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Utilizing MAXENT to Improve and Explain a Species Distribution Model for Freshwater Mussel Species in East Texas

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UTILIZING MAXENT TO IMPROVE AND EXPLAIN A SPECIES DISTRIBUTION MODEL FOR FRESHWATER MUSSEL SPECIES IN EAST TEXAS

By

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Abstract

Utilizing MAXENT to Improve and Explain a Species Distribution Model for Freshwater Mussel Species in East Texas

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One of the greatest challenges in landscape ecology has been determining the degree to which landscape level environmental characteristics effect the distribution of freshwater mussels. Freshwater mussels have long been regarded as valuable indicators of lotic system health because they are often the first organisms to exhibit a response to changes in their environment. Understanding distributional patterns of mussels is consequently a valuable conservation and management tool. Here, I evaluated the improvement of predictive modeling software by applying MAXENT to the distributions of two freshwater mussel species, the Texas Pigtoe (*Fusconia askewi*), a state threatened species, and the Rock Pocketbook (*Arcidens confragosus*), a species of concern. Existing species distribution models for these two mussel species were evaluated by the addition of sampling data from two unique watersheds, the Sulphur and Cypress River drainages. The Sulphur River was historically modified and has a biogeographically unique geology compared to most other rivers in East Texas. In addition to locating both species of interest, a range extension for the White Heelsplitter (*Lasmigona complanata*) was

produced on the lower Sulphur River. The Cypress River drainage is a set of watersheds that includes the Big Cypress Creek, Little Cypress Creek, and Black Cypress Creek. Compared to other East Texas Rivers the Cypress drainage is a relatively meandering bottomland system that is healthy along much of its length and empties into the Little Cypress Bayou near Louisiana. Each species distribution was modeled with 11 GIS derived environmental layers. I evaluated each environmental layer by the components these layers were built from and drew conclusions about associations of Texas Pigtoe and Rock Pocketbook with the most suitable habitat types in each important environmental layer. Improvement may depend on a complete understanding of a species fundamental niche and AUC values may not be an appropriate measure of model improvement. Freshwater mussel species will also associate significantly with specific components of each most highly contributing environmental layer.

Chapter One: Freshwater Mussel Ecology and Conservation

Introduction

Research in freshwater mussel ecology has recently shifted towards an interest in empirically linking environmental characteristics at the landscape level to patterns in freshwater mussel distributions (Newton et al., 2011). Environmental characteristics may include surface features, such as vegetation cover, urban sprawl, or agricultural development. Environmental characteristics may also include subsurface features, such as bedrock or aquifers. These attributes are variable across the landscape and are considered to be major contributors to the interactions between river biota and instream habitats (Allan et al., 1997; Allan, 2004). Methods for evaluation of landscape scale effects have been increasingly approached from the standpoint of one of the most imperiled animal groups in North America, the freshwater mussel (*Unionidae*) (Lydeard et al., 2004).

Freshwater mussels have long been regarded as valuable indicators of lotic system health because they are often the first organisms to exhibit a response to changes in their environment (Kabbes and Klocek, 2004). These changes can occur at multiple spatial scales. Extensive research on micro-scale habitat variations has shown the potential for alterations to the composition of mussel species present in a study area. Broader habitat variables such as landscape scale effects (Brown et al., 2010) and geology (Hopkins et al., 2009) have recently been proposed as equally significant contributors to changes in mussel diversity. Freshwater resources have always been popular locations for human activity so that land use, from forested to developed land, has elicited declines in populations of freshwater biota and shifts in the availability of habitat types for many species (Hopkins et al., 2009). These shifts can be attributed to an increase in run-off and ultimately sediment load in streams where cover has been removed from the surrounding landscape (Allan et al., 1997). The impacts of land use have long been recognized as they effect the composition of mussel communities and spatio-temporal changes in distributions of these animals (van der Schalie, 1938; Morris and Corkum, 1996; Arbuckle and Downing, 2002; Newton et al., 2011).

A combined understanding of habitat limiting factors and geographic distribution patterns are necessary to forging those empirical links between landscape activities and the associations with freshwater mussel occurrences (Burlakova et al., 2011). Species distribution models provide researchers a way to evaluate these associations. Improvement of a model by the addition of mussel sampling data from unique watersheds may help explain the correlations between mussel distributions and landscape characteristics. Geographically, the Sulphur and Cypress River drainages are unique compared to other watersheds in East Texas. The Sulphur River is a historically modified system that is still characteristically affected by unchecked past channelization and development (Minahan, 2004). The Cypress watershed consists of Big Cypress Creek, Little Cypress Creek, and Black Cypress Creek. This watershed is located in bottomland and is relatively pristine compared to other East Texas watersheds (Keeland and Young, 1997). All creeks in this watershed eventually converge into Little Cypress Bayou. Both watersheds are located in the Texoma Province which is delineated by the Red River drainage (Burlakova et al., 2011). The Sulphur and the Cypress watersheds are the only Texas freshwater rivers that belong to the Red River drainage and as such are unique in their biogeographical history. I hypothesized that the addition of mussel sampling data from the Sulphur and Cypress watersheds would improve a species distribution model that was originally created with mussel data from the Trinity, Neches, Angelina and Sabine Rivers. I hypothesized that species presence within a watershed would be correlated with specific environmental variables. I predicted that the degree to which these variables affect distribution would increase with the addition of sampling data from these rivers. I further predicted that individual species would demonstrate an association with specific components of each environmental variable that can be attributed to their respective ecological requirements. The purpose of the following research is to emphasize the importance of understanding how landscape characteristics can affect the distribution of mussel species. An approach such as this will demonstrate the utility of predictive modeling as it relates to freshwater mussel distributions and the implication for effective management of aquatic habitats. To meet this goal, the following objectives will be achieved:

- **Objective 1:** Quantify freshwater mussel assemblages within the Sulphur and Big Cypress River watersheds.
- **Objective 2:** Correlate distribution of two mussel species at each site with environmental variables using species distribution modeling.

- **Objective 3:** Evaluate the importance of including biogeographically unique watersheds in an existing MAXENT model.
- **Objective 4:** Identify specific environmental correlates of freshwater mussel distributions as they associate with environmental variables.

Sulphur and Cypress Watersheds

This study encompasses two watersheds in East Texas, the Sulphur and Cypress Rivers. The Cypress River study locations include the Big Cypress Creek, Little Cypress Creek, and Black Cypress Creek. Both river systems drain to the Red River in Louisiana but differ greatly in their respective hydrologic components and geomorphological characteristics. The Sulphur River is a highly modified system. Most of its length has been subjected to channelization or damming, resulting in a disconnection to its flood plain and an altered hydrologic profile (Minahan, 2003). There are two reservoirs within this basin, Cooper Lake and Wright-Patman Reservoir. Cooper Lake is located on the South Sulphur, which along with severe channelization and rerouting of this area, can be considered the most highly altered length of the Sulphur (Burgess, 2003). Wright-Patman Reservoir is located on the lower part of the mainstream Sulphur approximately 6.78 linear miles west of the Louisiana/Texas border. At the initiation of authorized realignment in the North Sulphur in the 1920's, likely to improve drainage for agricultural purposes, the Sulphur River was a naturally meandering, slow moving system. Channelization in the North Sulphur increased the velocity of this part of the river and ultimately caused a cascade of exponential problems that are still managed today including sediment deposition along the length of the Sulphur and debris input that results in localized flooding issues that are particularly hazardous to agricultural farmers (Minahan, 2003). To control the effects of the changes in the North Sulphur the Cooper Lake and Channels Project was implemented in 1955 with the purpose of relieving the disjunction between hydrologic characteristics of the North and South Sulphur, but halted in 1971 because of the passage of the National Environmental Policy Act (Minahan, 2003). The ultimate decision was made to discontinue the Cooper Lake Project where it was halted just west of HWY 37 resulting in a transition from channelized river to natural meander that continues to experience volatile environmental changes (Minahan, 2003). Today, riparian edge clearing because of decreases in flooding of channelized sections has caused erosion issues and debris accumulation downstream of areas like the HWY 37 debris pile and subsequent "natural" avoidance of these problems by the river, resulting in more frequent adjacent flooding and sediment deposition (Minahan, 2003). The ultimate significance of these problems is that consequences, such as altered flow regime and sedimentation, extend across miles of downstream river and edge, making the description of the Sulphur River overall as a highly modified system a concise one. In contrast, the Big Cypress River and its component tributaries is a relatively stable system. Flow regimes here are interrupted only once by Lake O' the Pines Reservoir, constructed by the U.S. Army Corps of Engineers in 1956. The majority of the watershed downstream of Jefferson, TX becomes a natural wetland as it approaches Caddo Lake, Texas' only natural lake (Keeland and Young, 1997). Channelization along the Cypress watershed is virtually non-existent and much of the river is well connected to its floodplain. Much of the land cover and topography of the lower half of the Big Cypress is dominated by a bottomland hardwood distribution, which is typical of East Texas watersheds (Burlakova et al.,2011). If it were not for the logjam that created Caddo Lake we might observe a vegetation type of bottomland hardwoods there today (Keeland and Young, 1997). The most significant conservation concern along this river is the retention of Bald Cypress in Caddo Lake, which are threatened by the controlled discharge from Lake O' the Pines.

So why is the Cypress watershed more natural than the Sulphur? Prior to 1900 the government promoted the destruction of wetland habitats because they were considered treacherous and of little value (Mitsch and Gosselink, 2000). In the last 40 years, researchers have been educating people on the value of wetlands and considerable federal protection, such as Section 404 and the Wetland Protection Act, has been implemented to conserve these habitats (EPA, 2012). It is likely that this awareness has contributed to protecting a majority of the Cypress watershed.

The unique biogeographical characteristics of these watersheds created an opportunity for comparison of mussel assemblages to other East Texas rivers located in the Sabine Province.

Freshwater Mussel Ecology

Throughout the last century, freshwater mussels of the family Unionidae were exploited at one time for their economic value and more recently studied for their academic value (Williams et al., 1993). In the past mussel shells were harvested for construction of buttons and jewelry (Coker, 1919) as well as a valuable food source. Of the 300 species extant in North America, 73 are considered critically imperiled, and 37 are listed as extinct (Strayer et al., 2004). In addition to historical harvesting, their complex life cycle, and sensitivity to environmental changes have drastically reduced the ability of these animals to survive (Howells et al., 1996). Mussels have a unique reproductive cycle that includes an obligate parasitic stage, glochidia, that utilizes the gills or fins of a host fish(es) for development (Lydeard et al., 2004). Many of the conservation concerns for these animals originate from habitat alterations that interrupt the potential for them to come into contact with their preferred host, and lack of identification of host species makes management difficult. To reach sexual maturity, glochidial mussels must become encysted upon a host fish, survive the host's immune system, and disperse into the substrate where they must anchor themselves successfully for up to 12 years for some species before they are capable of reproduction (Howells et al., 1996) . The reduction in dispersal ability combined with general intolerance for disturbances in the environment because of their sedentary nature inhibits settlement and can devastate recruitment for entire year classes (Vaughn and Taylor, 1999; Layzer and Madison, 1995).

Mussels can be found in a variety of lotic and lentic habitat types that include riffles and pools, and in many different substrates, such as sand, gravel and even clay. Substrate stability can largely be attributed in many areas to high mussel densities, known as mussel beds. Low densities of mussels may provide a control for study in areas where substrate is ideal and can suggest that the habitat is unsuitable because of other influences, such as shear stress (Statzner et al., 1988; Morales et al., 2006). Freshwater mussels are also benthic filter feeders. Their diet typically consists of algae, diatoms, phytoplankton of local variety and even sediment; though it has been suggested the latter is used for obtaining food particles (Gatenby et al., 1996; Coker et. al, 1921). Mussels are also considered ecosystem engineers for their ability to transfer nutrients from the water column to the substrate, stabilize benthic communities (bioturbation), and provide habitat structure and nutrients for other organisms (Vaughn et al., 2008; Howard and Cuffey, 2006; Gutierrez et al. 2003).These life history characteristics are what make mussels valuable bioindicators and essential members of aquatic ecosystems where the conservation of these types of benthic organisms may become a necessity for a healthy freshwater environment.

Landscape Characteristics

Perhaps one of the most important contributions to mussel distribution is the effect that land use and land cover have on mussel assemblages (Ford and Nicholson, 2006). Alteration of a watershed’s landscape has been demonstrated to change the assemblage of freshwater mussels not only in distributional aspects but composition as well from spatial scales ranging from stream level to entire watersheds (Groffman et al., 2003; Strayer et al., 2003; Newton et al., 2008). Agriculture, urbanization, and impoundments are the most notable anthropogenic inputs to rivers in east Texas (Allan et al., 1997). Use of landscapes for agricultural production has been shown to create long-term declines in stream biotic health (Diamond et al., 2002; Poole and Downing, 2004). Urban encroachment on stream riparian habitat decreases the quality of instream habitat. Influences in the landscape such as urban development can be monitored by population data of benthic organisms like freshwater mussels (Groffman et al., 2003; Kabbes and Klocek, 2004; Brown et al., 2010). Dams and other impoundments alter flow regimes and sediment transport, both of which directly impact freshwater mussel distributions. Interactions between mussel populations and altered environments can create the potential for a predictive model of management for streams (Vaughn and Taylor, 1999; Rahel, 2002; Gangloff et al., 2011; Pilger and Gido, 2012). Inclusion of this type of data is essential to understanding the contribution of allochthonous materials to an aquatic environment and the benefits of predictive modeling. To qualify the interactions between mussels and the environment, I utilized a set of environmental layers developed for the express purpose of correlating species occurrences with specific landscape attributes. The United States Geological Survey (USGS) in conjunction with agencies such as the Natural Resource Conservation Service (NRCS) and Texas Parks and Wildlife Department (TPWD) has made available geodatabases for use with a geographic information systems (GIS) program, such as ArcMap, that includes metadata (e.g., STATSGO) for environmental characteristics like soils, geology, and vegetation, to name a few. It is important that these environmental variables are temporally and spatially (e.g., corresponding grain and extent) complementary to the distributional data that are used (Anderson et al., 2003; Pearson et al., 2004). These environmental layers can be used to create a multitude of map types including population densities, climate zones, energy consumption, and more pertinent to this research land use and cover maps. Maps with this type of information contain layers that project features like surface, shape and size. These features can be presented in various formats (e.g., rasters, polygons, and points), linked to information (e.g., permeability of soils) and correlated to distributional data (Johnson et al., 2001). For this research I am interested in correlating the distribution of mussel species with the most suitable environmental layer subtypes (e.g., soils that contain high clay content) versus the least suitable subtypes. Species distribution models, such as MAXENT, produce visual distributions but do not provide an answer to why a species can be found at any particular point on a landscape. It is necessary to evaluate the correlations between mussel distributions and environmental layer subtypes being used in the model to answer this question.

Maximum Entropy Modeling

Present day technology has promoted a shift in our abilities to conduct research with the use of predictive modeling. Of the available software for predictive modeling, general linear models (GLM), general additive models (GAM), and machine learning software have arguably been the most successful. Some examples include BIOCLIM, a bioclimatic model that predicts changes in a species' distribution based on temporally diverse climate information (Beaumont et al., 2005), DOMAIN, which uses a "distance to" algorithm to make predictions (Carpenter et al., 2003), and GARP, potentially the most widely used presence-only package (Tsoar et al., 2007). With the advancement of species distribution modeling software such as MAXENT (Maximum Entropy), programs can now compute vast amounts of presence data across complicated algorithms and refine the accuracy of such models (Phillips et al., 2006). MAXENT does not utilize absence data because of the potential inaccuracy and deficiency of this kind of information (Anderson et al., 2003). MAXENT operates based on a conservative estimation of a species' realized niche (Hutchinson, 1957) but outputs a projection of probability of occurrence that defines its fundamental niche. In other words MAXENT is capable of utilizing the most precise estimation of available habitat types to create a continuous probability that accounts for species occurrence at the maximum availability of habitat types. A gradient such as this provides a high level of accuracy for the predictive powers of this model. Once the available environmental layers and distributional data have been input, MAXENT uses a deterministic algorithm to develop an optimal probability distribution similar to general linear and general additive models (Phillips et al., 2004). MAXENT then correlates known occurrences of species in their conservatively measured, variable environments and applies these data to areas with no record of that species. The output is AUC (area under the operating receiving curve) and it can range from 0 to 1. AUC is a measurement of the predictive power of a model. It estimates the probability that a presence point will have a higher suitability score than a random background point (pseudoabsence) on the map. Any value of 0.75 or greater is considered to indicate a useful model (Elith et al., 2006). In theory, like most modeling software, MAXENT will be more accurate with the addition of distributional data. Phillips et al. (2006) determined that the continuous nature of MAXENT’s predictions resulted in a more comprehensive map of species occurrences because the inclusion of habitat areas that were acceptable rather than just the optimized predictions that are apparent with GARP. Inclusion of all possible suitable habitats is very important from a management perspective. One of the major restrictions of this modeling technique is its inability to make predictions based on a finer scale. It is more appropriate to use this method at broader scales that are more likely to contain the most heterogeneous variety of available habitat types for the species in question (Phillips et al., 2006). By working at this extent, MAXENT provides a more accurate estimation of potential inhabitation of the ideal fundamental niche. In addition to this, MAXENT is a relatively young machine learning technique that is not available in standard software packages. Adjusting for errors, such as exponential growth of elevated predictions and extrapolation between disconnected study areas becomes a process of utilizing other statistical programs (Phillips et al., 2006). MAXENT, like all models, also makes assumptions about the environment including the lack of importance of interspecific and intraspecific interactions between biota, and that species occur at all locations where the environmental variables are favorable. This last assumption can be disadvantageous to a probability distribution model when studying a fluvial environment. As Newton et al. (2009) pointed out, there is a high degree of patchiness in regards to river environments and there is no adjustment within species distribution models to account for this disconnectivity. That said, conservative assessments of results are still very valuable for the predictions of species distributions.

Improvement and Explanation of an Existing Model

My research combines sampling data from two previous studies Troia (2010) and Dunithan (2012), the latter of which utilized MAXENT to predict the occurrence of rare species of freshwater mussels and fish in East Texas rivers. Dunithan (2012) demonstrated that MAXENT could accurately predict the distribution of rare mussel species with AUC values ranging from 0.78 to 0.91 for test samples in the Trinity, Angelina, Neches, and Sabine watersheds. The occurrence localities produced by the model indicated a correlation with actual distributional patterns seen during the study. The accuracy of species distributions was further supported by the differing probabilities between watersheds that are impacted by land use disturbances and those that generally are not. Variation within the landscape was associated at different levels with different species. However, Dunithan suggested that the use of landscape characteristics where rare species were occurring in real time may have exaggerated predictions of occurrence. I was interested in including sampling data from two watersheds that demonstrated very different geomorphologic and landscape characteristics from the watersheds that were sampled in this previous study. I also wanted to explain the associations of mussel species with specific habitat locations by evaluating the profiles of those landscapes. By including a more heterogeneous set of available habitat types for rare species, I suggested that MAXENT would be able to refine the fundamental niche for these species, reduce the over-predictive nature of the analyses, and provide a more concise contribution of environmental variables for each species.

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Chapter Two: Utilizing MAXENT to Improve and Explain an Existing Probability Model of Occurrences for Freshwater Mussel Species in East Texas

Introduction

There has recently been heightened interest in explanations of freshwater mussel habitat preferences based on large scale environmental parameters by malacologists. Changes in mussel communities as a result of land use have not gone undocumented (Allan et al., 1997; Strayer et al., 2003; Poole and Downing, 2004). Associations between mussel occurrences and landscape characteristics have been notoriously difficult to assess because of the broad extent to which landscape level activities affect fluvial systems (Newton et al., 2008). Explanatory variables are usually vague and can constitute a host of possible effects on mussel communities. The value of utilizing a species distribution model lies in the effectiveness of the constituent environmental layers. The inclusion of detailed descriptions of potentially suitable habitat types will provide links between general changes in the landscape and mussel distributions with less specious conclusions (Anderson et al., 2003). Demonstrating improvement of these models with the addition of data samples is important to validating the accuracy of a model's predictions. Being able to focus on the function of attributes of a habitat rather than subjective classifications of what is suitable habitat for mussels is the current goal of most research (Newton et al., 2008). If met, these goals can produce a framework for effective and economical management of potentially valuable freshwater mussel habitat.

I chose to evaluate two Unionid mussels, a state-threatened species, the Texas Pigtoe (*Fusconaia askewi*), and a species of concern, the Rock Pocketbook (*Arcidens confragosus*). The Texas Pigtoe has been historically reported in the Brazos, Neches, Sabine and San Jacinto rivers, and more recently in the Sulphur River (Howells et al., 1996). It is a smooth shelled species that prefers sand and gravel mixed substrates. The Rock Pocketbook was historically distributed throughout northeast Texas to the Guadalupe River (Howells et al., 1996). Current distribution is still relatively widespread but uncommon. Howells et al. (1996) indicates that this species prefers mud/sand/gravel substrates and can tolerate swift currents.

