NCKRI REPORT OF INVESTIGATION 10

STATISTICAL ANALYSIS AND REVISION OF ENDANGERED KARST SPECIES DISTRIBUTION, AUSTIN AREA, TEXAS

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Report of Investigation 10

Statistical Analysis and Revision of Endangered Karst Species Distribution, Austin Area, Texas

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Cover photo: Orion Knox in Electro-Mag Cave, Williamson County, Texas. Discovered by a geophysical survey, this cave is one of the more extensive and bio-diverse in the study area.

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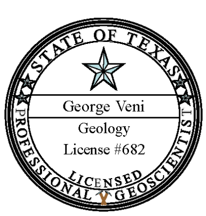

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Statistical Analysis and Revision of Endangered Karst Species Distribution, Austin Area, Texas

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Abstract

The cavernous outcrops in the Austin, Texas, area, exposed along the Balcones Fault Zone, contain seven troglobitic species of karst invertebrates, federally listed as endangered by the US Fish and Wildlife Service to insure their survival. Previous studies defined and updated 10 karst fauna regions (KFRs) as mostly distinct ecological regions which include endangered and non-endangered troglobite species. The KFRs are overlapped by four karst zones, which predict where the endangered karst species are most and least likely to be found in and beyond the KFRs. This report further evaluates and updates those boundaries, based in part on the development of a GIS model that maps the ranges of 39 troglobites limited to the study area from 479 localities.

The boundaries of the Central Austin, North Hays County, Post Oak Ridge, and South Travis County KFRs were confirmed. Minor changes were made to the Jollyville Plateau, McNeil-Round Rock, and Rollingwood KFRs. The Georgetown KFR was extended into what was the southern lobe of the North Williamson County KFR, which in turn was extended north into southern Bell County. The Cedar Park KFR was divided into the East Cedar Park and West Cedar Park KFRs. Eight informal KFRs were described as containing only non-endangered karst species as constraints on the distribution of the endangered karst species. An "Undesignated" KFR was created for small, biologically unstudied and geologically isolated karst areas until they could be examined to determine if they belong to a designated KFR and which one.

Karst Zone 1, where endangered karst species are known to occur, was expanded throughout most of the previous Karst Zone 2 areas based on new localities; it was reduced in the Rollingwood KFR based on the GIS modeling. Karst Zone 2, which has a high probability of containing the endangered species, changed in area proportionally to the changes in Karst Zone 1. Karst zones 3 and 4 were each split into two subzones to better identify their biological status and manage their ecosystems.

Introduction

The eastern margin of the Edwards Plateau in the vicinity of Austin, Texas, is a bio-geologically complex region. Species living in its caves and related voids have become physically isolated from each other through time, resulting in genetic isolation that has produced new species known to occur only within small geographic areas. The expansion of Austin and neighboring communities onto the karst where these species occur poses a threat to their survival due to the destruction and sealing 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 and 2000).

Seven troglobitic species of karst invertebrates in the Austin region are federally listed as endangered by the US Fish and Wildlife Service (USFWS) to insure their survival. Five were listed in September 1988 (USFWS, 1988) and a refinement of the taxonomy added two more species to the list in 1993 (USFWS, 1993). The species and their common names are:

Batrisodes texanus (Coffin Cave mold beetle)
Rhadine persephone (Tooth Cave ground beetle)
Tartarocreagris texana (Tooth Cave pseudoscorpion)
Tayshaneta myopica (Tooth Cave spider)
Texamaurops reddelli (Kretschmarr Cave mold beetle)
Texella reddelli (Bee Creek Cave harvestman)
Texella reyesi (Bone Cave harvestman)

In 1992, George Veni and Associates examined the stratigraphic, structural, and hydrological controls on cave development in the Austin area, coupled with an evaluation of the distribution of troglobitic species. While some troglobites occur broadly across the Edwards Plateau, the 1992 study focused on 38 species limited to the Austin area to determine if they were restricted to certain regions.

The "Austin area" was defined in 1992 as the contiguous range of the Cretaceous-age Edwards Limestone

Group extending north approximately 83 km from the Hays-Travis County line to the Williamson-Bell County line (Figure 1). While other carbonate units occur in the area and were considered, nearly all cave development was found in the Edwards which made it the *de facto* defining unit. The eastern limit of the area was bounded primarily by faults that down-throw the Edwards into the subsurface and below the water table. On average about 9–13 km to the west, the opposite boundary was defined primarily where the Edwards thins and is removed by erosion, although the southern 25 km are bounded by another major fault. Additionally, an isolated 33-km long, narrow, Edwards-capped plateau known as Post Oak Ridge in western Travis and eastern Burnet County was included in the study.

George Veni and Associates (1992) plotted the distribution of the 38 troglobite species and discovered that certain species occur in different areas. Statistically analyzing the percentage of species endemic to and shared with other areas, the Austin area was divided initially into 11 Karst Fauna Regions (KFRs; Figure 1):

1. Cedar Park
2. Central Austin
3. Georgetown
4. Jollyville Plateau
5. McNeil
6. North Hays County
7. North Williamson County
8. Post Oak Ridge
9. Rollingwood
10. Round Rock
11. South Travis County

The purpose of the KFRs was to identify major ecological communities that USFWS could use for species recovery. Although the statistical methods were simple, considering 33 species beyond the five listed at the time added statistical confidence to the results. The KFRs allowed USFWS to manage the species communities in ways that could potentially lead to delisting and/or preclude the need to list other rare species as endangered (e.g. USFWS, 1994).

An additional aspect of the study by George Veni and Associates (1992) was to delineate four endangered species habitat and management Karst Zones that were hand-drawn on twenty-two 7.5’ topographic quadrangles. They were defined as:

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 do not contain endangered cave fauna.

Due to the absence of directly observable features on the surface to define the extent of species’ underground habitat, these zones were based on biological and geological factors that could be used to estimate the likely boundaries of species’ habitat and areas of probable and improbable habitat. These zones have since been used by USFWS in several ways, but primarily as management zones, determining what level of action and research is needed in the protection and study of species and areas within them (e.g. USFWS, 2001).

In 2007, Veni and Martinez redrew the karst zones boundaries digitally in Geographic Information System (GIS) software and updated them based on an increase of 180 new localities for the endangered karst species above the 43 known in 1992. Additionally, they noted that the North Hays and Post Oak Ridge KFRs required no further consideration because the additional data made it clear those KFRs do not contain the endangered karst species. Further, they clarified a finding from the George Veni and Associates (1992) study that no significant difference was found between the McNeil and Round Rock KFRs and recommended they be combined into a single KFR: McNeil-Round Rock. Their first and strongest recommendation was for a more robust statistical analysis of species distribution, which is the subject of this report.

Of the 38 troglobite species evaluated by George Veni and Associates (1992) to create the KFRs, 34 belonged to only seven genera. They hypothesized that multiple species evolved due to factors that isolated the individual populations, facilitating genetic divergence. Since troglobites are, by definition, obligate cave animals that cannot survive on the surface, the absence of cavernous rock is the primary barrier to troglobite distribution. Consequently, three of the 38 species were endemic to the Post Oak Ridge KFR, which is separated from the other KFRs by non-cavernous rock, and none of the other 35 species from those KFRs were found on Post Oak Ridge.

