Voluntary Conservation Measure for US 281 from Loop 1604 to the Comal County Line, Bexar County

Statistical Analysis and Revision of Endangered Karst Invertebrate Species Distribution

San Antonio Area, Texas

CSJ(s): 0253-04-138 and 0253-04-146

January 2024

Prepared for the Texas Department of Transportation

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George Veni, PhD, John Cooper, and Wendy Dickerson

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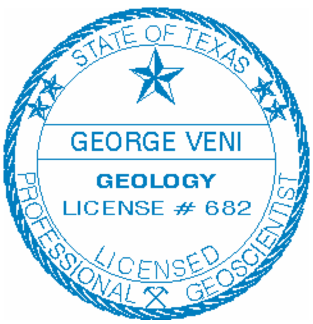

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Abstract

The cavernous outcrops exposed along the Balcones Fault Zone in the area of San Antonio, Texas, contain ten species or subspecies of karst invertebrates that are federally listed as endangered by the U.S. Fish and Wildlife Service. Previous studies defined six karst fauna regions in five karst zones in the San Antonio Area as mostly distinct ecological regions which include endangered and non-listed karst invertebrate species. The current work investigates all known localities of rare and endangered terrestrial invertebrate troglobites in the San Antonio Area and analyzes factors that might influence terrestrial invertebrate troglobite distribution. This report further evaluates and updates karst fauna region and karst zone boundaries, based in part on the development of a Geographic Information System model that maps the ranges of 35 karst invertebrate species from 212 localities within the study area.

The boundaries of all previously defined karst fauna regions were refined primarily based on recently available and more detailed geological mapping and karst invertebrate locality records. The current work describes seven informal karst fauna regions as containing only non-listed karst species as constraints on the distribution of the endangered karst species. Karst Zone 1, where endangered karst invertebrate species are known to occur, was expanded throughout most of the previous Karst Zone 2 based on newly discovered karst invertebrate localities. Karst Zone 2, which has a high probability of containing the endangered species, was reduced in area proportionally to the changes in Karst Zone 1 and the refined Karst Fauna Region boundaries. Karst Zones 3 and 4 were each split into two subzones to better define what we currently understand about their biological status and to better manage their ecosystems.

Introduction

The southeastern margin of the Edwards Plateau in the vicinity of San Antonio, Texas, is a bio-geologically complex region. Species living in its caves and related voids have become physically isolated from one another through time and across geographies, resulting in genetic isolation that has produced species that are documented to occur only within a few caves concentrated in small geographic areas. The expanding urbanization of the San Antonio region onto the karst where these species occur poses a threat to their survival due to the capping, closure, and/or destruction of caves and karst features, changes in nutrient and moisture input into the karst ecosystem, contaminants introduced into the karst ecosystem, and competition with and predation by non-native species introduced by urbanization (Elliott 1993, 2000; U.S. Fish and Wildlife Service [USFWS] 2000).

Investigations into local karst habitat and species distribution have been fueled in large part by regulatory requirements for development projects to comply with the Endangered Species Act. The Texas Department of Transportation funded this study to evaluate and modify karst fauna region (KFR) and karst zone boundaries as part of the implementation of conservation measures specified in the Biological Opinion resulting from formal consultation with the USFWS for impacts to federally listed karst invertebrates caused by improvements to US 281 (Consultation No. 02ETAU00-2015-F-0031). Nine species of karst invertebrates in the San Antonio Area were federally listed as endangered by the USFWS to ensure their survival (USFWS 2000). The species and their common names (where assigned) are:

- *Batrisodes (Excavodes) venyivi* (Helotes mold beetle)
- *Cicurina (Cicurella) baronia* (Robber Baron cave spider)
- *Cicurina (Cicurella) madla* (Madla's cave spider)
- *Cicurina (Cicurella) venii* (=madla) (no common name)
- *Cicurina (Cicurella) vespera* (Vesper cave spider)
- *Neoleptoneta (=Tayshaneta) microps* (Government Canyon cave spider)
- *Rhadine exilis* (no common name)
- *Rhadine infernalis* (no common name; 3 subspecies)
- *Texella cokendolpheri* (Robber Baron cave harvestman)

Since initial federal listing, there have been some taxonomic changes. *Neoleptoneta microps* was reassigned to the genus *Tayshaneta* (Ledford et al. 2011) and is discussed under that designation for the remainder of this report. *Cicurina venii* was made synonymous with *Cicurina madla* and, not included above, *Cicurina loftini* was made synonymous with *Cicurina vespera* (Hedin et al. 2018). Additionally, this report refers to ten listed species in order to include all three subspecies of *Rhadine infernalis*, including *Rhadine infernalis infernalis* and *Rhadine infernalis ewersi*, which were known at the time of endangered listing in 2000, and the more recently discovered *Rhadine infernalis* n. ssp.

The San Antonio Area defined in George Veni & Associates ([GVA] 1994) consisted predominantly of the northern half of Bexar County with minor extensions westward into Medina County. It encompassed the geologic formations from the Late Cretaceous Glen Rose Limestone through the Early Cretaceous Pecan Gap Chalk. The predominant cavernous rock units examined were the upper portion of the upper member of the Glen Rose, the Edwards Limestone Group, and the Austin and Pecan Gap chalks. In 2003, Veni expanded his definition of the San Antonio Area to include an area 12 kilometers (km) farther west into Medina County to the Medina River (GVA 2003).

George Veni & Associates (1994) coupled information about the stratigraphic, structural, and hydrological controls on cave development with an evaluation of the distribution of karst invertebrate species in the San Antonio Area. While some karst invertebrates occur broadly across the Edwards Plateau, that study focused on 19 species limited to the San Antonio Area to determine if they were restricted to certain cavernous regions within that area. Additionally, GVA (1994) delineated five karst zones to predict the likelihood of rare or endangered species occurring:

- Zone 1: areas known to contain endangered cave fauna;
- Zone 2: areas having a high probability of suitable habitat for endangered or other endemic invertebrate cave fauna;
- Zone 3: areas that probably do not contain endangered cave fauna; and
- Zone 4. areas which require further research but are generally equivalent to Zone 3, although they may include sections which could be classified as Zone 2 or Zone 5 as more information becomes available.
- Zone 5: areas which do not contain endangered cave fauna.

Sprawling urbanization, a high percentage of privately owned land, and lack of surface expression of caves and karst features across much of the San Antonio Area made this process especially challenging. Due to the absence of directly observable features on the surface that could be used to define the extent of species' underground habitat, karst zones were based on biological and geological factors that could be used to estimate the likely boundaries of species' habitat and to estimate areas of probable and improbable habitat. Karst zones have been used by USFWS primarily as management zones to determine what level of action and research is needed for the protection and study of the species within them (e.g., USFWS 2001b).

In 2003, Veni updated and redrew the San Antonio Area karst zone boundaries based on 74 confirmed localities of endangered karst invertebrates, an increase of over 50 localities since the 1994 study. The primary scope of the GVA (2003) report was to make recommendations on critical habitat delineation for those 74 localities. A related study by GVA (2007) in the Austin, Texas area, about 70 km to the northeast, focused on Austin Area karst zones and their first and strongest recommendation was for a more robust statistical analysis of species distribution, which is the subject of this report.

The plotted distribution of 19 karst invertebrate species in GVA (1994) revealed that communities of karst invertebrates could be distinguished between regions. Statistically analyzing the percentage of species endemic to and shared with other areas, the San Antonio Area was divided into six Karst Fauna Regions (KFRs):

- Alamo Heights
- Culebra Anticline
- Government Canyon

- Helotes
- Stone Oak
- UTSA

The purpose of establishing the KFRs was to define major ecological units that USFWS could use for species management and recovery. Although the statistical methods were simple, considering ten species beyond the nine listed at the time added greater statistical confidence to the results. The KFRs allowed USFWS to regulate actions within each ecological unit (i.e., KFR) in ways that could potentially lead to delisting and/or preclude the need to list other rare species as endangered (e.g., USFWS 2011).

George Veni & Associates (GVA 1992 and GVA 1994) hypothesized that multiple terrestrial invertebrate troglobite species of limited ranges evolved due to factors that isolated individual populations and facilitated genetic divergence. Because true troglobites are obligate cave animals that do not survive on the surface, the absence of cavernous rock is the primary barrier to their distribution. To explain differences in distribution of species in KFRs where limestone is contiguous, GVA (1994) examined terrestrial invertebrate troglobite distribution relative to streams and faults. He found that streams were the predominant factor isolating populations because they cut through the limestone, leaving less cavernous rock through which species could pass. Additionally, the limestone below streams is perennially or periodically below the water table, preventing the distribution of non-aquatic species. Faults effected no influence on species distribution except where the degree of displacement juxtaposed cavernous and non-cavernous rock.

These studies defined two types of boundaries to terrestrial invertebrate troglobite distribution and for the KFRs: barriers and restrictions. Barriers are boundaries beyond which terrestrial invertebrate troglobites cannot pass, such as areas lacking cavernous rock. Restrictions are boundaries where some gene flow is possible but is limited by space and/or time. Common examples are thin and/or narrow areas of cavernous limestone or times when the water table is low enough to allow terrestrial species to pass through areas that are normally inundated. Restrictions explain why some terrestrial invertebrate troglobite communities are not completely endemic but share some species with other KFRs.

The primary purpose of the current investigation is to analyze all known localities of rare and endangered terrestrial invertebrate troglobites in the San Antonio Area to conduct a robust, detailed, objective, statistical analysis of factors that might influence terrestrial invertebrate troglobite distribution, and use those results to modify KFR boundaries as appropriate to the results. This study's secondary purpose is to update karst zone boundaries in the San Antonio Area based on new localities and insights from the KFR analysis.

Methodology

This report was written upon completion of a parallel study for the Austin Area karst invertebrates by Veni and Jones (2021). The trials and lessons learned in creating research methods yielded nearly identical results for both studies. Both studies had identical goals, nearly identical karst ecosystems, the same first author; therefore, most of the introduction and methodology sections of this report, as well as portions of other sections, are adapted from Veni and Jones (2021) and adjusted in their details as needed without further citation. Specific relevant results from that report are cited as appropriate.

Rare and Endangered Species Data Collection

James Reddell maintains the most detailed and comprehensive database of species collected and observed in Texas caves. He provided a list for this study of all confirmed and tentative localities for the 10 listed species and 27 non-listed species known only from the study area. His list includes species beyond but adjacent to the known distribution of the endangered species to better define the limits of the listed species' ranges.

Review of Reddell's list and discussion with him and other taxonomists revealed that the spiders *Cicurina bullis* and *Cicurina neovespera* are generally considered synonymous, and the same is true of *Cicurina platypus* and *Cicurina puentecilla* (e.g., Paquin and Hedin 2004; Paquin and Dupérré 2009). Although synonymy is not yet published for these species, given the consensus on their status they are considered synonymous for the purposes of this study, reducing the number of non-listed species to 25 and total examined by this study to 35. Thus, the study area is defined by the extent of the mapped cavernous geologic units which contain those 35 species along the Balcones Fault Zone from the Medina River in Medina County, northeast approximately 80 km through Bexar County and to the Guadalupe River in Comal County (Figure 1). The analysis extends beyond the known range of the listed species within the study area to ensure that the study area contains the limits of the listed species distributions.

The 35 species analyzed for this effort are documented from 212 localities. Species occurred predominately in caves but also in some karst features too small to meet the Texas Speleological Survey ([TSS] 2020) definition of a cave, which requires a minimum 5 meters (m) of humanly traversable passage with no dimension of the entrance exceeding the cave's traversable length. There are 153 localities that contain at least one endangered karst invertebrate, 8 localities have no confirmed listed species but at least one species tentatively identified as belonging to one of the listed species, and the remaining 51 localities have no known confirmed or tentatively confirmed listed species. In the case of Black Cat Cave, USFWS recognizes the presence of *Rhadine exilis* for conservation purposes but also understands that uncertainty exists about the taxonomy of the species in this cave; therefore, *R. exilis* is designated as tentatively identified in that cave for the modeling purposes of this investigation.

The 35 species analyzed do not include all karst invertebrates known from within the study area. The ranges of widely distributed karst invertebrates provide no analytical insights to identify barriers or restrictions to species more sensitive to speciation and were therefore not included. Stygobites (aquatic troglobites) are also excluded from this analysis because their habitats and the factors affecting their distribution are not directly comparable to the endangered karst invertebrates.

Species distribution data from Reddell's database, USFWS species and location data, and recent discoveries of new localities was combined with cave location data from Texas Speleological Survey (TSS) and is presented in the Appendix. The TSS files are not generally open to the public and were made available for this research under the terms of a confidentiality agreement that restricts the distribution of specific cave locality coordinates to the primary authors and owners

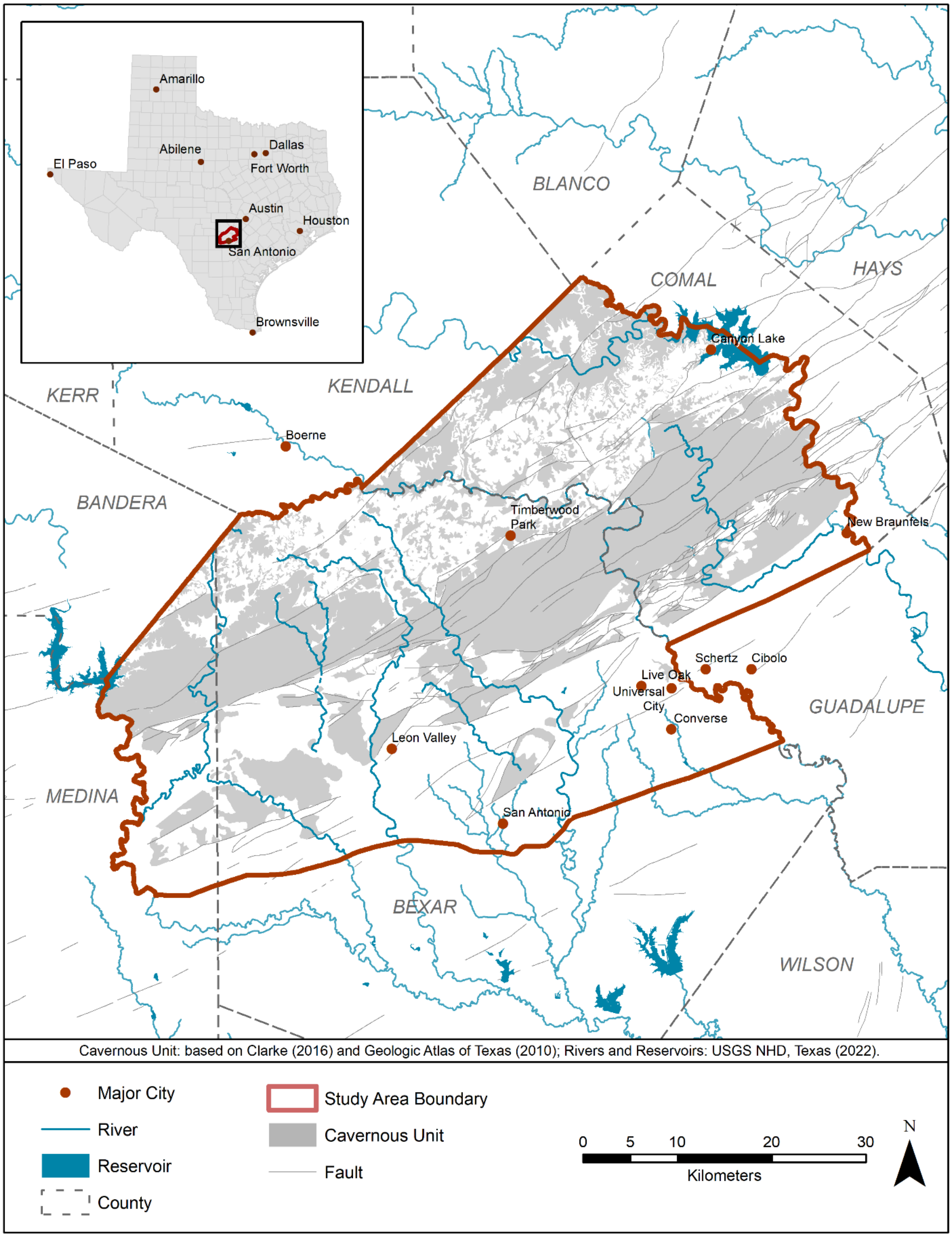

Figure 1. The study area is largely defined by the cavernous geologic units along the Balcones Fault Zone from the Medina River in Medina County, through Bexar County, and continuing northeast to the Guadalupe River in Comal County.

of this report. The credentials of the lead author (Veni) and Reddell include their past roles as TSS directors and current data managers, their combined experience thus facilitating a meticulous review of the data. Their efforts required the comparison of consulting and other reports to TSS records and rigorous data reconciliation as many caves and karst features are recorded by multiple names and codes, and in some cases were unknowingly listed multiple times. They scrutinized hundreds of reports, maps, and Google Earth images to verify that each locality in this study was included only once and in the correct location.

By agreement with USFWS and following the updates to the TSS database from this study; the cave names, alternate names, and coordinates in the database are considered authoritative. This effort also resulted in major improvements to the TSS database and Reddell's initial list of species localities. Only the primary references for each species at each locality are specified in the Appendix; complete citations for those sources are in the References section of this report. Where no published reference is known, or where unpublished updates occurred, Reddell was listed as a personal communication.

Austin Chalk Surface Mapping

The Austin Chalk is an important cavernous formation in the study area. Caves in the Alamo Heights and Culebra Anticline KFRs are formed within the Austin Chalk (Veni, 1994; Veni, 2003), yet prior geologic evaluation of those caves was limited by the absence of a detailed map of the unit. Clear variations in lithology are apparent, with some cavernous and poorly cavernous areas, but their stratigraphic relationship was unknown.

During this study, Cooper (2017) produced the first detailed stratigraphic section of the Austin Chalk for the San Antonio Area (Figure 2). For the effort described in the current report, he mapped cavernous and non-cavernous sections of the Austin Chalk within and outside of the identified KFRs in the greater Bexar County area to refine the delineation of the KFRs and karst zones within the Austin Chalk in Bexar County. Unless otherwise cited, all the information on the Austin Chalk presented below is based on Cooper (2017).

Field work was conducted over a two-week period in late January 2018 and late February 2020 to understand stratigraphically where caves were forming within the Austin Chalk. Caves within both the Alamo Heights KFR and the Culebra Anticline KFR were visited including Baseball, Chimney Cricket, Money Pit, Niche, Robber Baron, San Antonio Spring, San Pedro Park Spring, TMI, and World Newt caves. The stratigraphy of the Austin Chalk in each cave was investigated and correlated to Cooper's (2017) Bexar County Austin Chalk Composite Section to determine the part(s) of the Austin Chalk in which the caves are forming.

Green Mountain Road Cave is located in Austin Chalk and outside the mapped KFRs, and was recently documented to contain the endangered *Cicurina baronia* (USFWS 2021). Six Universal City caves along Cibolo Creek (Alectryonia, Another Prayer, Coon Crap, Gray, Gryphaea, and Whitetop), which are outside the KFRs and do not contain endangered species, were also visited to further understand cave development within the Austin Chalk. The abandoned Longhorn Quarry wall was visited to observe the entrance of The Labyrinth from a distance; we were not given permission to access this cave and only entered the publicly accessible areas of the property. Surface exposures of the Austin Chalk along the drainages of Cibolo, Culebra, Helotes, Leon, Olmos, Salado, and San Geronimo creeks, and road cuts along Bandera Road, Potranco

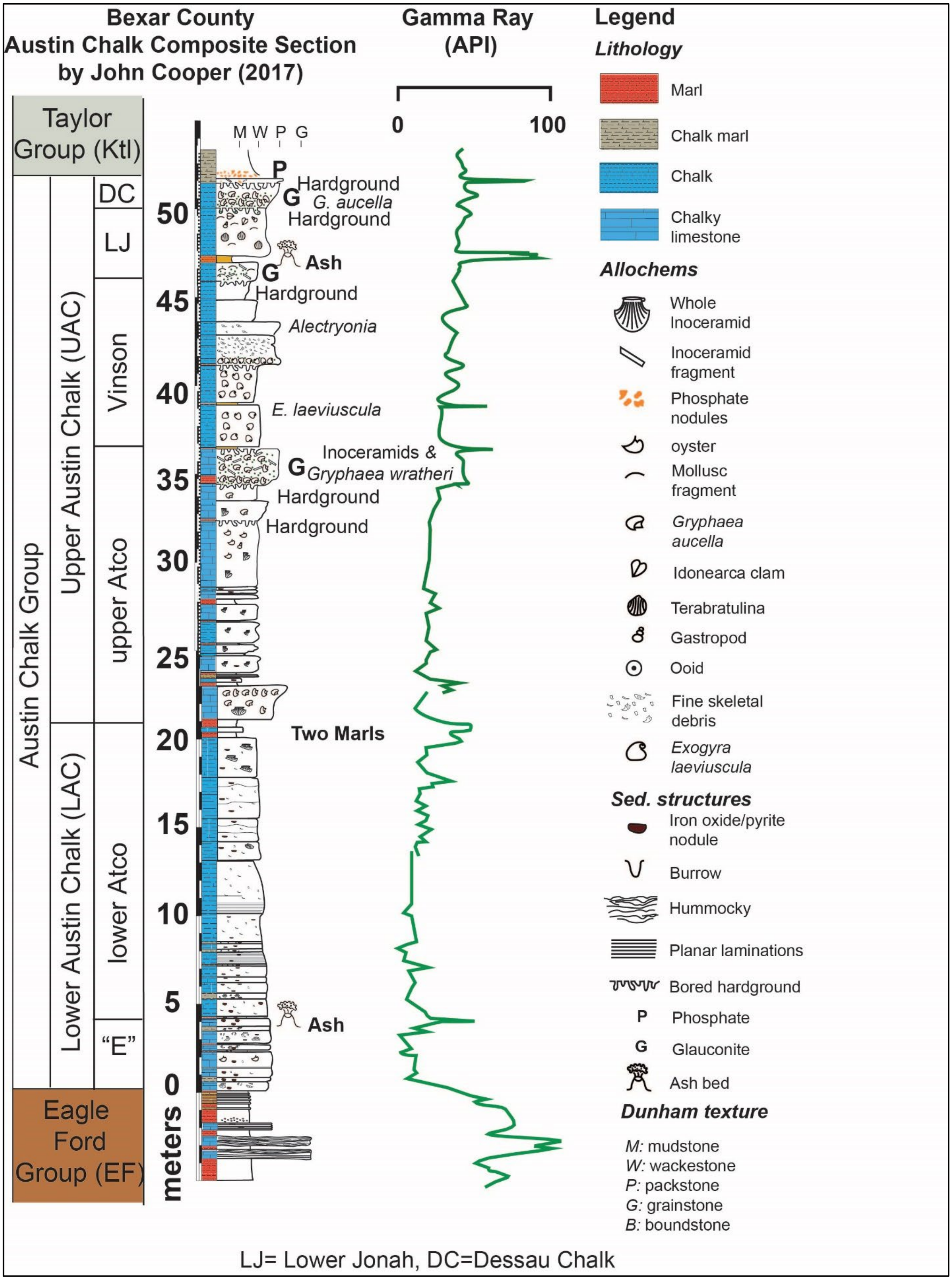

Figure 2. Composite cross section of the Austin Chalk in Bexar County (Cooper 2017).