The previous study by Dunithan (2012), which included mussel data samples from Troia (2010), incorporated a collection of mussel species occurrences that included the Texas Pigtoe and Rock Pocketbook from the Trinity, Angelina, Neches, and Sabine Rivers. Dunithan's study produced probabilities of distribution of freshwater mussels for the majority of East Texas but did not explain the associations of mussels to habitat types. I hypothesized that these species occurrences were correlating specifically with components in each of the most significantly contributing environmental layers and evaluation of these layers and the inclusive data would provide me with the opportunity to explain these associations. Improving the model would require adding data from two biogeographically unique watersheds, the Sulphur and Cypress, and assessing the compositional profiles of the most suitable habitat types within each important environmental layer. My objectives were to evaluate the improvement of species distributions for Texas Pigtoe and Rock Pocketbook, and explain the associations that the models produced between the environment and mussel occurrences with these modifications.

Methods

Sampling Design

Collection efforts for freshwater mussels were conducted from August to October, 2011 and June to September of 2012 in the Sulphur (Figure 2.1) and Big Cypress Rivers, including its tributaries Little Cypress, and Black Cypress (Figure 2.2). There were 14 sites sampled along the Sulphur River; two on the South Sulphur, one on the North Sulphur and 11 along the mainstem. There were 18 sites sampled along the Big Cypress River, five on the Little Cypress Creek, one on the Black Cypress and five on the mainstem. Each site contained a 150-200m reach that was sampled in 50m transects. Freshwater mussels were retrieved manually by researchers during a timed interval that met the equivalent of one person hour per transect when applicable. Locations that contained water deeper than wading depth were sampled with the use of SCUBA, in teams of two, and totaling one person hour per transect (Figure 2.1). Low visibility at all sites required the use of a 1m PVC quadrat, flipped continuously on end, to guide divers along linear cross sections of the transect. Living and recently dead specimens were isolated by transect, identified to species, and enumerated. All mussels were replaced with the exception of difficult or unknown specimens, which were retained as vouchers.

Additional sampling data from Black Cypress River was provided for my purposes by the United States Geological Survey (Reston, VA).

Modeling

My modeling procedure was based on the original methods by Dunithan (2012) that included the use of the species distribution modeling program MAXENT and a set of 11 environmental layers (Table 2.1). Each environmental layer was digitally derived from online geodatabases listed in the table and utilized with ArcMap 10.1. All layers were rasterized and the grid cell size of the constituent maps was 0.014 decimal degrees squared. I restricted MAXENT analyses to East Texas from the Sulphur River on the northern perimeter, the Trinity River on the western perimeter, the Angelina River on the southern perimeter, and the eastern border of Texas to complete the area. Within that predefined space are also the Sabine, Neches and Cypress watersheds.

The initial model included data previously collected by Dunithan (2012) and Troia (2010) using the 9 original layers and 3 modified layers to produce a baseline for comparison to the addition of alternate watersheds. I chose to focus on two species of interest that included the state-threatened Texas Pigtoe (*Fusconia askewi*) and a species of concern the Rock Pocketbook (*Arcidens confragosus*) because of the need for conservation of particularly imperiled species. Habitat suitability profiles were constructed for each species individually. My analysis combined the previous data with sampling data for both species collected on the Sulphur and Big Cypress Rivers. Habitat suitability profiles were constructed for each species using this model as Well. The crossvalidation method produced model-validating AUC values (area under the operator receiving curve values), which estimates the probability that a presence point will have a higher suitability score than a random background point (pseudoabsence) on the map. Values above an arbitrary designation of 0.75 were considered useful (Elith et al., 2009). I then isolated the three most significantly contributing environmental layers from each model and determined the mean habitat suitability scores (from MAXENT) for each component that constituted the total profile for those layers. I derived compositional profiles by locating the decoding information within the metadata and matching the habitat type with the constituent values it was built on. These analyses were performed using R (R Development Core Team, 2010) and a custom r-script for extracting and organizing the compositional data with its relevant habitat type. I then conducted Student's t-tests (Sokal and Rohlf, 1995) comparing the most suitable habitats (top average habitat suitability scores from Maxent) to the least suitable habitats (lowest average habitat suitability scores), separately for each environmental layer. I also analyzed significant differences between the mean habitat suitability scores of common environmental variable components of models before the addition of data and after the addition of data for each species. Finally, I made comparisons between the initial models for both species and also between the additive models for both species. Percent differences were calculated to demonstrate major changes across models.

Results

Texas Pigtoe *(Fusconaia askewi)*

The first model for Texas Pigtoe that included the initial data samples resulted in an AUC value of 0.936. The most significantly contributing environmental variables were soils, rock exposure, and vegetation (Table 2.2, Figure 2.3). Specifically, willow oak-water oak-blackgum forest was the most suitable vegetation (mean suitability = 0.26) and marsh barrier island was least suitable (mean= 0.0015) (Figure 2.4). The difference between the mean habitat suitability scores of the top 4 vegetation types and the bottom 4 vegetation types was marginally significant ($t= 1.94$, $p= 0.092$) (Table 2.3, Figure 2.5). The most suitable rock exposure type was terrace (mean= 0.87), and the least suitable was mudstone (mean = 0.0015; Figure 2.6). The difference between the top 5 and bottom 5 rock exposure types was significant ($t= 1.86$, $p= 0.05$) (Table 2.4, Figure 2.7). The most suitable soil type was TX282 (mean= 0.74), and the least suitable was TX534 (mean= 6.88×10^{-5}; Figure 2.8). Each soil type consisted of 12 components, the totality of which I termed compositional profile. Of these 12 components, THICK (thickness of the soil layers in inches) was the only variable that showed a significant difference between the most suitable soil types and the least suitable soil types ($t= 2.91$, $p= 0.0094$) (Table 2.5, Figure 2.9). Overall, the model suggested that Texas Pigtoe prefers habitats associated with specific riparian deciduous trees, terrace and sand formations, and thicker soils. The species does not prefer habitats that are associated with the presence of deviations from traditional cover types like forested areas to disturbed areas such as urban sprawl (mean= 0.0044) and agriculture (mean=0.0035).

The second model for Texas Pigtoe that included all collection samples improved the AUC value to 0.937. The most significantly contributing environmental variables were soils, rock exposure, and vegetation (Table 2.2, Figure 2.10). As with the first model, willow oak-water oak-blackgum forest was the most suitable vegetation cover (mean suitability= 0.30), and marsh barrier island was the least suitable (mean= 0.0020) (Figure 2.11). The difference between the top 4 vegetation types and the bottom 4 vegetation types was highly significant ($t= 7.18$, $p= \leq 0.001$) (Table 2.6, Figure 2.12). The most suitable rock exposure type was terrace (mean= 0.12), and the least suitable was mudstone (mean= 0.0059, Figure 2.13). The difference between the top 5 and bottom 5 rock exposure types was significant ($t =16.92$, $p = 0.0039$) (Table 2.7, Figure 2.14). The most suitable soil type was TX282 (mean= 0.72), and the least suitable was TX534 (mean= 0.00024) (Figure 2.15). The component THICK again showed an average significant difference between the most suitable soil types and the least suitable soil types ($t= 2.23$, $p= 0.039$) (Table 2.8, Figure 2.16). In addition to this component, the variables AWC (average water capacity of the soil in inches per inch) (Figure 2.17), and SLOPE (slope of the soil layers in percent) (Figure 2.18) also demonstrated a significant difference between the most suitable soil types and the lease suitable soil types ($t= 2.96$, $p= 0.0087$; $t=2.54$, $p= 0.021$) (Table 2.8). The addition of sampling data to this model nominally improved the AUC value and contributed to the increase of habitat suitability scores within each important environmental layer. The improved model suggests that Texas Pigtoe not only prefer habitats associated with specific riparian deciduous trees, terrace and sand formations, and thicker soils, but also soils with a higher capacity for retaining water and minimal slope. It is also notable for this model that additional data increased the disassociation of Texas Pigtoe with urban sprawls and agricultural lands (mean= 0.0003, mean= 0.0002).

Rock Pocketbook *(Arcidens confragosus)*

The first model for Rock Pocketbook that included the initial data samples resulted in an AUC value of 0.899. The most significantly contributing environmental variables were soils, vegetation, and rock exposure (Table 2.2, Figure 2.19). Within the rock exposure variable, sand was the most suitable habitat (mean= 0.087) and mudstone the least suitable (mean= 0.0015) (Figure 2.20). The difference between the top 5 and bottom 5 rock exposure types was significant (t= 2.3, p= 0.05) (Table 2.9, Figure 2.21). As with Texas Pigtoe, Rock Pocketbook prefer habitats dominated by willow oak-water oak-blackgum forest (mean=0.20) and rarely associate with pecan elm forests (mean= 0.00028) (Figure 2.22). The difference between the top 4 and bottom 4 vegetation types was significant (t= 2.55, p= 0.043) (Table 2.10, Figure 2.23). The most suitable soil type for Rock Pocketbook was TX282 (mean= 0.63) and the least suitable was TX639 (mean= 0.00027) (Figure 2.24). The average contribution of the HYGRP (hydrology of the soil layer) component was significantly different between the most suitable and least suitable soil types (t= 2.99, p= 0.05) (Table 2.11, Figure 2.25). The model shows that Rock

Pocketbook prefer habitats associated with sandy rock exposure characteristics, deciduous riparian tree species, and soils that have a higher capacity for retaining water.

The second model, which included all the sampling data, improved the AUC value to 0.915. The most significantly contributing environmental variables were soils, vegetation, and rock exposure (Table 2.2, Figure 2.26). Sand was again the most suitable rock exposure type (mean= 0.083) and siltstone was the least suitable (mean= 0.0012) (Figure 2.27). The difference between the top 5 most suitable and the bottom 5 least suitable rock exposure types was more significant for this model (t= 2.77, p= 0.022) (Table 2.12, Figure 2.28). The most suitable vegetation type for this model was water oak-elm-hackberry forest (mean= 0.22) and the least suitable was pecan elm forest (mean= 0.00017) (Figure 2.29). The difference between the top 4 most suitable vegetation types and the bottom 4 most suitable vegetation types was significant (t= 2.59, p= 0.041) (Table 2.13, Figure 2.30). The most suitable soil type was TX477 (mean=0.62) and the least suitable was TX188 (mean= 0.00019) (Figure 2.31). Within soil type, the contribution of HYGRP was again significantly different between the most suitable and least suitable soil types (t= 2.12, p=0.048) (Table 2.14, Figure 2.32). The additional data suggests that Rock Pocketbook still prefer habitats associated with sandy rock exposure characteristics, but may vary in their preference for riparian vegetation and soil types because of the change in most suitable habitats for these environmental variables. Hydrology of the ground water was important for determining the presence of Rock Pocketbook.

Comparisons of Common Attributes

The comparisons between the two Texas Pigtoe models demonstrated that there was a large amount of variation after new data were added. Sixty-seven percent of the soil types that were common in the top 10 most suitable soils significantly differed in regards to their mean habitat suitability scores between the two models (Table 2.15). However, the three most suitable soil types, TX282, TX222, and TX051, did not vary enough to indicate a significant difference. There was also variation within the association to vegetation types (Table 2.16). Sixty-nine percent of the vegetation types differed significantly including the top two most suitable types (willow oak-water oak-blackgum and water oak-elm hackberry forest). Observation of the mean habitat suitability scores indicated a significant difference of increased habitat suitability for each variable. The rank of suitability of rock exposure types remained consistent, however, the mean habitat suitability scores increased with the addition of data to the second model (Table 2.17). Seventy-eight percent of the rock exposure variables significantly differed in mean suitability scores with versus without the new data points.

Variation within the Rock Pocketbook models was low. Only 22 percent of the common soil types' suitability scores were significantly different between these two models (Table 2.15). Those soil types, TX123 and TX516, were not considered highly suitable habitat types by the model. Common rock exposure types also differed by 22 percent (Table 2.16). Those rock exposure types that differed, sand and sandstone, demonstrated increased mean habitat suitability scores with the addition of data samples to the second model. Twenty-three percent of the vegetation types significantly differed in mean suitability scores with versus without the new data points (Table 2.17). Among those types was water oak-elm-hackberry forest, which was associated with a decrease in mean habitat suitability score with the addition of data samples to the second model.

Comparisons of the first models of Texas Pigtoe and Rock Pocketbook demonstrated that there were 5 soil types out of the 10 most suitable that these two models had in common (Table 2.15). All of the mean habitat suitability scores of these soil types, with the exception of the most suitable soil type TX282, differed significantly. Fifty-six percent of the rock exposure types were also significantly different (Table 2.16). There was no significant difference in the suitability of the most suitable rock exposure type, terrace. Vegetation varied by 38 percent. Most vegetation types that differed between models were not considered to be most suitable habitat types by the model (Table 2.17). However, water oak-elm-hackberry forest was the second most suitable type for both models and it differed significantly. This vegetation type was more suitable for Rock Pocketbook than Texas Pigtoe (ROPO mean= 0.18, TEPI mean= 0.061).

The comparison of models for Texas Pigtoe and Rock Pocketbook that included additional data samples revealed significant differences within the environmental variables as well. There were 4 soil types that were common between both models, all of which had significantly different mean habitat suitability scores, with the exception of the most suitable soil type, TX282 (Table 2.15). Terrace and sand were the most suitable rock exposure types for both models and showed no significant difference between the mean habitat suitability scores. It should be noted that sand was more important than terrace for Rock Pocketbook but the mean habitat suitability score was not significantly different from sand in the Texas Pigtoe model. Overall, 33 percent of rock exposure types were significantly different between models (Table 2.16). Thirty-one percent of the vegetation types were significantly different (Table 2.17). Most of these vegetation types were not considered to be highly suitable by the model.

The average variation of suitability between models for the same species depended on the composition of the most suitable habitat types for those models. The Texas Pigtoe models displayed an average significant difference of 71.56 percent. The models with original data for both species and the models with additional data for both species also varied based on composition of the most suitable mean habitat suitability scores. The Rock Pocketbook models displayed an average significant difference of 22.51 percent. The models with the original data samples for both Texas Pigtoe and Rock Pocketbook displayed an average significant difference of 58.01 percent. The models with additional data samples for both Texas Pigtoe and Rock Pocketbook displayed an average significant difference of 46.37 percent.

Tables and Figures

Table 2.1. Environmental layers sources included in all MAXENT models.

Variable Categories	Habitat Attribute	Data Source	Relevant Time Period	Source Details
Aquifers	Sediments; Interstitial Chemistry	TWDB	1990	Aquifer delineations developed for the 1991 StateWater Plan
Geology	Sediments; Current; Interstitial Chemistry	UT-BEG	2007	Dataset containing rock unit data from the Geologic Atlas of Texas
Ground-water Recharge	Sediments; Interstitial Chemistry	USGS	2003	1-km resolution raster grid dataset estimating index of mean annual groundwater recharge
Kernelreservoirs	Sediments; Current; Temperature	TWDB	2007	Dataset of existing reservoirs in Texas greater than 5,000 acre-feet
Kernelroads	Sediments; Interstitial Chemistry	ESRI	2000	U.S. Detailed Streets and U.S. Census Block Centroid Populations were obtained from ESRI data CDs provided with ArcGIS software
Kernelsprings	Sediments; Interstitial Chemistry	USGS	1975-2005	Vector map containing digital data about spring flows and water quality
Landform	Sediments; Interstitial Chemistry	USGS	1964	A vector file of digital data that describes classes of land surface form (slope, local, relief, and profile)
Solar Radiation	Temperature	CRU	1961-1990	Solar radiation reaching the land surface
Soil Data	Sediments; Interstitial Chemistry	NRCS	1998-2007	NRCS Soil Data Viewer (STATSGO)
Topmodel	Sediments	USGS	1871-1997	5km raster dataset that represents average percentage of infiltration-excess overland flow in total stream flow
Vegetation Types	Sediments	TPWD	1972-1976	Vegetation types of Texas, including cropland and urban

Table 2.2. Percent contributions for the most significantly contributing environmental variables from all MAXENT models. AUC values range from 0.899 to 0.937 for all models and demonstrate improvement with the addition of data samples.

	Texas Pigtoe Original	Texas Pigtoe Combined	Rock Pocketbook Original	Rock Pocketbook Combined
Variable	Percent Contribution			
Soils	47	42. 5	54.2	53.6
Geology	18.8	22	9.6	10.5
Vegetation	17.7	21.3	12.6	11.6

	Texas Pigtoe Original	Texas Pigtoe Combined	Rock Pocketbook Original	Rock Pocketbook Combined
AUC	0.936	0.937	0.899	0.915

Table 2.3. Vegetation cover for the first Texas Pigtoe model is listed from highest to lowest mean habitat suitability score. The highest score is associated with the most suitable vegetation type for the presence of Texas Pigtoe using the initial data set.

MEAN	SE	VEGETATION COVER TYPE
0.26	0.0069	Willow Oak-Water Oak-Blackgum Forest
0.06	0.0024	Water Oak-Elm-Hackberry Forest
0.05	0.0022	Young Forest/Grassland
0.048	0.00097	Pine Hardwood
0.038	0.0069	Bald Cypress-Water Tupelo Swamp
0.016	0.0020	Lake
0.012	0.00027	Post Oak Woods/Forest
0.0066	0.00017	Post Oak Woods, Forest and Grassland Mosaic
0.0051	0.00014	Elm-Hackberry Parks/Woods
0.0043	0.00014	Urban
0.0035	0.00022	Crops
0.0034	0.00097	Pecan Elm
0.0027	0.00012	Bluestem Grassland
0.0015	0.00035	Marsh Barrier Island

Table 2.4. Rock exposure type for the first Texas Pigtoe model is listed from highest to lowest mean habitat suitability score. The highest score is associated with the most suitable rock exposure type for Texas Pigtoe using the initial data set.

MEAN	SE	ROCK EXPOSURE TYPE
0.087	0.0015	terrace
0.036	0.0023	sand
0.025	0.00054	sandstone
0.022	0.00090	fine-grained mixed clastic
0.014	0.0014	siltstone
0.0073	0.00032	clay or mud
0.0072	0.00058	limestone
0.0025	0.00	shale
0.0015	0.00	mudstone

Table 2.5. The compositional profiles for the first Texas Pigtoe model are listed by the most suitable soil types (MUID) and least suitable soil types. The highest mean habitat suitability score is associated with the most suitable soil type for the presence of Texas Pigtoe using the initial data set.

Compositional Profile for Most Suitable Soil Types														
MUID	MEAN	SE	AWC	CLAY	KFFACT	OM	PERM	THICK	HYGRP	DRAIN	SLOPE	LL	IFHYDRIC	AFLDFREQ
TX282	0.74	0.02	0.13	22.1	0.29	0.6	3.26	76.3	2.7	4.3	1.7	30.7	0.4	3.3
TX222	0.49	0.01	0.12	18.4	0.25	0.2	3.42	72.1	3	5.1	0.1	26.1	0.6	1.1
TX051	0.38	0.01	0.13	15.7	0.25	0.6	3.02	74.5	2	3.4	1.2	23.8	0.2	3.7
TX172	0.35	0.01	0.15	31.8	0.28	0.6	1.19	74.1	3.4	4.6	0.3	36.2	0.7	1.4
TX317	0.34	0.01	0.16	26	0.28	0.4	1.3	66	2.7	4.1	0	33.4	0	1.3
TX272	0.17	0.01	0.14	26.3	0.43	0.5	0.43	75.8	3.2	4.5	0.1	35.7	0.5	1.7
TX263	0.15	0.01	0.17	18.8	0.36	0.2	1.32	76.6	3	5.3	0.6	26.9	0.5	4
TX250	0.12	0.01	0.15	63.9	0.32	1	0.1	78.5	3.9	4.5	0.7	70.1	0.8	1.5
TX296	0.07	≤ 0.001	0.11	21.5	0.24	0.6	4.43	77.2	2	3	4.3	28.6	0	3.8
TX175	0.06	0.01	0.15	28.6	0.35	0.5	0.99	74.6	3.1	4.3	0.6	36.2	0.3	3.7
Compositional Profile for Least Suitable Soil Types														
MUID	MEAN	SE	AWC	CLAY	KFFACT	OM	PERM	THICK	HYGRP	DRAIN	SLOPE	LL	IFHYDRIC	AFLDFREQ
TX238	≤ 0.001	≤ 0.001	0.1	47.1	0.31	1	0.04	61.4	4	6.3	0.2	70.5	1	2
TX549	≤ 0.001	≤ 0.001	0.11	15.2	0.21	0.4	8.76	74.2	1.4	2.7	6.2	23.9	0.1	3.9
TX256	≤ 0.001	≤ 0.001	0.15	37.1	0.34	0.6	0.33	70.9	4	5.3	0.7	48.5	0.4	4
TX587	≤ 0.001	≤ 0.001	0.06	14.1	0.27	0.2	6.8	65.6	3.4	5.2	0.7	27.8	0.8	2
TX084	≤ 0.001	≤ 0.001	0.14	34.9	0.27	0.2	1.07	68.4	2.9	3.1	3.3	37.8	0	4
AR054	≤ 0.001	≤ 0.001	0.16	30.9	0.32	0.7	2.72	63.5	2.7	3.6	0.5	36.2	0.1	2.9
TX421	≤ 0.001	≤ 0.001	0.07	42.3	0.34	1.8	0.04	61.1	4	6.8	1	59.5	1	1.4
TX293	≤ 0.001	≤ 0.001	0.1	18.5	0.2	0.3	6.99	73.3	1.8	3.1	6.7	27.6	0.1	3.7
TX099	≤ 0.001	≤ 0.001	0.17	24.7	0.4	0.9	2.03	65.2	2.3	3	0	30.1	0	1.9
TX534	≤ 0.001	≤ 0.001	0.13	15.1	0.24	0.5	2.28	78.8	4	5.4	0.6	34.2	0.4	2.8

Table 2.6. Vegetation cover for the second Texas Pigtoe model is listed from highest to lowest mean habitat suitability score. The highest score is associated with the most suitable vegetation type for the presence of Texas Pigtoe using the combined data set.