To explain the differences in distribution of species in the other KFRs where the limestone is contiguous, George Veni and Associates (1992) examined troglobite distribution relative to streams and faults. They

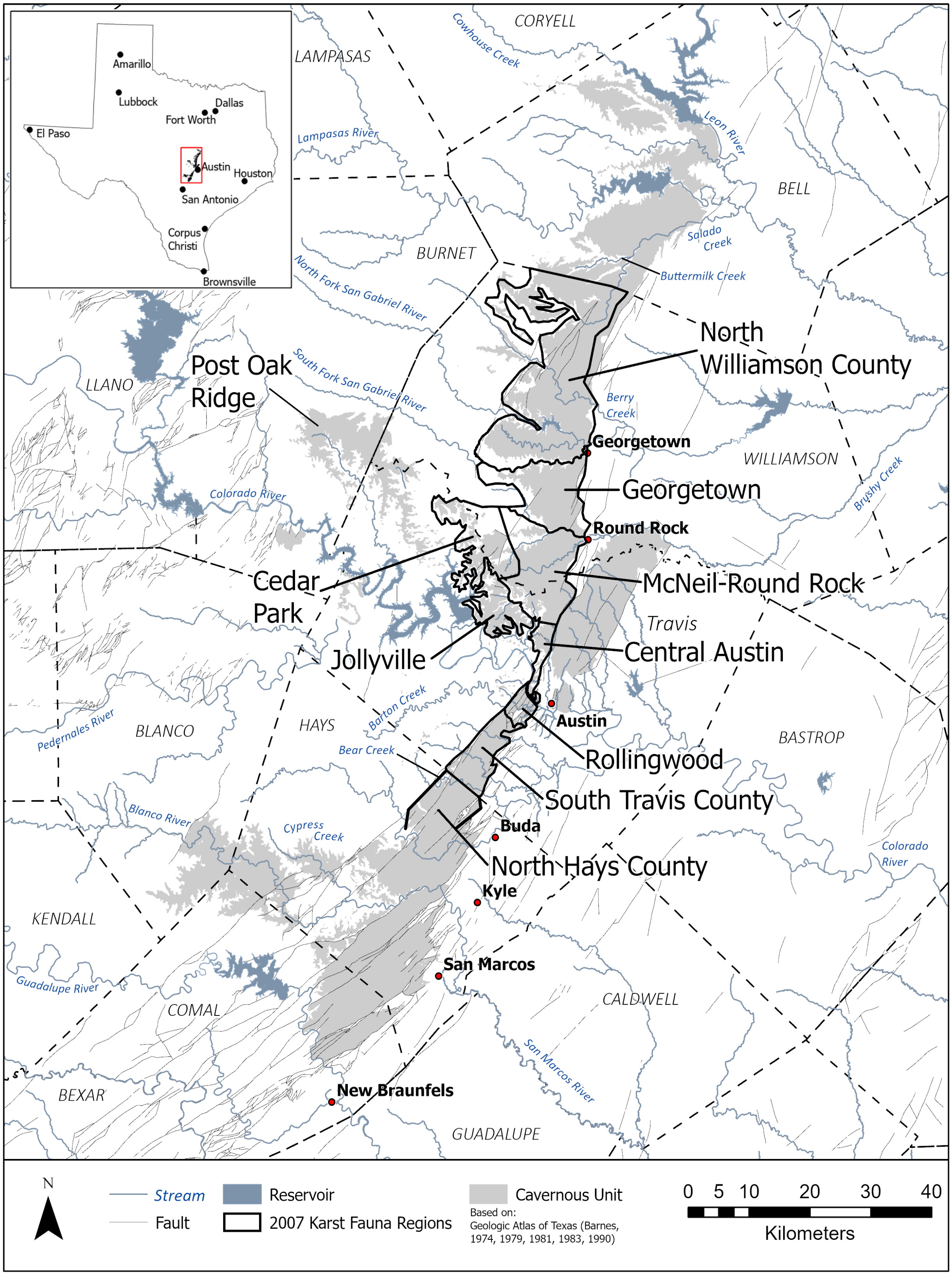

Figure 1. *Study area location map with cavernous unit and 2007 karst fauna regions per Veni and Martinez (2007).*

found 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 and because the species are not aquatic, they cannot exist in or easily pass through such conditions. Also the effects of faults on species distribution were examined and no influence was found, except where the degree of displacement juxtaposed cavernous and non-cavernous rock. Supporting these results, they also studied related endangered species in the San Antonio, Texas, area about 70 km to the southwest and those data yielded the same conclusions (Veni, 1994).

These studies defined two types of boundaries to troglobite distribution and for the KFRs: barriers and restrictions. Barriers are boundaries beyond which 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 along streams that occasionally run dry, lowering the water table allowing species to pass occasionally. Restrictions explain why some troglobite communities are not completely endemic but share some species with other KFRs.

Zara Environmental (2010b) used similar methods to establish KFRs in Hays County. Their study, using three measures of endemicity by Mainali (published later in 2014), included both terrestrial and aquatic species with the goal of identifying areas of overall greater karst biodiversity for protection, as opposed to the prior studies that focused on the federally listed terrestrial troglobites.

A few authors suggest the KFR boundaries and justifications require revision. For example, White et al. (2009) suggest relay ramps of block-faulted limestone may play a greater role in troglobite distribution than certain streams. Van Kampen-Lewis and White (2019) argue that the South Fork of the San Gabriel River may not be a boundary between the Georgetown and North Williamson County KFRs due to the presence of the federally listed mold beetle, *Batrisodes texanus*, on each side of the river.

The primary purpose of this investigation is to include all the known localities of rare and endangered troglobites in the Austin area, along with geologic and hydrologic data, into a GIS model to conduct a robust, detailed, objective, statistical analysis of factors that might influence troglobite distribution, and use those results to modify KFR boundaries as appropriate to the results. This study's secondary purpose is to update the karst zone boundaries based on new localities and insights from the GIS analysis.

Methodology

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 seven listed species, plus 32 non-listed troglobite species known only from the study area. His list includes species beyond but adjacent to the known distribution of the federally listed species in order to better define the limits of the listed species' range. Based on this distribution of species, the study area is defined by the cavernous geologic units (described in the following subsection) containing the 39 species along the Balcones Fault Zone from the Guadalupe River in Comal County, northeast approximately 160 km to the Leon River in Bell and Coryell counties (Figure 1).

The 39 species are known from a total of 479 localities, predominately caves but also a well and some karst features not large enough to qualify as caves by the Texas Speleological Survey (2020) definition of a minimum 5 m of humanly traversable passage and with no dimension of the entrance exceeding the cave's traversable length. At least one federally listed species is known in 255 localities, 36 localities have no known listed species but at least one species tentatively identified as listed, and no confirmed or tentatively confirmed listed species are known in the remaining 188 localities.

The 39 species do not include all troglobites known in the study area. The ranges of troglobites which are widely distributed across central Texas provide no analytical insights to identify barriers or restrictions to species more sensitive to speciation. Stygobites (aquatic troglobites) are also excluded from this analysis because their habitats and the factors affecting their distribution are not directly comparable to the federally listed terrestrial troglobites. The published status of species in certain localities, whether tentative or confirmed, has changed based on new data and consultation with USFWS and the biologists specializing in those taxa. Those changes are noted in the references in Table 1 (available online). In other cases, while USFWS does not formally recognize the status of some species (notably the division between *Batrisodes cryptotexanus* and *Batrisodes* *texanus*), they accept them for the purposes of this investigation.

Reddell's list was converted into a spreadsheet (Table 1, available online). The 479 localities are sorted by rows for each locality and columns for each species. Additional data are added from the files of the Texas Speleological Survey (TSS), a non-profit corporation organized to collect, maintain, and make available information on caves and karst features in Texas. Those data primarily included the location coordinates for each locality, recorded in latitude and longitude with a datum of NAD 1983, estimated precision of the coordinates, and all known alternate names for the localities. Four additional columns are included in Table 1 (available online): county, KFR (initial), KFR (revised) per any revisions from this study, and references. Only the primary references for each species at each locality are included. Where no published reference is known, or where unpublished updates occurred, Reddell was listed as a personal communication.