Road, and Wiseman Boulevard farther west on the Culebra Anticline, were also investigated to understand the outcrop nature and trends of regional faulting. The prominent 30-cm thick Gryphaea oyster bed at 35 m on the Bexar County Austin Chalk Composite Section was found as far west as the Culebra Anticline region and as far east as Cibolo Creek around Universal City. This regional marker bed enabled confident stratigraphic correlations of the Austin Chalk across Bexar County.

After observations from surface exposures and within the caves, the Austin Chalk was divided into two units:

1. Upper cavernous section (UAC) with clean beds of fossiliferous limestone and chalk with interbedded clays, consisting of the Upper Atco, Vinson, Jonah, and Dessau formations, and
2. Lower non-cavernous section (LAC) with more clay-rich chalk and marl, consisting of "E" bench (Ewing 2013) and the Lower Atco Formation.

Where surface exposures were sparse, several water well logs from the Texas Water Development Board's Groundwater Data Viewer enabled confident surface mapping of the Austin Chalk. Surface geologic maps of the Austin Chalk were drafted using the Geologic Atlas of Texas (GAT) San Antonio Sheet (Barnes 1983; Texas Commission on Environmental Quality 2004) as a base map for the greater Bexar County area. Additional geologic maps in the Bexar County area were reviewed for refinement of geologic contacts and fault lines (Arnow 1963; Collins 1993a, 1993b, 1994a, 1994b, 1995, 2000). Further care was taken to update the GAT base map by hand drawing in contacts between the UAC and LAC sections within areas mapped as Austin Chalk. Some contacts were revised for the upper boundary of the Austin Chalk with the overlying Taylor Group and the lower boundary with the underlying Eagle Ford Group. As a note, the Taylor Group, which overlies the Austin Chalk, has been mapped as the Pecan Gap Formation on the GAT and the terms are synonymous here.

Some fault traces were added, as well as inferred fault traces, based on the above referenced geologic maps, along with field work done in this study. A slight revision to the GAT base map was made by re-mapping the surface at Robber Baron Cave as Pecan Gap, which was mapped as Austin Chalk on the GAT. The entrance to Robber Baron is at the bottom of a 9-m deep sinkhole and occurs right at the contact between the UAC and the overlying Pecan Gap. The biggest revision to the surface maps was in the Culebra Anticline region farther west into Medina County, where a large part of the surface exposure on the southwest flank of the anticline is mapped on the GAT as the Anacacho Formation, a tongue of high-energy carbonate facies originating from the Uvalde Salient farther to the west. After visiting road cuts along Potranco Road, several localities mapped as the Anacacho and Pecan Gap formations on the GAT were re-mapped as the UAC.

After the study was concluded, the maps reveal a large portion of areas near Castle Hills, northeast of Leon Valley, Alamo Heights, and the Culebra Anticline as well as portions of the southwestern flank of the anticline, Garden Ridge, and Universal City all rest on exposure of UAC. Most of these areas are already urbanized, the exception being certain portions of the Culebra Anticline that warrant further investigation.

The subdivision of the Austin Chalk into the LAC and the UAC is a simplification of convenience for distinguishing cavernous and non-cavernous sections. X-ray fluorescence data confirm that chalk beds in the "E" bench and Lower Atco Formation have appreciably higher clay contents than chalk beds in the Upper Atco, Vinson, Jonah, and Dessau which are more carbonate rich. It is likely that the clay content with massive chalk beds is a large determining factor for which stratigraphic sections of the Austin Chalk are cave-forming. The results of this mapping are incorporated into the Geographic Information System (GIS) model used for the current analysis.

Karst Fauna Region Analysis

Conceptual Approach

We studied and attempted multiple methods to identify the most accurate means of evaluating the distribution of the karst invertebrate species. Veni and Jones (2021) extensively modeled and assessed many factors involving geology, hydrology, cave microclimates, surface climate, vegetation, and soils for their potential effects on species distribution. Most of these factors lacked sufficient data, sufficiently detailed data, or the needed resolution of data. Other data factors varied in quality and resolution over the study area in ways that might bias the results.

Following this extensive evaluation, the best method was determined to be identifying and analyzing the range of distribution for each species first, prior to modeling the effects of various physical conditions on the species' distribution. The clustering of multiple range margins was then interpreted to reflect the presence of a barrier or restriction to species distributions *a posteriori*. Given that the localities occur irregularly spaced across a broad area, exact range alignments are not expected; however, geologic contacts, faults, streams, soils, and other factors can be examined carefully in areas where the range margins cluster to determine if they may create a barrier or restriction. Where no hydrogeological explanation is found for a cluster of range margins, subsurface ecological conditions are assumed as the likely cause.

Hydrogeologic Data

George Veni & Associates (1994) described the hydrogeologic factors resulting in cave development within the study area and how those factors relate to the distribution of the endangered species. The study area is in the Balcones Fault Zone at the southeastern corner of the Edwards Plateau, where predominantly Cretaceous-age carbonate rocks are found outcropping. These rocks dip slightly to the southeast where they are downfaulted into the subsurface and buried under younger and mostly clastic geologic units.

Karst aquifer development and major groundwater flow patterns are generally downdip, northwest to southeast, changing to the northeast along structural strike on the southeastern edge of the Edwards Plateau where springs discharge into base level rivers. Sharp et al. (2019) provides the most recent and comprehensive review of the Edwards Aquifer, the primary aquifer in this study area. Veni (1988) provides the most comprehensive published report on Bexar County caves, supplanted on the Alamo Heights KFR by Veni and Heizler (2009), Camp Bullis by Zara Environmental LLC and George Veni & Associates (2011), and Government Canyon State Natural Area by Miller (2018). This study's mapping of the Austin Chalk further supports the hypogenic model of cave development by Veni and Heizler (2009). Depths and patterns of cave development vary throughout the study area, affecting species distribution in different ways locally. While caves are present throughout the study area, not all contain karst invertebrate species, presumably because nutrients, humidity, temperature, or other conditions are not suitable.

The modeled analyses of karst species distribution for this investigation were conducted using ArcGIS Pro 2.8.0 (ArcPro) by Environmental Systems Research, Inc. (Esri). Basic data layers in the GIS model include cultural features and boundaries and major streams. The most critical data layer is the geological mapping of the area provided by two sources. The U.S. Geological Survey (USGS) provides continuous detailed mapping of the Glen Rose and Edwards limestones, in west-to-east order, for Medina County (Clark et al. 2020) and Bexar County and Comal counties (Clark et al. 2016). Mapping of the units younger than the Edwards Limestone, including the Austin and Pecan Gap chalks, is primarily from the less detailed San Antonio sheet of the 1:250,000 scale GAT (Barnes 1983), although portions of those units and other units are included along the margins of the USGS maps.

Several geologic units were lumped into a single “cavernous unit” for the purposes of this analysis. In descending (youngest to oldest) stratigraphic order those units are the:

- Austin Chalk (UAC);
- Edwards Limestone Group (Person and Kainer formations);
- Glen Rose Limestone, Upper Member: Cavernous and Upper Fossiliferous hydrostratigraphic units; and
- Glen Rose Limestone, Lower Member: Little Blanco, Doeppenschmidt, Rust, and Honey Creek hydrostratigraphic units.

Variations and some special consideration in the geology must be noted:

- The mapping of the UAC is approximate in some areas, and a few caves whose entrances plot in the Pecan Gap are entirely formed in the UAC. To include these caves and thin areas of Pecan Gap where entrances to Austin Chalk caves may occur, the boundaries of the UAC were expanded by 300 m.
- The Del Rio Clay and Georgetown Formation are generally non-cavernous but thin and, in some areas (too small for the map scale), may be breached by erosion or collapse to expose the underlying cavernous Edwards Limestone.
- The Cavernous Hydrostratigraphic Unit of the Glen Rose becomes less cavernous to the northwest and is non-cavernous in adjacent Kendall County.
- The Camp Bullis Hydrostratigraphic Unit is predominantly non-cavernous but is known to contain a few small caves.
- The Upper Fossiliferous Hydrostratigraphic Unit becomes less cavernous westward, with no caves known west of Interstate 10 and is excluded from the cavernous unit in that area.
- Small hills ringed by the cavernous unit but capped by non-cavernous rock were mapped as entirely within the cavernous unit because cavernous conditions should extend beneath those caps.

In addition to the above-listed rocks, areas geologically mapped as alluvium or other Quaternary-age deposits, but underlain by these rocks, were also included as part of the cavernous unit because several caves and karst features with entrances extend through these deposits into cavernous habitat below.

The general steps for the analysis of the data are illustrated schematically in Figure 3. The model begins with two parallel data paths. In the first path, the coordinates of the species' localities in the Appendix ("All Cave Locations" in Figure 3) are plotted ("XY Table To Point") as points on the map ("All Cave Points"). These points ("All Cave Points") are then selected ("Select By Attribute") by species listed in the Appendix as confirmed for a locality ("Confirmed Species"). The tentative species localities are not used in the model's analysis. While the range of confidence in tentative species identification varied, James Reddell identified those of high confidence. The tentative species are plotted later in the analysis as an informal check on the model's output.

The second path prepares the GIS "cost surface" on which the ranges were modeled. The first step of this path is the selection of the rock unit polygons ("Texas Rock Units") by the cavernous units described above ("Cavernous Units"). Next, the cavernous unit's polygons are exported ("Polygon to Raster") to a raster cost surface ("Cavernous Units Cost Surface") set at 1-m resolution and including the limits of precision for all cave and karst feature coordinates.

The two paths join with the merging of the "Cavernous Units Cost Surface" and the "Confirmed Species." Before the model is run further per Figure 3, and as described in the following subsection, the "Confirmed Species" localities are plotted to verify their occurrence in the cavernous unit. Some caves plotted outside the mapped cavernous unit, which was expanded to include those caves in the following instances:

- Since the edge of the UAC could not be mapped precisely throughout the study area, its estimated boundary was expanded as much as an additional 200 m in a few areas of the Culebra Anticline to include known caves.
- La Cantera Cave No. 2, Mastodon Pit, UTSA Feature No. 50, and Vogel's Sink plotted in the Del Rio, which thinly covers the Edwards Limestone in those areas, except at the cave entrances in areas too small to appear on the geologic map.
- Darling's Pumpkin Hole plots in a thin outcrop of the non-cavernous Upper Evaporite Hydrostratigraphic Unit of the Upper Glen Rose, and Kappelman Salamander Cave plots in a thin portion of the Bulverde Hydrostratigraphic Unit of the Lower Glen Rose; each drop into and is formed in the cavernous Upper Fossiliferous and Little Blanco hydrostratigraphic units, respectively.
- Allan Clark (USGS, personal communication 2021), field-checked and confirmed that the mapped boundary of Upper Fossiliferous in Clark et al. (2016) near Cannonball needed slight adjustment to include the cave area.
- Clark also field checked to confirm the mapping (Clark et al. 2016) around F-150 Cave as non-cavernous, but the cave is in a small, unmapped, discontinuous bed of limestone and the cavernous unit was expanded slightly to include that approximate area.

<u>Species Ranges</u>

Unlike surface species which are more easily observed and have habitat conditions that are mapped readily, defining the range of karst invertebrate distribution is based on sparse information. The purpose of including 25 non-listed species in this study, which depend on

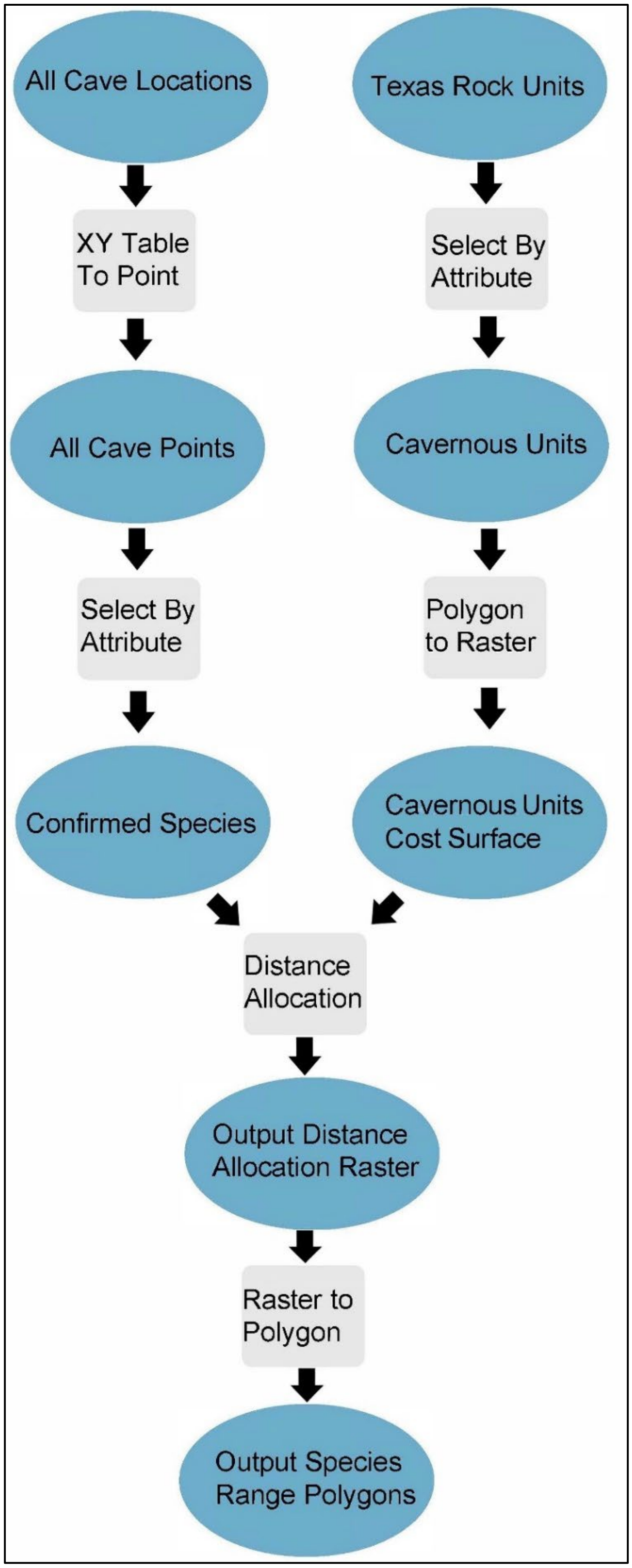

Figure 3. Schematic workflow of ArcPro model for analyzing species ranges (Veni and Jones 2021).

habitat conditions similar or identical to the endangered species, is to provide a richer data set for analysis than can be derived from the ten endangered species alone.

Most species in the study area are allopatric (i.e., ranges do not overlap) in their genera. This fact is used to define most species ranges (Table 1). After attempts and refinements with different ArcPro tools and methods, the following range determination method was applied to the allopatric species:

1. A 3-km travel radius was established around all localities in the model for a given species. The 3-km radius extends with the ArcPro distance allocation tool from the coordinates of each cave entrance ("Distance Allocation", Figure 3); caves are treated as if they only have one entrance since multi-entrance caves are few in the study area and typically less than 30 m apart—less than 1% of the radius. Based on field experience and study of the distribution of the 35 species, in addition to 39 related species in the Austin area (Veni and Jones 2021), 3 km is determined to be an approximate average default range for all species from a known locality.
2. Travel radii or other range margins described in the following steps do not extend beyond the limit of the cavernous unit. In addition, by use of the distance allocation tool, range distances are based on the distance of travel for the species within the cavernous unit rather than a Euclidean (straight line) distance from the cave entrance. Thus, range distances measure distance around and through the cavernous unit, rather than extending across gaps in the unit.
3. If a given species is known from multiple caves farther than 3 km apart, the 3-km radii are extended to two-thirds the distance of the cave farthest from its nearest neighbor with that same species (Table 1). If a non-cavernous area occurs along the straight-line path between the caves, the two-thirds distance is the shortest distance possible through the cavernous unit. The two-thirds distance is found to produce biologically realistic ranges, as opposed to shorter distances that barely connect the ranges, while not extending the ranges unrealistically from the known localities. Once connected by this method, these combined ranges from all caves with a certain species defined the range of that species ("Output Distance Allocation Raster), which is exported ("Raster to Polygon") to polygon format ("Output Species Range Polygons") (Figure 3). This method demonstrates that a species range has the capacity to extend at least that two-thirds distance from a location given enough time and no physical or biological impediments, but it only applies to the individual species assessed in those caves; the distance for other species of the same genus may differ and are determined separately by the same method.
4. The range of a given species can be limited in some areas by the edge of the cavernous unit, as described in Step 2 above, but it can also be limited by encountering the ranges of other species of the same genus. Because the species are allopatric, they cannot occupy the same area. Where the modeled ranges of the individual species will otherwise overlap, the distance allocation tool is used on all species within the same genus with a set maximum distance to divide the overlap equally between adjacent ranges.

Table 1. Range distances per species.

Species	Range distance (m)	Basis
Batrisodes excavodes shadeae	3,000	Standard radius
Batrisodes venyivi	4,490	Two-thirds distance from Cave No. 189 to Helotes Hilltop Cave
Cicurina baronia (Alamo Heights KFR)	5,120	Two-thirds distance from OB3 to Robber Baron Cave
Cicurina baronia (isolated area)	3,000	Standard radius
Cicurina brunsi	3,000	Standard radius
Cicurina bullis-neovespera	6,570	Two-thirds distance from Elm Springs Cave to Power Pole Hole
Cicurina madla	3,000	Standard radius
Cicurina platypus-puentecilla	6,540	Two-thirds distance from Black Cat Cave to Natural Bridge Caverns
Cicurina reclusa	3,000	Standard radius
Cicurina vespera	3,000	Standard radius
Rhadine bullis	3,000	Standard radius
Rhadine exilis	3,000	Standard radius
Rhadine infernalis ewersi	3,000	Standard radius
Rhadine infernalis infernalis	3,000	Standard radius
Rhadine infernalis new	3,000	Standard radius
Rhadine ivyi	3,000	Standard radius
Rhadine specum	3,000	Standard radius
Rhadine specum crinicollis	3,000	Standard radius
Rhadine specum gentilis	3,000	Standard radius
Rhadine specum specum	3,000	Standard radius
Rhadine sprousei	3,000	Standard radius
Speodesmus falcatus	3,826	Two-thirds distance from Elmore Cave to Root Toupee Cave
Speodesmus ivyi (Alamo Heights KFR)	3,000	Standard distance
Speodesmus ivyi (Stone Oak KFR)	13,473	Two-thirds distance from Cavern of the Morning Star to Cueva Cave
Speodesmus ivyi (isolated area)	3,000	Standard distance
Speodesmus reddelli	5,233	Two-thirds distance from Goat Cave to Suprise Cave
Tartarocreagris amblyopa	3,000	Standard radius
Tartarocreagris reyesi	7,413	Two-thirds distance from Up the Creek Cave to Young Cave No. 1
Tayshaneta bullis	3,000	Standard radius
Tayshaneta madla	3,000	Standard radius
Tayshaneta microps	3,000	Standard radius
Tayshaneta sprousei	3,000	Standard radius
Tayshaneta whitei (Culebra Anticline KFR)	3,000	Standard radius
Tayshaneta whitei (Government Canyon KFR)	11,453	Two-thirds distance from Lithic Ridge Cave to Nisbet Cave
Texella cokendolpheri	3,000	Standard radius
Texella elliotti	3,756	Two-thirds distance from Headquarters Cave to Winston's Cave
Texella hilgerensis	3,000	Standard radius
Texella tuberculata	3,680	Two-thirds distance from Logan's Cave to Surprise Sink
Texella youngensis	3,000	Standard radius

Four special circumstances require manual modifications to the modeled Output Species Range Polygons. First, some *Rhadine* species are sympatric. While these carabid beetles may occupy the same cave, they do not occupy the same ecological niche in the cave, which allows their co-existence. Gómez, et al. (2016) divided the *Rhadine* genus into two groups based on morphology: robust: (*Rhadine infernalis*) and slender (*Rhadine bullis, Rhadine exilis, Rhadine ivyi , Rhadine specum, Rhadine sprousei*).

Second, Elliott (2004) describes similar sympatry in some *Speodesmus* millipedes, where *Speodesmus ivyi* is diminutive and more soil-dwelling, allowing sympatry among these species. The *Speodesmus* genus is also divided into two groups: robust (*Speodesmus falcatus*, *Speodesmus reddelli*) and diminutive (*Speodesmus ivyi*). These sympatric species are plotted using the steps described above, except as robust or slender/diminutive groups. Reddell further notes (personal communication, 2020) that across genera in every case of sympatry in terrestrial invertebrate troglobites in the region, one species is more cave-adapted than the other, reflecting different periods where ancestor species began to occupy or reoccupy cave habitats.

The third special circumstance is where a species' range is divided by the smaller range(s) of other species. As described in Veni and Jones (2021), these situations are interpreted as areas once occupied by the species with the larger range until extirpated from the intervening area by the invasion of a competitive terrestrial invertebrate troglobite of the same genus. In these cases, the maximum range distance from a cave is based on the maximum distance within any of the subranges, without crossing the range of the intervening species. While the species may have once occurred in the intervening area, its distribution between caves in that area is unknown and unlikely to have spanned that entire distance.

Where overlaps in ranges occur, they are generally divided equally, as in Step 4 above. Where one range substantially overlaps the range of another, the range is defined based on two considerations, both of which can apply to different parts of the same range:

1. If the halfway distance between the nearest caves for the different species is within the smaller range, that smaller range is truncated at that distance.
2. If the halfway distance between the nearest caves for the different species is outside of the smaller range, the limit of the smaller range defines the boundary.