MEAN	SE	VEGETATION COVER TYPE
0.30	0.007225	Willow Oak-Water Oak-Blackgum Forest
0.26	0.006425	Water Oak-Elm-Hackberry Forest
0.056	0.001017	Pine Hardwood
0.054	0.002275	Young Forest/Grassland
0.042	0.008064	Bald Cypress-Water Tupelo Swamp
0.025	0.000764	Post Oak Woods/Forest
0.024	0.002092	Lake Houston
0.015	0.000512	Elm-Hackberry Parks/Woods
0.014	0.00036	Post Oak Woods, Forest and Grassland Mosaic
0.010	0.000276	Crops
0.0073	0.000303	Urban
0.0035	0.000185	Bluestem Grassland
0.0028	0.001038	Pecan Elm
0.0020	0.000501	Marsh Barrier Island

Table 2.7. Rock exposure type for the second Texas Pigtoe model is listed from highest to lowest mean habitat suitability score. The highest score is associated with the most suitable rock exposure type for Texas Pigtoe using the combined data set.

MEAN	SE	ROCK EXPOSURE TYPE
0.12	0.0017	terrace
0.11	0.0037	sand
0.028	≤ 0.001	sandstone
0.022	≤ 0.001	fine-grained mixed clastic
0.016	0.0014	siltstone
0.011	≤ 0.001	limestone
0.0087	≤ 0.001	clay or mud
0.0076	≤ 0.001	shale
0.0059	≤ 0.001	mudstone

Table 2.8. The compositional profiles for the second Texas Pigtoe model are listed by the most suitable soil types (MUID) and least suitable soil types. The highest mean habitat suitability score is associated with the most suitable soil type for the presence of Texas Pigtoe using the combined data set.

Compositional Profile for Most Suitable Soil Types												
MUID	AWC	CLAY	KFFACT	OM	PERM	THICK	HYGRP	DRAIN	SLOPE	LL	IFHYDRIC	AFLDFREQ
TX282	0.13	22.1	0.29	0.6	3.26	76.3	2.7	4.3	1.7	30.7	0.4	3.3
TX222	0.12	18.4	0.25	0.2	3.42	72.1	3	5.1	0.1	26.1	0.6	1.1
TX051	0.13	15.7	0.25	0.6	3.02	74.5	2	3.4	1.2	23.8	0.2	3.7
TX172	0.15	31.8	0.28	0.6	1.19	74.1	3.4	4.6	0.3	36.2	0.7	1.4
TX317	0.16	26	0.28	0.4	1.3	66	2.7	4.1	0	33.4	0	1.3
TX250	0.15	63.9	0.32	1	0.1	78.5	3.9	4.5	0.7	70.1	0.8	1.5
TX272	0.14	26.3	0.43	0.5	0.43	75.8	3.2	4.5	0.1	35.7	0.5	1.7
TX263	0.17	18.8	0.36	0.2	1.32	76.6	3	5.3	0.6	26.9	0.5	4
TX175	0.15	28.6	0.35	0.5	0.99	74.6	3.1	4.3	0.6	36.2	0.3	3.7
TX316	0.16	20.9	0.29	0.5	1.43	68.9	3.2	4.7	0.2	28.6	0.5	1.4
Compositional Profile for Least Suitable Soil Types												
MUID	AWC	CLAY	KFFACT	OM	PERM	THICK	HYGRP	DRAIN	SLOPE	LL	IFHYDRIC	AFLDFREQ
TX417	0.14	24.5	0.26	0.1	2.6	77.4	2.3	3.8	3.5	30.7	0.1	3.9
TX458	0.1	38.2	0.22	0.2	0.65	64.9	3.5	3.9	4.7	49.9	0	4
TX639	0.16	71.4	0.26	2.9	0.66	73.4	4	7	0	71.7	1	1
TX238	0.1	47.1	0.31	1	0.04	61.4	4	6.3	0.2	70.5	1	2
TX256	0.15	37.1	0.34	0.6	0.33	70.9	4	5.3	0.7	48.5	0.4	4
TX421	0.07	42.3	0.34	1.8	0.04	61.1	4	6.8	1	59.5	1	1.4
TX587	0.06	14.1	0.27	0.2	6.8	65.6	3.4	5.2	0.7	27.8	0.8	2
TX549	0.11	15.2	0.21	0.4	8.76	74.2	1.4	2.7	6.2	23.9	0.1	3.9
TX293	0.1	18.5	0.2	0.3	6.99	73.3	1.8	3.1	6.7	27.6	0.1	3.7
TX534	0.13	15.1	0.24	0.5	2.28	78.8	4	5.4	0.6	34.2	0.4	2.8

Table 2.9. Rock exposure type for the first Rock Pocketbook model is listed from highest to lowest mean habitat suitability score. The highest score is associated with the most suitable rock exposure type for Rock Pocketbook using the initial data set.

MEAN	SE	ROCK EXPOSURE TYPE
0.087	0.0015	terrace
0.036	0.0023	sand
0.025	≤ 0.001	sandstone
0.022	≤ 0.001	fine-grained mixed clastic
0.014	0.001493	siltstone
0.0073	≤ 0.001	clay or mud
0.0072	≤ 0.001	limestone
0.0025	≤ 0.001	shale
0.0015	≤ 0.001	mudstone

Table 2.10. Vegetation cover for the first Rock Pocketbook model is listed from highest to lowest mean habitat suitability score. The highest score is associated with the most suitable vegetation type for the presence of Rock Pocketbook using the initial data set.

MEAN	SE	VEGETATION COVER TYPE
0.20	0.0068	Willow Oak-Water Oak-Blackgum Forest
0.18	0.0084	Water Oak-Elm-Hackberry Forest
0.052	0.0036	Urban
0.032	0.0012	Post Oak Woods, Forest and Grassland Mosaic
0.031	≤ 0.001	Pine Hardwood
0.031	0.0016	Young Forest/Grassland
0.022	≤ 0.001	Post Oak Woods/Forest
0.011	≤ 0.001	Lakes
0.010	0.0027	Bald Cypress-Water Tupelo Swamp
0.0057	≤ 0.001	Elm-Hackberry Parks/Woods
0.0041	≤ 0.001	Crops
0.0012	≤ 0.001	Marsh Barrier Island
≤ 0.001	≤ 0.001	Bluestem Grassland
≤ 0.001	≤ 0.001	Pecan Elm

Table 2.11. The compositional profiles for the first Rock Pocketbook model are listed by the most suitable soil types (MUID) and least suitable soil types. The highest mean habitat suitability score is associated with the most suitable soil type for the presence of Rock Pocketbook using the initial data set.

Compositional Profiles for Most Suitable Soil Types												
MUID	AWC	CLAY	KFFACT	OM	PERM	THICK	HYGRP	DRAIN	SLOPE	LL	IFHYDRIC	AFLDFREQ
TX282	0.13	22.1	0.29	0.6	3.26	76.3	2.7	4.3	1.7	30.7	0.4	3.3
TX250	0.15	63.9	0.32	1	0.1	78.5	3.9	4.5	0.7	70.1	0.8	1.5
TX317	0.16	26	0.28	0.4	1.3	66	2.7	4.1	0	33.4	0	1.3
TX357	0.13	28.4	0.29	0.8	1.39	79.9	3.1	4.7	0.7	38.5	0.7	1.8
TX316	0.16	20.9	0.29	0.5	1.43	68.9	3.2	4.7	0.2	28.6	0.5	1.4
TX123	0.11	27.9	0.24	0.6	3.11	70.6	2.5	3	8.3	33.5	0	4
TX172	0.15	31.8	0.28	0.6	1.19	74.1	3.4	4.6	0.3	36.2	0.7	1.4
TX574	0.14	65.5	0.32	1.8	0.1	76	3.8	4.5	0	69.2	0.1	1.5
TX568	0.06	7.2	0.15	0.8	12.23	82.2	1.3	1.8	6.2	21	0.1	3.7
TX516	0.12	23.6	0.27	0.8	3.68	75.4	2	3.2	2.9	30.7	0	3.9
Compositional Profiles for Least Suitable Soil Types												
MUID	AWC	CLAY	KFFACT	OM	PERM	THICK	HYGRP	DRAIN	SLOPE	LL	IFHYDRIC	AFLDFREQ
TX037	0.12	31.3	0.33	0.5	1.93	86.2	3.5	3.8	4.8	41.6	0	4
TX162	0.15	37.9	0.34	1	0.24	70.8	4	5.3	0	50.1	0.3	3.9
TX475	0.13	29.5	0.31	0.9	2.15	80.5	3.4	4	2.8	41.9	0	3.9
TX454	0.13	29.3	0.32	0.6	1.22	76	3.5	3.9	2.2	39.3	0	3.8
TX346	0.17	32	0.36	0.8	0.39	65.5	3.9	5.3	0.4	41.6	0.3	3.8
TX188	0.15	44.7	0.3	2.2	0.44	72.2	3.5	3.5	3.3	57.8	0	3.7
TX119	0.14	43.3	0.33	0.9	0.16	75.2	3.9	3.8	2.3	55	0	3.9
TX638	0.18	65.6	0.23	2.9	1.23	63.7	4	6.8	0.1	68.1	1	1.1
TX293	0.1	18.5	0.2	0.3	6.99	73.3	1.8	3.1	6.7	27.6	0.1	3.7
TX639	0.16	71.4	0.26	2.9	0.66	73.4	4	7	0	71.7	1	1

Table 2.12. Rock exposure type for the second Rock Pocketbook model is listed from highest to lowest mean habitat suitability score. The highest score is associated with the most suitable rock exposure type for Rock Pocketbook using the combined data set.

MEAN	SE	ROCK EXPOSURE TYPE
0.082	0.0038	sand
0.074	0.0014	terrace
0.048	≤ 0.001	sandstone
0.029	≤ 0.001	fine-grained mixed clastic
0.012	≤ 0.001	shale
0.0044	≤ 0.001	mudstone
0.0040	≤ 0.001	limestone
0.0028	≤ 0.001	clay or mud
≤ 0.001	≤ 0.001	siltstone

Table 2.13. Vegetation cover for the second Rock Pocketbook model is listed from highest to lowest mean habitat suitability score. The highest score is associated with the most suitable vegetation type for the presence of Rock Pocketbook using the combined data set.

MEAN	SE	VEGETATION COVER TYPE
0.22	0.0093	Water Oak-Elm-Hackberry Forest
0.19	0.0066	Willow Oak-Water Oak-Blackgum Forest
0.057	0.0039	Urban
0.038	≤ 0.001	Post Oak Woods, Forest and Grassland Mosaic
0.038	0.0022	Post Oak Woods/Forest
0.033	≤ 0.001	Pine Hardwood
0.029	≤ 0.001	Young Forest/Grassland
0.015	≤ 0.001	Lake
0.013	0.0038	Bald Cypress-Water Tupelo Swamp
0.0078	≤ 0.001	Elm-Hackberry Parks/Woods
0.0043	≤ 0.001	Crops
≤ 0.001	≤ 0.001	Marsh Barrier Island
≤ 0.001	≤ 0.001	Bluestem Grassland
≤ 0.001	≤ 0.001	Pecan Elm

Table 2.14. The compositional profiles for the second Rock Pocketbook model are listed by the most suitable soil types (MUID) and least suitable soil types. The highest mean habitat suitability score is associated with the most suitable soil type for the presence of Rock Pocketbook using the combined data set.

Compositional Profiles for Most Suitable Soil Types												
MUID	AWC	CLAY	KFFACT	OM	PERM	THICK	HYGRP	DRAIN	SLOPE	LL	IFHYDRIC	AFLDFREQ
TX477	0.13	19.6	0.25	0.7	5.56	78.7	2.2	2.9	2.9	28.2	0	3.8
TX282	0.13	22.1	0.29	0.6	3.26	76.3	2.7	4.3	1.7	30.7	0.4	3.3
TX250	0.15	63.9	0.32	1	0.1	78.5	3.9	4.5	0.7	70.1	0.8	1.5
TX317	0.16	26	0.28	0.4	1.3	66	2.7	4.1	0	33.4	0	1.3
TX357	0.13	28.4	0.29	0.8	1.39	79.9	3.1	4.7	0.7	38.5	0.7	1.8
TX123	0.11	27.9	0.24	0.6	3.11	70.6	2.5	3	8.3	33.5	0	4
TX172	0.15	31.8	0.28	0.6	1.19	74.1	3.4	4.6	0.3	36.2	0.7	1.4
TX316	0.16	20.9	0.29	0.5	1.43	68.9	3.2	4.7	0.2	28.6	0.5	1.4
TX516	0.12	23.6	0.27	0.8	3.68	75.4	2	3.2	2.9	30.7	0	3.9000001
TX574	0.14	65.5	0.32	1.8	0.1	76	3.8	4.5	0	69.2	0.1	1.5
Compositional Profiles for Least Suitable Soil Types												
MUID	AWC	CLAY	KFFACT	OM	PERM	THICK	HYGRP	DRAIN	SLOPE	LL	IFHYDRIC	AFLDFREQ
TX475	0.13	29.5	0.31	0.9	2.15	80.5	3.4	4	2.8	41.9	0	3.9000001
TX293	0.1	18.5	0.2	0.3	6.99	73.3	1.8	3.1	6.7	27.6	0.1	3.7
TX520	0.09	31.9	0.23	0.6	1.02	52.5	3.7	3.6	2.9	41.2	0	3.8
TX626	0.14	33.5	0.36	0.9	0.32	67.9	3.9	4.5	2.4	43.4	0	3.9000001
TX162	0.15	37.9	0.34	1	0.24	70.8	4	5.3	0	50.1	0.3	3.9000001
TX638	0.18	65.6	0.23	2.9	1.23	63.7	4	6.8	0.1	68.1	1	1.1
TX454	0.13	29.3	0.32	0.6	1.22	76	3.5	3.9	2.2	39.3	0	3.8
TX346	0.17	32	0.36	0.8	0.39	65.5	3.9	5.3	0.4	41.6	0.3	3.8
TX639	0.16	71.4	0.26	2.9	0.66	73.4	4	7	0	71.7	1	1
TX188	0.15	44.7	0.3	2.2	0.44	72.2	3.5	3.5	3.3	57.8	0	3.7

Table 2.15. The soil habitat types (MUID) that were common between individual species (Texas Pigtoe original and combined models; Rock Pocketbook original and combined models) and common between models of different data inclusion (both species with original data; both species with combined data). Highlighted components submit the most control over what is considered the most suitable habitats within each model.

Comparisons of Common Soil MUIDs								
	Common MUIDs of ROPO Models	p-value	Common MUIDs of TEPI Models	p-value	Common MUIDs of Original Data	p-value	Common MUIDs of Combined Data	p-value
Code	ROPO		TEPI		ROPO_TEPI_ORIG		ROPO_TEPI_COMB	
MUID	TX282	0.96	TX282	0.66	TX282	1	TX282	1
	TX250	0.14	TX222	0.35	TX250	≤ 0.001	TX250	≤ 0.001
	TX317	0.32	TX051	0.31	TX317	≤ 0.001	TX317	≤ 0.001
	TX357	0.79	TX172	0.02	TX172	≤ 0.001	TX172	≤ 0.001
	TX123	≤ 0.001	TX317	0.002	TX316	≤ 0.001		
	TX172	0.65	TX250	≤ 0.001				
	TX316	1	TX272	0.002				
	TX516	0.047	TX263	≤ 0.001				
	TX574	0.23	TX175	≤ 0.001				

Table 2.16. The rock exposure types that were common between individual species (Texas Pigtoe original and combined models; Rock Pocketbook original and combined models) and common between models of different data inclusion (both species with original data; both species with combined data). Highlighted components submit the most control over what is considered the most suitable habitats within each model.

Comparisons of Common Rock Exposure Types								
	Common Rock Exposure Types of TEPI Models	p-value	Common Rock Exposure Types of ROPO Models	p-value	Common Rock Exposure Types of Original Data	p-value	Common Rock Exposure Types of Combined Data	p-value
Code	TEPI		ROPO		ROPO_TEPI_ORIG		ROPO_TEPI_COMB	
Geology Type	Terrace	≤ 0.001	Terrace	0.23	Terrace	1	Terrace	1
	Sand	≤ 0.001	Sand	≤ 0.001	Sand	0.0086	Sand	1
	Sandstone	≤ 0.001	Sandstone	0.018	Sandstone	≤ 0.001	Sandstone	≤ 0.001
	Fine-grained Mixed Clastic	0.3	Fine-grained Mixed Clastic	0.1	Fine-grained Mixed Clastic	≤ 0.001	Fine-grained Mixed Clastic	≤ 0.001
	Siltstone	0.13	Siltstone	0.51	Siltstone	1	Siltstone	1
	Clay or Mud	≤ 0.001	Clay or Mud	0.97	Clay or Mud	1	Clay or Mud	1
	Limestone	≤ 0.001	Limestone	0.57	Limestone	0.98	Limestone	1
	Shale	NA	Shale	1	Shale	≤ 0.001	Shale	≤ 0.001
	Mudstone	NA	Mudstone	1	Mudstone	≤ 0.001	Mudstone	0.99

Table 2.17. The vegetation types that were common between individual species (Texas Pigtoe original and combined models; Rock Pocketbook original and combined models) and common between models of different data inclusion (both species with original data; both species with combined data). Highlighted components submit the most control over what is considered the most suitable habitats within each model.

	Comparisons of Common Vegetation Types							
	Common Vegetation Types of TEPI Models	p-value	Common Vegetation Types of ROPO Models	p-value	Common Vegetation Types of Original Data	p-value	Common Vegetation Types of Combined Data	p-value
Code	TEPI		ROPO		ROPO_TEPI_ORIG		ROPO_TEPI_COMB	
Vegetation Type	Willow Oak-Water Oak- Blackgum Forest	≤ 0.001	Willow Oak-Water Oak- Blackgum Forest	0.78	Willow Oak-Water Oak- Blackgum Forest	1	Willow Oak-Water Oak- Blackgum Forest	1
	Water Oak-Elm_Hackberry Forest	≤ 0.001	Water Oak-Elm_Hackberry Forest	0.0013	Water Oak-Elm_Hackberry Forest	≤ 0.001	Water Oak-Elm_Hackberry Forest	1
	Young Forest/Grassland	0.36	Young Forest/Grassland	0.78	Young Forest/Grassland	1	Young Forest/Grassland	1
	Pine Hardwood	≤ 0.001	Pine Hardwood	0.082	Pine Hardwood	1	Pine Hardwood	0
	Bald Cypress-Water Tupelo Swamp	0.36	Bald Cypress-Water Tupelo Swamp	0.25	Bald Cypress-Water Tupelo Swamp	1	Bald Cypress-Water Tupelo Swamp	1
	Post Oak Woods/Forest	≤ 0.001	Post Oak Woods/Forest	≤ 0.001	Post Oak Woods/Forest	≤ 0.001	Post Oak Woods/Forest	≤ 0.001
	Post Oak Woods/Forest-Grassland	≤ 0.001	Post Oak Woods/Forest-Grassland	≤ 0.001	Post Oak Woods/Forest-Grassland	≤ 0.001	Post Oak Woods/Forest-Grassland	≤ 0.001
	Elm-Hackberry Parks/Woods	≤ 0.001	Elm-Hackberry Parks/Woods	0.98	Elm-Hackberry Parks/Woods	0.12	Elm-Hackberry Parks/Woods	1
	Urban	≤ 0.001	Urban	0.19	Urban	≤ 0.001	Urban	≤ 0.001
	Crops	≤ 0.001	Crops	0.14	Crops	0.014	Crops	1
	Pecan Elm	0.68	Pecan Elm	0.81	Pecan Elm	1	Pecan Elm	0.99
	Bluestem-Grassland	≤ 0.001	Bluestem-Grassland	1	Bluestem-Grassland	1	Bluestem-Grassland	1
	Marsh Barrier Island	0.17	Marsh Barrier Island	0.99	Marsh Barrier Island	0.78	Marsh Barrier Island	0.98

Figure 2.1. The Sulphur River was sampled for freshwater mussels at 14 sites, 2 of which were located on the South Sulphur, 1 on the North Sulphur, and 11 on the mainstem. Sites in green indicate locations that were shallow enough to accomplish a manual search of the entire reach. Sites in red indicate locations where the use of SCUBA was required.