To protect the species' localities and the privacy of their landowners, location coordinates are excluded from the version of Table 1 (available online) attached to this report. Further, all maps in this report do not show those locations. All raw and processed data from this study, including all specific locations, were provided to the USFWS for review prior to the completion of this report.

The TSS files are not generally open to the public. TSS does provide data upon formal request to support research and other needs. For this project, the lead author (Veni) and Reddell had full access to the TSS files. Both are past TSS directors and current data managers, which allows them to more rigorously review the files for information. They spent hundreds of hours comparing consulting reports (provided by USFWS) and other reports to the TSS records. Many caves and karst features are recorded by multiple names and codes. Consequently, some 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. Several people and organizations provided valuable primary and supplemental information. Reddell and Veni determined the location and identity of many caves by studying and improving the coordinates of caves and karst features without species pertinent to this study, which were used as landmarks for geographic orientation and verification. By agreement with USFWS, the cave names, alternate names, and coordinates in the TSS database, and following the updates to the database from this study, are considered authoritative. While the above work is crucial to this investigation, it also resulted in major improvements to the TSS database. To avoid any potential conflict of interest, Reddell and Veni conducted this work with the TSS materials as TSS volunteers.

The detailed review of TSS and other records also updated Reddell's initial list of species and recorded in Table 1 (available online). The locations and species localities were reviewed multiple times for accuracy and completeness, including a meticulous comparison where USFWS personnel reviewed the locations and species recorded in their files.

Karst Fauna Region Analysis

Conceptual Approach

We studied and attempted multiple methods to identify the most accurate means of evaluating the distribution of the troglobite species. We also considered modeling and tested many factors involving geology, hydrology, cave microclimates, surface climate, vegetation, and soils for their potential effects on species distribution. Most didn't have sufficient data, sufficiently detailed data, or the needed resolution of data. Other data 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 as reversing the analysis. Rather than model the effects of various physical conditions on the species' distribution, we determined and analyzed the range of distribution for each species. The clustering of multiple range margins is 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 and Associates (1992) described in detail the hydrogeologic factors resulting in cave development in the study area and how they relate to the distribution of the endangered species. In summary, the study area is in the Balcones Fault Zone at the eastern edge of the Edwards Plateau. Predominantly Cretaceous-age carbonate rocks occur throughout the area. These rocks dip slightly to the east 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, west to east, changing to the structural strike, north and south, along the eastern edge of the karst where springs discharge into base level rivers; Sharp et al. (2019) provide the most recent and comprehensive review of the Edwards Aquifer, the primary aquifer of the study area. 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 appropriate habitat for troglobites if nutrients, humidity, temperature, and other conditions are not suitable.

The modeled analyses of karst species distribution for this investigation were conducted using the geographic information system (GIS) software ArcGIS Pro 2.6.0 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 map of the 1:250,000 scale Geologic Atlas of Texas, which define this study's geological formation boundaries and major faults. The portion of the Geologic Atlas within the study area includes parts of the following published sheets: Austin (Barnes, 1974), Llano (Barnes, 1981), San Antonio (Barnes, 1983), Seguin (Barnes, 1979), and Waco (Barnes, 1990).

Since troglobite species are found only in caves or related underground habitat, 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;
- Georgetown Formation;
- Edwards Limestone and equivalent Fredericksburg Group and in Bell County the equivalent undivided Denton Clay, Fort Worth Limestone, Duck Creek Limestone, Kiamichi Clay, and Edwards Limestone;
- Walnut Formation (in the Post Oak Ridge area where it is cavernous and not in the Bell-Coryell County area where it is not);
- Lower Member of the Glen Rose Limestone;
- undivided mapping of the Hensel Sand and Cow Creek Limestone along part of the Pedernales River; and
- Marble Falls Limestone.

While some portions of the undivided units above are not cavernous, the map resolution requires their inclusion. Most of the species and all the federally listed karst species occur in the Edwards Limestone or equivalent Fredericksburg Group ("Edwards Limestone" is used in this report to generically refer to both). Except for the Pennsylvanian age Marble Falls Limestone, all rocks in the cavernous unit are Cretaceous in age.

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 since troglobite habitat extends below these shallow deposits. This is demonstrated by several caves and karst features with entrances that extend through these deposits into cavernous habitat below.

Similarly, Bandit Cave, Big Mouth Cave, Five Pocket Cave, McGlothin Sink, McNeil Quarry Cave, Rocky Horror Pit, and Spyglass Cave plot in non-cavernous units. In each of these situations, either the Del Rio Clay or the undivided Del Rio Clay and Georgetown Formation thinly cover the Edwards Limestone, except at the cave entrances in areas too small to appear on the geologic map. Thus, areas where these and other cave entrances and karst features are known in mapped non-cavernous units, and where the outcrops of those units are small, thin, and surrounded by the cavernous unit such that habitat for troglobites almost certainly extends under the non-cavernous units and might be exposed by construction on the surface, were included as part of the cavernous unit. The largest non-cavernous area included in this way is about 3 km long by 1 km wide. Prior to this analysis, several Edwards Limestone caves were known to have entrances surrounded by the otherwise non-cavernous and thin Georgetown Formation, which is why the Georgetown was included initially among the cavernous units.

The general steps for the ArcPro analysis of the data are programmed in Python and illustrated schematically in Figure 2. The model begins with two parallel data paths. In the first path, the coordinates of the species' localities in Table 1 (available online) ("All Cave Locations" in Figure 2) 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 Table 1 (available online) as confirmed for a locality ("Confirmed Species"). The tentative species localities

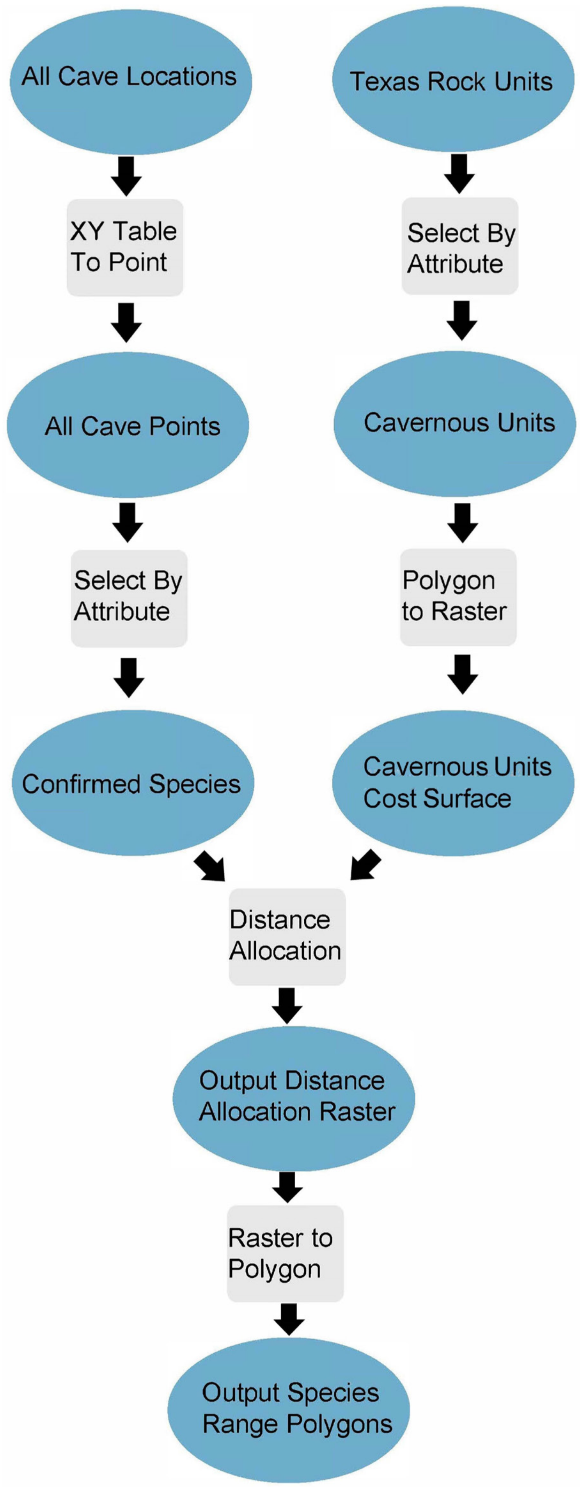

Figure 2. *Schematic workflow of ArcPro model for analyzing species ranges.*

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 as an informal validation of the model output and show that the high confidence tentative localities are within the vicinity of the confirmed species.