The fourth special circumstance is where sympatry exists, but there is insufficient information to consider them functionally allopatric, or in different niches, as with *Rhadine* and *Speodesmus*. This occurs in this study area with the combined *Cicurina bullis-neovespera,* the combined *Cicurina platypus-puentecilla*, and *Cicurina madla* with *Cicurina vespera*. Their ranges are plotted as overlapping, following Steps 1–3 above but not Step 4. Following the four special manual adjustments described above, the final Output Species Range Polygons are illustrated in Figures 4-12.

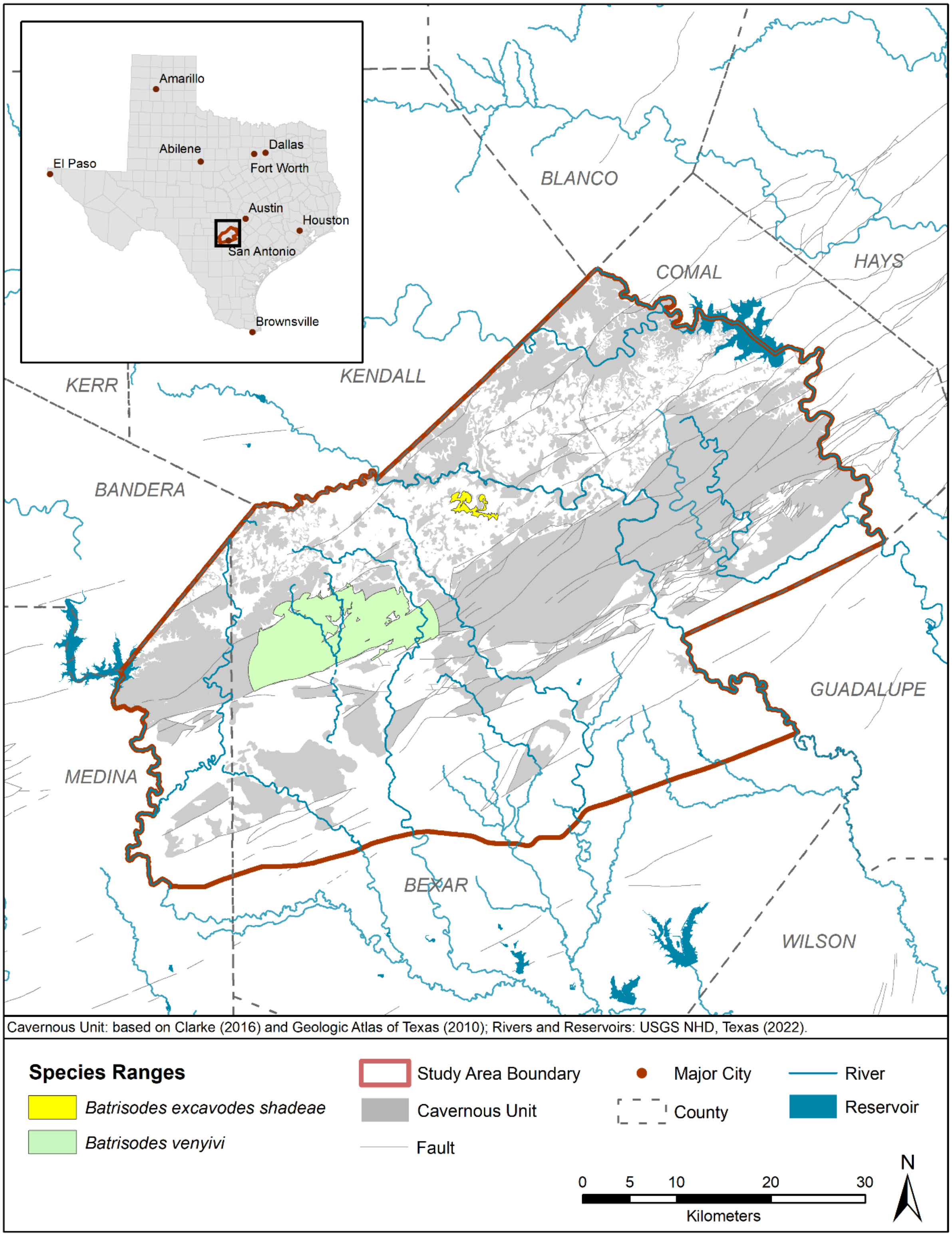

Figure 4. Ranges of Batrisodes species in the San Antonio Area.

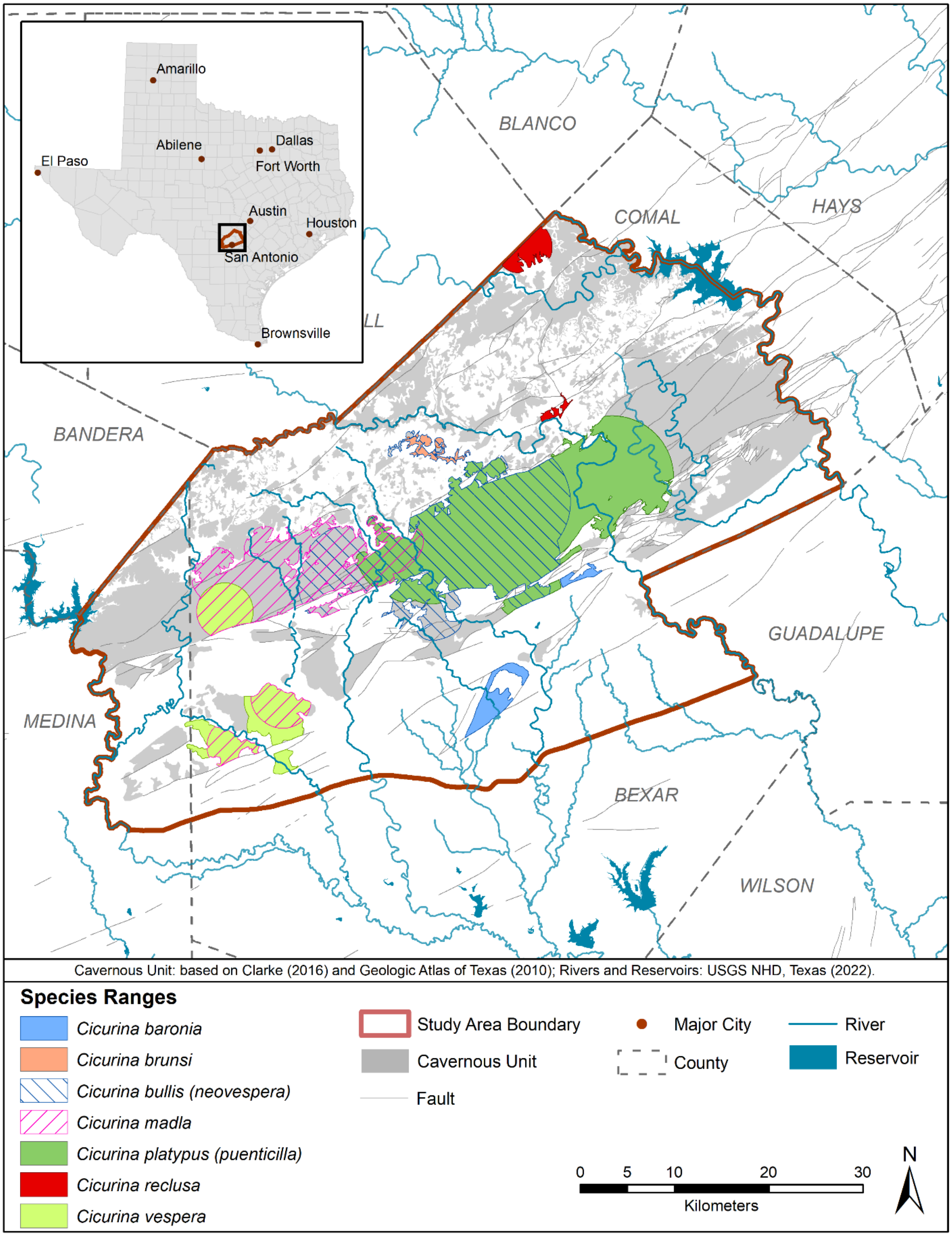

Figure 5. Ranges of Cicurina species in the San Antonio Area.

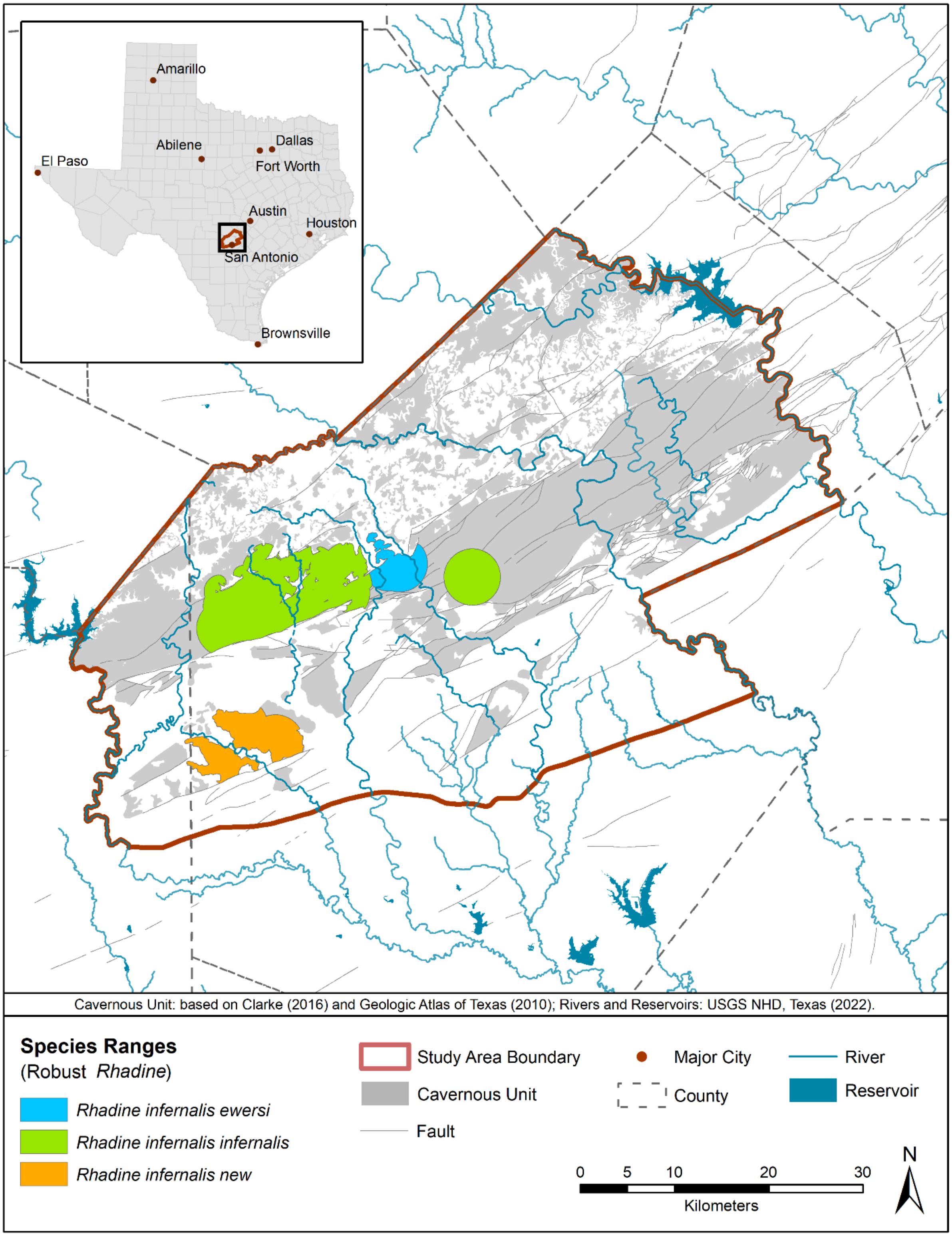

Figure 6. Ranges of robust Rhadine species in the San Antonio Area.

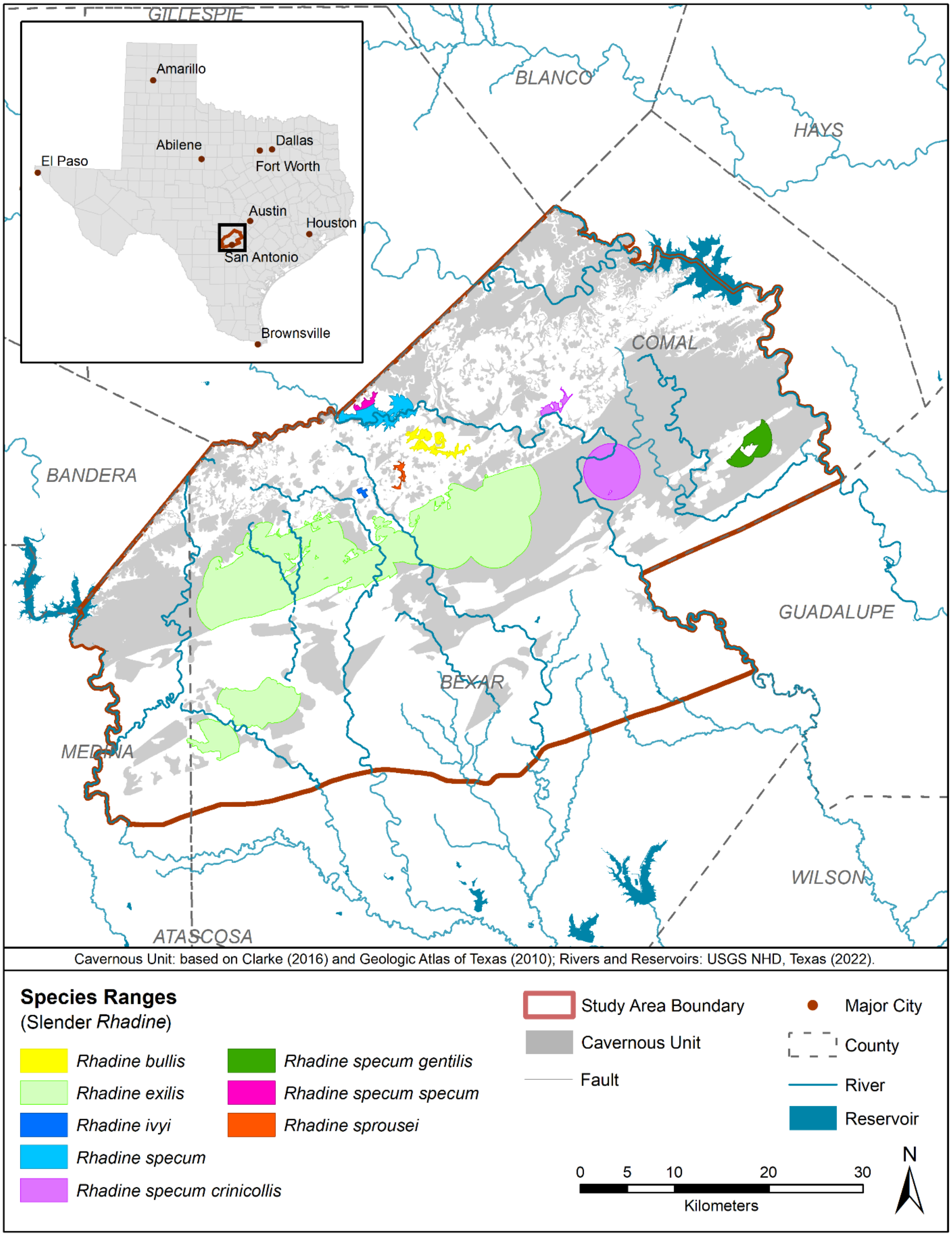

Figure 7. Ranges of slender Rhadine species in the San Antonio Area.

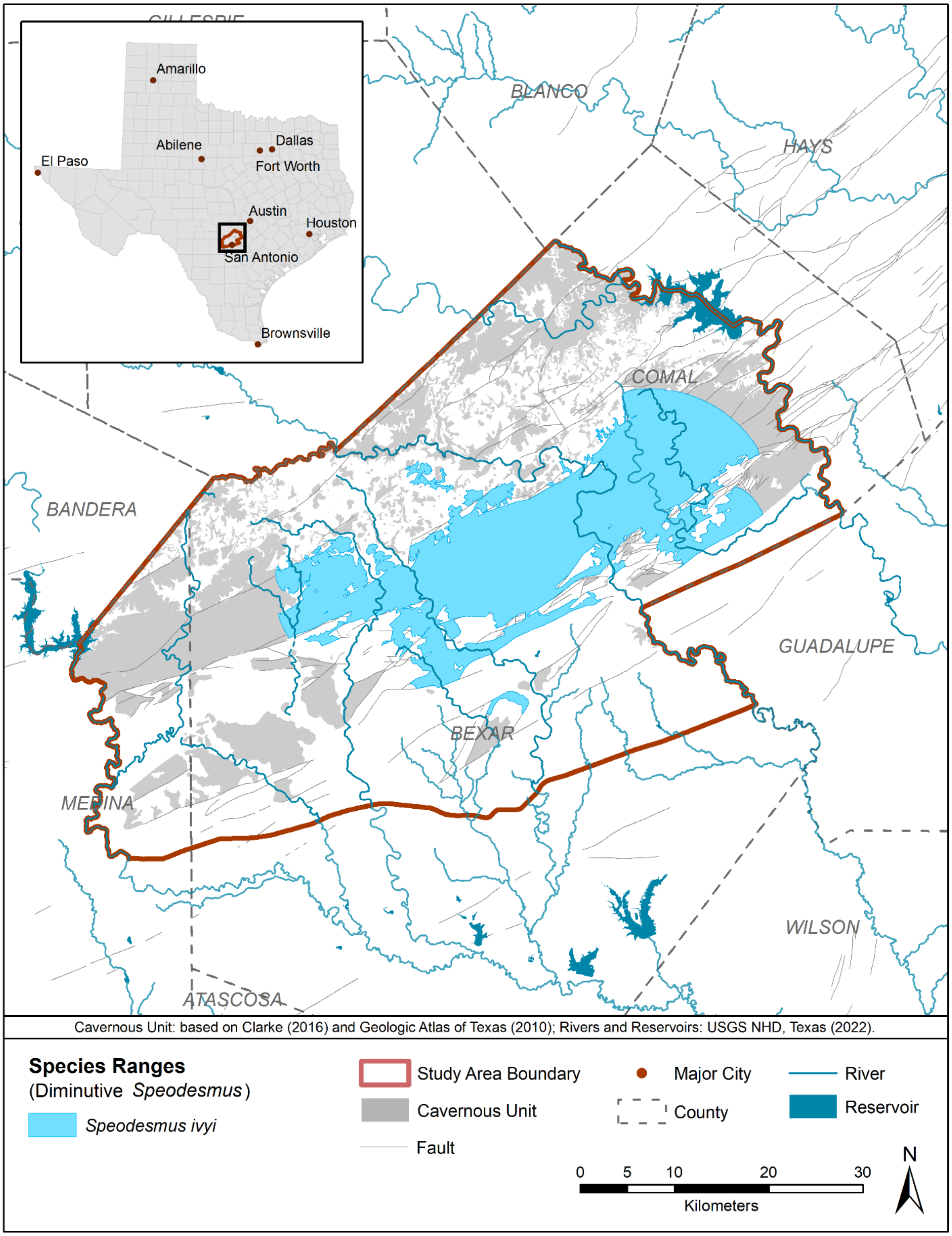

Figure 8. Range of diminutive Speodesmus species in the San Antonio Area.

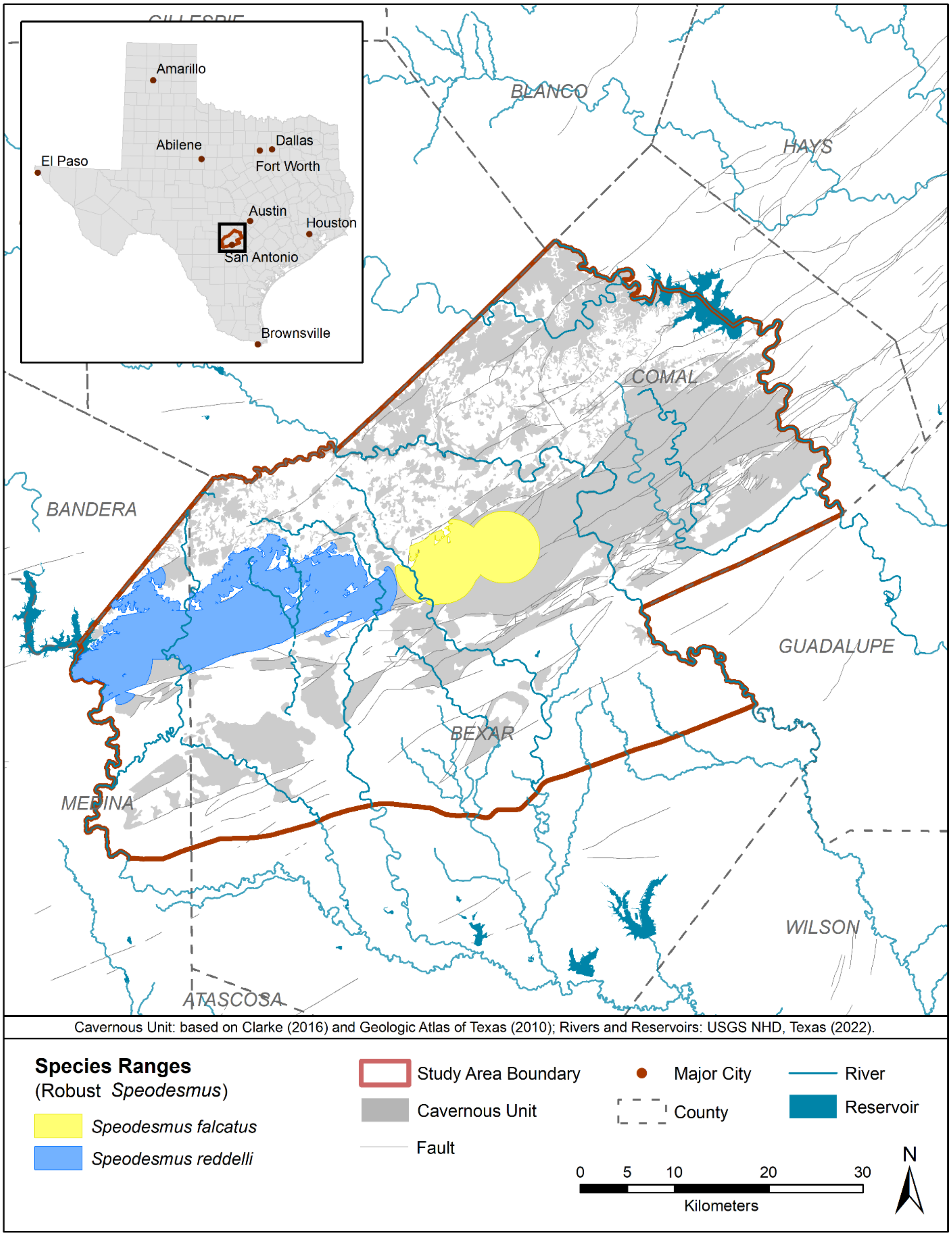

Figure 9. Ranges of robust Speodesmus species in the San Antonio Area.