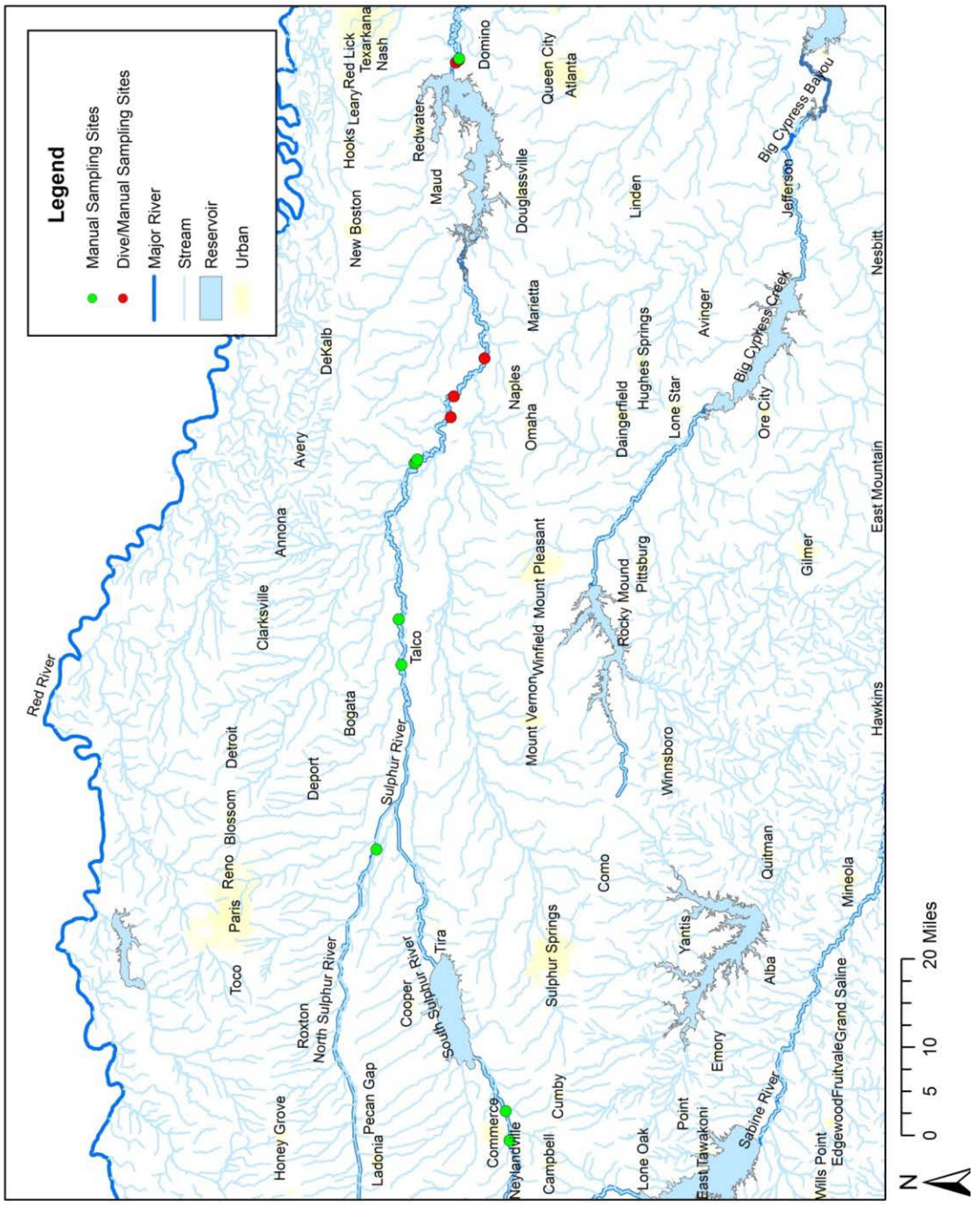


Figure 2.2. The Big Cypress River was sampled for freshwater mussels at 18 sites, 5 of which were located on the Little Cypress Creek, and 1 on the Black Cypress.

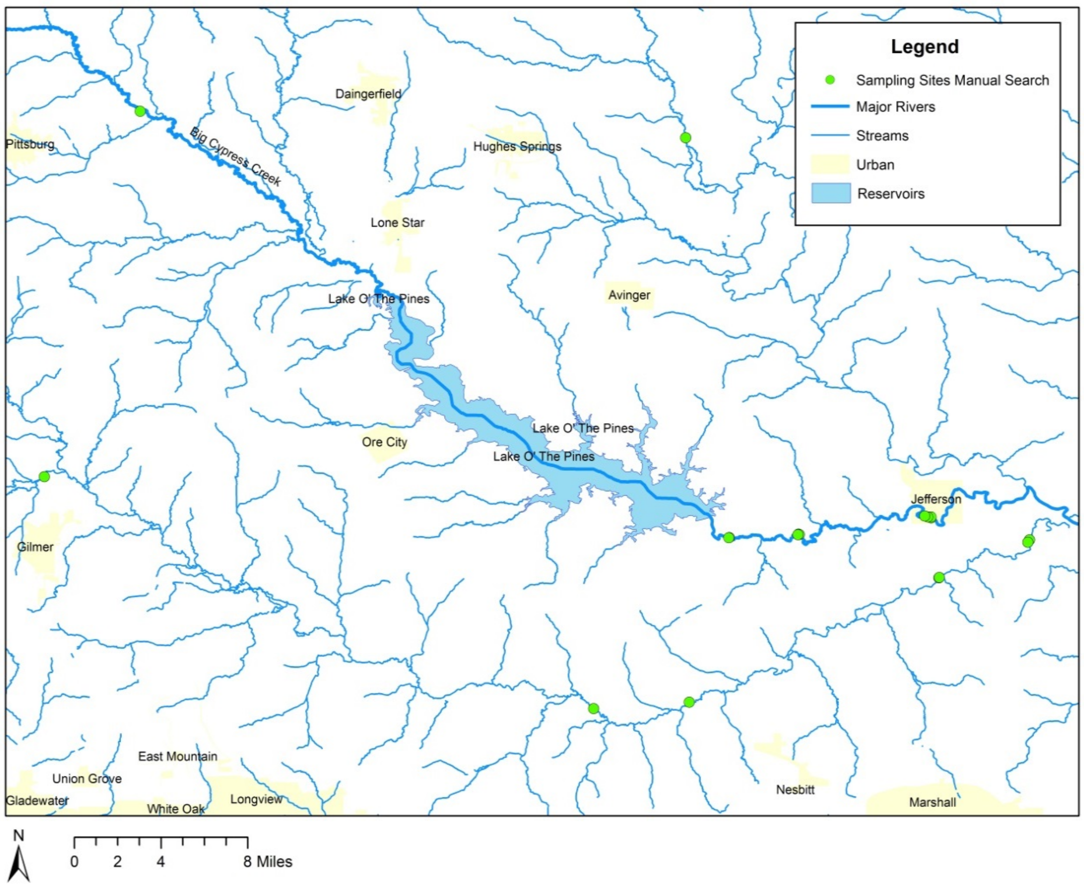


Figure 2.3. Probability distribution of Texas Pigtoe (*Fusconaia askewi*) for the initial model with original data samples. Sampling sites are located within the Sabine, Neches, Angelina, and Trinity Rivers.

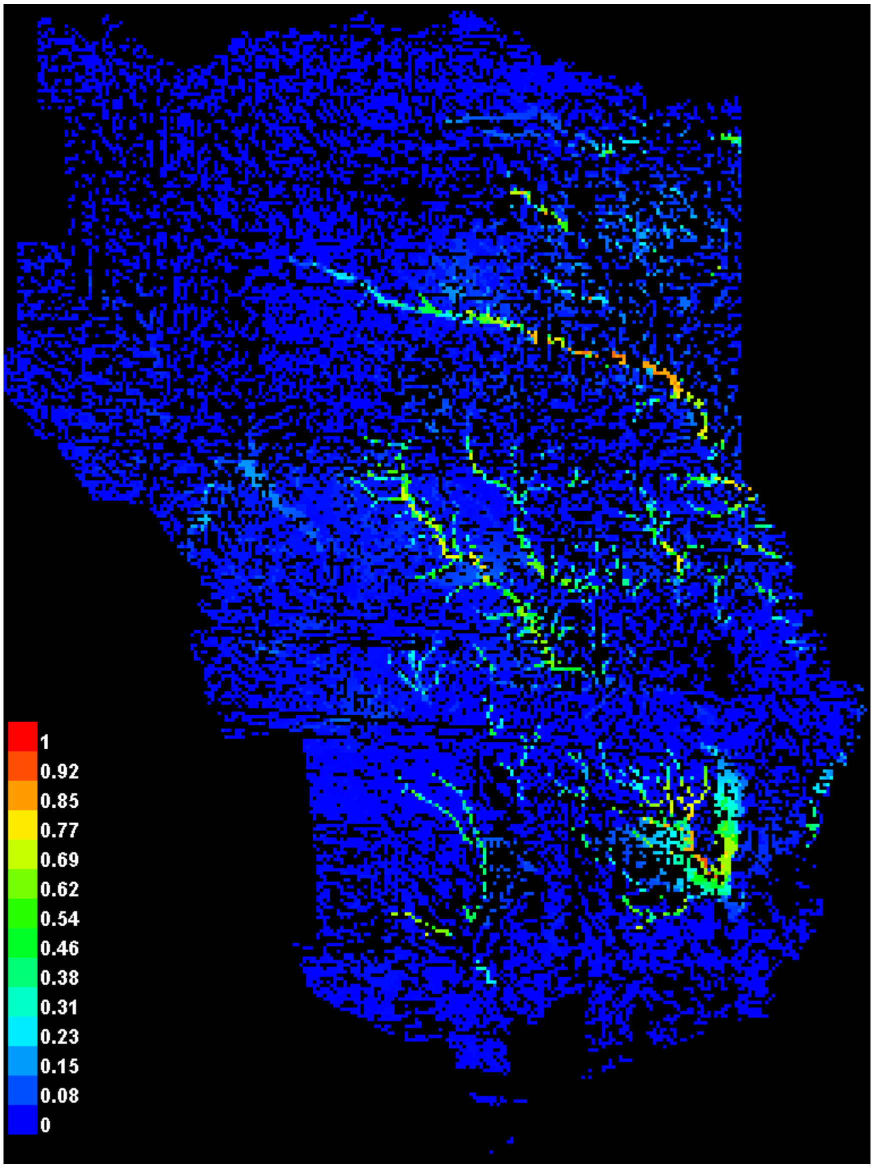


Figure 2.4. Mean habitat suitability scores for the 4 most suitable vegetation types and 4 least suitable vegetation types. Values are derived from the initial species distribution model of Texas Pigtoe (*Fusconaia askewi*) with the original data samples.

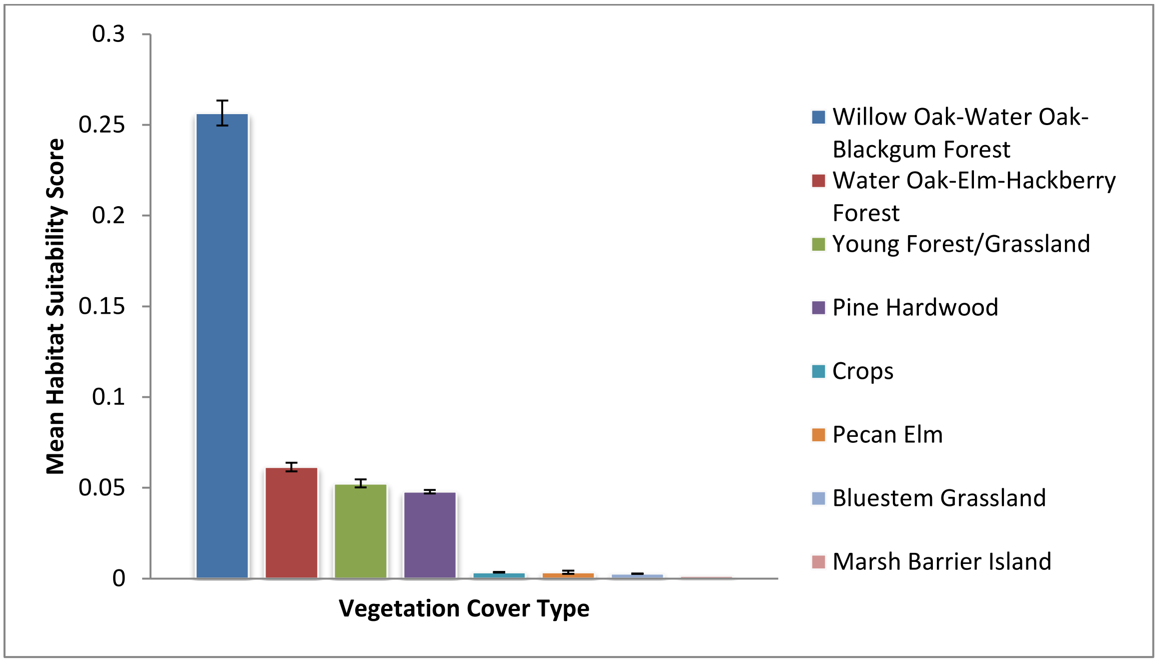


Figure 2.5. The mean habitat suitability scores of the 4 most suitable vegetation types and 4 least suitable vegetation types are significantly different for Texas Pigtoe (*Fusconaia askewi*). Data derived from the initial species distribution model.

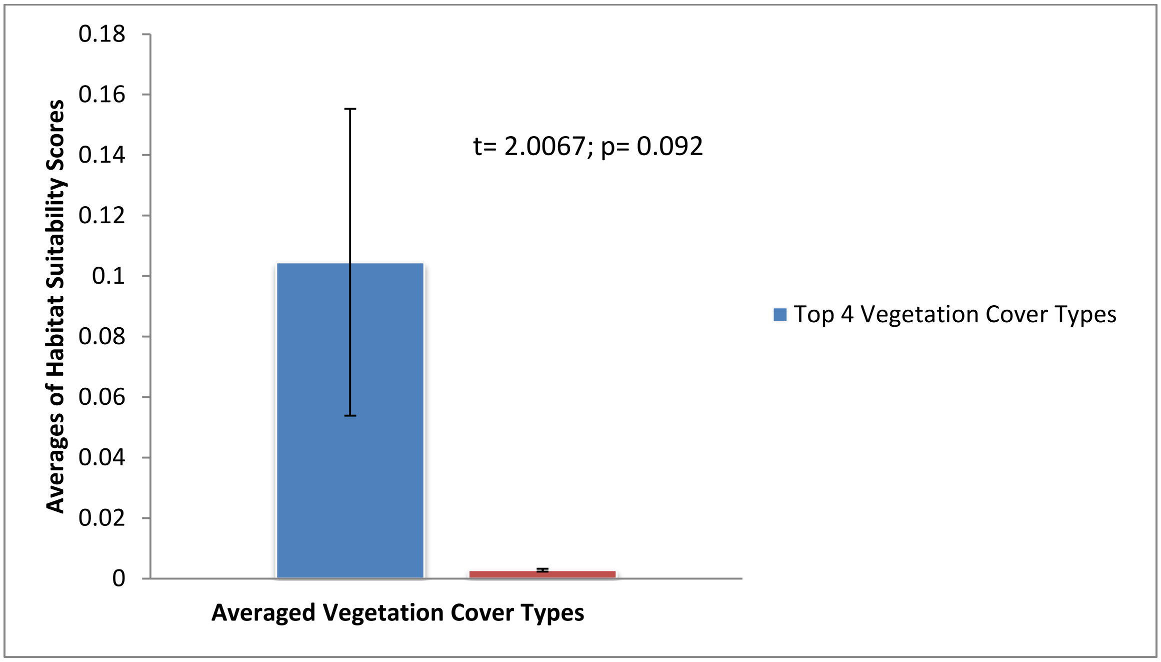


Figure 2.6. Mean habitat suitability scores for all rock exposure types. Values are derived from the initial species distribution model of Texas Pigtoe (*Fusconaia askewi*) with the original data samples.

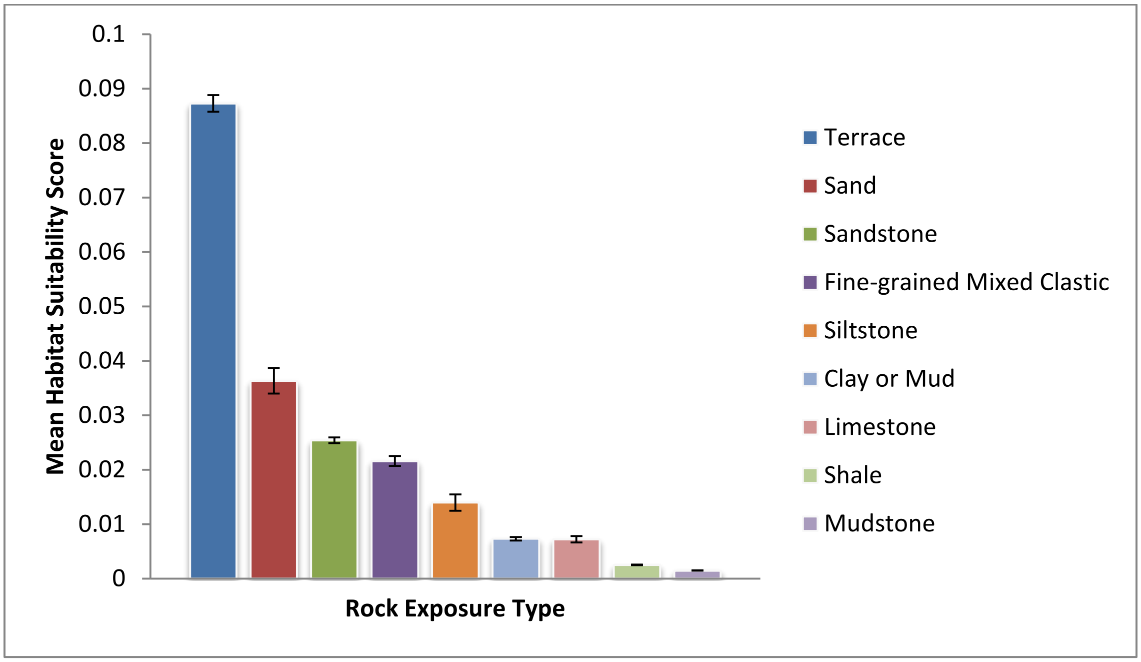


Figure 2.7.The mean habitat suitability scores of the 5 most suitable rock exposure types and 5 least suitable rock exposure types are significantly different for Texas Pigtoe (*Fusconaia askewi*). Data derived from the initial species distribution model.

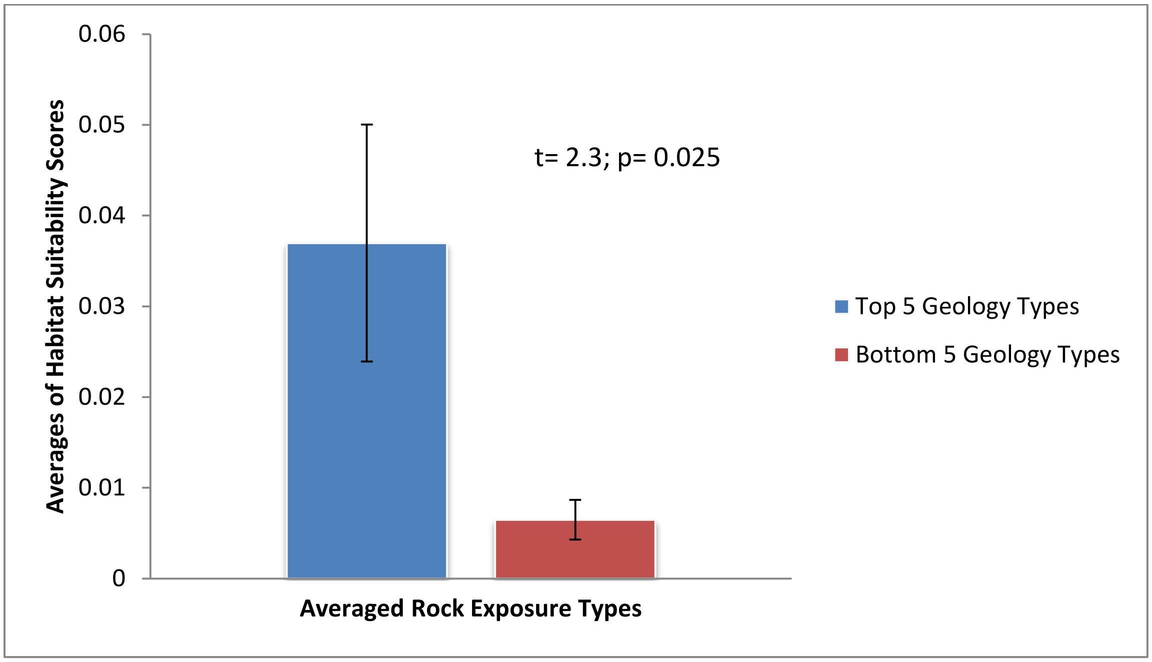


Figure 2.8. Mean habitat suitability scores for the 5 most suitable soil types and 5 of the least suitable soil types. Values are derived from the initial species distribution model of Texas Pigtoe (*Fusconaia askewi*) with original data.