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 Texas Geologic Database rock unit polygons ("Texas Rock Units") by the cavernous units described above ("Cavernous Units"). Next, the cavernous units polygons are exported ("Polygon to Raster") to a raster cost surface ("Cavernous Units Cost Surface").

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 2, and as described in the following subsection, the Confirmed Species localities are plotted to confirm their occurrence in the cavernous unit.

Limits in the precision of the coordinates for five caves (identified in Table 1 [available online], Adjusted Locations), and/or resolution of geologic mapping, requires adjusting the caves' locations, generally within a few tens of meters, so they will plot within the cavernous unit. One adjustment extends beyond that range. Uncertainties in the precision of Bee Creek Cave's location and the surrounding geology result in the cave's location being over 200 m from the currently mapped boundary of the cavernous unit. Although the cave's location is adjusted to within the cavernous unit for the purposes of this study, future confirmation of the cave's location and the extent of the cavernous unit in this area may require adjusting the local boundaries of the surrounding KFR and karst zone.

Species Ranges

Unlike surface species which are more easily observed and have habitat conditions that are mapped readily, defining the range of troglobites is based on often random and sparse information. The purpose of including 32 non-endangered troglobites in this study, which depend on habitat conditions similar or identical to the endangered species, is to provide a richer data set for analysis than can be derived from the seven endangered species alone.

Most troglobites in the study area are allopatric in their genera. This fact is used to define species ranges. After many attempts and refinements with different ArcPro tools and methods, the following range determination method is applied to the allopatric species:

1. Areas within a 3-km travel radius are 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"); 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 39 species, 3 km is determined as an approximate average default range for all troglobites from a known locality.
2. These radii, or other range margins in the following steps, do not extend beyond the limit of the cavernous unit. In addition, by use of the distance allocation tool, the 3-km or other range distances below 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, they measure distance around rather than extending across gaps in the unit.
3. If a given species is known from multiple caves further than 3 km apart, the 3-km radii are extended to two-thirds the distance of the cave furthest from its nearest neighbor with that same species (recorded in Table 2). 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" in Figure 2), which is exported ("Raster to Polygon") to polygon format ("Output Species Range Polygons"). 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.

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. James Reddell (personal communication, 2020), based on morphology, divides the *Rhadine* genus into two groups:

<u>Robust:</u>
Rhadine persephone
Rhadine russelli
<u>Slender:</u>
Rhadine new species 1
Rhadine new species 2
Rhadine austinica
Rhadine noctivaga
Rhadine subterranean mitchelli
Rhadine subterranea subterranea

These species are then plotted mostly by the above four steps. Reddell further notes that across genera in every case of sympatry in 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.

In an opposite situation to *Rhadine*, the second special circumstance is that troglobitic *Batrisodes* and *Texamaurops* species mold beetles are closely related and allopatric, allowing them to be modeled together.

The third special circumstance is where a species' range is divided by the smaller range(s) of other species. These situations are interpreted as areas once occupied entirely by the species with the larger range, until extirpated from the intervening area by the invasion of a competitive 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 formerly occurred in the intervening area, its distribution between caves in that area is unknown and unlikely to have spanned that entire distance. The same principle applies to species occurring in different KFRs separated by the absence of the cavernous unit. In those situations, the principle of this third circumstance remains the same, except that the populations were divided by stream down-cutting to remove the

Table 2. *Range distances per species.*

Species	Range distance (m)	Basis
Aphrastochthonius muchmoreum	3,000	Standard radius
Batrisodes cryptotexanus	3,000	Standard radius
Batrisodes reyesi (Georgetown KFR subrange)	3,000	Standard radius
Batrisodes reyesi (McNeil-Round Rock KFR subrange)	3,000	Standard radius
Batrisodes reyesi (Post Oak Ridge KFR subrange)	8,456	Distance from Collaboration Cave to GCWA Cave
Batrisodes texanus (northern subrange)	3,000	Standard radius, constrained by *Batrisodes cryptotexanus* species range
Batrisodes texanus (southern subrange)	4,330	Distance allocation model using 2/3 distance from Sunless City Cave to Temples of Thor Cave, constrained by *Batrisodes cryptotexanus* species range
Cicurina bandida	3,000	Standard radius
Cicurina browni	3,000	Standard radius, constrained by *Cicurina buwata* species range
Cicurina buwata	4,200	Distance from Fossil Garden Cave to LakeLine Cave, constrained by *Cicurina browni* and *Cicurina travisae* species ranges
Cicurina coryelli	3,000	Standard radius
Cicurina travisae	3,000	Standard radius for both subranges
Cicurina vibora	11,125	Distance from Chagas Cave to Rattlesnake Filled Cave
Dichoxenus n. sp.	3,000	Standard radius
Eidmannella reclusa	8,991	Distance from Near Miss Cave to Plethodon Cave
Mexichthonius exoticus	3,000	Standard radius
Rhadine austinica	3,000	Standard radius
Rhadine n. sp. 1	3,000	Standard radius for both subranges, with eastern subrange constrained by *Rhadine* n. sp. 2 and *Rhadine subterranea subterranea* species ranges
Rhadine n. sp. 2	3,000	Standard radius, constrained by *Rhadine* n. sp. 1 species eastern subrange and *Rhadine subterranea subterranea* species subrange
Rhadine noctivaga	6,157	Distance allocation model using 2/3 distance from Coffin Cave to Cricket Cave, constrained by *Rhadine subterranean mitchelli* species range
Rhadine persephone	4,166	Distance from Lakeline Mall Trap No. 6 to Stovepipe Cave
Rhadine russelli	6,663	Distance from GCWA Cave to Lunsford Cave
Rhadine subterranean mitchelli	3,000	Standard radius for all three subranges, with the northern subrange constrained by *Rhadine noctivaga* and *Rhadine subterranea subterranea* species ranges, the southeastern subrange constrained by *Rhadine subterranea subterranea* species range
Rhadine subterranea subterranea	3,000	Standard radius, constrained by *Rhadine* n. sp. 1 species eastern subrange, *Rhadine* n. sp. 2 species range, and *Rhadine subterranea mitchelli* northern and southeaster species subranges
Speodesmus bicornourus (northern subrange)	6,250	Distance allocation model using 2/3 distance from Bat Well Cave to Cobb Cavern
Speodesmus bicornourus (southern subrange)	3,427	Distance allocation model using 2/3 distance from Get Down Cave to Ireland's Cave
Speodesmus castellanus	3,000	Standard radius
Speodesmus n. sp. (eastern subrange)	12,765	Distance allocation model using 2/3 distance from Michaelis Cave to Slaughter Creek Cave
Speodesmus n. sp. (western subrange)	3,000	Standard radius
Tartarocreagris altimana	3,000	Standard radius, constrained by *Tartarocreagris intermedia* species range
Tartarocreagris attenuata	3,000	Standard radius, constrained by *Tartarocreagris infernalis and Tartarocreagris texana* species ranges
Tartarocreagris infernalis (northern subrange)	5,058	Distance from Beck Ranch Cave to Lakeline Cave, constrained by *Tartarocreagris attenuata* and *Tartarocreagris domina* species ranges
Tartarocreagris infernalis (southern subranges)	3,000	Standard radius for both southern subranges, constrained by *Tartarocreagris texana* species range for the southwestern subrange