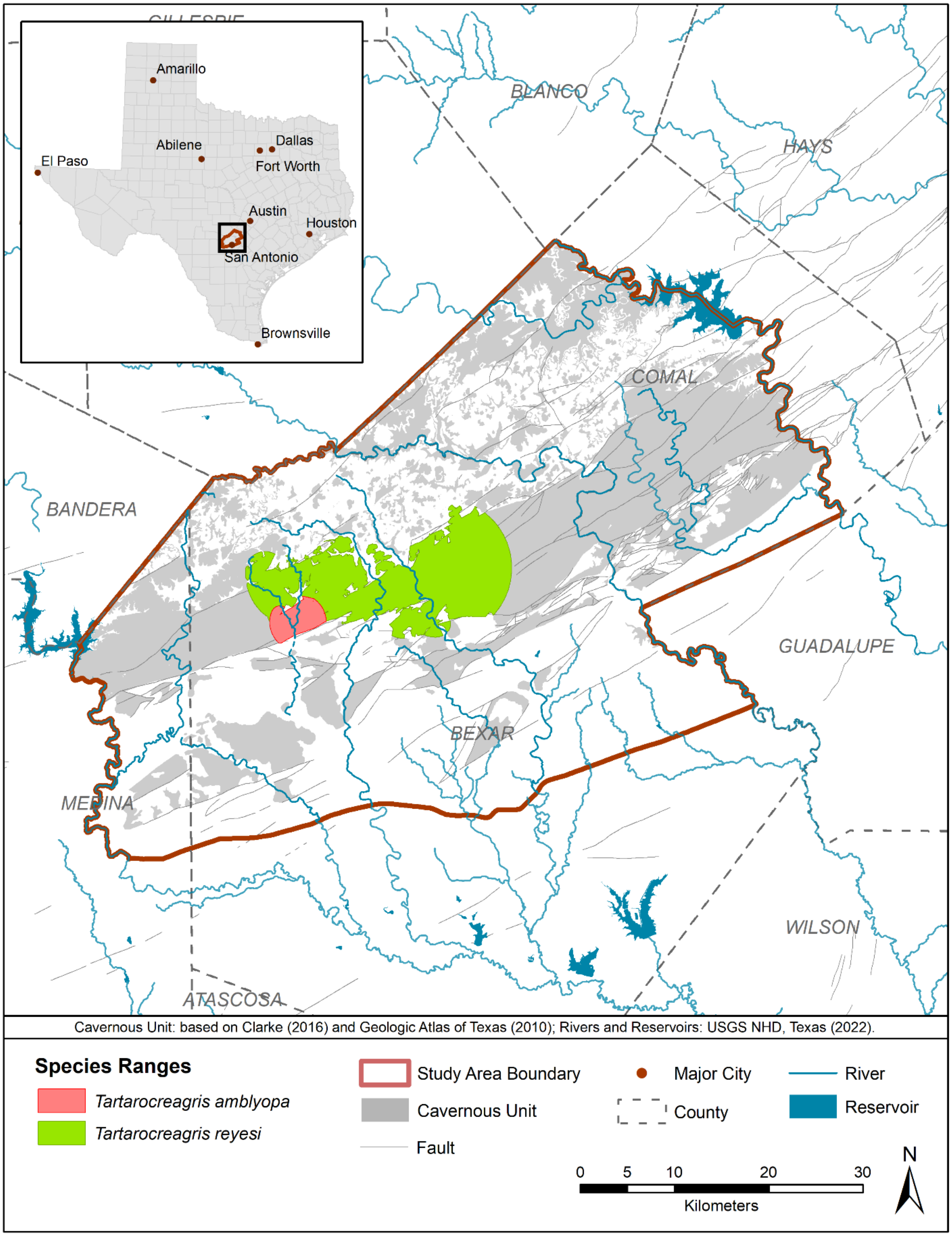

Figure 10. Ranges of Tartarocreagris species in the San Antonio Area.

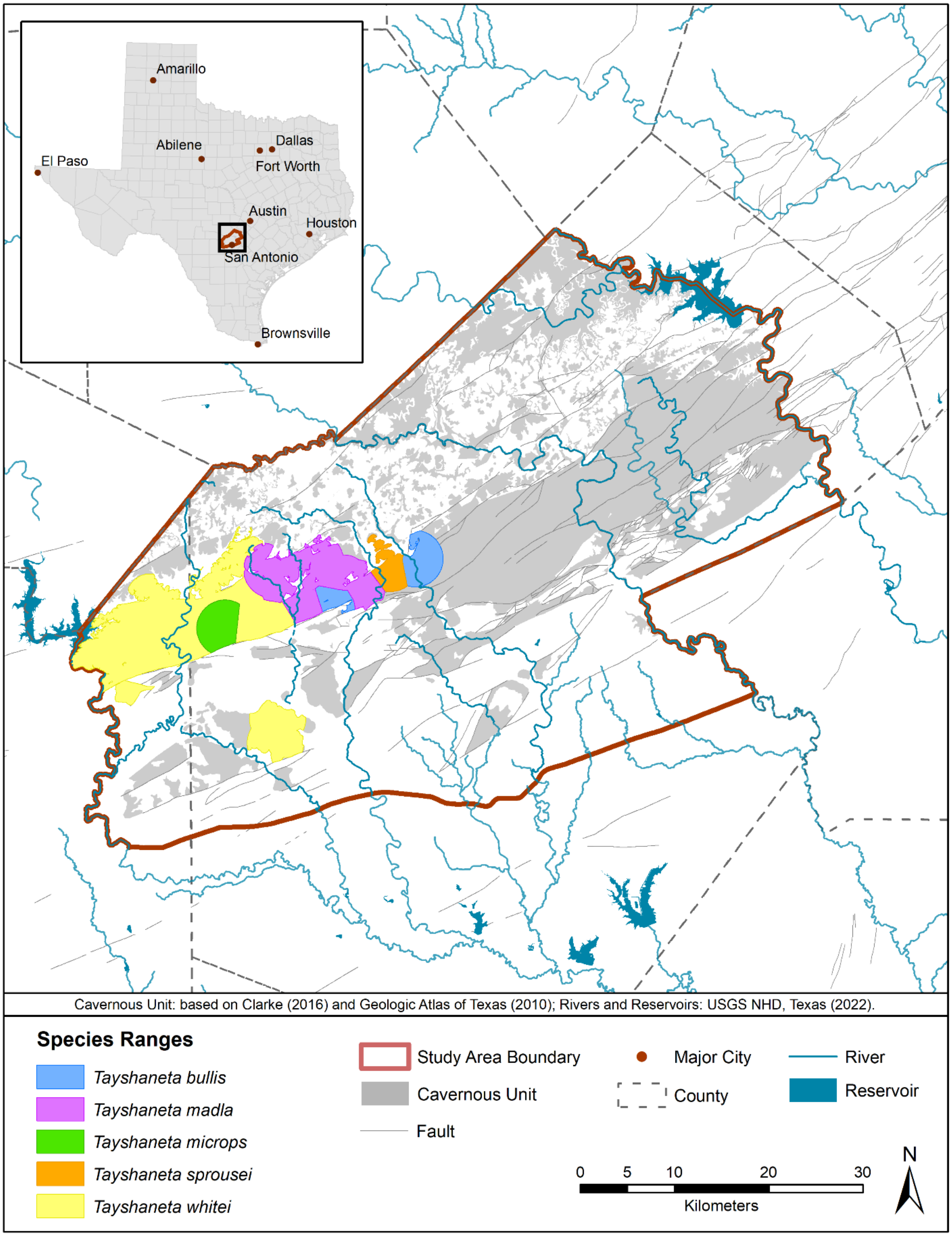

Figure 11. Ranges of Tayshaneta species in the San Antonio Area.

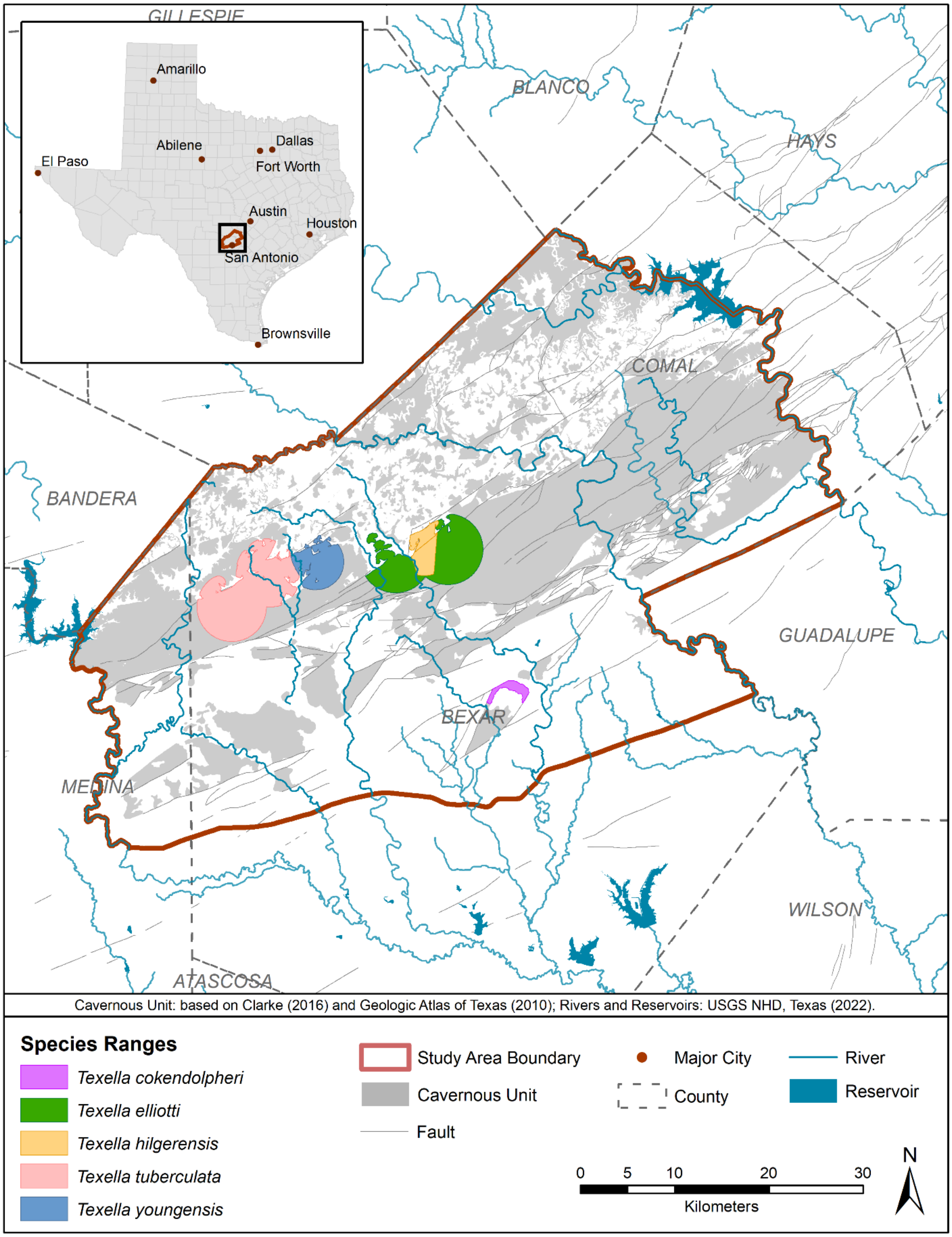

Figure 12. Ranges of Texella species in the San Antonio Area.

Karst Fauna Region Boundary Analysis Methodology

Figure 13 illustrates the breath of all the modeled species ranges used to evaluate the KFR boundaries and combines all the range margins from Figure 4 through Figure 12 for examination and analysis. KFR boundaries are evaluated based on the clustering of species range margins as identified through the following steps and factors:

1. The margins of the cavernous unit are considered natural KFR boundaries, where clustering is expected for many species. No additional consideration is given to clustering along these boundaries unless something unusual is discovered.
2. Clusters are defined as three or more range margins within an area of width no greater than the approximate average length of the range margins. The range margin length, for the purposes of defining clusters, is the straight-line distance between a margin's end points at the edges of the cavernous unit where the overall trend is linear. Where a margin is generally circular or oval, the diameter of the circle or linear axis of the oval is the length. This definition and measure of clustering only applies to areas of contiguous cavernous rock.
3. If the species reflected by the clustered range margins represent at least 50% of the species analyzed that occur in that cluster area, then that cluster suggests a potential KFR boundary. It is important to reemphasize that a KFR boundary is not necessarily a barrier to species dispersion over time, but it can be a restriction, allowing limited dispersion while still promoting speciation.
4. The individual ranges within a cluster at a potential KFR boundary are reexamined to determine if any special factors, such as modeling artifacts, need consideration in assessing their significance toward evaluating the presence or absence of a KFR boundary.
5. If the clustered range margins still represent at least 50% of the species analyzed that occur in that cluster area, without equivocation, the cluster area is considered verified as indicating the presence of a barrier or restriction to species distribution.
6. The location and alignment of the cluster area, along with the actual species localities, are compared to mapped geologic and hydrologic features to determine if such feature(s) account for the cluster. If so, a KFR boundary is drawn along that feature. The KFR boundary occurs within or adjacent to the cluster area.
7. If no known geologic or hydrologic feature accounts for a cluster, it is assumed to result from biological factors beyond the scope of this study to assess (e.g., nutrient and moisture variations in cave habitats, competition, displacement by competing species, etc.), and the KFR boundary is drawn along the axis of the cluster.

While the previously established KFR boundaries are known and discussed below for comparison, this evaluation is conducted without consideration of those boundaries.

Each range margin and cluster is examined carefully for modeling artifacts that might result in erroneous interpretation. The primary potential modeling artifact considered in the above seven steps is that the modeled species ranges can extend into areas where a given species has not been documented to occur. If the modeled range for a species extends beyond a possible KFR boundary, but the species is not present past that possible boundary, that is

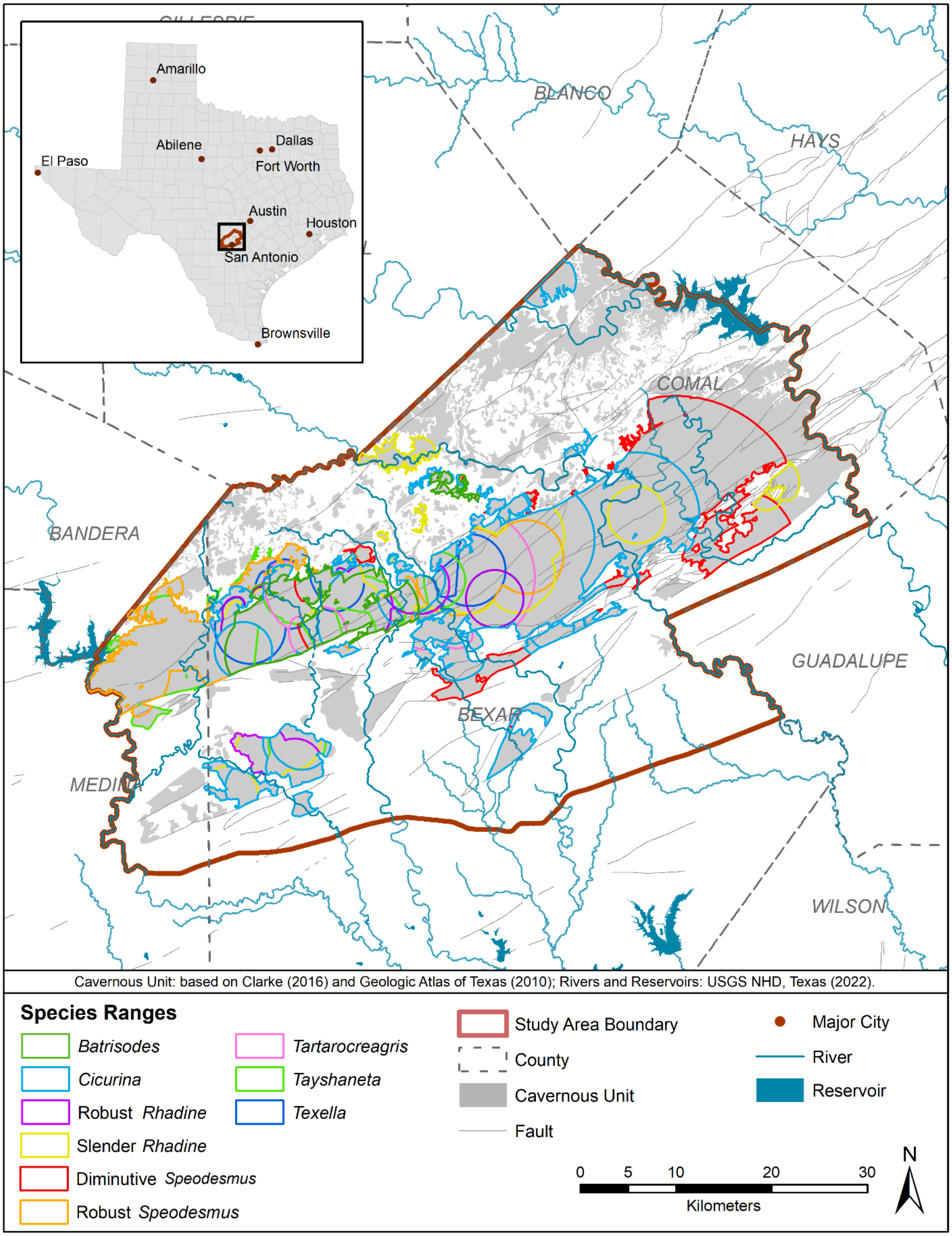

Figure 13. Combined ranges of all species analyzed in the San Antonio Area.

considered supporting evidence for the existence of a KFR boundary. In all cases, all available data (geologic, hydrologic, genetic, evolutionary, etc.) for a cluster area and its species are considered in KFR boundary decisions.

Karst Zone Analysis Methodology

The most critical of the karst zones is Zone 1, where endangered species are known to occur. When the existing karst zone maps were first drafted in 1994, fewer than 30 caves were known from the study area to contain species then petitioned for endangered listing. When GVA (2003) updated the karst zones, 78 caves were known or reported to contain listed species. That study, and a similar revision of karst zones in the Austin area (GVA 2007), found that wherever caves with habitat appropriate for the listed species were found in Zone 2, the endangered species were often found, confirming Zone 2 as an area of high probability for containing the endangered species.

Of the 212 localities included in this study, the majority contain listed species. A total of 153 localities are caves or karst features confirmed as containing endangered karst species and eight are reported as potentially containing them. The increase in localities confirmed to contain endangered species required additional revision of Zone 1 for more effective species management, study, and protection. The need for Zone 1 revision is not limited to the discovery of new endangered species localities but is also compelled by the better understanding of their ranges through this report's KFR boundary analyses.

Additionally, the remaining three zones (Zones 2, 3, 4) are revised as needed with three notable changes from the earlier zone maps. First, Zone 4 was originally defined as an area of uncertain cave potential. That is no longer the case following recent detailed geologic mapping of those areas; Zone 4 is eliminated, with Zone 5 of GVA (2003) now changed to Zone 4 to better match the four karst zones designations defined in the Austin area (Veni and Jones 2021).

The second and third zone changes are that Zone 3 was defined previously as "areas that probably do not contain endangered cave fauna" and Zone 4 (previously Zone 5) as "areas which do not contain endangered cave fauna." New data and better understanding of management needs expands and more precisely redefines those zones as:

- Zone 3a: areas suitable for terrestrial invertebrate troglobite species but which have a low probability of containing endangered karst invertebrate species because the habitat is occupied by other terrestrial invertebrate troglobite species;
- Zone 3b: areas which have a low probability of containing endangered karst invertebrate species because they are poorly suited for terrestrial invertebrate troglobite species;
- Zone 4a: areas suitable for terrestrial invertebrate troglobite species but which do not contain endangered karst invertebrate species because the habitat is occupied by other terrestrial invertebrate troglobite species;
- Zone 4b: areas which do not contain terrestrial invertebrate troglobite species.

These same zone distinctions were proposed for the Austin area by Veni and Jones (2021).

In general, the karst zones are delineated based on lithology as follows:

- Zones 1 and 2 occur in the cavernous unit.
- Zone 3a is in the cavernous unit but where KFR boundary modeling indicates the endangered karst invertebrate species are nearby but probably not present.
- Zone 3b is in areas of the cavernous unit covered by poorly cavernous or non-cavernous alluvium or rock, which includes areas of the Del Rio Clay and Georgetown Formation, and areas of the Austin Chalk's UAC and the Glen Rose Limestone's Camp Bullis Hydrostratigraphic Unit.
- Zone 4a is in areas of the cavernous unit which are sufficiently distant from the endangered karst invertebrate species to preclude their presence, and where a different suite of terrestrial invertebrate troglobites is established as occupying the habitat that would otherwise be occupied by the endangered karst species.
- Zone 4b is all adjacent non-cavernous geologic units.

This classification system is based on the presence or absence of caves and karst features in those lithologies.

Zone boundaries are revised based on current understanding of cave and karst development (e.g., Ford and Williams 2007; Palmer 2007), karst conditions occurring specifically in the study area (Veni 1988; Zara Environmental LLC and George Veni and Associates 2011; Veni 2018), and on biological information and KFR modeling of the distribution of endangered and non-listed species. The main principles used to delineate zone boundaries are to identify hydrogeologic and/or topographic features that may restrict the distribution of the endangered species and to examine the KFR modeling's distribution of endangered and non-listed species for indications that zone boundaries are valid. Contacts between geologic units where caves are common, versus geologic units where caves are rare or absent, are the most reliable factors in delimiting Zone 1 boundaries. These boundaries sometimes occur in valleys where erosion has removed one unit and exposed another and can also occur along faults where one unit may be juxtaposed against another.