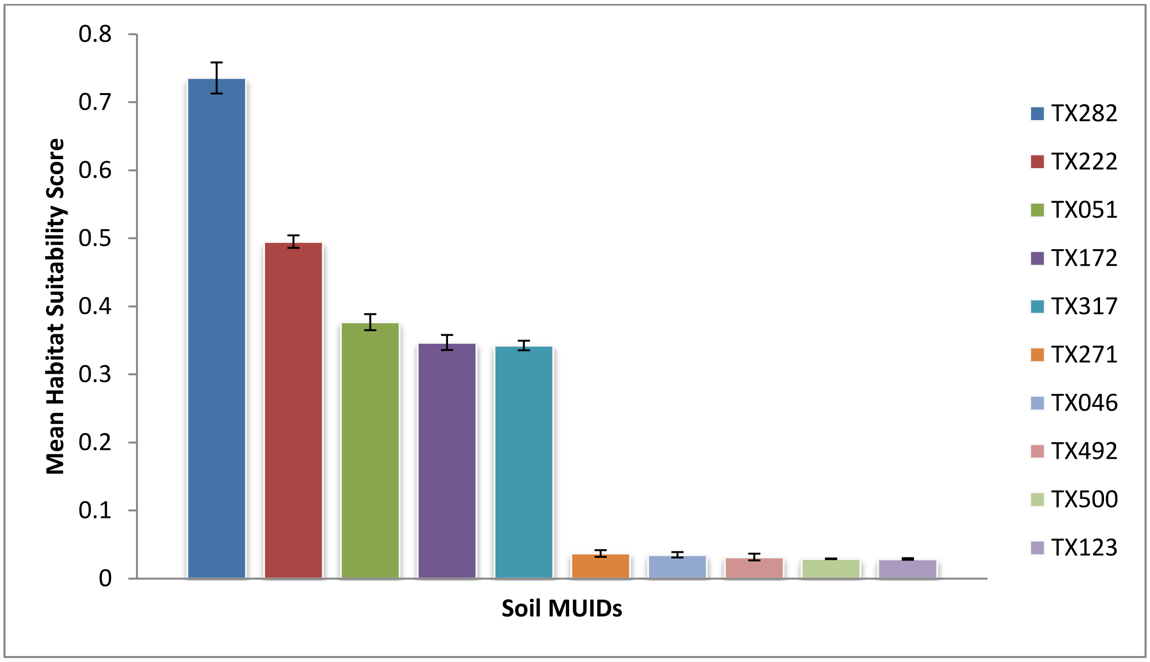


Figure 2.9 The mean habitat suitability scores of the 10 most suitable soil types and the 10 least suitable soil types are significantly different for Texas Pigtoe (*Fusconaia askewi*). Data derived from the initial species distribution model.

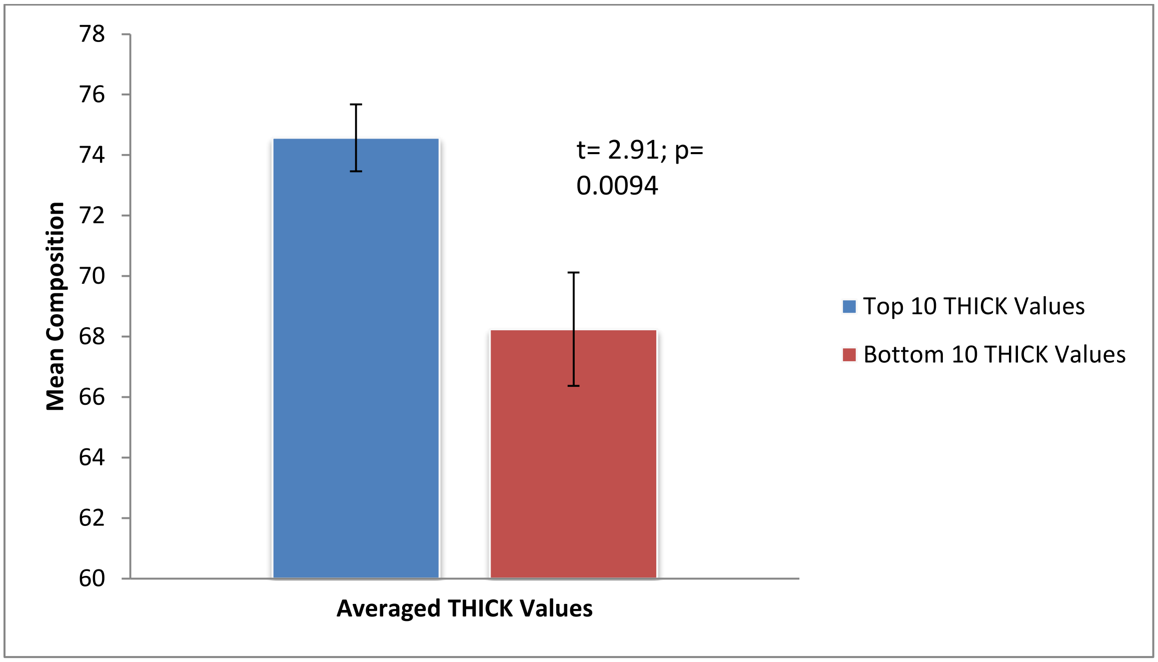


Figure 2.10. Probability distribution of Texas Pigtoe (*Fusconaia askewi*) for the second model with combined data samples. Sampling sites are located within the Sabine, Neches, Angelina, Trinity, Sulphur, and Big Cypress Rivers.

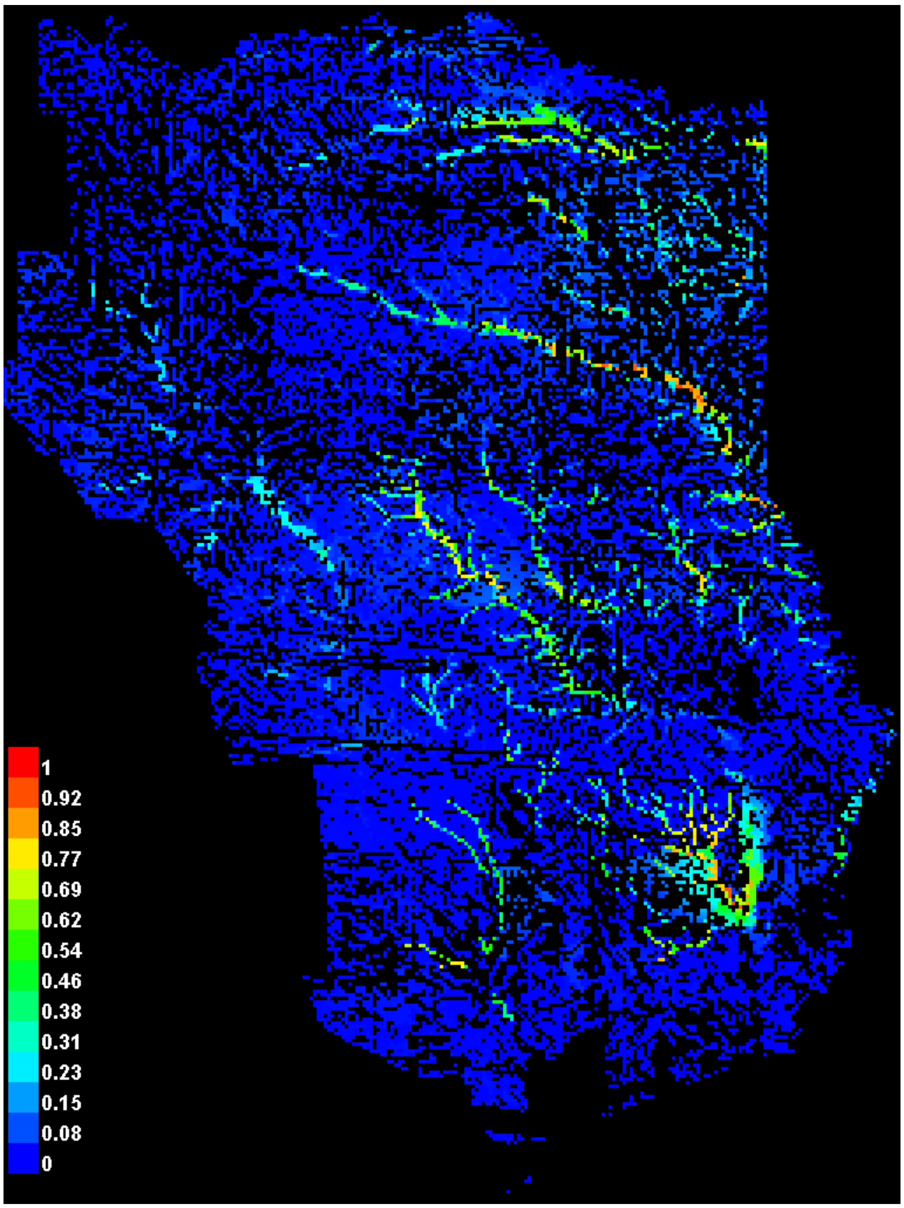


Figure 2.11. Mean habitat suitability scores for the 4 most suitable vegetation types and 4 least suitable vegetation types. Values are derived from the second species distribution model of Texas Pigtoe (*Fusconaia askewi*) with the combined data samples.

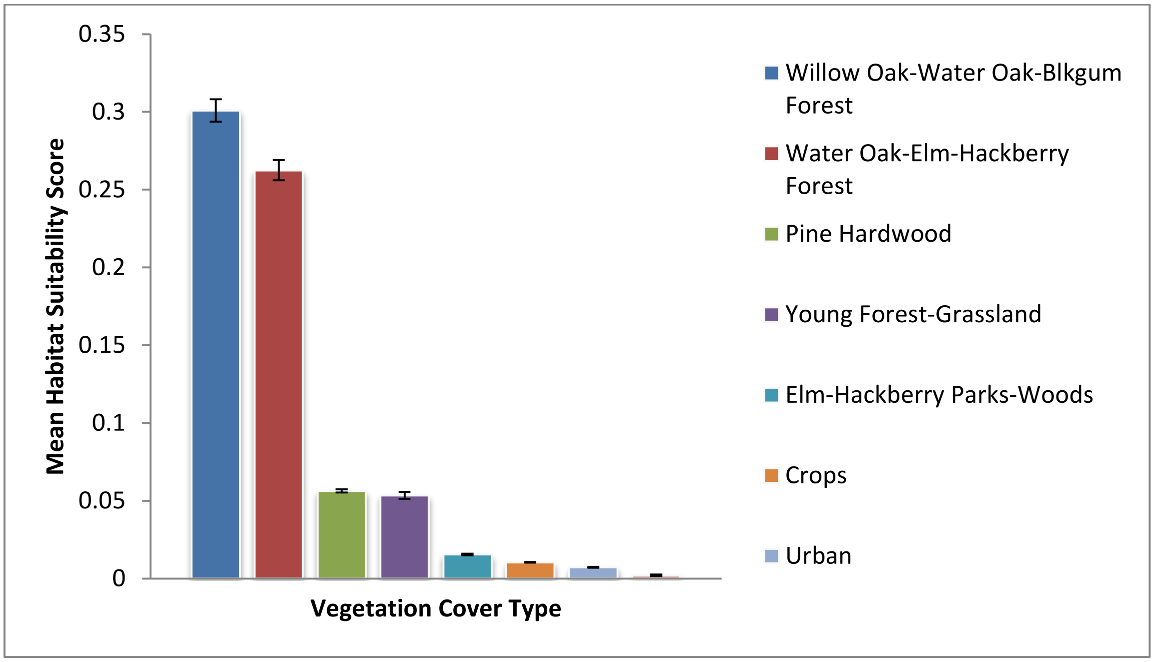


Figure 2.12. The mean habitat suitability scores of the 4 most suitable vegetation types and 4 least suitable vegetation types are significantly different for Texas Pigtoe (*Fusconaia askewi*). Data derived from the second species distribution model.

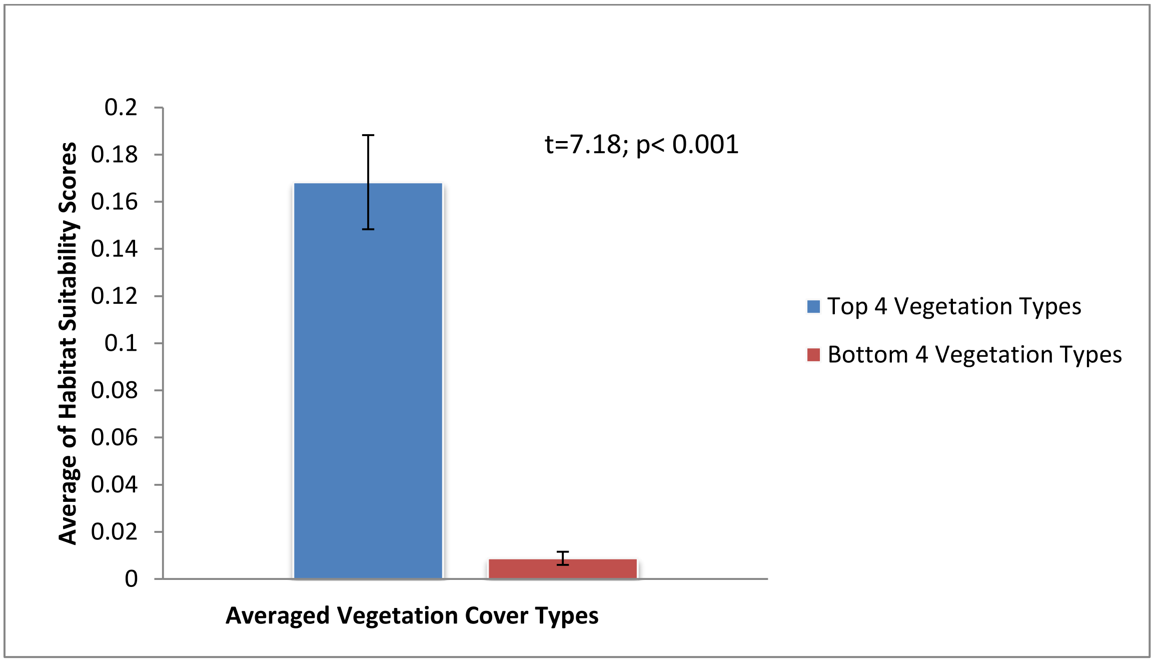


Figure 2.13. Mean habitat suitability scores for all rock exposure types. Values are derived from the second species distribution model of Texas Pigtoe (*Fusconaia askewi*) with the combined data samples.

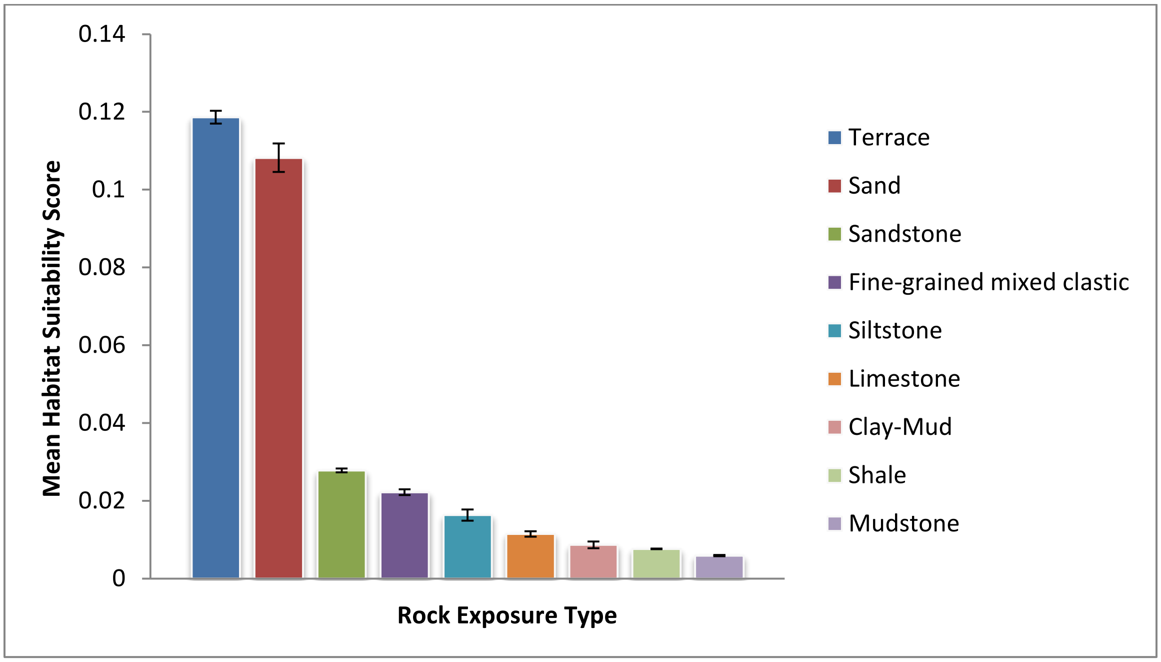


Figure 2.14. The mean habitat suitability scores of the 5 most suitable rock exposure types and 4 least suitable rock exposure types are significantly different for Texas Pigtoe (*Fusconaia askewi*). Data derived from the second species distribution model.

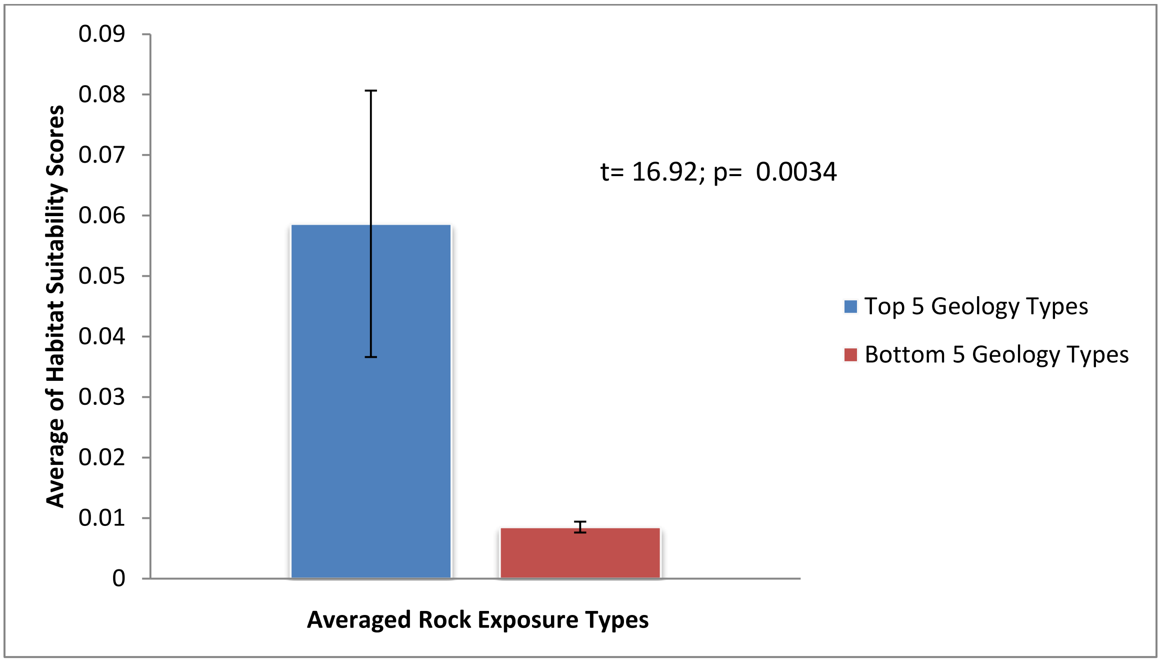


Figure 2.15. Mean habitat suitability scores for the 5 most suitable soil types and 5 of the least suitable soil types. Values are derived from the second species distribution model of Texas Pigtoe (*Fusconaia askewi*) with combined data.

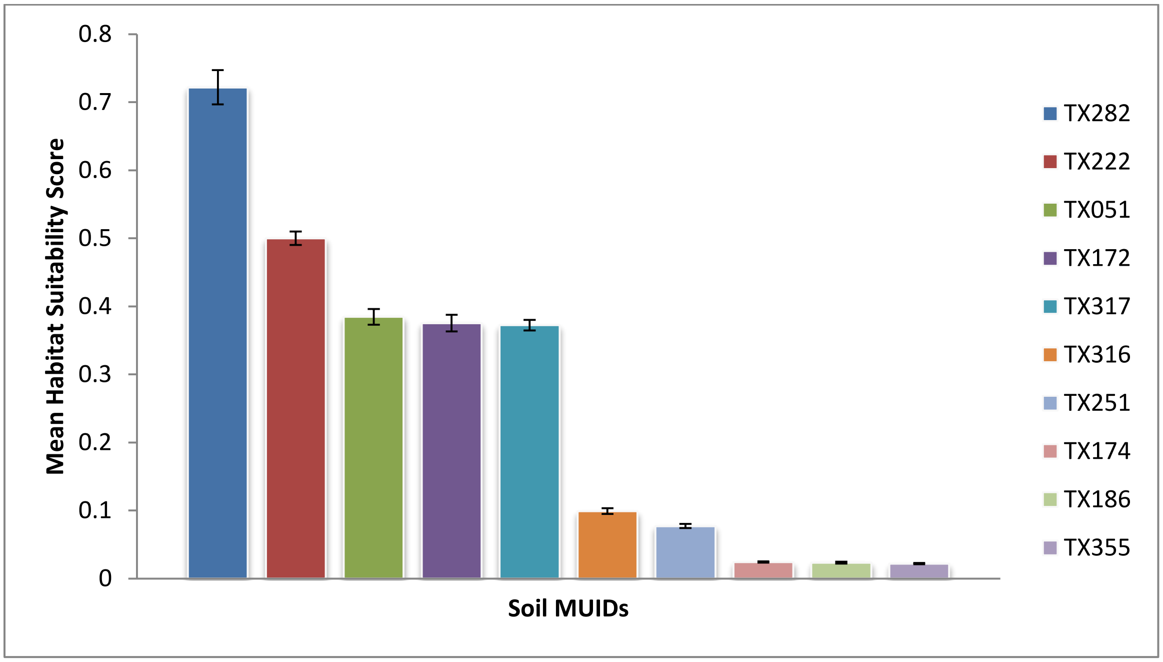


Figure 2.16. The mean habitat suitability scores of the 10 most suitable soil types and the 10 least suitable soil types are significantly different for Texas Pigtoe (*Fusconaia askewi*). Data derived from the second species distribution model.