Table 2 (continued). *Range distances per species.*

Species	Range distance (m)	Basis
Tartarocreagris domina	3,000	Standard radius, constrained by *Tartarocreagris infernalis* species range
Tartarocreagris intermedia	3,000	Standard radius, constrained by *Tartarocreagris altimana* species range
Tartarocreagris proserpina	3,000	Standard radius
Tartarocreagris texana	3,000	Standard radius, constrained by *Tartarocreagris attenuata* species ranges and *Tartarocreagris infernalis* species southwest species subrange
Texamaurops reddelli	3,000	Standard radius
Tayshaneta anopica	3,000	Standard radius
Tayshaneta myopica	9,395	Distance from Millipede Annex Cave to Tight Pit Cave
Tayshaneta sandersi	3,000	Standard radius
Texella mulaiki	6,666	Distance allocation model using 2/3 distance from Big Mouth Cave to Pulpit Cave, constrained by *Texella spinoperca* species range
Texella reddelli	3,000	Standard radius, constrained by *Texella spinoperca* species range
Texella reyesi	5,133	Distance allocation model using 2/3 distance from Cotterell Cave to Hole-in-the-Road Cave, constrained by the Colorado River and *Texella reddelli* species range
Texella spinoperca	3,000	Standard radius, constrained by *Texella mulaiki* and *Texella reddelli* species ranges

cavernous rock, instead of by an intervening species.

Where overlaps in ranges occur, they are generally divided equally, as in Step 4 above. However, where one range substantially overlaps the range of another, the range is defined based on two considerations. First, 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. Second, if the halfway distance is outside of the smaller range, the limit of the smaller range defines the boundary. Both circumstances can apply to different parts of the same range.

The fourth special circumstance is where sympatry exists, but there is insufficient information to consider them functionally allopatric, in different niches, as with *Rhadine*. This only occurs in this study with *Speodesmus* new species and *Speodesmus bicornourus* millipedes. Their ranges are plotted as overlapping, following Steps 1–3 above but not Step 4.

Following the four special manual adjustments, the final Output Species Range Polygons are plotted as Figures 3–12.

Karst Fauna Region Boundary Analysis

Figure 13 illustrates the species ranges used to evaluate the KFR boundaries. It combines all the range margins from Figures 3–12 for examination; due to the complexity and scale of Figure 13, Figures 3–12 should be used to more easily identify specific species ranges. KFR boundaries are evaluated based on the clustering of species range margins as in Figure 13 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, and 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, that 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 after this scrutiny 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.

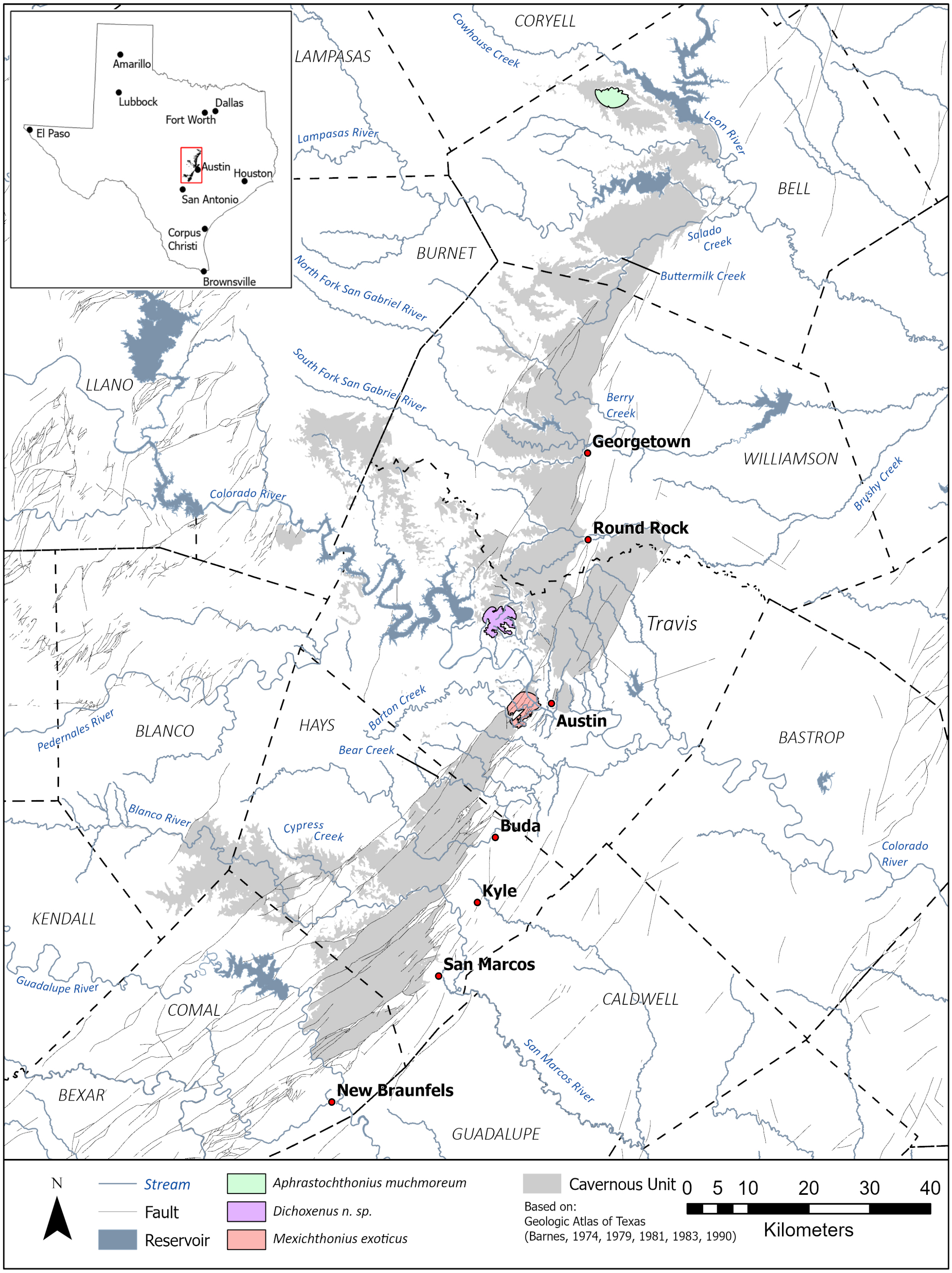

Figure 3. *Ranges of* Aphrastochthonius, Dichoxenus, *and* Mexichthonius *species.*