Many Zone 1 boundaries are not simple to define. Except for the newly added factors 5 and 6 below, the following zone delineation methodology follows that established by GVA (2007). Where no known discontinuity occurs in the cavernous unit, and for lack of other possible options, Zone 1 boundaries can be drawn along creek beds and the locally narrowest or lowest drainage divide. These locations are where the limestone is thinnest and may pose some restrictions on species distribution. Faults with cavernous rock on either side do not seem to restrict species distribution, but they may be selected as a Zone 1 boundary if other possibilities are exhausted. While some caves form along faults, fault planes filled with calcite or gouge are unlikely sites for cave development. Other factors considered in the delineation of Zone 1 boundaries include:

1. The lowest known cave elevation is compared with the lowest topographic elevation to be sure at least the known cavernous zone in the rock is encompassed, assuming the rock is essentially horizontally bedded in the area.
2. The distribution of karst invertebrates in different caves is examined. If the fauna assemblages are similar, then the caves may warrant grouping into a single zone. The quality of specimen collections is weighed such that collections conducted only once,

under poor conditions, cursorily, and/or by non-specialists in the collection of cave species (if these factors are known), are given greater weight for similarity of species. This is because if rare fauna are found under poor collecting conditions, it suggests that even more species are present and could be found during good collecting conditions by those with more experience, thus more detailed studies would likely yield more similarities with other caves.

3. The type and extent of cave development in an area is considered as an indication of how realistic it may be for cavernous voids to occur in locations considered as zone boundaries.
4. The presence of other caves in the area, especially if they occur between caves with endangered species, demonstrates the presence of a potential habitat for the species, unless the caves have been carefully surveyed (with approximate habitat discovered) and the listed species were not found.
5. The GIS-modeled ranges of the endangered karst species, primarily, with some consideration of the non-listed species, are used as guides to support their likely presence.
6. The distribution of tentatively identified endangered species is not a primary factor in delineating Zone 1 boundaries; however, their presence (especially if high confidence exists in the tentative identification) may assist in refining boundary details.

The above factors are not always consistent. For example, the geology may suggest a restriction, but the biology may indicate the opposite. All available factors and information are considered to determine which features and locations are the most likely boundaries. While the above methods are focused on Zone 1, they are also applied to other zones if additional considerations are needed beyond lithology and the species present.

Karst Fauna Region Boundary Analysis

The following subsections report on the use of GIS modeling to evaluate the KFR boundaries established by GVA (1994; Figure 14) and any potential KFR boundaries suggested by the model's range clusters in Figure 13. They include information on other boundaries for the KFRs, but do not evaluate them unless the GIS model or other factors indicate that additional consideration is warranted. The KFR evaluations occur in a general clockwise, southeast-to-northwest order, with a southward detour to the Alamo Heights KFR and back to the Culebra Anticline. The conclusions section of this report provides summary descriptions and a map of all KFRs based on the following assessments.

Culebra Anticline KFR Boundaries

George Veni & Associates (1994) describes the Culebra Anticline KFR as an isolated KFR, about 19 km east-to-west and 9 km north-to-south (Figure 14). It primarily includes the Austin Chalk and the Pecan Gap Chalk, to a far lesser degree, over the geologic structure known as the Culebra Anticline. Barnes' (1983) geologic map shows the Culebra Anticline bounded by faults to the south and covered by younger and non-cavernous geologic units to the north and about 3 km west into Medina County. All caves currently known from this KFR are formed in the Austin Chalk, not including entrances in the Pecan Gap that lead into the Austin Chalk below. Since some cave entrances are in the Pecan Gap, most of the existing boundaries of the KFR are better defined as at the area of contiguous Austin Chalk and Pecan Gap Chalk outcrops

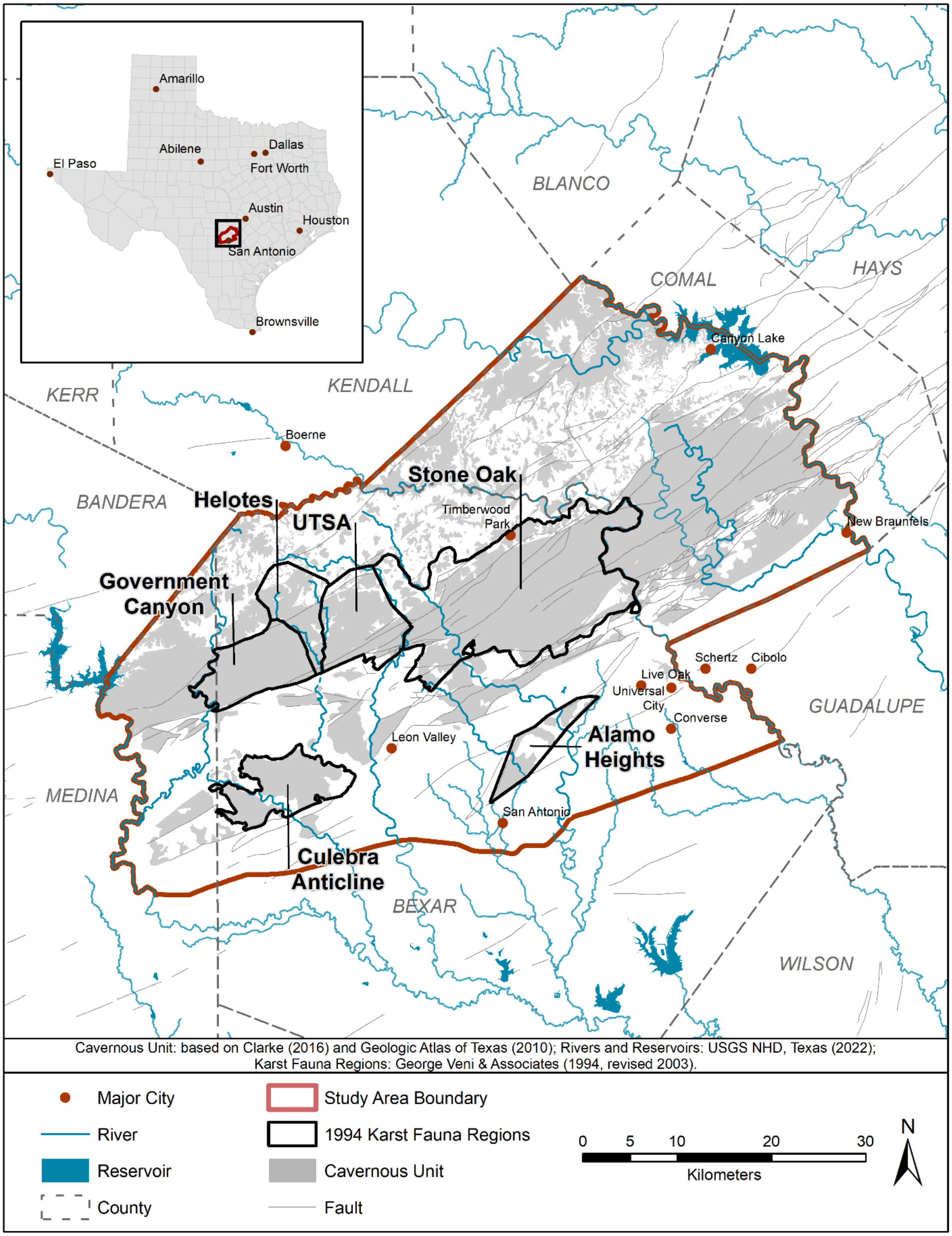

Figure 14. Previously defined Karst Fauna Region boundaries in the San Antonio Area (George Veni & Associates 1994 and revised in 2003).

west of Culebra Creek over the Culebra Anticline, including areas mapped as alluvium that cover those units. This incorporates areas mapped by Barnes (1983) as Anacacho Limestone, some of which were found to be Austin Chalk during this study. It also includes one isolated section of Austin Chalk, approximately 2.3 km north-to-south and 1.8 km east-to-west along Loop 1604, which is now known to contain several caves and sinkholes, eight of which provide habitat to the endangered spider *Cicurina vespera* (Figure 5). Additionally, the Culebra Anticline KFR is expanded to include a section of Pecan Gap at the east end of Culebra Creek and seven sections of Austin and Pecan Gap to the northwest, all of which are mapped as isolated outcrops but separated only by alluvium that covers the intervening areas.

East of Culebra Creek, the Pecan Gap Chalk extends 17 km to the Alamo Heights KFR. Only two caves are known in this area of Pecan Gap, neither well described nor biologically studied. None of the species known in the Culebra Anticline KFR are documented to occur in the Alamo Heights KFR, indicating this area of the Pecan Gap is a barrier to distribution and supports the Pecan Gap portion of Culebra Creek as a KFR boundary.

North and northeast of Culebra Creek, the Austin Chalk continues about 6 km to the Edwards Limestone of the Government Canyon and UTSA KFRs, but GVA (1994) did not include this area within the Culebra Anticline KFR due to the near absence of caves and the observed presence of poorly cavernous strata. To evaluate this area's status as a potential KFR boundary, Figure 13illustrates six species ranges within the Culebra Anticline KFR:

1. *Cicurina madla* (Figure 5),
2. *Cicurina vespera* (Figure 5),
3. *Rhadine exilis* (Figure 7),
4. *Rhadine infernalis infernalis* (Figure 6),
5. *Rhadine infernalis* n. ssp. (Figure 6), and
6. *Tayshaneta whitei* (Figure 11).

Only one species is limited to the Culebra Anticline, *Rhadine infernalis* n. ssp. (Figure 6), and the others occur in the Culebra Anticline and Government Canyon and/or UTSA KFRs. In addition to these six species, Figure 13 shows the ranges of eight species in the Government Canyon and UTSA KFRs that are adjacent to outcrops of Austin Chalk which extend to the Culebra Anticline KFR:

1. *Batrisodes venyivi* (Figure 4),
2. *Cicurina bullis-neovespera* (Figure 5),
3. *Speodesmus reddelli* (Figure 9),
4. *Tartarocreagris amblyopa* (Figure 10),
5. *Tayshaneta bullis* (Figure 11),
6. *Tayshaneta madla* (Figure 11),
7. *Tayshaneta microps* (Figure 11), and
8. *Texella tuberculata* (Figure 12).

With the ranges of eight of the 14 species (57.1%) not extending from the Culebra Anticline to the Government Canyon and/or UTSA KFRs, this distribution suggests a potential KFR boundary.

Genetic studies of the region's karst invertebrates demonstrate differences within some Culebra Anticline species from individuals of the same species in the nearby KFRs. For example, *Cicurina loftini* and *Cicurina venii* were considered distinct species limited to the Culebra Anticline KFR for several years until lumped with *Cicurina vespera* and *Cicurina madla*, respectively (Hedin et al. 2018). The morphologic and genetic differences between the former *C. loftini* and *C. venii* with *C. vespera* and *C. madla* from the Government Canyon and UTSA KFRs may suggest some speciation of the Culebra Anticline populations, but would require further investigation.

Barnes (1983) and Clark et al. (2016) show several faults between the Culebra Anticline and the KFRs to the north that might affect species distribution and speciation as restrictions, not barriers, to gene flow given that five of the species in the Culebra Anticline KFR also occur in the Government Canyon and/or UTSA KFRs. Because the faults have been present for millions of years, they should become more permeable by dissolution over time and thus less restrictive to gene flow, contrary to what is suggested by the pattern of evident speciation observed Therefore, it seems more likely that erosion of the UAC in the area between the Culebra Anticline and Governmental Canyon/UTSA KFRs has thinned and removed much of the potential habitat, progressively isolating the Culebra Anticline populations.

This study's identification of the UAC north of Culebra Creek and a previously unrecorded zone of extensive karstification in that area in addition to the two caves previously known demonstrates its potential for possessing habitat for karst invertebrates. The absence of karst invertebrates, due to inappropriate conditions at the known caves, makes it impossible to determine (using these methods) if this area should be part of the Culebra Anticline KFR or the KFRs slightly to the north. Any new cave found in this area should be studied to help clarify its biological status. Until further information is available, Culebra Creek should remain as the most likely KFR boundary for the Culebra Anticline's eastern limit in the Austin Chalk. The creek is likely a restriction to distribution because it is in the poorly cavernous LAC, any karst features are likely filled and/or buried with alluvium, and episodic flooding creates poor habitat conditions.

Government Canyon KFR Boundaries

The Government Canyon KFR is the westernmost in a series of contiguous KFRs extending across the northern third of Bexar County, predominantly in the Edwards Limestone and the Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose Limestone. It was initially defined as extending 6 km north of the Haby Crossing Fault to another major unnamed fault, and 13 km east from San Geronimo Creek to the 6-km long boundary with the Helotes KFR along Los Reyes Creek (5 km) and below where it joins Helotes Creek (1 km). This KFR was informally expanded by GVA (2003) 10 km farther west to the Medina River by the expansion of Karst Zone 2 during that study (Figure 14).

In examining the boundaries for this KFR and its contiguous KFRs in the Edwards and Glen Rose limestones, changes in the geological and biological understanding of those limestones must first be presented. When the KFRs were established in 1994 and the karst zones reevaluated in 2003, the uppermost section of the Upper Member of the Glen Rose was recognized as cavernous, but it had not been mapped or lithologically described. Consequently, the boundaries for Government Canyon and its contiguous KFRs to the east were based primarily on the mapped position of the Edwards Limestone. By the time of this current study, the geology of the area is mapped and described in detail, including the Glen Rose Limestone, for Medina County (Clark, et al. 2020) and Bexar and Comal counties (Clark et al. 2016). This new mapping, along with greater understanding of cave development in each hydrostratigraphic unit (e.g., Veni 2005) and study of its terrestrial invertebrate troglobite fauna allows more accurate delineation of the KFR boundaries and inclusion of that upper Glen Rose cavernous section (now named the Cavernous Hydrostratigraphic Unit) and other cavernous and non-cavernous units for consideration in defining boundaries. In this report, "Cavernous Hydrostratigraphic Unit" refers to the uppermost section of the Glen Rose Limestone and "cavernous unit" refers to the collective cavernous rocks in the area used in this study's modeling of species distribution. As a general comment on cave development, most cave entrances are found in the Edwards Limestone, and it is not unusual for those caves to extend down into the Upper Glen Rose.

Most of the Government Canyon KFR is deeply dissected Edwards Limestone with some valleys in the underlying Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose Limestone. GVA (1994) established San Geronimo Creek as the Government Canyon KFR's western boundary. While cavernous rock extended west beyond the creek, there were no biological collections from the few known caves to determine the biological affinity of that area. While relatively few caves are still known and biologically studied in that area, Figure 13 shows two of this investigation's 35 species west of the creek (*Speodesmus reddelli*, Figure 9 and *Tayshaneta whitei*, Figure 11). Both are present on each side of the creek, and no species is known only from its west side, suggesting San Geronimo Creek poses no barrier or significant restriction to distribution and, therefore, is not a KFR boundary.

Reddell (personal communication, 2021) finds no overlap in species across the Medina River at the west end of the KFR. The perennial flow of the river prevents terrestrial invertebrate species from crossing under the river, creating a barrier to species distribution. The southern boundary of the Government Canyon KFR, along the Haby Crossing Fault, abuts the Austin Chalk and is discussed in the previous section on the Culebra Anticline KFR.

The updated geologic mapping for the area shows the cavernous unit extends 5.8 km north of the Government Canyon KFR, along the Bexar-Medina County line, to a fault that strikes to the southwest where this northward extension of the cavernous unit is cut off where Mescal Creek flows into Medina Lake. Ten caves are now known from the area, which remains poorly explored for caves, with only one cave receiving what TSS describes as a small and "hasty examination" of its fauna. Despite this fact, one of the 35 species studied in this report was recovered. This indicates reasonable potential for the listed species to be found by thorough studies in this portion of the cavernous unit, and that the Government Canyon KFR should be extended north to this southwest striking fault. The cavernous unit does extend north beyond the fault as narrow and generally thin outcrops and almost certainly a short distance to the west near Mescal Creek where Clark et al.'s (2020) geologic mapping ends at the Bandera County line; however, there is currently insufficient evidence to include those areas in the Government Canyon KFR. A nearly straight north-side alignment of the KFR boundary for 5.8 km along the Bexar-Medina County line reflects a difference in mapping between Clark et al. (2016) and Clark et al. (2020) and is beyond the scope of this study to resolve.

The eastern boundary of the Government Canyon KFR abuts the Helotes KFR. Figure 13 illustrates a cluster of six range margins in the Los Reyes and Helotes Creek area along that boundary:

1. *Cicurina bullis-neovespera* (Figure 5),
2. *Speodesmus ivyi* (Figure 8),
3. *Tartarocreagris amblyopa* (Figure 10),
4. *Tartarocreagris reyesi* (Figure 10),
5. *Tayshaneta madla* (Figure 11),
6. *Tayshaneta whitei* (Figure 11).

Additionally, six species are also known to occur in both KFRs:

1. *Batrisodes venyivi* (Figure 4),
2. *Cicurina madla* (Figure 5),
3. *Rhadine infernalis infernalis* (Figure 6),
4. *Rhadine exilis* (Figure 7),
5. *Speodesmus reddelli* (Figure 9),
6. *Texella tuberculata* (Figure 12).

The six range margins have an average length of 3.58 km and occur within a 3.1-km width, qualifying as a cluster. Of these 12 species in the area, the range of *Speodesmus ivyi* requires closer scrutiny. This species in not known in either the Helotes or UTSA KFRs. Its closest known occurrence is in the Stone Oak KFR, 12.5 km from the Government Canyon-Helotes KFR boundary. In circumstances like this, the modeled range would be considered a modeling artifact (e.g., Veni and Jones, 2021) and the range discounted from this specific range boundary analysis; however, two exceptional factors compel keeping the range of *Speodesmus ivyi* in this analysis. First, the species' distribution is probably not well represented due to a bias in biological collection methods. *Speodesmus ivyi* may have lower detection probability than *Speodesmus reddelli* because it is often found in soil and may remain unnoticed during many collections. Some collectors (the lead author on this report included) did not collect small *Speodesmus* for years believing they were immature *Speodesmus reddelli*. Second, *Speodesmus ivyi* has the greatest span between known localities of the 35 species examined at over 20 km (Table 1), which is significantly farther from a known locality than the Government Canyon-Helotes KFR boundary. This 20-km distance also extends out of the Stone Oak KFR, which may suggest the species could cross the boundaries into the UTSA and Helotes KFRs. Consequently, six of the 12 species in the area (50%) are considered to occur at their range margins in a range margin cluster, suggesting the cluster is a potential KFR boundary.

The cavernous unit occurs throughout most of the Los Reyes Creek and Helotes Creek area. Clark et al. (2016) show faulting is perpendicular to the creeks, and the species are distributed on either side of the various faults, therefore faulting plays no role as a significant barrier or restriction to species distribution. However, three factors do have limiting effects on species distribution:

1. The cavernous unit is significantly thinner in the creek valleys and absent in two locations, totaling about a sixth of the valley length, reducing the available area for species to cross between KFRs.

2. Periodic flooding of the creeks can inundate the habitat and often keeps it too moist for the species' habitat. This effect is exacerbated by the Cavernous Hydrostratigraphic Unit of the Upper Glen Rose comprising the cavernous unit below the creek beds. The high amount of clay in the Cavernous Hydrostratigraphic Unit retains more moisture than the purer Edwards Limestone, which may diminish habitat quality for endangered karst invertebrates.
3. Additionally, while the Cavernous Hydrostratigraphic Unit is certainly cavernous, it is notably less cavernous than the surrounding Edwards Limestone.

Based on the above factors, Los Reyes Creek and its downstream continuation as Helotes Creek is a KFR boundary and a restriction to species distribution because it limits but does not prevent troglobitic species from crossing the boundary. The KFR boundary at the upstream end of Los Reyes Creek is discussed in the next section.

Helotes KFR Boundaries

The Helotes KFR was first delineated as a roughly triangular area between Los Reyes Creek to the west (boundary with the Government Canyon KFR) and Helotes Creek to the east (boundary with the UTSA KFR)(Figure 14). It begins at the confluence with Los Reyes Creek and extends about 10 km north to the limit of the watershed between the creeks, reaching a maximum width of 5.6 km where the fault on the north side of the Government Canyon KFR extends northeast across both creeks. The area is characterized by caves formed mostly in isolated outcrops of Edwards Limestone on hilltops, and some cave development in the underlying Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose.

Updated geologic mapping for the area (Clark et al. 2016) shows the cavernous unit extends across much of the northern section of the creeks' watersheds to a northeast-striking fault 3.6 km north of the intersection of Texas Highway 16 and Shadow Canyon Drive. The broader extent of the cavernous unit from earlier studies of the area show it extends between the Government Canyon and Helotes KFRs north of the Los Reyes Creek along its watershed boundary. No caves are currently known in that area. The area remains largely unexplored for caves, with only five new caves reported about 4-5 km to the southeast since Veni's (2003) report, and none studied biologically. Based on the new geologic mapping, a more realistic boundary between the Government Canyon and Helotes KFRs in this area is to divert the Helotes boundary from Los Reyes Creek, about 900 m south of its northern limit, northeast along a fault and deep tributary creek about 1.8 km to the edge of the cavernous unit on the east side of Chimenea Creek, then north 1.3 km to the northeast-striking fault. The Government Canyon KFR boundary will also change to follow the edge of the cavernous unit around the head of Los Reyes Creek to the deep tributary creek to the cavernous unit's edge on west side of Chimenea Creek, north to the northeast-striking fault, and southeast along the east side of San Geronimo Creek to the main portion of the Government Canyon KFR. The cavernous unit does extend north beyond these modified boundaries as narrow and generally thin outcrops, where there is currently insufficient evidence to include those areas in either KFR. Additionally, the northeast end of the Helotes KFR is reduced in size and limited to the main outcrops of the cavernous unit, which is notably smaller in extent than the original KFR in this area.

The new geologic mapping by Clark et al. (2016) divides the cavernous unit into north and south sections beginning at a fault 2.2 km north of the confluence of Los Reyes and Helotes Creeks.

This non-cavernous area spans a 200-m stretch of Los Reyes Creek and a 2.9-km span of Helotes Creek. It could be expected to split the KFR except there is no clear justification for such action. Analysis of the 35 species show that seven occur in the Helotes KFR and five occur both north and south of the non-cavernous area. This biological affinity is likely because at its narrowest, the non-cavernous area is only 24 m wide, indicating that division of the cavernous unit by erosion in that area is a geologically recent phenomenon.