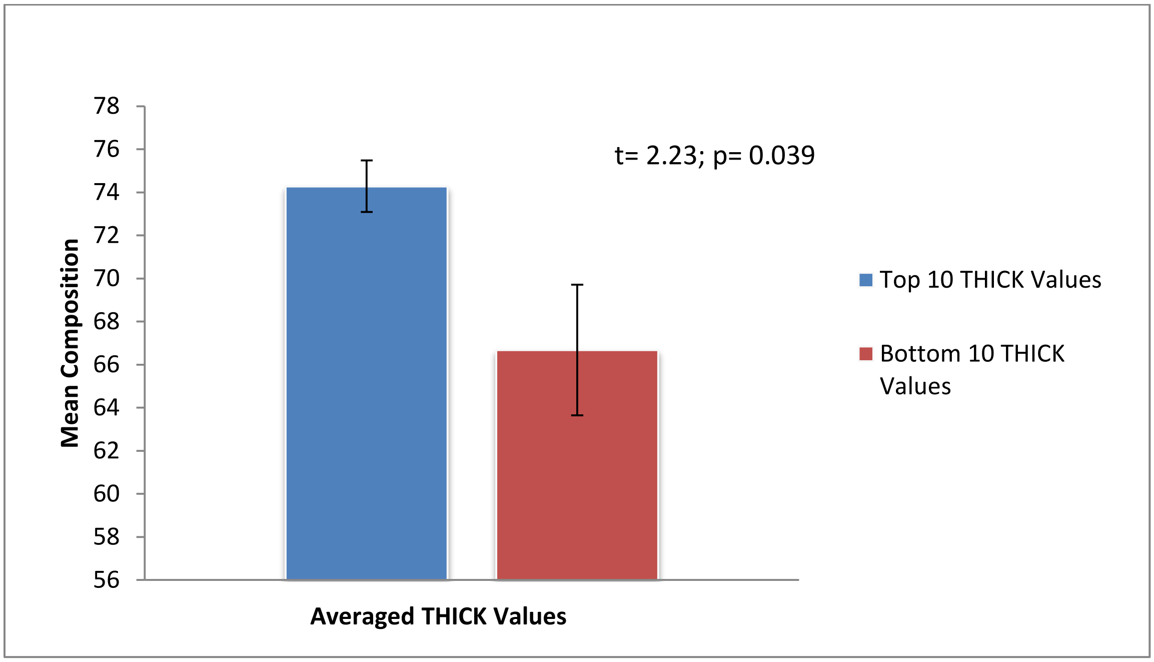


Figure 2.17. The mean habitat suitability scores of the 10 most suitable soil types and the 10 least suitable soil types are significantly different for Texas Pigtoe (*Fusconaia askewi*). Data derived from the initial species distribution model.

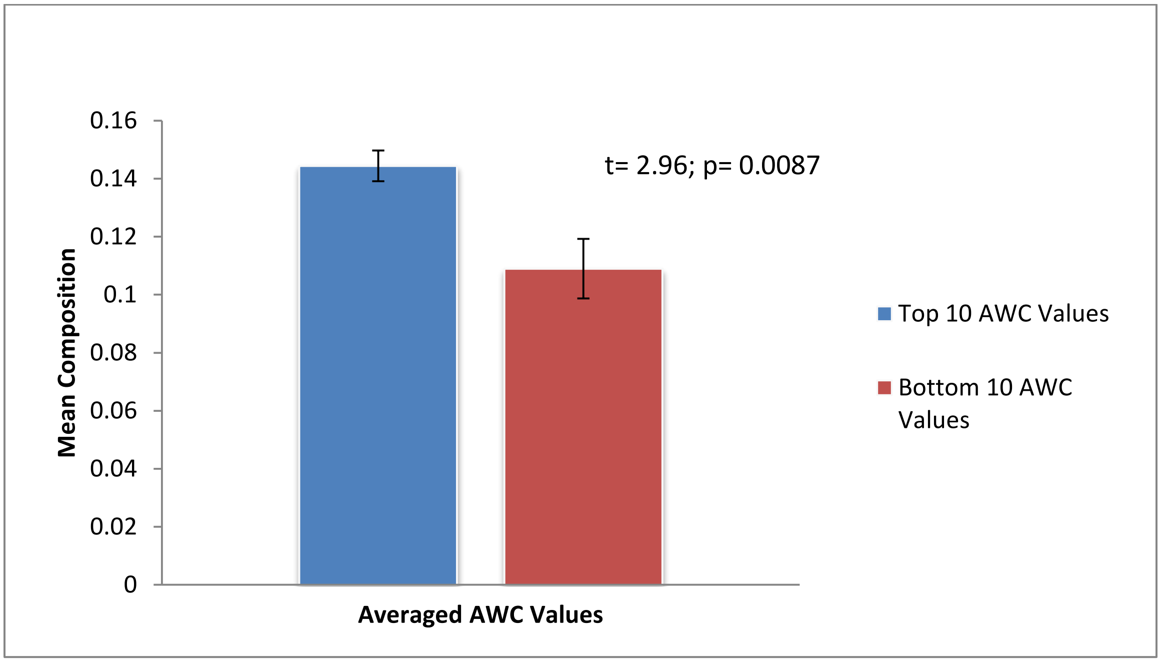


Figure 2.18. The mean habitat suitability scores of the 10 most suitable soil types and the 10 least suitable soil types are significantly different for Texas Pigtoe (*Fusconaia askewi*). Data derived from the initial species distribution model.

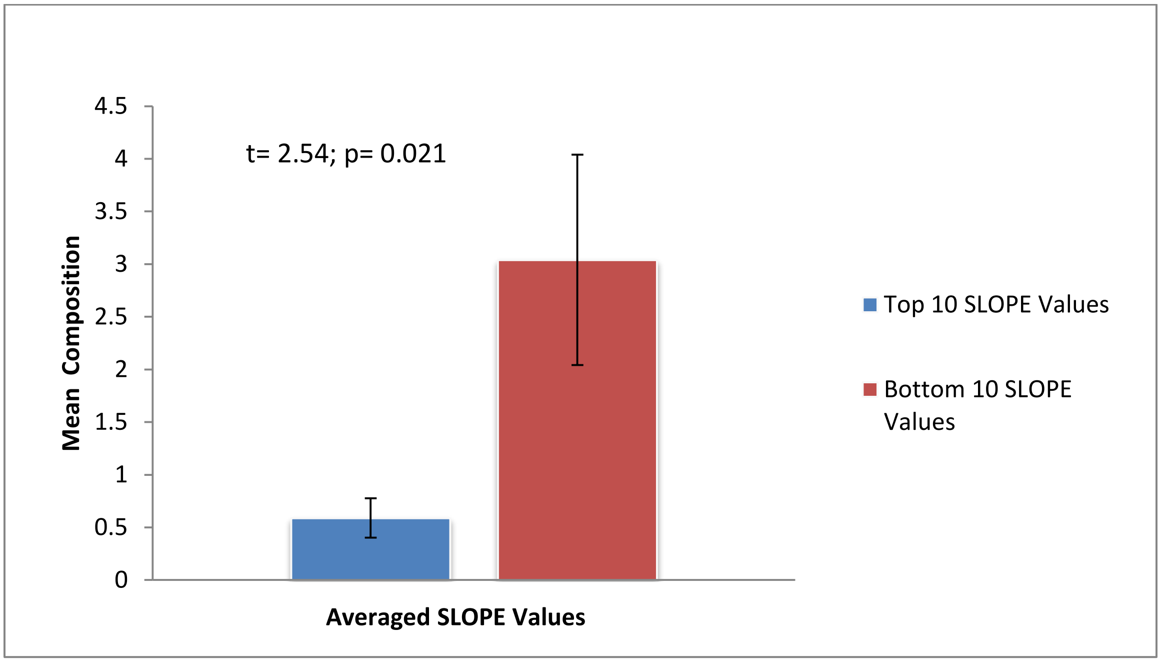


Figure 2.19. Probability distribution of Rock Pocketbook (*Arcidens confragosus*) for the initial model with original data samples. Sampling sites are located within the Sabine, Neches, Angelina, and Trinity Rivers.

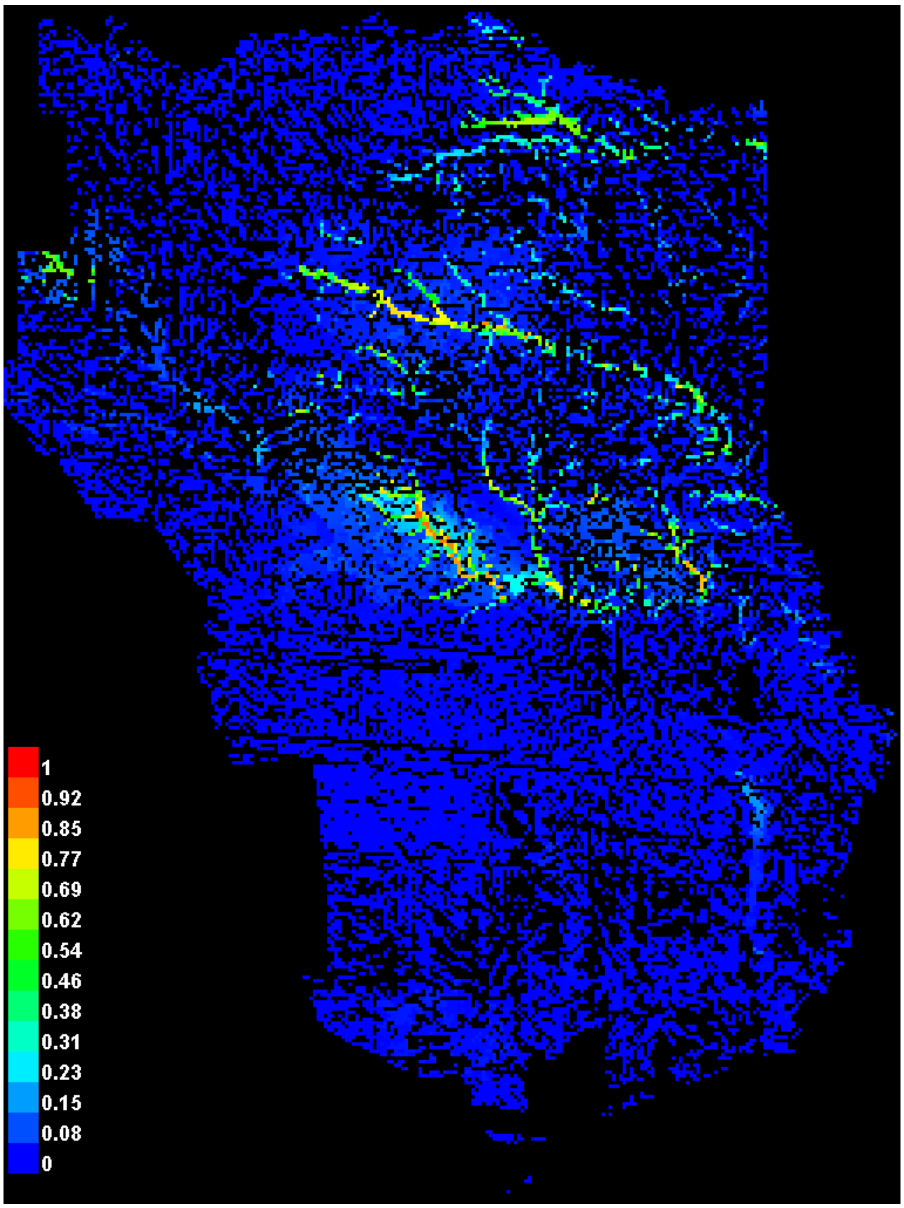


Figure 2.20. Mean habitat suitability scores for all rock exposure types. Values are derived from the initial species distribution model of Rock Pocketbook (*Arcidens confragosus*) with the original data samples.

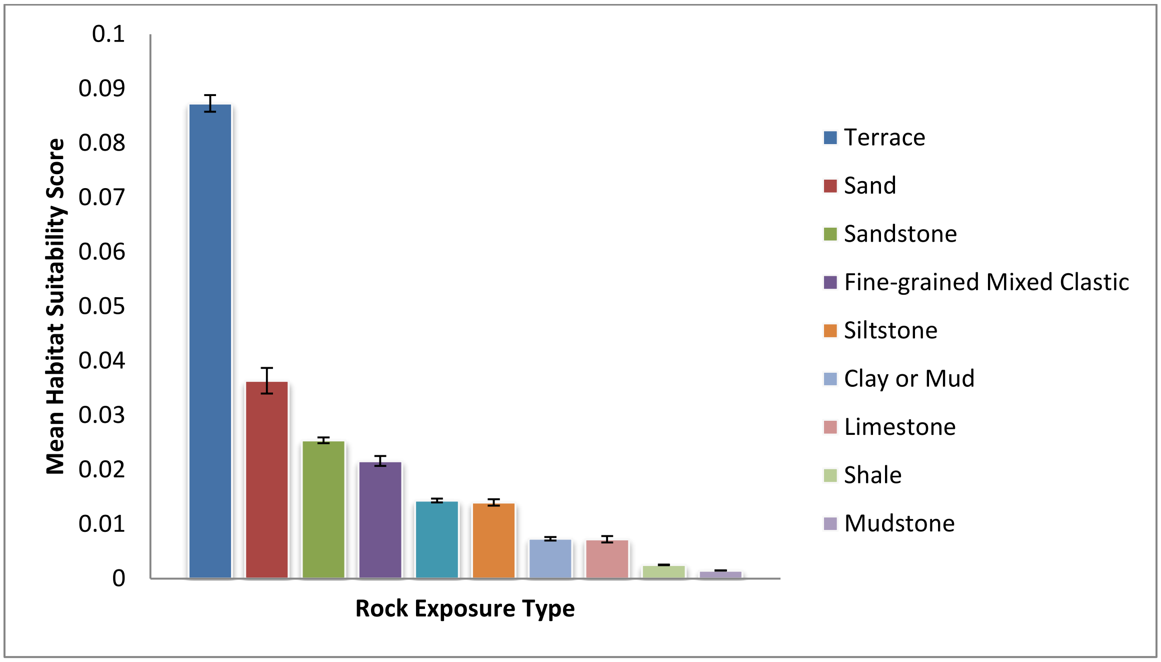


Figure 2.21. The mean habitat suitability scores of the 5 most suitable rock exposure types and 5 least suitable rock exposure types are significantly different for Rock Pocketbook (*Arcidens confragosus*). Data derived from the initial species distribution model.

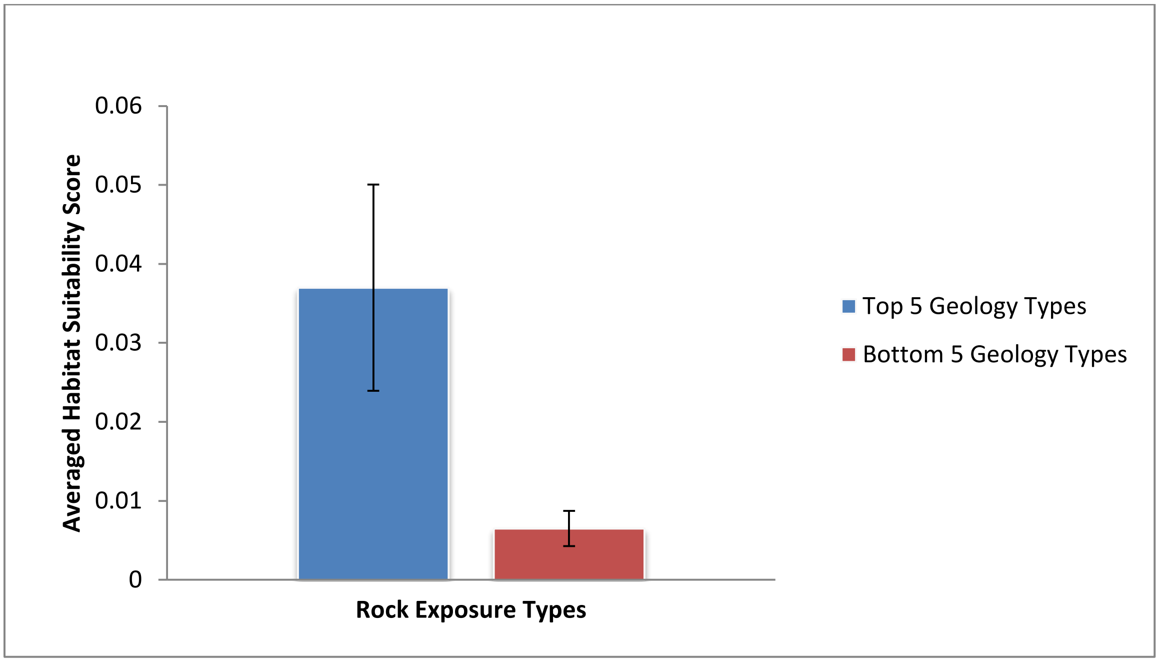


Figure 2.22. Mean habitat suitability scores for the 4 most suitable vegetation types and 4 least suitable vegetation types. Values are derived from the initial species distribution model of Rock Pocketbook (*Arcidens confragosus*) with the original data samples.

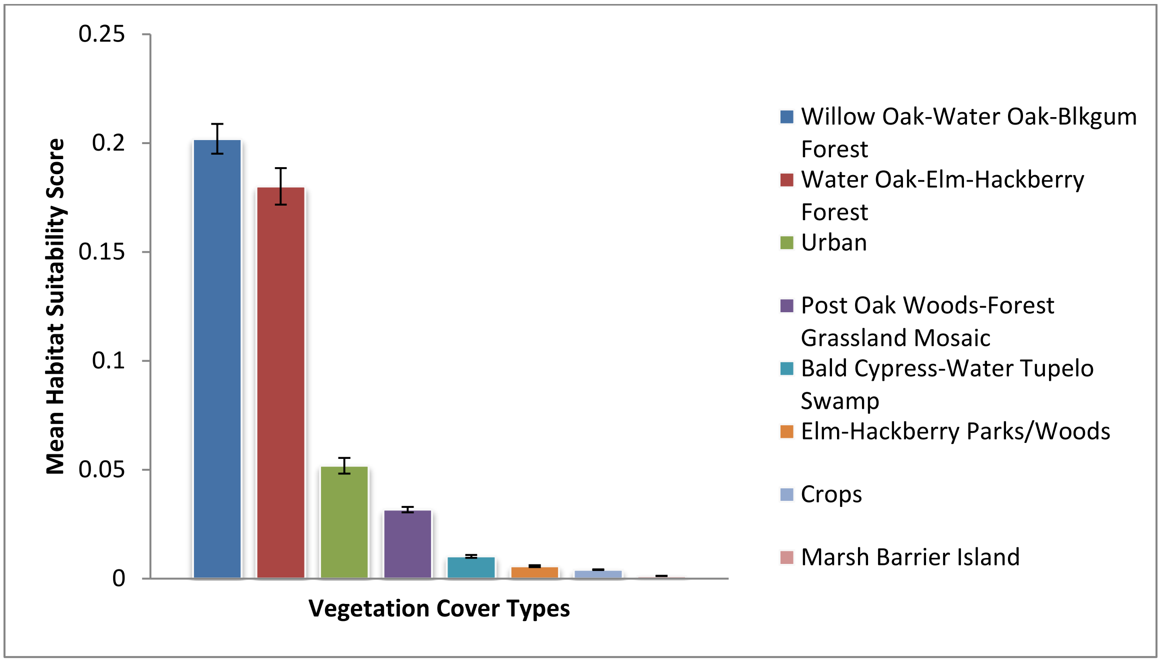


Figure 2.23. The mean habitat suitability scores of the 4 most suitable vegetation types and 4 least suitable vegetation types are significantly different for Rock Pocketbook (*Arcidens confragosus*). Data derived from the initial species distribution model.