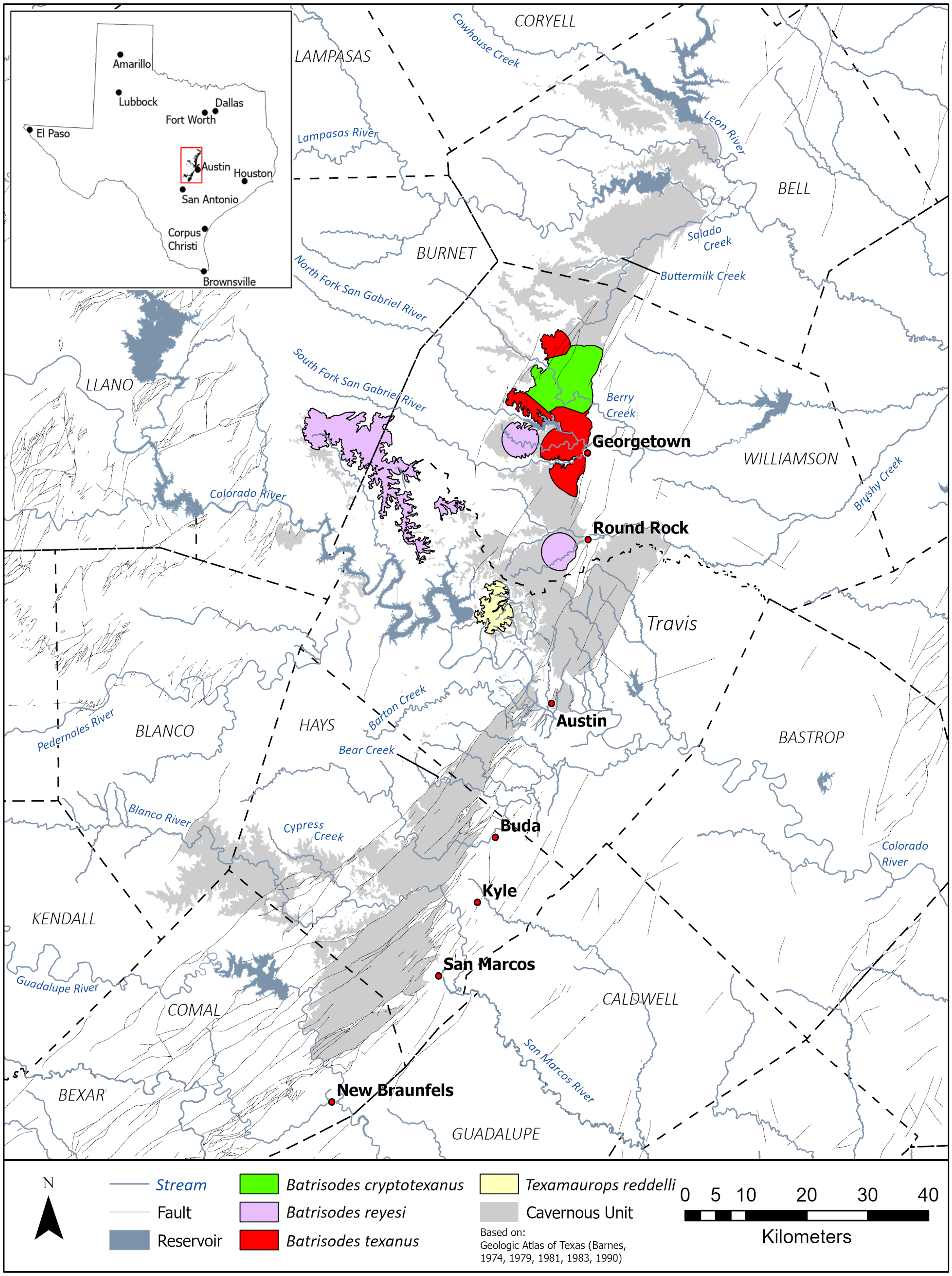

Figure 4. *Ranges of* Batrisodes *and* Texamaurops *species.*

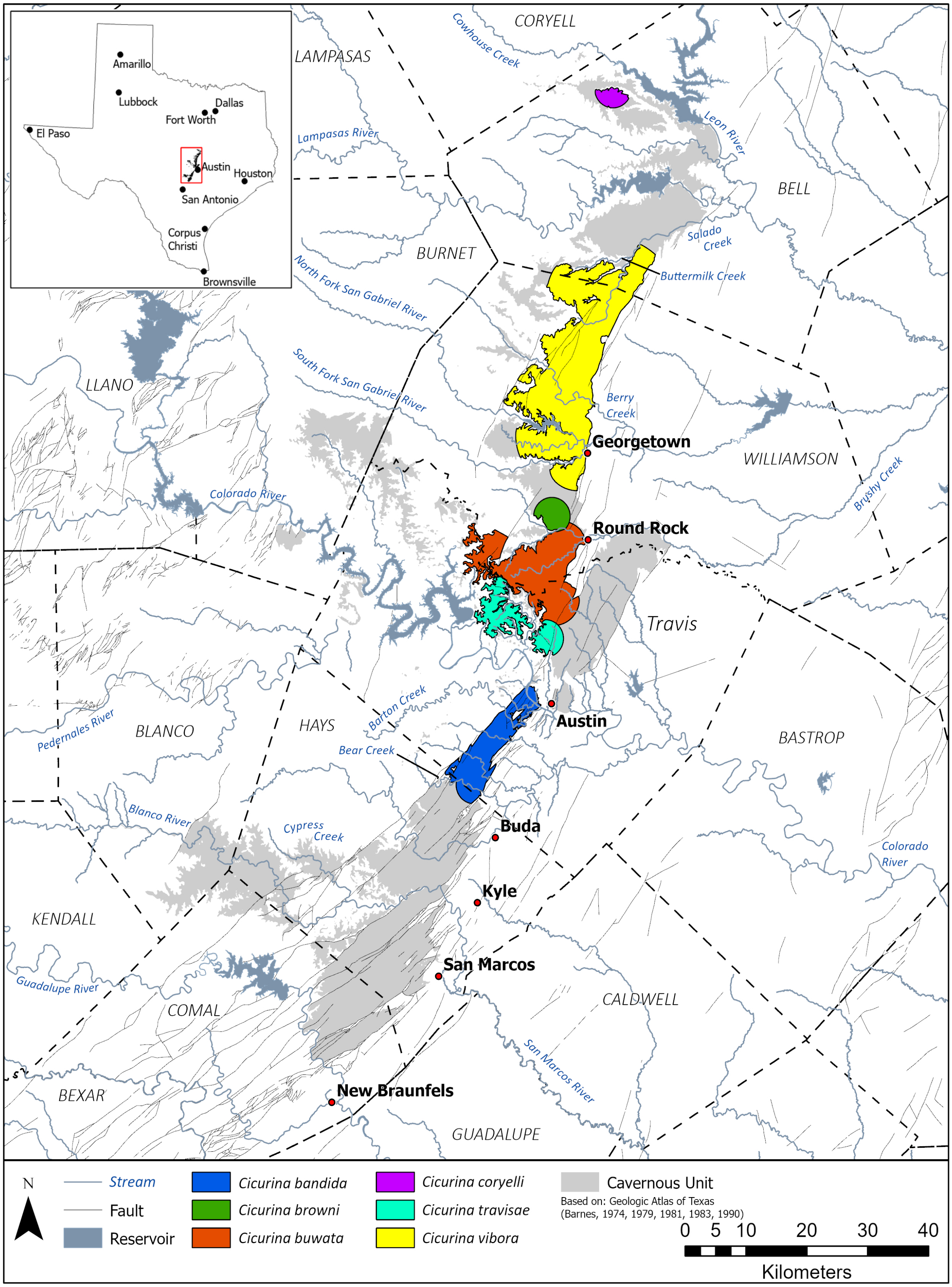