Figure 13 illustrates a cluster of seven range margins along Helotes Creek, which is the Helotes KFR's boundary with the UTSA KFR:

1. *Cicurina bullis-neovespera* (Figure 5),
2. *Speodesmus ivyi* (Figure 8),
3. *Tartarocreagris amblyopa* (Figure 10),
4. *Tayshaneta madla* (Figure 11),
5. *Tayshaneta whitei* (Figure 11),
6. *Texella tuberculata* (Figure 12),
7. *Texella youngensis* (Figure 12).

Additionally, six species are also known to occur in both the Helotes and UTSA KFRs:

1. *Batrisodes venyivi* (Figure 4),
2. *Cicurina madla* (Figure 5),
3. *Rhadine infernalis infernalis* (Figure 6),
4. *Rhadine exilis* (Figure 7),
5. *Speodesmus reddelli* (Figure 9),
6. *Tartarocreagris reyesi* (Figure 10).

The seven range margins have an average length of 3.36 km and occur within a 3.1-km width, qualifying as a cluster. These ranges also demonstrate some of the complex biogeography of the region and the varying effects of restrictions on species distribution in different areas. The central to northern 2.9 km of Helotes Creek is non-cavernous, limiting the potential routes for species to move between KFRs to a 3.3-km wide area to the south and a 1.3-km wide area to the north of the non-cavernous area. *Tayshaneta madla* extends across Helotes Creek between the Helotes and UTSA KFRs to the north, while none of the seven species are documented to occur on either sides of the creek to the south. With seven of the 13 species (54%) at their range margins in this area, they form a range margin cluster and suggest a potential KFR boundary.

In examining the geologic factors that may affect species distribution along Helotes Creek, they are identical to those described above for the Government Canyon's eastern KFR boundary along Los Reyes and Helotes creeks. Based on the above factors, Helotes Creek is a KFR boundary and a restriction to terrestrial invertebrate species distribution because it limits but does not prevent troglobitic species from crossing the boundary.

UTSA KFR Boundaries

The UTSA KFR was originally delimited as bounded by Helotes Creek on the west (boundary with the Government Canyon and Helotes KFRs), Leon Creek 8 km to the east (boundary with the Stone Oak KFR) and extending about 10 km north from major faults to the limits of the Edwards Limestone as mapped in 1994 (Figure 14). It is characterized by a continuous belt of Edwards Limestone along its southern boundary and Edwards Limestone on ridges to the north with intervening valleys predominantly in the Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose Limestone.

Following updated geologic mapping for the area (Clark et al. 2016), the western boundary for the UTSA KFR still follows Helotes Creek, as described in the previous section. The southern boundary along major faults, near and roughly parallel to Loop 1604, is changed. It is refined for newly mapped positions for the faults, but mostly changed to the southwest where it is extended about 5.5 km to Helotes Creek to include areas of Edwards Limestone, some of which are overlain by thin sections of the Georgetown Formation, Del Rio Clay, and Buda Limestone. One Edwards Limestone cave with *Cicurina madla* (Feature 1604-083-02) was found in this area under the Del Rio Clay by the Texas Department of Transportation ([TxDOT]; 2022), who also encountered karst features and a notable cave in the Buda Limestone in the vicinity. When considered with other karst feature data in the TSS database, the inclusion of these lithologies in at least this area is warranted.

The northern boundary is mostly unchanged but refined to follow the edge of the cavernous unit north to a northeast trending fault located 260 m south of the intersection of Scenic Loop and Babcock Road, excluding narrow and generally thin outcrops that continue north of the fault where there is currently insufficient evidence to include those areas in the KFR. More caves are known in the northern section of the UTSA KFR than the northern areas of the Government Canyon and Helotes KFRs, but most of the area is unexplored for caves and most of the known caves have seen little or no biological study.

Figure 13 illustrates a cluster of nine range margins along Leon Creek, which is the UTSA KFR's eastern boundary with the Stone Oak KFR:

1. *Batrisodes venyivi* (Figure 4),
2. *Cicurina platypus-puentecilla* (Figure 5),
3. *Rhadine infernalis ewersi* (Figure 6),
4. *Rhadine infernalis infernalis* (Figure 6),
5. *Speodesmus falcatus* (Figure 9),
6. *Speodesmus reddelli* (Figure 9),
7. *Tayshaneta madla* (Figure 11),
8. *Tayshaneta sprousei* (Figure 11),
9. *Texella elliotti* (Figure 12).

Additionally, five species are also known to occur in both the UTSA and Stone Oak KFRs:

1. *Cicurina bullis-neovespera* (Figure 5),
2. *Cicurina madla* (Figure 5),
3. *Rhadine exilis* (Figure 7),
4. *Speodesmus ivyi* (Figure 8),
5. *Tartarocreagris reyesi* (Figure 10).

The nine range margins have an average length of 3.32 km and occur within a 3.26-km width, qualifying as a cluster. With nine of the 14 species (64.3%) at their range margins in this area, they form a range margin cluster and suggest a potential KFR boundary.

Geologic factors that may affect species distribution along Leon Creek are similar to those described above for the KFR boundaries along Los Reyes and Helotes creeks. The primary difference is that along that 3.4-km stretch of Leon Creek (measured as a straight line from where it crosses onto the cavernous unit to where it exits the cavernous unit), a thicker section of the unit is present below the creek, and more of the more cavernous and less clay-rich Edwards Limestone for about 1.8 km. Esquilin et al.'s (2012) potentiometric elevations place the water table about 55-82 m below the creek bed, depending on location and water table conditions, through which the karst species may move between KFRs. Based on the above factors, Leon Creek is a KFR boundary and a restriction to terrestrial invertebrate species distribution because it limits but does not prevent troglobitic species from crossing the boundary.

Stone Oak KFR Boundaries

Unlike the deeply stream-cut topography of the KFRs west of Leon Creek, the Stone Oak KFR has mostly near-level to gently rolling hills and valleys. It was initially defined as extending east about 24 km from Leon Creek (eastern boundary with the UTSA KFR) to Cibolo Creek, widening north-to-south from 7.7 km along Leon Creek to 12 km along Cibolo Creek (Figure 14). Like the contiguous KFRs to the west, it is bounded by faults to the south and the limits of cavernous rock in the interstream watersheds to the north. The area is underlain primarily by Edwards Limestone with some sections in the Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose Limestone.

Notable modifications are needed in the western and northern parts of the Stone Oak KFR following the updated geologic mapping for the area by Clark et al. (2016). The western boundary still follows Leon Creek, as described in the previous section, but reduced from 7.7 km to 3.4 km in width due to the reduced width of the cavernous rocks estimated by GVA (1994). The northern boundary is reduced primarily to the major northeast-trending fault across the KFR between the cavernous unit and mostly non-cavernous rocks to the north. The fault crosses US Highway 281 2.8 km south of Cibolo Creek. Small outcrops of the cavernous unit north of the fault are included in the KFR based on the actual and modeled distribution of the species in Table 1. At the west end of the KFR, two localities of the endangered *Rhadine infernalis ewersi* occur north of the fault. Also, north of the fault in central Camp Bullis, a broad expanse of the cavernous unit north of the fault suggests listed karst invertebrate species could be found there. This area extends to within 310 m of an isolated section of the cavernous unit predominantly on Camp Bullis where the caves and their fauna are well studied. That geologically recent eroded gap in the cavernous unit has two non-listed species known from the Stone Oak KFR, *Cicurina bullis-neovespera* and *Speodesmus ivyi*, plus a tentative locality for *Speodesmus falcatus*. It also has two species endemic to that isolated section of the cavernous unit: *Cicurina brunsi* and *Rhadine bullis*. With the ranges of 50% of the known species on one or both sides of this 310-m gap, this isolated section is separate from the Stone Oak KFR. The presence of six other endemic species in other isolated sections of the cavernous unit north of the major northeast-trending fault (*Rhadine bullis*, *Rhadine ivyi*, *Rhadine reclusa*, *Rhadine specum*, *Rhadine specum specum*, *Rhadine sprousei*) further support the fault as a northern boundary for the Stone Oak KFR.

Over 30 caves are known in the area of the Stone Oak KFR boundary along Cibolo Creek, but only two caves are biologically studied, and each are about 5 km on either side of the creek. Figure 13 illustrates a cluster of four range margins along Cibolo Creek:

1. *Cicurina bullis-neovespera* (Figure 5),
2. *Rhadine exilis* (Figure 7),
3. *Rhadine specum crinicollis* (Figure 7),
4. *Speodesmus falcatus* (Figure 9),

Only one species is known to occur on both sides of the creek: *Speodesmus ivyi* (Figure 8). The four range margins have an average length of 9.84 km and occur within a 5.38-km width, qualifying as a cluster. With four of the five species (80%) at their range margins in this area, they form a range margin cluster and suggest a potential KFR boundary. Additionally, it must be noted that while the range of *Cicurina platypus-puentecilla* extends east past the cluster, into Comal County beyond Cibolo Creek, all its known localities are more than 5 km west of Cibolo Creek. Further indirect support for this cluster is that *Rhadine specum gentilis* is known only from Comal County 18 km east of Cibolo Creek. While the evidence for this cluster is significant, it should be reexamined for possible refinement when more of the caves in the area, especially those closer to Cibolo Creek, are studied biologically.

Hydrogeologically, the area along Cibolo Creek is similar to Leon Creek, relative to the distribution of terrestrial invertebrate troglobites. Faulting is perpendicular to the creek and has no significant effect on the species. The upstream half of the 11.3-km stretch of Cibolo Creek (measured as a straight line from where it crosses onto the cavernous unit to where it exits the cavernous unit), is on the Cavernous Hydrostratigraphic Unit of the Upper Glen Rose. The downstream half is on the more cavernous and less clay-rich Edwards Limestone. Esquilin et al.'s (2012) potentiometric elevations place the water table only about 35-50 m below the creek bed, depending on location and water table conditions, through which the karst species may move between KFRs. Based on the above factors, Cibolo Creek is a KFR boundary and a restriction to terrestrial invertebrate species distribution because it limits but does not prevent troglobitic species from crossing the boundary.

The southern boundary of the Stone Oak KFR remains unchanged along the faults that juxtapose the Edwards Limestone with other rocks, except where the faults' mapped positions are refined by Clark et al. (2016). Of the 13 species known in the Stone Oak KFR, only *Speodesmus ivyi* occurs south in the Alamo Heights KFR. This strongly supports the faults as a KFR boundary; however, the modeled ranges of *Cicurina bullis-neovespera* and *Cicurina platypus-puentecilla* (Figure 5) extend through a 400-m wide section of Edwards Limestone up to nearly 5 km into an approximately 16.4-km long by 1.2-km wide section of block-faulted Austin Chalk, discussed in more detail below in the section on the Alamo Heights KFR.

Alamo Heights KFR Boundaries

The Alamo Heights KFR was defined originally as the outcrop of Austin Chalk and Pecan Gap Chalk bounded within the horst beginning near San Pedro Park in San Antonio, and which heads northeast about 14 km, reaching a maximum width of 3.5 km, and pinching out near

O'Connor Road roughly midway between Nacogdoches Road and Interstate Highway 35 (Figure 14). All known caves in the KFR are formed in the Austin Chalk, although some have entrances is the Pecan Gap. Eastward, the Pecan Gap continues for 17 km to the Culebra Anticline KFR, with only two biologically unstudied caves of undetermined extent and geologic origin.

Until recently, the boundaries of the Alamo Heights KFR seemed firm. The faults delimited the area clearly and none of the three species were known in other KFRs. Data collected for this report show *Texella cokendolpheri* is still endemic to the Alamo Heights KFR (Figure 12), while *Speodesmus ivyi* also occurs north in the Stone Oak KFR (Figure 8), but more importantly, the endangered species *Cicurina baronia* is now known 5 km north of the northeast end of the Alamo Heights KFR in Green Mountain Road Cave near the east end of the Austin Chalk fault block described in the previous section as 16.4 km long by 1.2 km wide (Figure 5). This area had not been assigned to any KFR. The nearest cave to Green Mountain Road Cave within that Austin Chalk fault block is 11 km to the west with three other caves beyond the fault block and up to 18.5 km away. All four other caves besides Green Mountain Road Cave are sealed, small, and seem unlikely to have significant terrestrial invertebrate troglobite fauna assemblages, a hypothesis supported by a biological survey in the largest cave.

Of the 13.3 km between Green Mountain Road Cave and Robber Baron Cave, the nearest locality with *Cicurina baronia*, about 8 km are underlain by the Pecan Gap as indicated by the non-cavernous area between the ranges of the species shown in Figure 5. Only one small cave is known in the Pecan Gap, 16.3 km east of Robber Baron, and it contains no terrestrial invertebrate troglobites which suggests the Pecan Gap is a barrier or restriction to the distribution of terrestrial invertebrate troglobites. Contrary to the more generalized geologic map by Barnes (1983), which locates the entrance of Robber Baron Cave in the Austin Chalk, Cooper (2017) unambiguously placed the cave's entrance in the Pecan Gap during this study and otherwise found the cave is formed entirely in the Austin Chalk 9 m below. This demonstrates that sufficient water and nutrients penetrate the Pecan Gap to support Robber Baron Cave's ecosystem, since the entrance is a relatively young feature and the cave's ecosystem was almost certainly well-established before the entrance collapsed and opened the cave to surface water and organic debris.

Robber Baron Cave is a hypogenic maze cave and the longest cave in Bexar County with 1,636 m of known passages. The cave's history strongly indicates the cave is much longer than its currently known extent (Veni and Heizler 2009) and reports abound of caves in the surrounding area with some leading into mazes. Of the 24 other caves known in the Alamo Heights KFR, most have been sealed by urbanization decades ago, a few others are springs or are small in size and may not provide suitable dark zone to support terrestrial invertebrate troglobite populations unless they have sufficient mesocavernous space, and only one has been biologically studied: OB3, which also contains *Cicurina baronia* and is 6.3 km southwest of Robber Baron Cave.

The second most extensive cave in the Alamo Heights KFR (The Labyrinth) is open but the entrance is located on private property and permission for access could not be obtained for its study. The Labyrinth, like Robber Baron, is a maze cave, probably hypogenic in origin, with 610 m of surveyed passages and over 100 unexplored passages. Significantly, this cave is also formed in the Austin Chalk directly below the Pecan Gap. Robber Baron would be unknown if not for the collapse of its entrance through the Pecan Gap, and The Labyrinth would be unknown if it were not exposed in the wall of a currently inactive quarry. The Labyrinth is located within the northeast corner of the Alamo Heights KFR and approximately midway between Robber Baron Cave and Green Mountain Road Cave. Given the absence of biological data from The Labyrinth, it cannot be said with certainty that *Cicurina baronia* or other species known from the Alamo Heights KFR occur there, but this cave does represent the most likely known path for the distribution of *Cicurina baronia* under the Pecan Gap to Green Mountain Road Cave and demonstrates that extensive cave development under the Pecan Gap is not unique to Robber Baron Cave.

Based on this new information, the northern portion of the Alamo Heights KFR is expanded to include Green Mountain Road Cave through the following boundary changes:

1. The eastern edge of the KFR is extended 6.25 km, along the fault with the mean trend of 40 degrees which delimits the east side of the KFR and the Alamo Heights horst. It ends at the intersection with the south side of the Green Mountain Road Cave fault block (covered by alluvium at that intersection but obvious to interpolate by extending the two fault trends 300 and 700 m).
2. The KFR boundary follows the fault on south side of Green Mountain Road Cave fault block about 2 km to where the Austin Chalk is exposed, then turns along the contact of the Austin Chalk 1.5 km northwest to a fault boundary with the Buda Limestone. The KFR boundary then extends along that fault 3.7 km down its mean trend of 234 degrees back to the fault on the south side of the Green Mountain Road Cave fault block. This location is 2.9 km west of Green Mountain Road Cave, close to the modeled 3-km range of *Cicurina baronia* at that cave and only 100 m and 1.3 km east of the modeled ranges of *Cicurina platypus-puentecilla* and *Cicurina bullis-neovespera*, respectively (Figure 5).
3. Barnes (1983) does not show any fault extending south from this location. Not having other geologic features for guidance, the KFR boundary is extended 11.8 km along a 223-degree trend to the north end of the west 25-degree trending fault of the Alamo Height horst and KFR. This section of the boundary approximately follows an unnamed tributary to Salado Creek and two small faults near the horst.

While this study and earlier analyses (GVA 1994, GVA 2003; Veni and Martinez, 2007) of KFR boundaries found that faults are not barriers or significant restrictions to terrestrial invertebrate troglobite distribution unless juxtaposing cavernous and non-cavernous rock, they provide the only known guidance for these new boundaries until more information is available.

Karst Zone Revision

Figure 15 illustrates the karst zones as defined by GVA (2003). The following analysis focuses on the distribution of Zone 1, which has increased in size from that work (GVA 2003) based on new endangered species localities. Consequently, Zone 2, where there was a high probability for endangered species but not known until this revision, has reduced in size. Zone 4 of GVA (2003) is eliminated because geologic mapping which had not been conducted at that time is now available. Zone 5 of GVA (2003) is now classified as Zone 4 as of this report. Zones 3 and 4 are expanded substantially beyond the limits of GVA (2003) because the study area for this investigation was expanded. As described earlier in this report, Zones 3 and 4 are now divided into two sub-zones each based on their potential for endangered karst invertebrate species due to biological factors (other species occupy those ecological niches) or geological factors (the rock is poorly cavernous or non-cavernous).

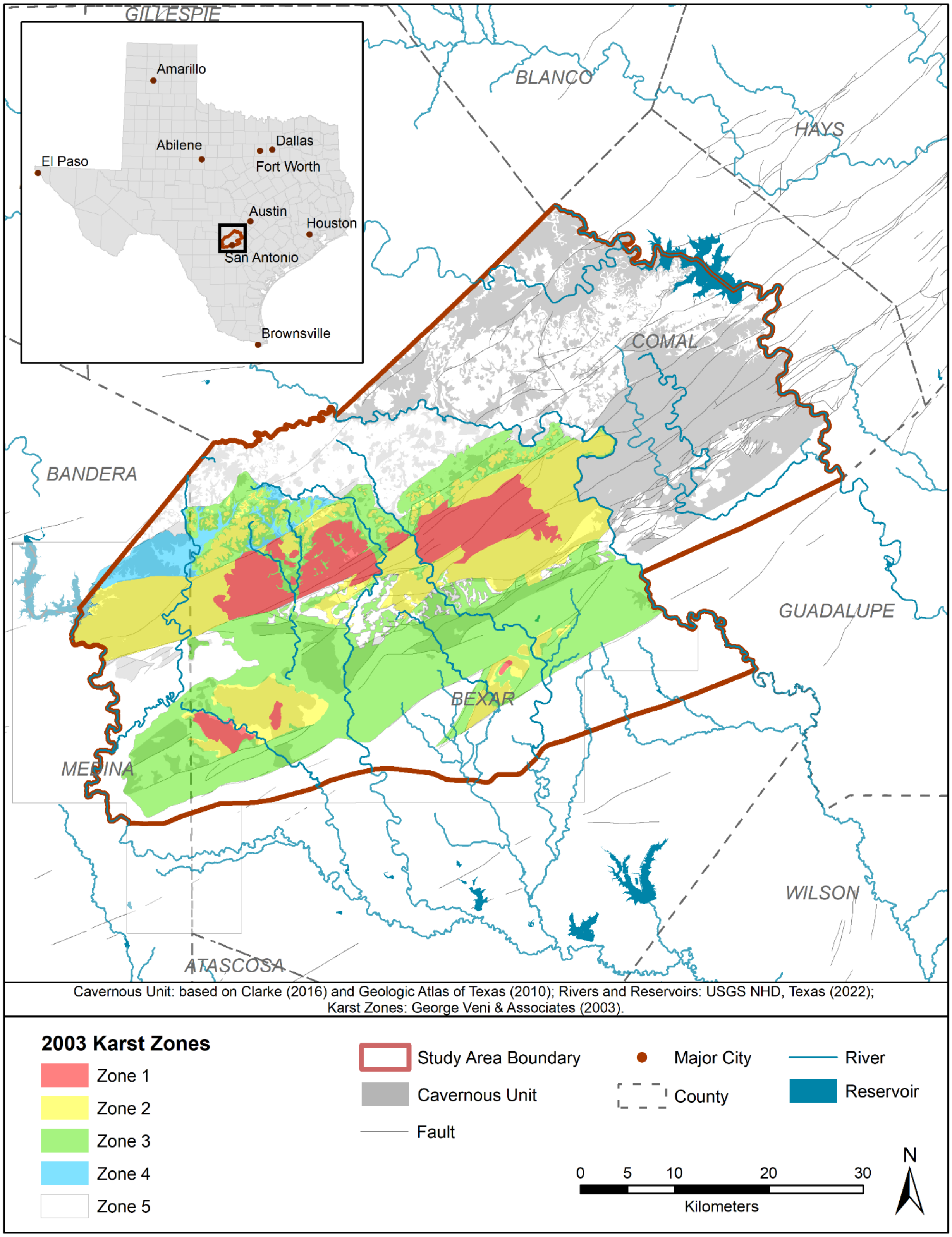

Figure 15. Previously defined Karst Zone boundaries in the San Antonio Area (George Veni & Associates, 2003).

Additional informal KFRs, which are not part of the KFR boundary analysis in the previous section, are presented here only as a mechanism to describe those areas which constrain the distribution of the endangered invertebrate species beyond the formal KFRs evaluated above. Further, the mapped boundaries of two informal KFRs (Central Medina and Interstate Highway 35) extend beyond the defined study area in order to capture the known extent of karst features and geologic units known to support karst feature formation in those regions. Fully analyzing, describing, and/or defining these "informal KFR" areas exceeds the scope of this report.

It is also beyond the scope of this report to describe the methodology and rationale for each specific karst zone boundary in detail. However, a general description of and explanation for the zone boundaries follows below, described southwest-to-northeast by KFR (both formal and informal) in three stratigraphic south-to-north tiers:

- Austin Chalk-Pecan Gap: Culebra Anticline (formal), Central San Antonio (informal), Alamo Heights (formal), and Interstate Highway 35 (informal).
- Edwards Limestone: Central Medina (informal), Government Canyon (formal), UTSA (formal), Stone Oak (formal), New Braunfels (informal).
- Glen Rose Limestone: Northern Bexar (informal), Western Comal (informal).

The conclusions section of this report provides summary descriptions and a map of all karst zones based on the following assessments. The additional informal KFR boundaries, as approximated and described below, are also displayed in the KFR map in the conclusions section, along with the formal KFR boundaries as described in the previous section.