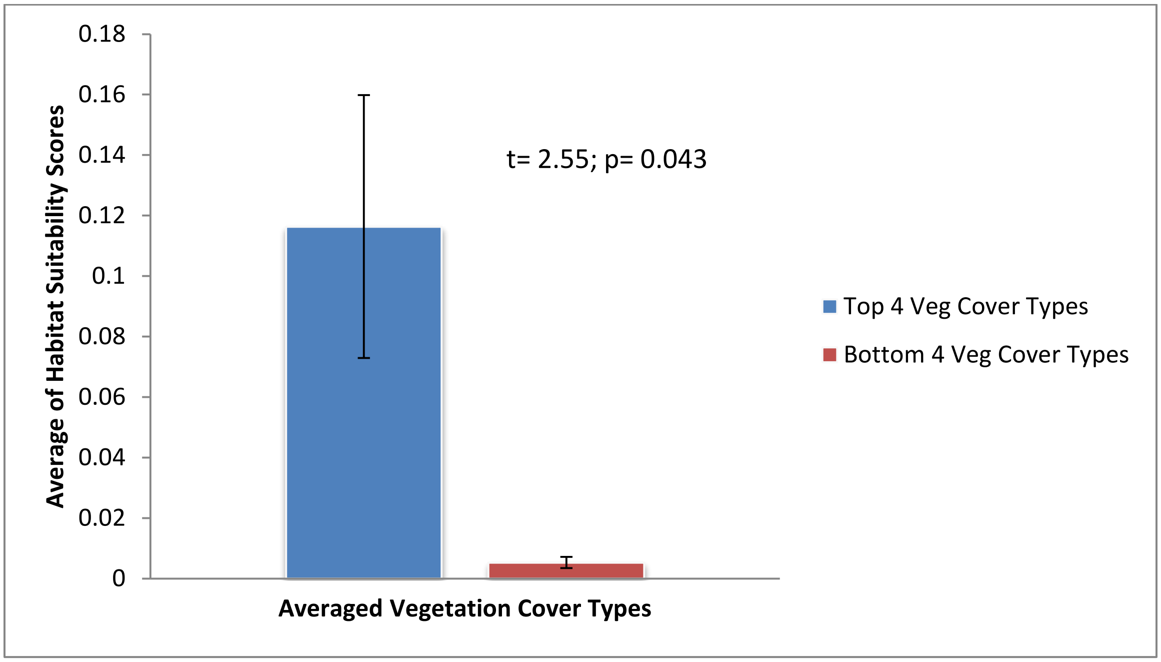


Figure 2.24. Mean habitat suitability scores for the 5 most suitable soil types and 5 of the least suitable soil types. Values are derived from the initial species distribution model of Rock Pocketbook (*Arcidens confragosus*) with original data.

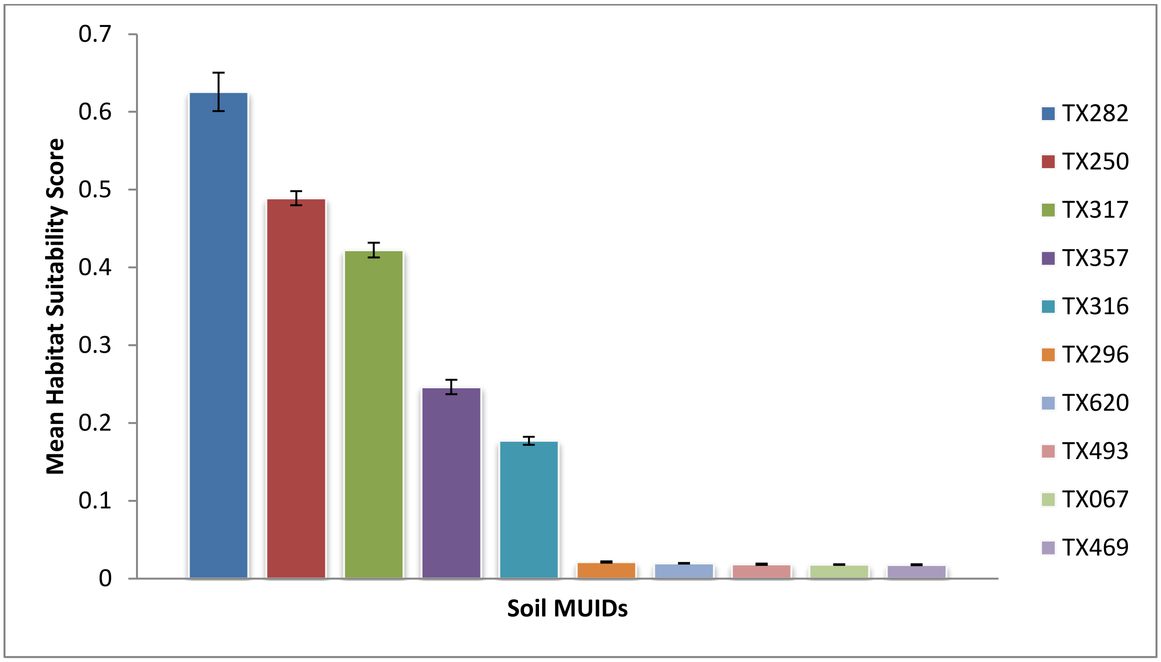


Figure 2.25. The mean habitat suitability scores of the 10 most suitable soil types and the 10 least suitable soil types are significantly different for Rock Pocketbook (*Arcidens confragosus*). Data derived from the initial species distribution model.

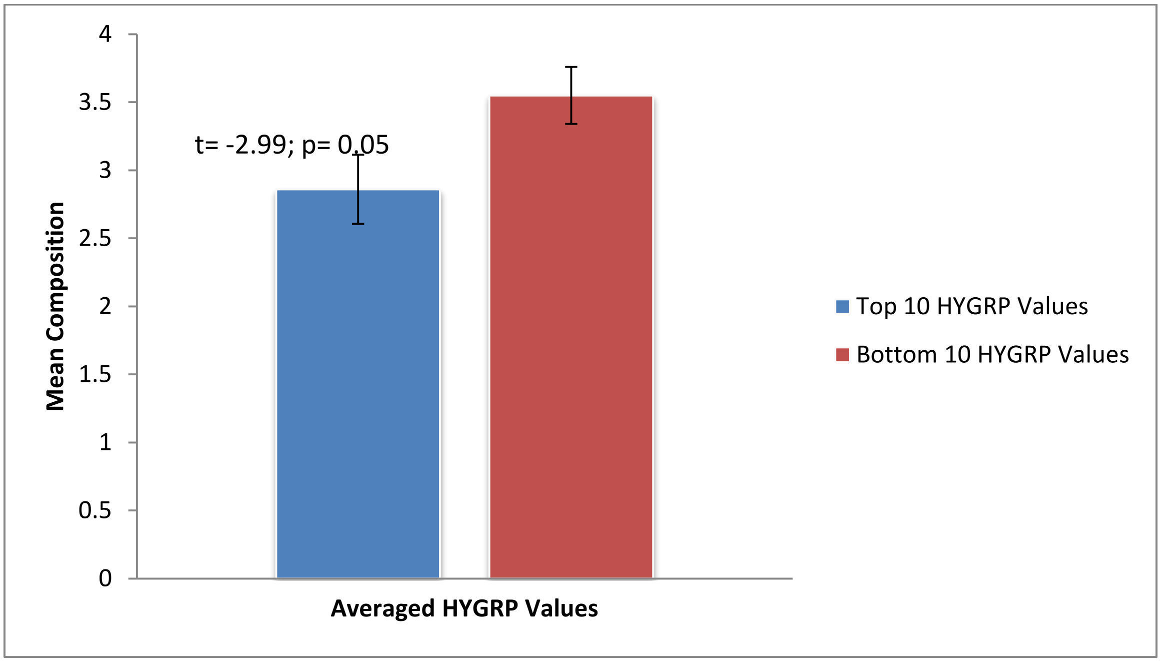


Figure 2.26. Probability distribution of Rock Pocketbook (*Arcidens confragosus*) for the second species distribution model with combined data samples. Sampling sites are located within the Sabine, Neches, Angelina, Trinity, Sulphur, and Big Cypress Rivers.

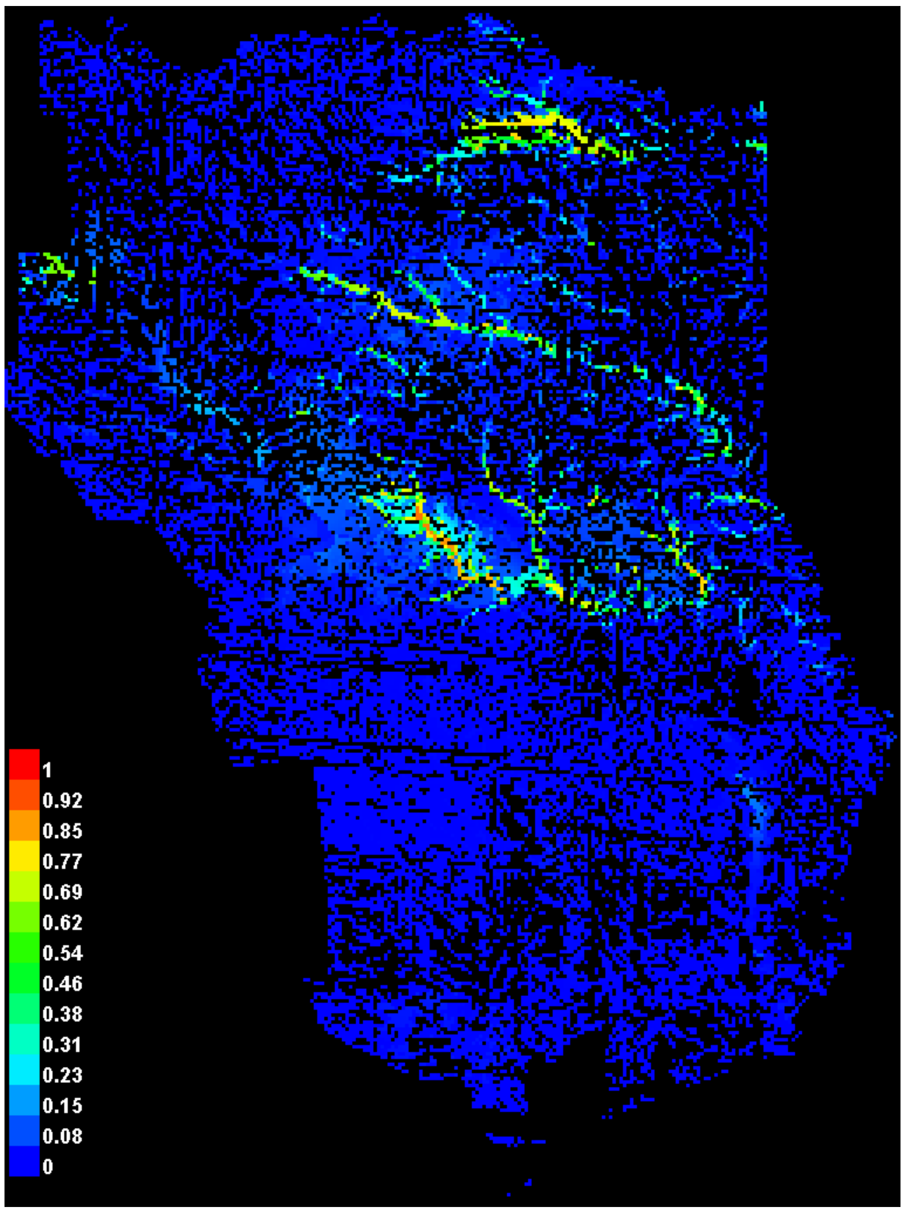


Figure 2.27. Mean habitat suitability scores for all rock exposure types. Values are derived from the second species distribution model of Rock Pocketbook (*Arcidens confragosus*) with the combined data samples.

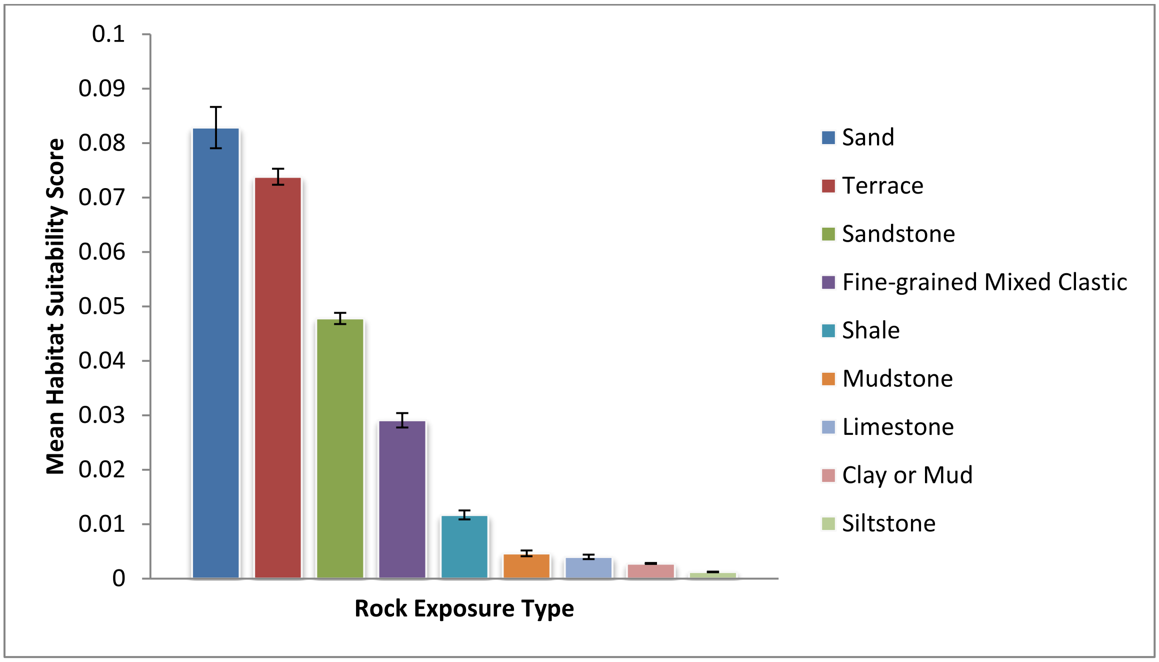


Figure 2.28. The mean habitat suitability scores of the 5 most suitable rock exposure types and 5 least suitable rock exposure types are significantly different for Texas Pigtoe (*Fusconaia askewi*). Data derived from the second species distribution model.

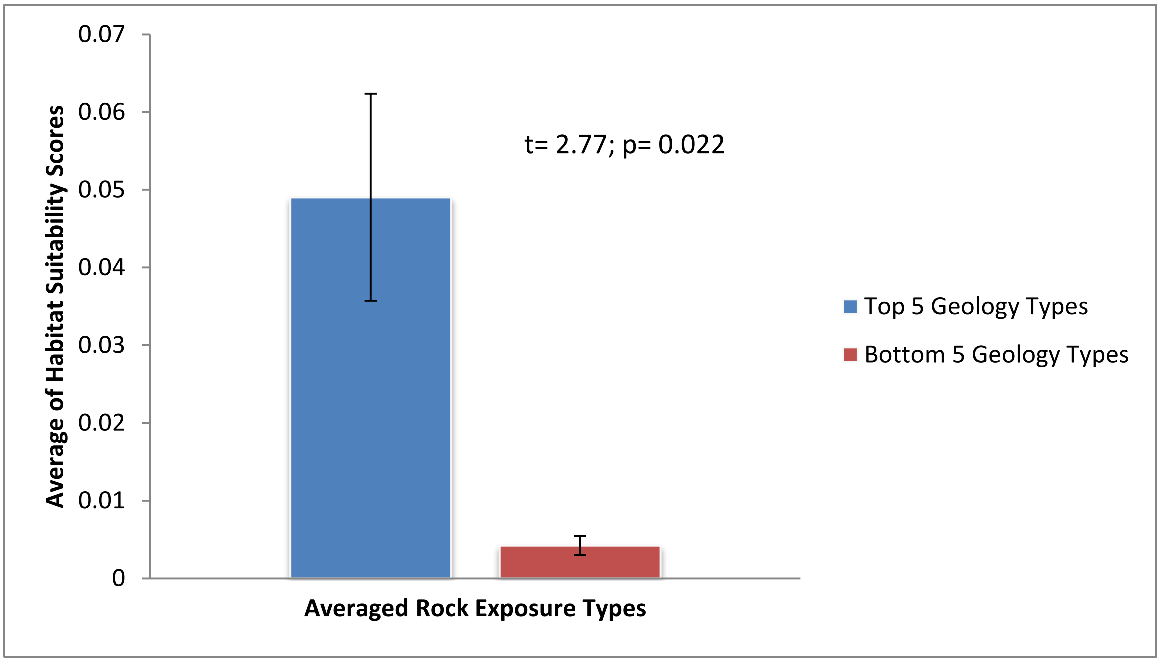


Figure 2.29. Mean habitat suitability scores for the 4 most suitable vegetation types and 4 least suitable vegetation types. Values are derived from the second species distribution model of Rock Pocketbook (*Arcidens confragosus*) with the combined data samples.

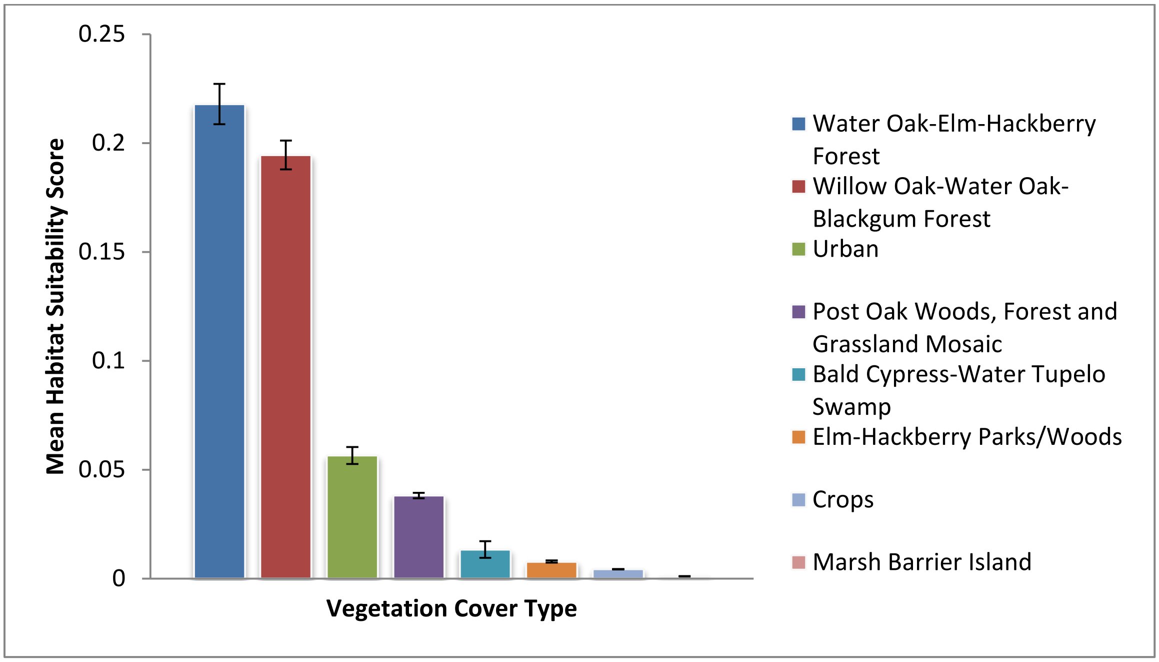


Figure 2.30. The mean habitat suitability scores of the 4 most suitable vegetation types and 4 least suitable vegetation types are significantly different for Rock Pocketbook (Arcidens confragosus). Data derived from the second species distribution model.

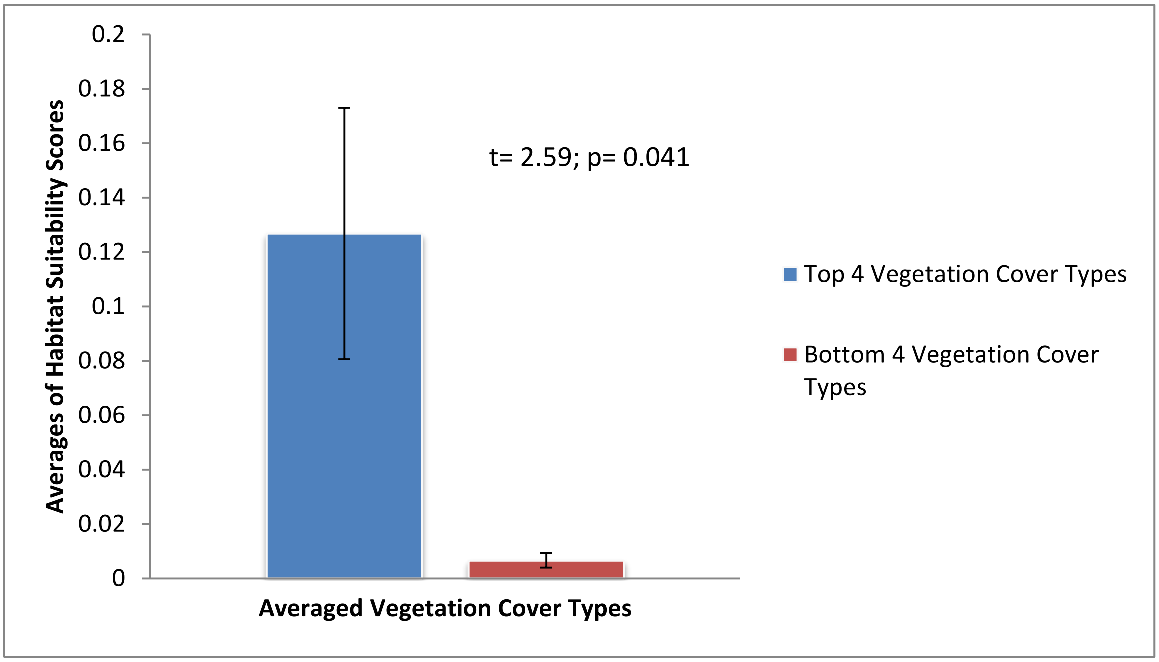


Figure 2.31. Mean habitat suitability scores for the 5 most suitable soil types and 5 of the least suitable soil types. Values are derived from the second species distribution model of Rock Pocketbook (*Arcidens confragosus*) with combined data.