***Figure 5.** Ranges of Cicurina species.*

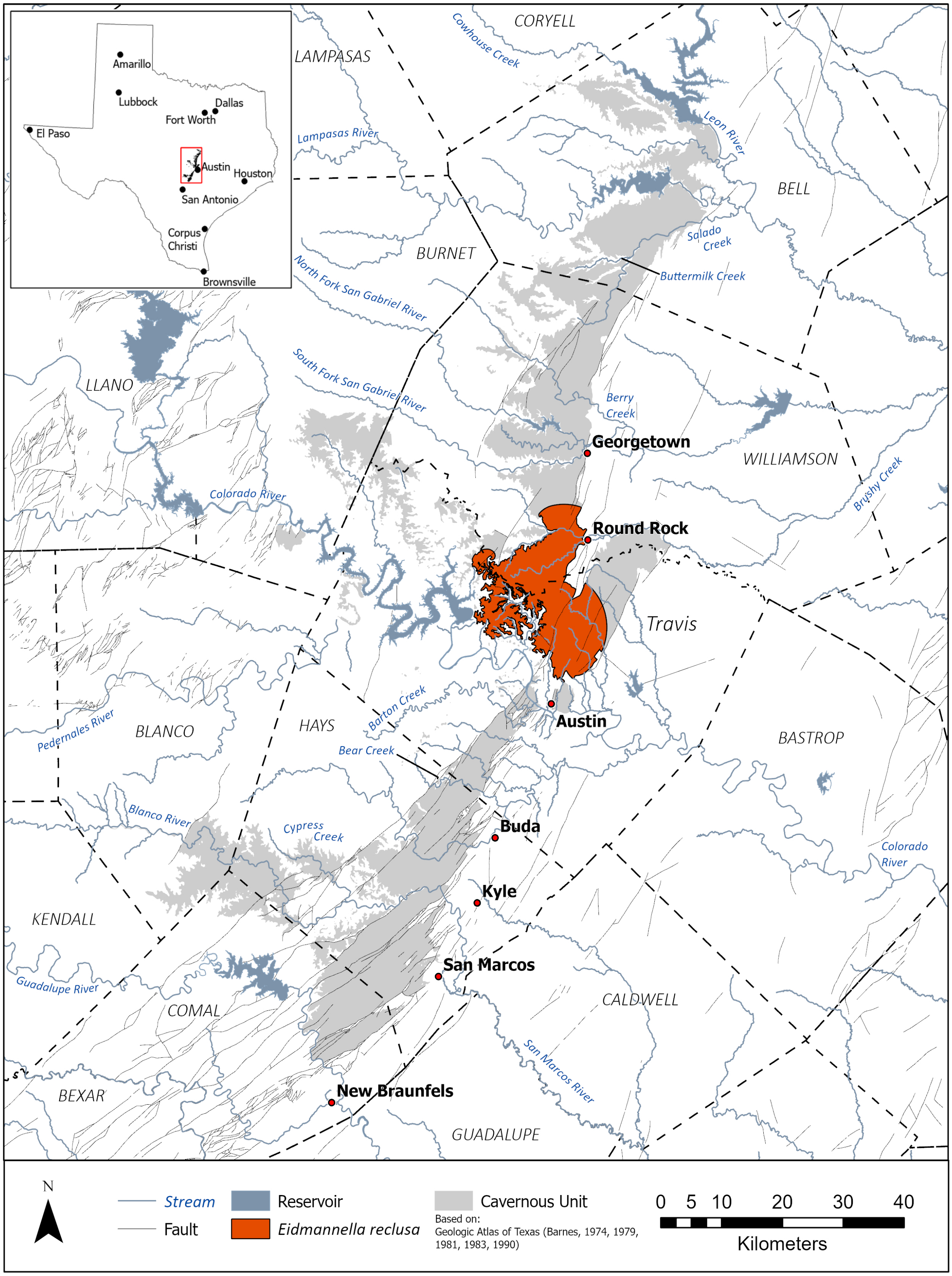

Figure 6. *Range of* Eidmannella reclusa.