Culebra Anticline Karst Fauna Region

The boundaries of this KFR are defined earlier in this report. Five endangered species and subspecies are known:

1. *Cicurina madla* (Figure 5),
2. *Cicurina vespera* (Figure 5),
3. *Rhadine exilis* (Figure 7),
4. *Rhadine infernalis* n. ssp. (Figure 6), and
5. *Tayshaneta microps* (Figure 11).

Their distribution ranges extend widely throughout the central portion of the KFR where the UAC is exposed, and their modeled ranges fill those areas except for three small areas along the distal margins ranging from 180-670 m wide and where no apparent restrictions to distribution are known. Given these results, all of the UAC within the modeled ranges is classified as Zone 1. The outcrops of the UAC outside of the modeled ranges are classified as Zone 2 because they are potential habitat with few or no known studies for caves in those areas.

Outcrops of the LAC, Pecan Gap Chalk, and Anacacho Limestone are classified as Zone 3b. The Anacacho Limestone is poorly studied for caves and karst features. It is Cretaceous in age, like all other rocks in the study area, and up to about 150 m thick and occurs in several outcrops up to 140 km west of the Medina River. Most recently described by Swezey and Sullivan

(2004), it includes chalk and marl units which likely explain why no caves are known in the rock, except possibly for an unconfirmed cave marked on the USGS topographic map west of Uvalde.

Central San Antonio Karst Fauna Region

No endangered karst invertebrate species are documented from this informal KFR. It was included in this study to constrain the distribution of the endangered karst species. It is informally designated as the outcrops of the Austin Chalk, Pecan Gap Chalk, and overlying alluvial deposits east of Culebra Creek for 26 km to the Alamo Heights KFR. A small section of this informal KFR extends west of the creek to include the Austin and Pecan Gap outcrops and associated alluvium directly south of the Government Canyon KFR. The Central San Antonio KFR is bounded to the north by faults which mark the southern boundary of the Government Canyon, UTSA, and Stone Oak KFRs, and to the south by faults that mark the southern limit of the Austin and Pecan Gap in that area and extrapolated along fault trends where covered by alluvium.

Several small caves are known in this KFR. Most are sealed by urbanization and unstudied. Terrestrial invertebrate troglobites are not known from any of the caves due to insufficient study or inadequate habitat conditions, where known, such as the caves being too small or flooding periodically. No modeled ranges of the endangered species extend into this KFR; however, the modeled ranges of *Speodesmus reddelli* and *Tayshaneta whitei* extend into the westernmost outcrop of the UAC and the modeled ranges of *Cicurina bullis-neovespera*, *Cicurina platypus-puentecilla*, *Speodesmus ivyi*, and *Tartarocreagris reyesi* extend into the UAC east of Interstate Highway 10 (Figure 13). Given this high modeled potential distribution of troglobites into the KFR, where the modeled ranges extend into portions of the UAC, that section of the cavernous unit is classified as Zone 2. Areas of the UAC that do not include any of the modeled ranges have few and poorly studied caves and are classified as Zone 3a until more information is available. The remaining areas are classified as Zone 3b.

Alamo Heights Karst Fauna Region

The boundaries of this KFR are defined earlier in this report. Two endangered species are known:

1. *Cicurina baronia* (Figure 5), and
2. *Texella cokendolpheri* (Figure 12).

Their distribution in three caves and modeled ranges span the north and south ends of the KFR. The ranges do not include the north-of-central portion of the KFR due to the discontinuous nature of the cavernous unit. Given these results, all of the KFR within the modeled ranges is classified as Zone 1. Based on the known development of extensive Austin Chalk caves below the Pecan Gap in this KFR, all remaining portions of the KFR mapped as outcrops of the Pecan Gap are classified as Zone 2 and areas covered by alluvium along Salado Creek and its tributaries are classified as Zone 3b due to poorer habitat conditions.

Interstate Highway 35 Karst Fauna Region

No endangered karst invertebrate species are documented from this informal KFR. It was included in this study to constrain the distribution of the endangered karst species. It is informally designated as the outcrops of the Austin Chalk (and a sliver of adjacent Edwards

Limestone in the Bracken [town, not cave] area), Pecan Gap Chalk, and overlying alluvial deposits northeast of the Alamo Heights KFR for 27 km to the Guadalupe River. The Interstate Highway 35 KFR is bounded to the north by faults which mark the southern boundary of the Stone Oak KFR and informal New Braunfels KFR (described below), and to the south by faults that mark the southern limit of the Austin and Pecan Gap in that area and extrapolated along fault trends where covered by alluvium.

Ten caves are known in this informal KFR. Nine are formed in the Austin Chalk. Seven occur within a 130-m long section of cliffs along Cibolo Creek as paleosprings, draining nearby upland recharge down the steep hydraulic gradient to the creek. One is the only cave known as formed entirely in the Pecan Gap Chalk and not through it into the underlying Austin Chalk. None of these caves have conditions that seem likely to provide habitat to the endangered species. An estimated 120 m away, in Bexar County, is Schertz-Cibolo Cave. Long covered by urbanization, this biologically unstudied cave has 467 m of mapped maze passages that are almost certainly formed in the Austin Chalk, which would be a third example of extensive cave development below the Pecan Gap. The entrances of the two remaining caves are entirely in the Austin Chalk, about 4 and 6 km to the north, and biologically unstudied. One floods violently and is poorly explored, often blocked by flood debris. The other has 66 m of maze passages.

Terrestrial invertebrate troglobites are not known from any of the caves in this informal KFR due to insufficient study. Appropriate habitat conditions likely exist in the two longest caves. None of the modeled ranges for the endangered species or non-listed terrestrial invertebrate troglobites extend into this informal KFR due to its discontinuities in the cavernous unit. Given this proven continuation of extensive cave development below the Pecan Gap west of Cibolo Creek, the outcrops of the Austin Chalk and Pecan Gap (and a small possible upland terrace deposit shown by Barnes 1983) west of the creek are classified as Zone 2 and areas covered by alluvium along Cibolo and Salado creeks and their tributaries are classified as Zone 3b due to poorer habitat conditions. East of Cibolo Creek, which is a likely restriction to terrestrial invertebrate troglobite distribution, the outcrop of the Austin Chalk is classified as Zone 3a (although this needs to be confirmed by biological collections) and the rest of the area is classified as Zone 3b.

Central Medina Karst Fauna Region

No endangered karst invertebrate species are documented from this informal KFR. It was included in this study to constrain the distribution of the endangered karst species. It is informally designated as the outcrops of the Edwards Limestone and stratigraphically equivalent Devils River Limestone from the Medina River west 27 km to Hondo Creek. The Central Medina KFR is bounded to the north and south by limits of the Edwards and Devils River limestones, which occur mostly along faults, and where removed by erosion to the north and covered by younger rocks and alluvium to the south.

Twenty caves are known in this informal KFR but only two have seen biological study. Reddell (personal communication, 2021) found no caves in his database for this informal KFR or the vicinity farther west with advanced terrestrial invertebrate troglobites, like the 35 modeled in this study, whose species occur east of the Medina River. Conversely, the modeled ranges for the endangered species do not extend west of the Medina River and while *Speodesmus* *reddelli* occurs within 3 km of the river and *Tayshaneta whitei* within 150 m of the river, there is currently no evidence that either occurs west of the river. Given this information, the Central Medina KFR is potentially Zone 4a but is classified as Zone 3a until it receives additional biological studies.

Government Canyon Karst Fauna Region

The boundaries of this KFR are defined earlier in this report. Six endangered species are known:

1. *Batrisodes venyivi* (Figure 4),
2. *Cicurina madla* (Figure 5),
3. *Cicurina vespera* (Figure 5),
4. *Rhadine exilis* (Figure 7),
5. *Rhadine infernalis infernalis* (Figure 6), and
6. *Tayshaneta microps* (Figure 11).

As a group, they are well distributed throughout the eastern third of the Government Canyon KFR and their modeled ranges extend west to within 500-2,400 m of San Geronimo Creek and north to within 900-2,700 m of the KFR's northern boundary. The non-listed *Texella tuberculata* also extends as close as 500 m of San Geronimo Creek while the ranges of *Speodesmus reddelli* and *Tayshaneta whitei* reach west to the Medina River. These three non-listed species also range through much of the area on the north side of the KFR beyond the modeled range of the endangered species (Figure 13).

The areas west and north of the endangered species' ranges are not well explored for caves. Twenty are known and most have not been biologically studied. Several seem likely to contain biologically appropriate habitat based on their descriptions. In consideration of the above information, the cavernous unit of the Government Canyon KFR is classified as Zone 1 to the limits of the endangered species' modeled ranges; the remaining portions of the cavernous unit it are classified as Zone 2. Areas of non-cavernous rock surrounded by the KFR, or surrounded in combination with an adjacent KFR, are classified as Zone 4b.

Helotes Karst Fauna Region

The boundaries of this KFR are defined earlier in this report. Four endangered species are known:

1. *Batrisodes venyivi* (Figure 4),
2. *Cicurina madla* (Figure 5),
3. *Rhadine exilis* (Figure 7), and
4. *Rhadine infernalis infernalis* (Figure 6).

As a group, they are distributed throughout the southern two-thirds of the Helotes KFR and their modeled ranges extend to within 2.4 km of the KFR's northern boundary. The non-listed *Speodesmus reddelli*, *Tayshaneta madla*, and *Texella tuberculata* also occur in the KFR and their ranges come within 250 m of the KFR's northern edge. The modeled ranges of *Speodesmus ivyi*, *Tartarocreagris amblyopa*, *Tartarocreagris reyesi*, and *Texella youngensis* extend into the Helotes KFR but the species have not yet been found there; therefore, any implications of their ranges should be considered cautiously.

The area north of the endangered species' ranges has not been explored for caves and none are known at the time of this study. Considering the presence of caves in the same hydrogeologic situation nearby with proven or likely terrestrial invertebrate troglobite habitat, such caves are likely to occur in that section of the Helotes KFR. Based on the above information, the cavernous unit of the Helotes KFR is classified as Zone 1 to the limits of the endangered species' modeled ranges; the remaining portions of the cavernous unit are classified as Zone 2. Areas of non-cavernous rock surrounded by the KFR, or surrounded in combination with an adjacent KFR, are classified as Zone 4b.

UTSA Karst Fauna Region

The boundaries of this KFR are defined earlier in this report. Four endangered species are known:

1. *Batrisodes venyivi* (Figure 4),
2. *Cicurina madla* (Figure 5),
3. *Rhadine exilis* (Figure 7), and
4. *Rhadine infernalis infernalis* (Figure 6).

As a group, they are distributed throughout the southern two-thirds of the UTSA KFR and their modeled ranges extend to within 1.7 km of the KFR's northeast boundary. The non-listed *Cicurina bullis-neovespera*, *Speodesmus reddelli*, *Tartarocreagris reyesi*, *Tayshaneta madla*, and *Texella youngensis* also occur in the KFR and their ranges extend throughout the KFR.

The area in the northeast corner of the endangered species' ranges has not been explored for caves and none are known at the time of this study. Considering the presence of caves in the same hydrogeologic situation nearby with proven or likely terrestrial invertebrate troglobite habitat, such caves are likely to occur in that section of the UTSA KFR. Based on the above information, the cavernous unit of the UTSA KFR is classified as Zone 1 to the limits of the endangered species' modeled ranges and the remaining portions of the cavernous unit are classified as Zone 2. The areas of the Georgetown Formation, Del Rio Clay, and Buda Limestone that overlay the cavernous unit in the KFR's southwest corner are classified as Zone 3b. Areas of non-cavernous rock surrounded by the KFR are classified as Zone 4b.

The one exception to the above Zone 3b classification is near the southern boundary of the KFR where Feature 1604-083-02 is located below the Del Rio Clay near a fault. The fault extends west to an isolated outcrop of Edwards Limestone and east to a smaller isolated Edwards outcrop, then about 300 m further east to the main contiguous Edwards outcrop. Fractures associated with this fault likely resulted in cave and conduit development that allow *Cicurina madla* to occur in this area. Therefore, the two isolated Edwards outcrops are connected along the fault to the main Edwards outcrop by a Zone 1 area that extends 100 m from each side of the fault.

Stone Oak Karst Fauna Region

The boundaries of this KFR are defined earlier in this report. Four endangered species are known:

1. *Cicurina madla* (Figure 5),
2. *Rhadine exilis* (Figure 7),

3. *Rhadine infernalis ewersi* (Figure 6), and
4. *Rhadine infernalis infernalis* (Figure 6).

As a group, they are distributed mostly throughout the northern portion of the western two-thirds of the Stone Oak KFR. More specifically, they are all within the Kainer Formation of the Edwards Limestone Group (with some extending through the Kainer down into the Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose Limestone). This distribution reflects an access bias. When focused biological study began in this KFR, most of the Edwards Limestone's Person Formation was covered by urban development and caves in the remaining area were not available for study. The Person Formation is also significantly less exposed in the study area, but it has caves with endangered species only 400-1,100 m west of Leon Creek in the UTSA KFR, and potentially in the Stone Oak KFR if the tentative occurrences in Black Cat Cave and Encino Park Cave are confirmed in the future.

The modeled ranges of the endangered species extend as much as 2.5 km south and southeast into the Person Formation, and east to within 3.9 km of the KFR boundary at Cibolo Creek. The non-listed *Cicurina bullis-neovespera*, *Cicurina platypus-puentecilla*, *Speodesmus ivyi*, and *Tartarocreagris reyesi*, also occur in the KFR and two of their ranges extend throughout the KFR (Figure 13).

Thirty-seven caves are known between Cibolo Creek and the modeled range of the caves with endangered species. Many of those caves have not been studied biologically. A notable group of deep, extensive, and biologically unstudied caves for the area, which collectively represent a significant gap in the understanding of terrestrial invertebrate troglobite biogeography in the Stone Oak KFR, include Baling Wire Cave, Corkscrew Cave, Looserock Cave, Poison Ivy Pit, Tobacco Can Hole, and Whistledrop, all described by Veni (1988).

Based on the above information, the cavernous unit of the Stone Oak KFR is classified as Zone 1 to the limits of the endangered species' modeled ranges and the remaining portions of the cavernous unit are classified as Zone 2. Areas of non-cavernous rock surrounded by the KFR are classified as Zone 4b.

New Braunfels Karst Fauna Region

No endangered karst invertebrate species are documented from this informal KFR. It was included in this study to constrain the distribution of the endangered karst species. It is informally designated as the contiguous outcrops of the Edwards Limestone and Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose Limestone between Cibolo Creek and the Guadalupe River, 23 km to the northeast. Also included are small, adjacent, sections of Austin Chalk in the faulted area about 8 km north of Interstate Highway 35. From the southeast along the Comal Springs Fault, where the Edwards Limestone is in contact with the Pecan Gap Chalk, the New Braunfels KFR extends 15-18 km northwest to the Hidden Valley and associated faults. They can be traced in the study area from the Canyon Lake Gorge spillway 21 km southwest into the northeast corner of Bexar County.

None of the modeled ranges for the listed species extend into this informal KFR but *Speodesmus ivyi* is present and extends about 18 km northeast into the New Braunfels KFR from the Stone Oak KFR. Other species known from this informal KFR are *Rhadine specum gentilis* (Figure 7), which is endemic to this KFR, and *Rhadine specum crinicollis* (Figure 7), which is only known from Natural Bridge Caverns and a cave about 9 km to the northwest in the Western Comal KFR (informal KFR, described below). While about 70 caves are known in the New Braunfels KFR, few have been biologically investigated; however, based on data currently available in this region, the cavernous unit in this KFR is classified as Zone 3a. Areas of non-cavernous rock surrounded by the KFR are classified as Zone 4b.

Northern Bexar Karst Fauna Region

No endangered karst invertebrate species are documented from this informal KFR. It was included in this study to constrain the distribution of the endangered karst species. It is informally designated as the narrow outcrops of the cavernous unit extending north from the northern boundaries of the Government Canyon, Helotes, UTSA, and Stone Oak KFRs. It includes isolated sections of the cavernous unit between those KFRs and the Northern Bexar KFR's boundary along Balcones and Cibolo Creeks 2-7 km to the north. Its western boundary extends as much as 4 km into Medina County to the Bandera County line where detailed geologic mapping ends.

Along the southern margin of the Northern Bexar KFR, the cavernous unit is predominantly the Edwards Limestone and Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose Limestone. Farther north, the Upper Fossiliferous Hydrostratigraphic Unit is more common; at lower elevations near Balcones and Cibolo creeks, the Little Blanco, Doeppenschmidt, and Rust hydrostratigraphic units of the Lower Member of the Glen Rose crop out. Given the abundance of varied and relatively small sections of cavernous rock, often isolated by faulting and topography, there is high potential for speciation. Additionally, the degree of cave development varies significantly within some units. For example, about 6 km east of this KFR, the Cavernous Hydrostratigraphic Unit produces Natural Bridge Caverns, the largest cave by volume in Texas. Yet, along Balcones Creek and north into Kendall County, that unit is not cavernous. A more detailed study of this KFR will likely subdivide it, as done by Veni and Reddell (1999) for Camp Bullis.

Camp Bullis is the most studied section in the Northern Bexar KFR. All localities in this KFR for the species evaluated by this study occur on Camp Bullis and are in three of the six areas identified by Veni and Reddell (1999) as potential KFRs (with minor changes due to changes in geologic mapping):

1. <u>Edwards Outlier KFR</u>: This is a series of hills capped with Edwards Limestone and the Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose Limestone along the southwest boundary of the military installation. It contains the only known locality of *Rhadine ivyi* (Figure 7).
2. <u>Upper Glen Rose Biostrome KFR</u>: Seven major outcrops of a biostrome, now known as the Upper Fossiliferous Hydrostratigraphic Unit, were delineated as one KFR should they biologically connect where the unit does not appear at the surface. The results of this study suggest they may be divided into at least two KFRs. *Rhadine sprousei* (Figure 7) is known only from one cave in this unit in Lewis Valley in the central part of Camp Bullis. *Batrisodes excavodes shadeae* (Figure 4) and *Rhadine bullis* (Figure 7) are known only from eight caves in the Upper Fossiliferous in the Meusebach Creek area of northeast Camp Bullis. Additionally, *Speodesmus ivyi* (Figure 8) is known from one of the caves and *Cicurina bullis-neovespera* (Figure 5) is known from a ninth cave. These two additional species occur primarily in the Stone Oak KFR and their presence indicates a

recently developed gap between the Upper Fossiliferous and the cavernous unit extending from Stone Oak.

3. Cibolo Creek KFR: Described as the outcrop of the Lower Member of the Glen Rose Limestone along Cibolo Creek (now mapped in that area as five hydrostratigraphic units) along the north boundary of Camp Bullis, these units contain one species. *Rhadine specum* (Figure 7) is known from three caves south of Cibolo Creek in the Northern Bexar KFR and four caves north of the creek in the Western Comal KFR, suggesting no restriction to terrestrial invertebrate troglobite distribution along this section of the Northern Bexar-Western Comal boundary.

Based on these findings, the cavernous unit of the Northern Bexar KFR is classified as Zone 3a, with intervening non-cavernous areas classified as Zone 4b.

Western Comal Karst Fauna Region

No endangered karst invertebrate species are documented from this informal KFR. It was included in this study to constrain the distribution of the endangered karst species. It is similar to the Northern Bexar KFR and informally designated as the narrow outcrops of the cavernous unit extending west from New Braunfels to the Kendall County line where detailed geologic mapping ends. The southern boundary of the Western Comal KFR is the Northern Bexar KFR along Cibolo Creek. Its northern boundary follows the Guadalupe River northwest about 20 km to Rebecca Creek, then follows the creek 5 km to the county line to include one of the species sites included in the Appendix.

Along the eastern margin of the Western Comal KFR, the cavernous unit is predominantly the Edwards Limestone and Cavernous Hydrostratigraphic Unit of the Upper Member of the Glen Rose Limestone. The Upper Fossiliferous Hydrostratigraphic Unit occurs to the southwest along Cibolo Creek, and at lower elevations near Cibolo Creek and along the Guadalupe River, the Little Blanco, Doeppenschmidt, Rust, and Honey Creek hydrostratigraphic units of the Lower Member of the Glen Rose crop out. Given the abundance of varied and relatively small sections of cavernous rock, often isolated by faulting and topography, there is high potential for speciation, especially in the Upper Glen Rose. Additionally, the degree of cave development varies significantly within some units. For example, the Upper Fossiliferous Hydrostratigraphic Unit has several caves within 8 km of US Highway 281 and Cibolo Creek but thins and has no caves 14 km to the north in the Guadalupe River watershed.

Four species occur in the Western Comal KFR:

1. *Rhadine specum* (Figure 7) was described in the previous section as occurring along both sides of Cibolo Creek, in both the Northern Bexar and Western Comal KFRs.
2. *Rhadine specum specum* (Figure 7) is at the north end of the same outcrop of the cavernous unit as *Rhadine specum*, with the nearest localities of the two different subspecies about 1.4 km apart.
3. *Rhadine specum crinicollis* (Figure 7) is found 21 km east of *Rhadine specum specum* in what is mapped as an isolated portion of the cavernous unit comprised of the Little Blanco Hydrostratigraphic Unit of the Lower Member of the Glen Rose Limestone. However, this species occurs in the Cavernous Hydrostratigraphic Unit of the Upper Glen Rose in Natural Bridge Caverns 9 km to the southeast, which indicates the units connect in the subsurface across a fault.

4. *Rhadine reclusa* (not included in the 35 species analyzed in this effort) occurs17.5 km north of the Little Blanco locality for *Rhadine specum crinicollis* (Figure 7). As a distinctive species, instead of subspecies of *Rhadine specum*, it suggests the Guadalupe River is a barrier to terrestrial invertebrate troglobite distribution.

Based on these findings, the cavernous unit of the Western Comal KFR is classified as Zone 4a, with intervening non-cavernous areas classified as Zone 4b.

Conclusions

Formal Karst Fauna Regions

The GIS analysis of karst invertebrate species distribution across the varied hydrogeological landscape of the study area proves a useful tool to objectively quantify the potential presence of KFR boundaries, especially with the substantial limits on available data and types of data for the distribution model. The results of this study support the initial hypothesis from 1994, used conceptually to define Karst Zone 2, that if cavernous rock is present and appropriate habitat conditions exist, then its caves will likely contain terrestrial invertebrate troglobitic species. KFR boundaries occur where cavernous rock is absent, thin and/or narrow, and filled at least periodically with water. Faults create restrictions and barriers only where they juxtapose cavernous and non-cavernous rock. While some faults and other geologic factors may have local effects on karst invertebrate species distribution, no effects are seen within the KFRs.