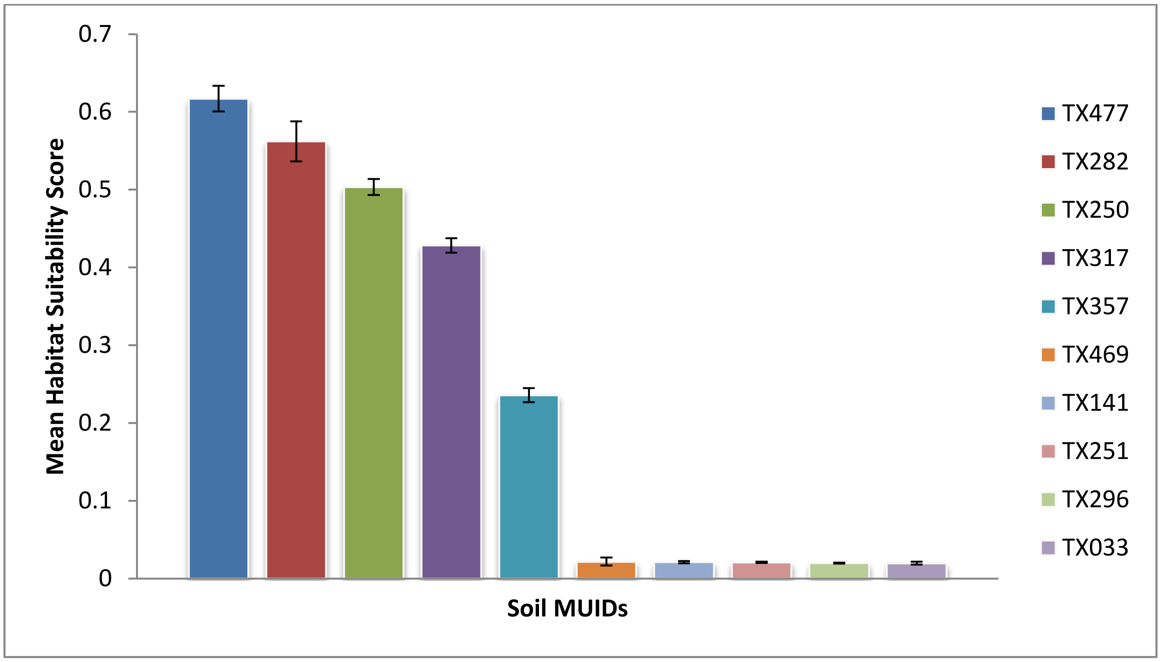
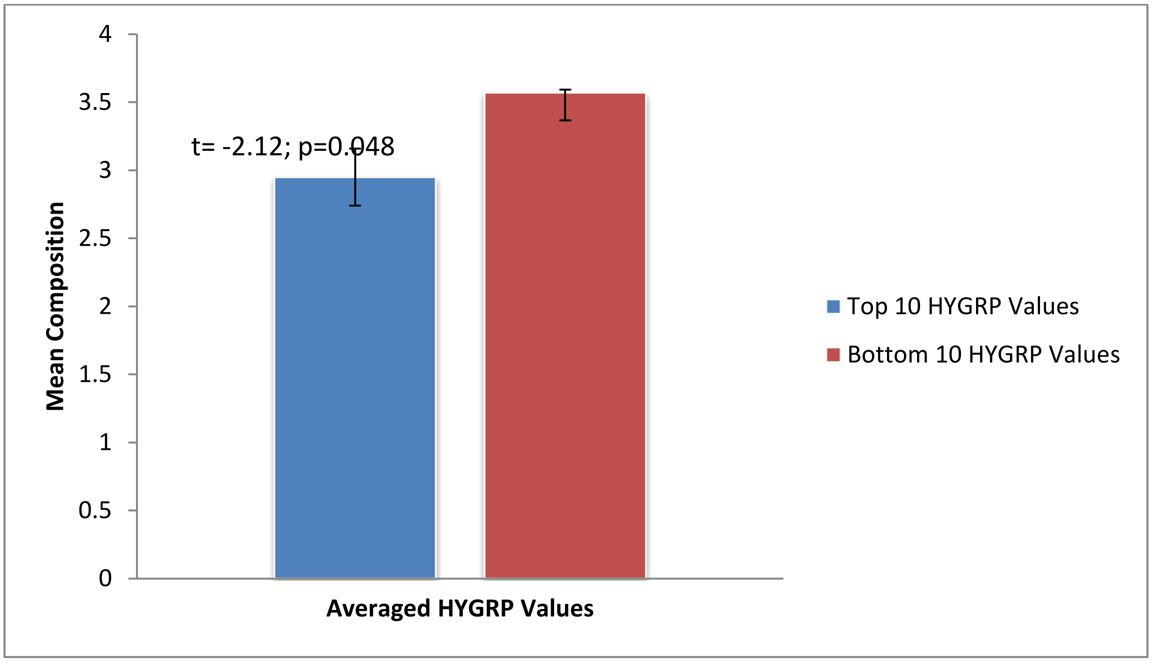


Figure 2.32. The mean habitat suitability scores of the 10 most suitable soil types and the 10 least suitable soil types are significantly different for Rock Pocketbook (*Arcidens confragosus*). Data derived from the combined species distribution model.



Discussion

From a conservation perspective, species distribution models can be important in determining the distribution of a threatened species. That said, the quantity of data necessary to yield an accurate distribution map has not been determined. The utility of species distribution models is that the model can be trained with additional data and an output of assessment can be produced that accesses the general success of incorporating that quantity of data (Phillips et al., 2006). Those data can then be used to explain associations between species presences and the environmental preferences they exhibit. The preferences of freshwater mussels are thought to be governed at some level by the environmental characteristics of the surrounding landscape (Harding et al., 1998). The associations of freshwater mussels and environmental variables can be evaluated by incorporating mussel sampling data from two unique watersheds in a model previously constructed with sampling data in biogeographically different regions. The addition of new data will improve the model's predictive abilities by advancing our knowledge of what is considered suitable habitat for a species.

In my study, the improvement in AUC values supported the hypothesis that including two additional watersheds of varying geomorphology would improve an initial species distribution model (Dunithan, 2012) at least for Rock Pocketbook (*Arcidens confragosus*). However, the improvement for Texas Pigtoe (*Fusconaia askewi*) was marginal even though overall the mean habitat suitability scores for the most suitable habitats increased with the addition of data from the Sulphur and Cypress watersheds. One reason for this low improvement may be that this species is habitat specific and varies little in the types of substrate or other fluvial characteristics it requires. If that is the case then the model suggests that there are very similar habitat types within all watersheds regardless of the geomorphology where Texas Pigtoe can be found. Conversely, if we take a closer look at the output maps it is evident that the addition of data only affects the highlighting in the Sulphur and Big Cypress Rivers, with an appearance of suitable habitat in the Trinity as well. The probabilities of distribution within the watersheds of the original data change very little. Instead the model is adjusting the parameters of acceptable habitat for Texas Pigtoe, and this information is not necessarily reflected in the AUC values. Additionally, recent work on the Trinity River by Zara Environmental revealed the presence of Texas Pigtoe in the Fort Worth area (Krejca pers. comm., 2013). The suggestion is that there are characteristics that these three watersheds share that make habitats suitable for Texas Pigtoe. Burlakova et al. (2011) utilized biogeographic regions to describe the distributional habits of freshwater mussels in East Texas. They demonstrated that the Texoma Province (containing the Sulphur and Cypress Rivers) and the Sabine Province (containing the Trinity River) have the most similar fauna. In relation to the models here, I suggest that the upper Trinity is biogeographically similar to the Sulphur River because of the Trinity's proximity to the Texoma Province. This is why the addition of sampling data from the Sulphur and Cypress watersheds initiated the indication of suitable habitat in the upper Trinity River rather than the original set of data samples. The similarities between the three watersheds are most likely those components that were considered to be most significant in the models of combined data, THICK (thickness of the soils in inches), AWC (average water capacity in inches per inch), and SLOPE (slope of soil layers in percent), willow oak and water oak forest cover, and terrace and sand formations. These watersheds therefore have suitable habitat that contains thick soils (mean= 75 inches), a higher capacity for water retention within the soils, minimal slope, vegetation within the riparian zones, and terrace and sand fluvial formations. In addition, the AUC value is not designed to reflect differences in patterns of change between models (Peterson et al., 2007; Jeschke and Strayer, 2008). The output value is simply not sophisticated enough in its derivation to account for these differences. Rather, the actual deviation from the original mean habitat suitability scores of the variable components is more useful for answering the question of why mussels associate with certain habitat types.

Because the inclusion of more spatially heterogeneous habitats provides MAXENT with a set of increasingly comprehensive options for comparison, it is reasonable to predict that the addition of alternative watersheds would improve the accuracy of the modeling program (Phillips et al., 2006). The models that compared the individual species probability distributions for Rock Pocketbook before and after the addition of new data samples produced an increase in AUC values. The model also produced higher mean habitat suitability scores for many of the components within each of the most significant environmental variables. These results are visible in the output distribution maps as a decrease in ambiguous areas with regards to the probability of distribution for both species (Figures 2.10, 2.26). The results are supported biologically for two reasons: (1) the addition of alternative watersheds increases the knowledge of a species fundamental niche and therefore gives MAXENT additional parameters that it will use to more precisely define those nominally suitable habitats (Phillips et al., 2004) and (2) MAXENT can define a species realized niche using additional data with a higher degree of certainty in addition to a redefinition of what is marginally acceptable habitat (Phillips et al., 2006). An example of this ability is detectable in the increased suitability scores of individual components within the environmental variables I used. The end product is a reduction in marginal habitat coverage and an increase in the identification of the most suitable habitat types for that species.

I further demonstrated that the model building environmental variables can be used to define specific associations between these freshwater mussel species and geomorphological characteristics in the surrounding landscape. Price et al. (2011) outlined changes within alluvial systems as being a product of environmental characteristics such as geology, pedogenic regimes, and alterations within riparian zones. Soil was inevitably the most important environmental variable in every model. Arbuckle and Downing (2002) described soils as being one of the most influential, broad scale effectors of mussel distributions. It is unclear whether soil properties are directly affecting distributions or exaggerating hydrologic properties such as sedimentation, which has been shown to affect the survivability of mussels (Box and Mossa, 1999). My results likely describe a combination of both. In the output for the initial data set of Texas Pigtoe distributions, thicker soils were important. Because broad scale environmental influences can be the source point for changes to the biological integrity of a system, the variation in thickness of soils may be correlated with cascading effects that can contribute to the alteration of species distributions (Bedoya et al., 2011). For instance, Texas Pigtoe are a smooth shelled species and may not tolerate high shear stress (Goodding et al., 2012). Shear stress is associated with increases in flow that could be a result of severe slope and lower water capacity of the soils. Both of these attributes become prevalent, as well as thickness of the soils, with the addition of data from the Sulphur and Cypress

Rivers. Groffman et al. (2003) described the importance of a robust soils profile as being a buffer to the concept of hydrologic drought. Drought is one scenario where dewatering of the riparian zone occurs as a result of lowering of the water table. The Sulphur River being a modified system likely has a decreased ability to retain water in the surrounding watershed, especially with consideration to the highly channelized nature of the upper reaches (Minahan, 2003). When a river is channelized the drainage of the surrounding landscape increases especially within the riparian zones. The draw-down effect would then likely decrease the capacity of soils to retain surface water and exaggerate the effects of severe slope. Mwakalila et al. (2002) suggested that the through flow zone around or close to the riparian districts of an alluvial system is thought to be more important than ground water as an effector of baseflow because of its soil and alluvium structure. Lateral drainage is directly affected by altering these regimes, the results of which are high relief watersheds that influence a shift towards high-gradient streams exhibiting substrate changes unsuitable for mussels (Arbuckle and Downing, 2002). Habitat characteristics such as these became apparent with the Rock Pocketbook models. The hydrology of the groundwater, with well drained soils and moderate infiltration rates, was an increasingly important environmental component for this species. In addition to increases in water loss from the surrounding landscape, erosion caused by altering soil or riparian zone structures can translate to excessive allochthonous inputs. These alterations can manifest as sediment deposition, and hydrological changes once the displaced materials enter the fluvial environment (Allan, 2004). The structure of the Sulphur River often exhibits these characteristics. As with most ecological systems, the morphology of soils and its components is often directly affected by similar environmental variables, and so it is important to recognize that these cascading affects actually consist of more than just one factor.

Soils variables can also be affected by the trends that are seen within geological data, such as the rock exposure variables incorporated in this study. Among the variables that Brutsaert (2005) outlined as important effectors of baseflow were geomorphology of the landscape and the function and arrangement of riparian aquifers and near-surface soils. Using the surficial descriptions within the geology layer, it is evident that rock exposures refer to a variety of geological formations at surface and sub-surface intervals. Terrace formations are typically associated with fluvial systems and become the most important component for a majority of the models. The one exception is the second Rock Pocketbook model in which sand is paramount. Despite this close association with riverscapes, terraces were not found at all sites and therefore represent a rock exposure type that is very important for mussel distributions. So the preference of these species for terrace-like habitat may actually be a product of the association of specific geological processes at the surface and sub-surface of the environment around these study sites. Mwakalila et al. (2002) demonstrated that easily eroded bedrock intensifies channel formation and pedogenesis, which could explain the adjacently important sand and sandstone associations within each model. Areas of extremely folded bedrock exhibit increases in the frequency of fracturing and promote less connectivity to surface water.

Processes such as these have a direct effect on the amount of water that is received as baseflow in rivers within the perimeter of this type of bedrock (Smith, 1981). The more permeable geological layers promote dewatering, a process that freshwater mussels generally do not tolerate (Layzer and Madison, 1995). Complex interactions between surface and subsurface characteristics such as these provide a reasonable explanation as to why permeable layers such as limestone disassociated with species distributions and more directly influential surface layers became most important for the presence of mussels.

Perhaps the most interesting results were the outputs for the vegetation environmental variable. All models suggested that willow oak or water oak dominates the most suitable vegetation type for both mussel species. A relationship such as this is not surprising considering these plants are bottomland species that associate closely with floodplain and riparian habitat (Hupp et al., 1993). It is possible that these results are artefactual in nature because of the preferred habitat of this type of vegetation (Roura-Pascual et al., 2009). However, it is more probable that the existence of vegetation in riparian areas may indicate a preference in general for habitat that is not impacted by development. A close inspection of the Rock Pocketbook models indicates a definitive association with willow oak and water oak and nothing else of significance. Howells et al. (2000) conducted a study on the B.A. Steinhagen Reservoir for which surveys of mussel species survival were recorded over a 6 year period of drawdowns. They found that in general mussels were intolerant of fluctuating water levels at as little as 2.0

meters. Specifically, Rock Pocketbook densities plummeted and subsequent surveys conducted by Karatayev and Burlakova (2007) produced no live individuals and only 3 shells. With evidence of a plain aversion to dewatering events, it is probable that this species does well in habitats that do not suffer drastic low water events. When vegetation cover is removed from riparian zones, for example to accommodate urban development, cascading effects such as sedimentation cause shifts in the available habitat for freshwater mussels (Box and Mossa, 1999; Brown et al., 2010). Urban areas are therefore associated with characteristic changes within proximal river reaches. The stripping of vegetation and implementation of concrete surfaces or other impermeable landscapes that is common with development causes an increase in overland flow that, when in close proximity to a river, can increase the input of what would otherwise have been stored water (Wang et al., 2001). This phenomenon inevitably exaggerates the flow regime in the affected portion of a river system often causing channel incision and flashier hydrological conditions (Groffman et al., 2003). Wang et al. (2012) further supported this by suggesting that urban sprawl affects the substrate particle size within a streambed by reducing the average mass of particles. This is consistent with substrate types that are common in a modified system like the Sulphur River, which often mimics the silty clay and fine sand of substrate in the B.A. Steinhagen Reservoir, and could explain why Rock Pocketbook are associating with forested areas rather than development, such as urban areas. Additionally, heavier textured species most likely cannot tolerate dynamic fluctuations in a flow regime because they are less mobile with this type of morphology

(Howells et al., 2000). Interestingly, the infiltration and overland flow layer (TOPMODEL) did not rank as a significant contributor to the model. It might be expected that Rock Pocketbook associate closely with this particular environmental variable if dewatering events were major effectors of distributional habits for this species. However, this layer is developed as an average percentage of input across the landscape and as such may not be built with a fine enough resolution to pick up on the finer scale occurrences of this uncommon species associating with urban development. An adjustment of resolution to a fine scale would perhaps alter the results of this particular association. It may be that Rock Pocketbook are less-habitat specific in their preferences considering Texas Pigtoe did not associate with this land cover type and so can tolerate the presence of urban areas. They could also be taking advantage of environmental changes caused by human disturbance. It would be advantageous to evaluate this species' habitat preferences with more detailed vegetation layers.

The results of this study highlight the need for additional research with landscape scale variables. Researchers are still attempting to minimize erroneous correlations between mussel species and landscape level variables. While I was able to demonstrate that the addition of alternative watersheds is valuable in improving a model, the promotion of the study of empirical links to specific components of these watersheds is important. The two species in this study demonstrated model validating differences between the most suitable habitat types and least suitable habitat types despite the marginal change in AUC for Texas Pigtoe. It is important to understand the degree to which the construct of the environmental layers affects the output of the model. Additional research should include the use of profile components, such as HYGRP, as individual layers. By incorporating this level of detail, associations between mussel species occurrences and environmental characteristics at the landscape level may be more accurately reported (Newton et al., 2008).

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Appendix A

Table 1. Cumulative sampling data for all locations where Texas Pigtoe (*Fusconaia askewi*) and Rock Pocketbook (*Arcidens confragosus*) were collected in the Sulphur and Cypress watersheds.

Sampling Data Sulphur River										
-95.05754	33.39098	Sulphur	1905 Bridge 1/4 mi down	6-Jun-12	2	0.66	50	Rock Pocketbook	1	dead
-94.72572	33.30706	Sulphur	East of 259	7-Aug-12	Dive/Manual	1.5	1 Team	Rock Pocketbook	1	Live
-94.14342	33.29873	Sulphur	Hwy 59	12-Aug-12	Dive/Manual	1.5	1 Team	Rock Pocketbook	1	Live
-94.79568	33.36132	Sulphur	Shirleys 3	14-Oct-12	3	1	50	Rock Pocketbook	1	live
-94.79568	33.36132	Sulphur	Shirleys 3	14-Oct-12	3	1	50	Texas Pigtoe	1	dead
-95.05754	33.39098	Sulphur	1905 Bridge 1/4 mi down	6-Jun-12	1	0.83	50	Texas Pigtoe	2	dead
-95.05754	33.39098	Sulphur	1905 Bridge 1/4 mi down	6-Jun-12	3	0.66	50	Texas Pigtoe	1	live
-95.05754	33.39098	Sulphur	1905 Bridge 1/4 mi down	6-Jun-12	3	0.66	50	Texas Pigtoe	3	dead
-94.79963	33.36264	Sulphur	Shirleys 2	13-Oct-12	1	1	50	Texas Pigtoe	1	live
-94.79511	33.36057	Sulphur	Shirleys 3	14-Oct-12	1	1	50	Texas Pigtoe	3	dead
-94.76900	33.36169	Sulphur	Shirleys 3	14-Oct-12	4	1	50	Texas Pigtoe	1	dead
Sampling Data Big Cypress River										
-94.57822	32.62505	Little Cypress	Hwy 450	5-Jun-12	3	1.00	50	Rock Pocketbook	1	live
-94.51662	33.00145	Black Cypress	Hwy 11	15-Jun-12	1	0.83	50	Texas Pigtoe	1	dead
-94.51662	33.00145	Black Cypress	Hwy 11	15-Jun-12	1	1.10	50	Texas Pigtoe	2	live
-94.51662	33.00145	Black Cypress	Hwy 11	15-Jun-12	1	1.10	50	Texas Pigtoe	1	dead
-94.28793	32.73478	Little Cypress	N Hwy 134	4-Sep-11	3	0.75	50	Texas Pigtoe	1	dead
-94.28793	32.73478	Little Cypress	N Hwy 134	4-Sep-11	3	0.75	50	Texas Pigtoe	6	dead