Most of the KFR boundaries are restrictions, not barriers, to karst invertebrate species distribution. Some boundaries may not have restricted species in the past, as indicated by certain species occurring on each side of a boundary, but the boundaries are based on current conditions which dictate management needs. Whether or not endangered karst invertebrate species are present in an area also depends on biogeographical factors beyond the scope of this investigation to assess, such as competition with other species and microclimatic conditions.

Figure 16 illustrates the KFRs of the study area as defined or redefined by this study, including the informally designated KFRs. The extents of the Central Medina and IH 35 informal KFRs are mapped outside of the study area based on the understood limits of geological boundaries; however they were not evaluated in sufficient detail to include them within the boundaries of the study area, which was designed to contain the range limitations of listed species. The most significant difference between Figure 16 and the highly generalized 1994 boundaries of Figure 14 is that the new boundaries are as precise as possible. Following the GVA (2003) karst zone update and initial conversion into GIS, USFWS schematically illustrated the KFRs in various mapping applications, including areas now recognized as non-cavernous on the chance that terrestrial invertebrate troglobites might be found with further study. Following 28 years of additional study by many researchers, the KFR boundaries now follow the edge of the cavernous unit to the precision limits of the mapping scale.

Following are summary descriptions of the boundaries of the six formal and previously designated KFRs which contain endangered karst invertebrate species. The six additional informally defined KFRs in the karst zone analysis of this report are not included below because their boundaries are only approximated.

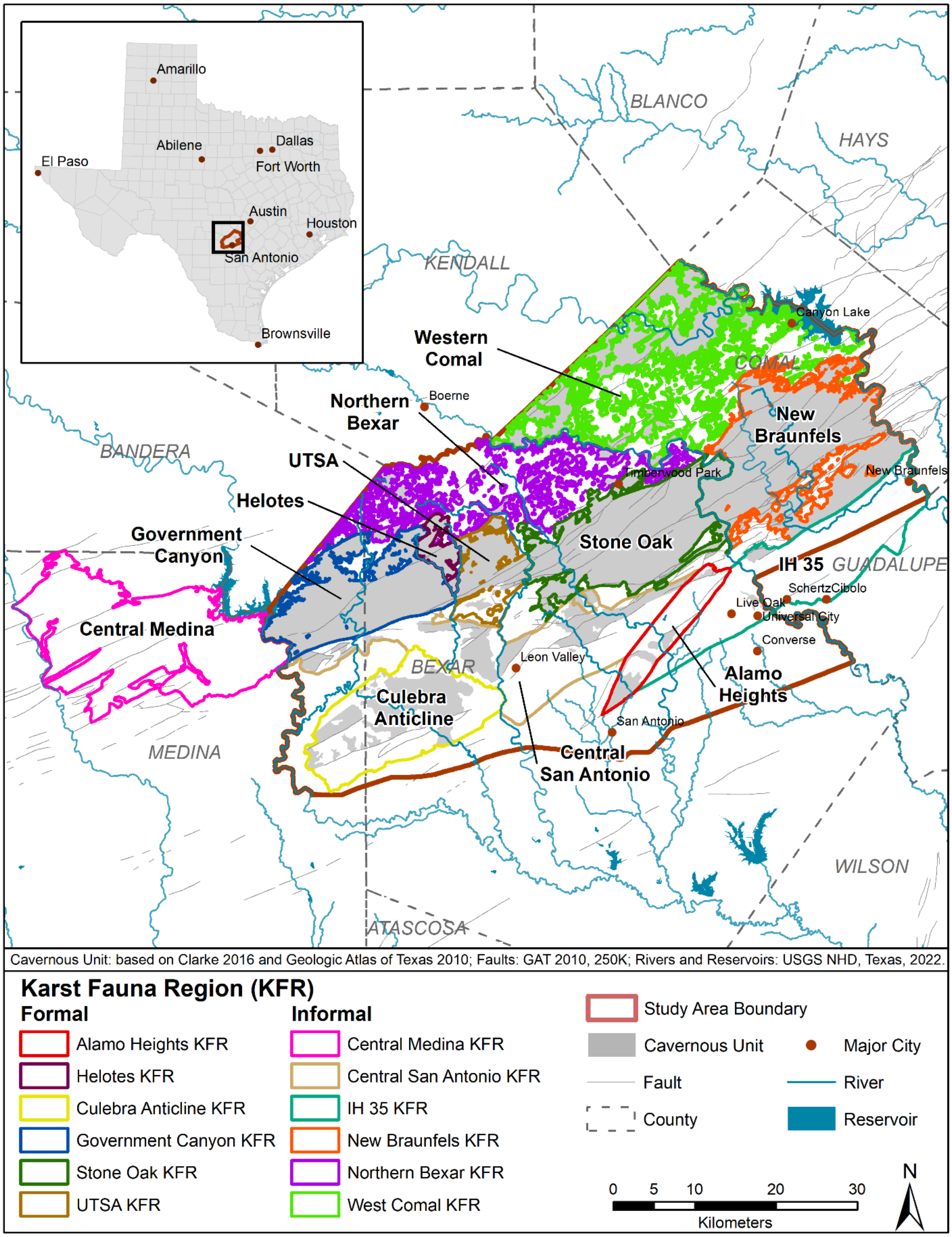

Figure 16. Formal and informal San Antonio Area Karst Fauna Region (KFR) boundaries identified through GIS analysis of geology and karst invertebrate species distribution as understood in 2023.

Culebra Anticline Karst Fauna Region

Bounded to the northeast by Culebra Creek, the Culebra Anticline KFR's other boundaries are delineated by the edges of the cavernous unit along erosional contacts, predominantly to the north and west, and faults predominantly to the south. Five endangered karst invertebrates are known to occur in this KFR: *Cicurina madla*, *Cicurina vespera*, *Rhadine exilis*, *Rhadine infernalis* n. ssp., and *Tayshaneta microps*.

Government Canyon Karst Fauna Region

The Government Canyon KFR is bounded by faults to the south, the Medina River to the west, and faults and erosional contacts with non-cavernous units to north and east, and predominately Los Reyes and Helotes creeks to the east. Six endangered karst invertebrates occur in this KFR: *Batrisodes venyivi*, *Cicurina madla*, *Cicurina vespera*, *Rhadine exilis*, *Rhadine infernalis infernalis*, and *Tayshaneta microps*.

Helotes Karst Fauna Region

A roughly triangular area, the Helotes KFR is bounded to the west by Los Reyes Creek, to the east by Helotes Creek, and the predominantly eroded limit of the cavernous unit to the north. Four endangered karst invertebrates occur in this KFR: *Batrisodes venyivi*, *Cicurina madla*, *Rhadine exilis*, and *Rhadine infernalis infernalis*.

UTSA Karst Fauna Region

The UTSA KFR is bounded by Helotes Creek on the west, Leon Creek 8 km to the east, major faults marking the limits of the cavernous unit to the south, and the predominantly eroded limit of the cavernous unit to the north. Four endangered karst invertebrates occur in this KFR: *Batrisodes venyivi*, *Cicurina madla*, *Rhadine exilis*, and *Rhadine infernalis infernalis*.

Stone Oak Karst Fauna Region

Leon Creek and Cibolo Creek mark the respective west and east limits of the Stone Oak KFR. Contacts of the cavernous unit along faults or where covered by younger rocks delimits the KFR to the south. The northern boundary is the eroded and faulted limit of the cavernous unit. Four endangered karst invertebrates occur in this KFR: *Cicurina madla*, *Rhadine exilis*, *Rhadine infernalis ewersi, and Rhadine infernalis infernalis*.

Alamo Heights Karst Fauna Region

The Alamo Heights KFR is the outcrop of Austin Chalk and Pecan Gap Chalk bounded within the horst beginning near San Pedro Park and extending north to an east-west Austin Chalk fault block along Loop 1604. Two endangered karst invertebrates occur in this KFR: *Cicurina baronia* and *Texella cokendolpheri*.

Karst Zones

Karst zones defined in GVA (2003) were redefined from the five previous zones. This report adds two subzones for Zone 3 and the new Zone 4 to better identify their biological status and manage their ecosystems. Updates to the karst zones are summarized in Table 2. Terrestrial troglobite distribution modeling, especially for the endangered species, proved a valuable tool in revising the karst zones, along with the incorporation of new species localities, the improvement of cave location precisions, and other associated updates and location information.

Figure 17 illustrates new karst zones following the results of this investigation. It includes zone determinations for the informally designated KFRs, including those informal KFRs whose boundaries extend beyond the defined study area, to constrain and describe the likely distribution of the endangered karst species. Table 2 summarizes the notable karst zone changes below, with a primary focus on the formal and previously designated KFRs which contain endangered karst invertebrate species:

Karst Zone 1

Karst Zone 1 was expanded in the Culebra Anticline, Government Canyon, Helotes, UTSA, and Stone Oak KFRs. Karst Zone 1 was only expanded in the newly added section of the Alamo Heights KFR.

Karst Zone 2

Karst Zone 2 was reduced proportionally to the enlarged Zone 1 areas and changes in the KFR boundaries.

Karst Zone 3a

Karst Zone 3a was established for the Edwards Limestone and the Cavernous Hydrostratigraphic Unit in the Central Medina and New Braunfels KFRs and in the hydrostratigraphic units below the Cavernous Hydrostratigraphic Unit in the Northern Bexar KFR.

Karst Zone 3b

Karst Zone 3b was established for various lithologies in the Central San Antonio, Alamo Heights, and Interstate Highway 35 KFRs.

Karst Zone 4a

Karst Zone 4a was established for the Western Comal KFR.

Karst Zone 4b

Karst Zone 4b was established for the non-cavernous rocks in the Government Canyon, Helotes, North Bexar, Stone Oak, UTSA, and Western Comal KFRs.

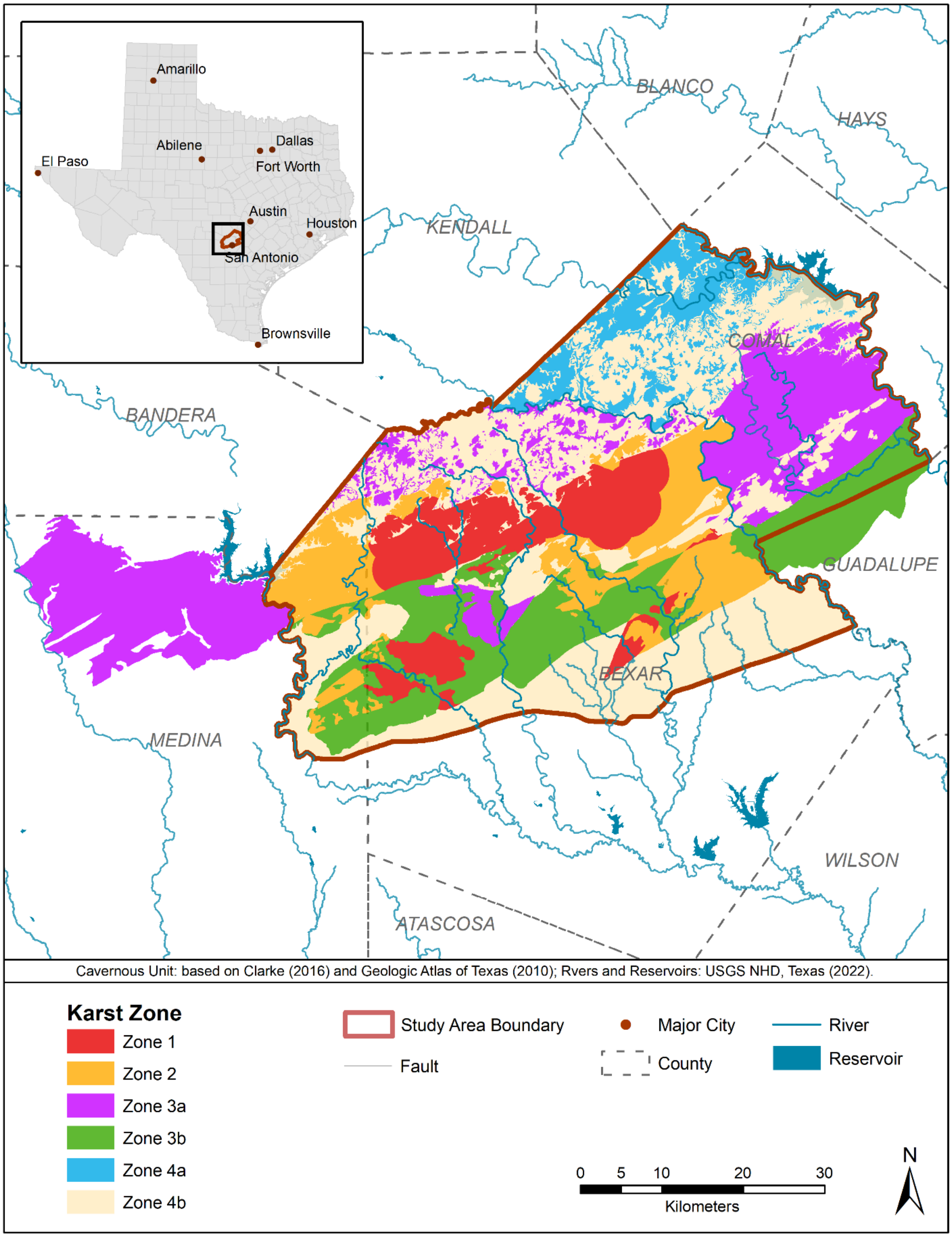

Figure 17. Karst Zone boundaries as defined by this report's analysis.

Table 2. Summary of karst zone revisions as a result of this study.

<table>
<tr><th>2003 Karst Zone Definition</th><th>Revision</th><th>2023 Revised Karst Zone Definition</th></tr>
<tr><td>Zone 1: Areas known to contain endangered terrestrial karst invertebrates.</td><td>Revised boundaries to reflect new localities and species range knowledge.</td><td>Zone 1: Areas known to contain endangered terrestrial karst invertebrates.</td></tr>
<tr><td>Zone 2: Areas having a high probability of suitable habitat for endangered or other endemic terrestrial karst invertebrates invertebrates.</td><td>Revised boundaries to reflect data findings.</td><td>Zone 2: Areas having a high probability of suitable habitat for endangered or other endemic terrestrial karst invertebrates.</td></tr>
<tr><td rowspan="2">Zone 3: Areas that probably do not contain endangered terrestrial karst invertebrates.</td><td rowspan="2">Refined into two zone distinctions.</td><td>Zone 3a: Areas suitable for terrestrial karst invertebrates but which have a low probability of containing endangered species because the habitat is occupied by other terrestrial karst invertebrates species.</td></tr>
<tr><td>Zone 3b: Areas which have a low probability of containing endangered species because they are poorly suited for terrestrial karst invertebrates.</td></tr>
<tr><td>Zone 4. Areas which require further research but are generally equivalent to Zone 3, although they may include sections which could be classified as Zone 2 or Zone 5 as more information becomes available.</td><td>Eliminated due to a better understanding derived from geological mapping.</td><td></td></tr>
<tr><td rowspan="2">Zone 5: Areas which do not contain endangered terrestrial karst invertebrates.</td><td rowspan="2">Renamed Zone 4 and refined into two sub-zones.</td><td>Zone 4a: Areas suitable for terrestrial karst invertebrates species but which do not contain endangered species because the habitat is occupied by other terrestrial karst invertebrates.</td></tr>
<tr><td>Zone 4b: Areas which do not contain terrestrial karst invertebrates.</td></tr>
</table>

Recommendations

The following recommendations are offered in descending order of importance:

1. Genetic data were used in this report in different capacities. In some cases, genetic results have identified, confirmed, or changed species identifications. In other situations, genetic subclades could support or refute the modeling results. No genetic data were available for some taxa, and identification of those species is based on morphologic studies. As genetic data become available for more of the seven genera examined in this report, further analysis could establish standards for what level of genetic differentiation, *irrespective of species name*, suggests the presence of a KFR boundary. Therefore, we recommend that the next update of this analysis include a study and review of all available genetic data for the included genera.
2. During the data collection phase of the study, we noted that some biological surveys seemed to focus on finding the endangered species but not on documenting the full ecological communities of the caves. Consequently, less information was available for understanding the ecological conditions of the species. Studies similar to this one would benefit from a richer data set; therefore, we support thorough biological surveys of all caves.
3. Detailed mapping of the Austin Chalk and Pecan Gap Chalk is needed throughout the study area. While the recent mapping conducted of those units is quite helpful, this study was not designed or funded to conduct extensive and detailed mapping. Until further mapping of the Austin Chalk and Pecan Gap Chalk can be completed, we recommend that care be taken when reviewing surface exposures mapped by Barnes (1983) as the Pecan Gap when cavernous sections of the Austin could occur below.
4. Biological studies of caves at the east end of the Stone Oak KFR are needed to better define that KFR boundary, especially because of the uncertain status of *Rhadine exilis* in Black Cat Cave (the species westernmost potential locality) which has become marginal habitat due to impacts from Bulverde Road. We recommend that additional biological collections in other caves could instead resolve the species' status in that area.
5. Biological study of The Labyrinth is needed to confirm this study's hypothesis on the distribution of *Cicurina baronia*, along with a hydrogeologic study to better evaluated the species' potential distribution and the boundaries of the Alamo Heights KFR. Since most of the Austin Chalk and Pecan Gap Chalk in the study area is highly urbanized, thorough biological and hydrogeological investigation of any caves discovered or opened by construction in these geologic units is strongly encouraged to refine the understanding of their cave development and terrestrial invertebrate troglobite distribution.
6. Additional searches for and biological study of caves in the Central Medina KFR are needed to confirm its status as Zone 3a or possibly Zone 4a.
7. Searches for biological studies of caves are needed in the following hydrostratigraphic units: Cavernous, Upper Fossiliferous, Little Blanco, Doeppenschmitt, and Rust. These units are either known to change lithologically in their potential to form caves across the study area, or their potential requires further evaluation. Such information would help further refine KFR and Karst Zone boundaries.

8. *Cicurina bullis* and *Cicurina neovespera* are presently recognized formally as separate species. Informally, they are believed to be synonymous and are thus combined in this study's analyses. The same applies to *Cicurina platypus* and *Cicurina puentecilla*. The status of this synonymy needs to be confirmed. If refuted, the modeling of this study should be rerun.
9. *Cicurina* species have generally been considered sympatric, although occasional allopatry has recently been discovered (Hedin et al. 2018) and included for eight caves in this study. Ecological studies are needed to determine if allopatry truly occurs, or if they occupy different ecological niches and remain functionally sympatric. Should allopatry be proven, this study's model should be rerun. Ecological studies will also prove valuable toward more effect habitat management efforts.
10. *Speodesmus ivyi* is broadly distributed across multiple KFRs and warrants genetic study to determine if this distribution is accurate or if it represent multiple species or species subclades. While this species is not listed as endangered, better understanding its distribution is valuable in better defining KFR boundaries.
11. In relation to the above recommendations, the further use of genetics to determine the timing of species division would be important in evaluating species evolution relative to changing geological factors, and in evaluating the development of new species that invade and fragment the ranges of older species.

Acknowledgments

The Texas Department of Transportation funded this study and provided years of logistical support, hundreds of data points, field and reporting assistance, and technical expertise that was instrumental in the completion of this work.

This study would not have been possible without the assistance of James Reddell, Curator Emeritus of Cave Invertebrates at The University of Texas at Austin, who provided the extensive list of species for analysis and the list of caves in which they occur. He worked tirelessly to assure maximum quality control on the species' identification and the sometimes confusing and difficult identification and location of their caves, and to provide additional valuable insights to their ecology.

Zara Environmental LLC contracted this study and were excellent partners. Krista McDermid, President; Peter Sprouse, Founder; and previous employees Clover Clamons, PG and Brian Cowan, PG all proved supportive and helpful. Dr. Jean Krejca, Founder, provided valuable biological insights and Wendy Dickerson, GIS Analyst, was tremendous in her work on the GIS model, mapping, and reporting that were critical to this project.

Special appreciation goes to Jenny Wilson, USFWS Karst Invertebrate Lead, who worked closely with us to improve the quality of the data and provide additional biological guidance to ensure this study was well conceived and designed to best recover the endangered karst species.

In memoriam, Dr. Stirling Robertson, of the Texas Department of Transportation, did more than simply administer the project, but provided crucial understand of the study's needs, postponing its deadline until important genetic work was completed and applying additional funds for the geologic mapping of the Austin Chalk.

Several individuals contributed meaningfully to the analyses in this study. Michael Jones, formerly Cave and Karst Science Specialist with the National Cave and Karst Research Institute (NCKRI), provided instructions in how to create the model employed successfully by Veni and Jones (2021). Allan Clark of the USGS provided helpful geologic information for use in the model. Dr. William R. Elliott (retired Missouri State Cave Biologist) gave valuable insights on *Speodesmus* sp. millipedes, as Dr. Marshal Hedin (Professor and Associate Chair of Biology at San Diego State University) did for *Cicurina* sp. spiders and Dr. Joel Ledford (Lecturer at University of California Davis) did for *Tayshaneta* sp. spiders.

Lastly, one of the most basic yet critical aspects of this investigation was to establish cave locations as accurately as possible for analysis. The TSS graciously provided access to its extensive digital database of caves and karst features, as well as access to its physical files through the assistance of TSS Directors Logan McNatt and Merideth Turner. In return, extensive new and updated information generated by this project was added to the TSS database to make it a more effective resource for future research. New and improved cave location coordinates and associated information and access were also kindly provided by:

Jenny Blair, Blair Wildlife Consulting
Chris Collins, SWCA Environmental Consultants
Valerie Collins, Pape-Dawson Engineers
Andy Grubbs, Hays Environmental Consulting
Mike Harris, Texas Cave Management Association
Dr. Marshal Hedin, San Diego State University
Niki Lake, Texas Parks and Wildlife Department (retired)
Walker Lazo, Pape-Dawson Engineers
Bennett Lee, Texas Cave Management Association
Kurt Menking, Texas Speleological Survey
Marvin Miller, Texas Speleological Survey
Joe Mitchell, Texas Speleological Survey
Linda Palit, Texas Cave Management Association
Dr. Caleb Phillips, Texas Tech University
Joe Ranzau, Texas Cave Management Association
Peter Sprouse, Zara Environmental LLC
Chris Thibodaux, Camp Bullis (retired)
Stephen Van Kampen-Lewis, SWCA Environmental Consultants
Cyndee Watson, U.S. Fish and Wildlife Service
Dr. Kemble White, Cambrian Environmental
Jenny Wilson, U.S. Fish and Wildlife Service

We thank them all for their support.

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