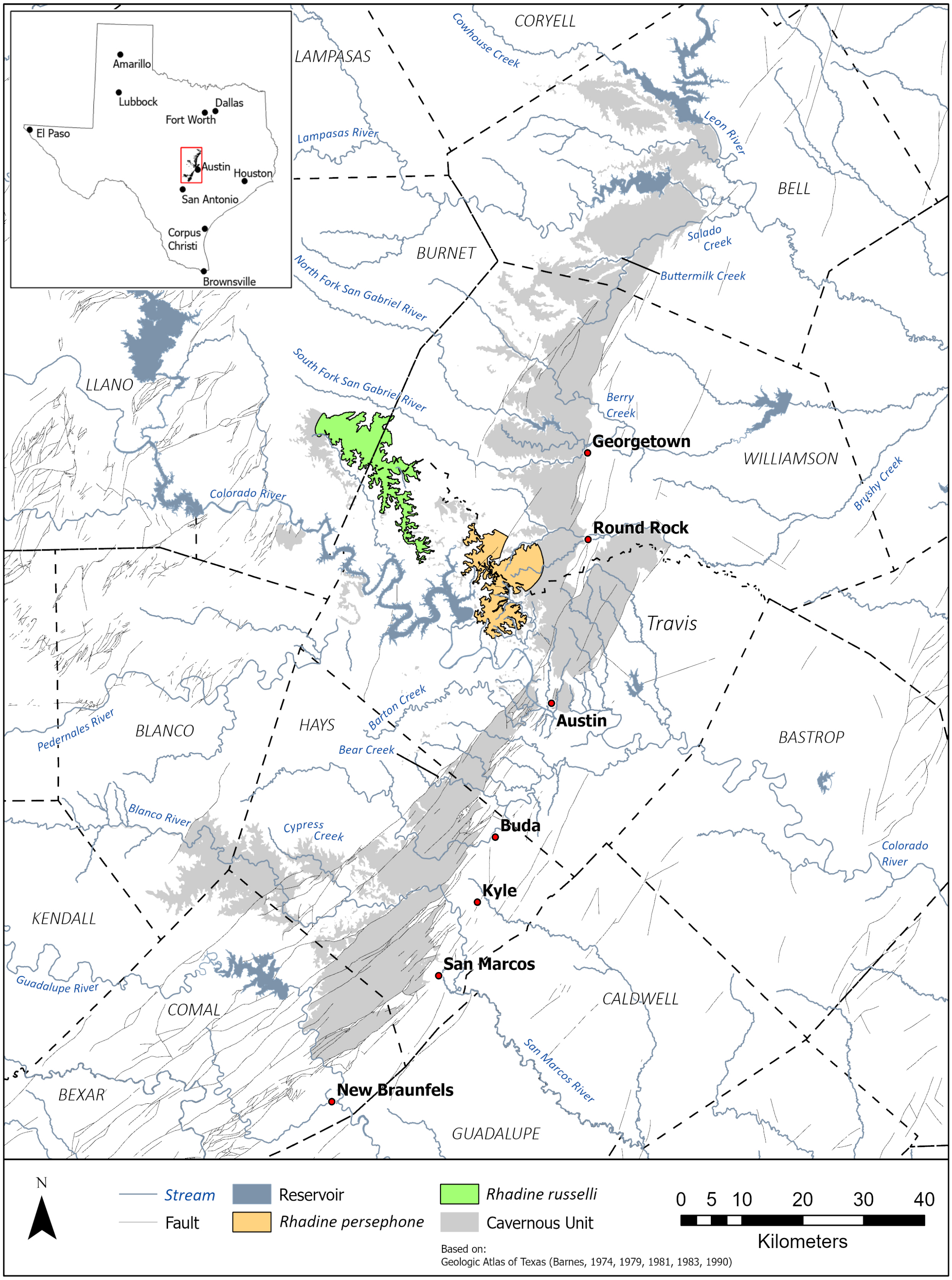

Figure 7. *Ranges of robust* Rhadine *species.*

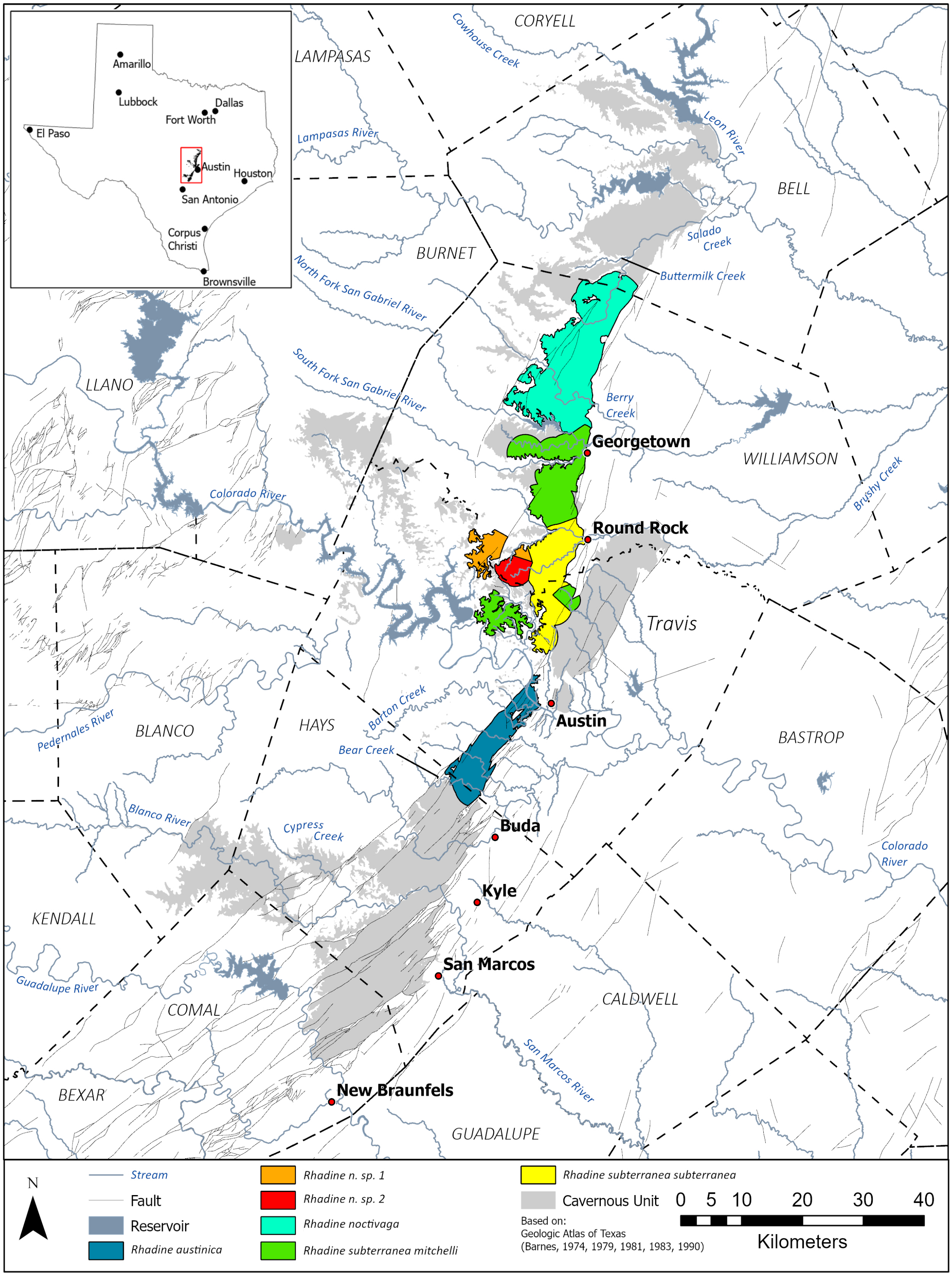

Figure 8. *Ranges of slender* Rhadine *species.*

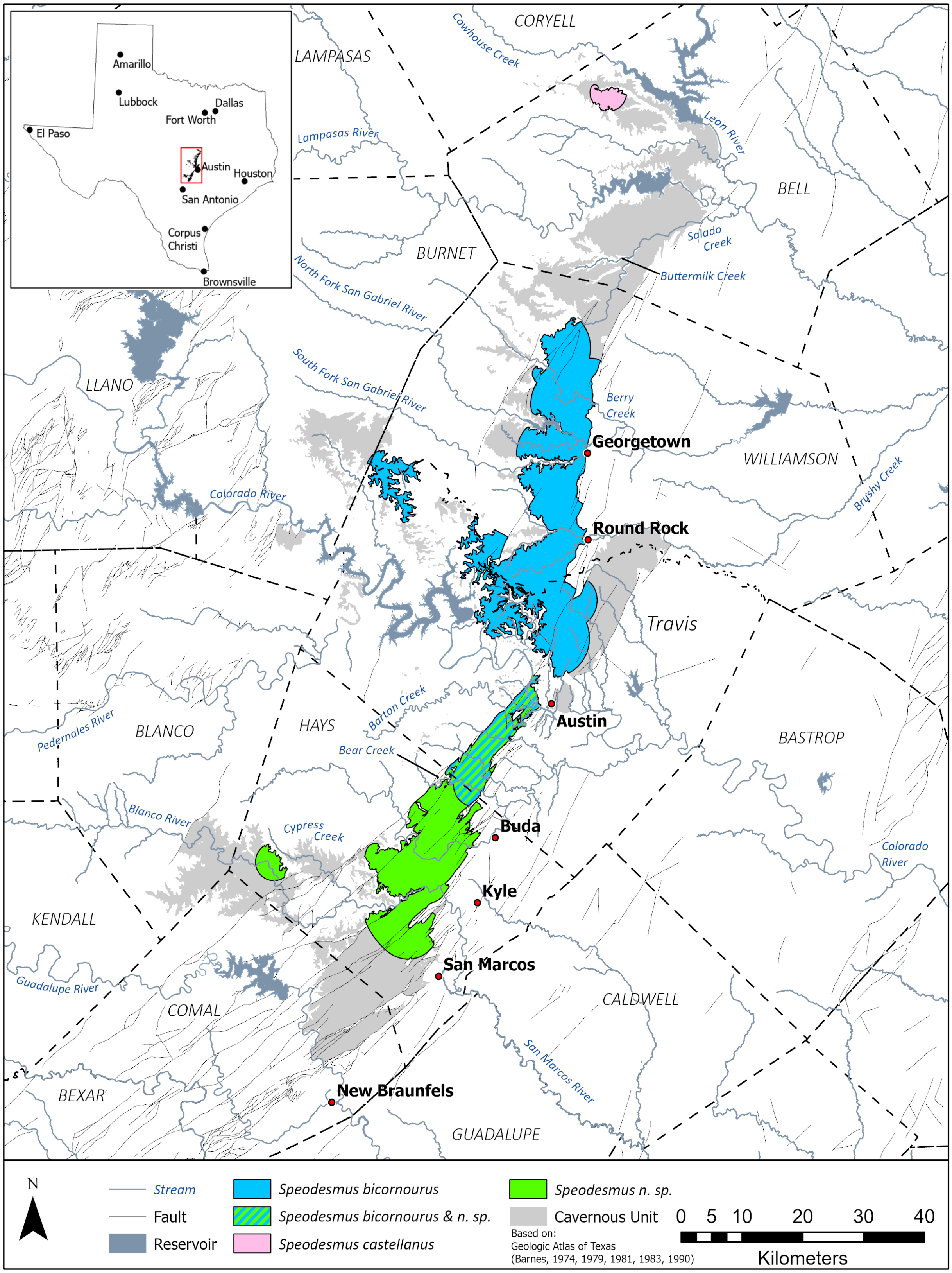

Figure 9. *Ranges of* Speodesmus *species.*

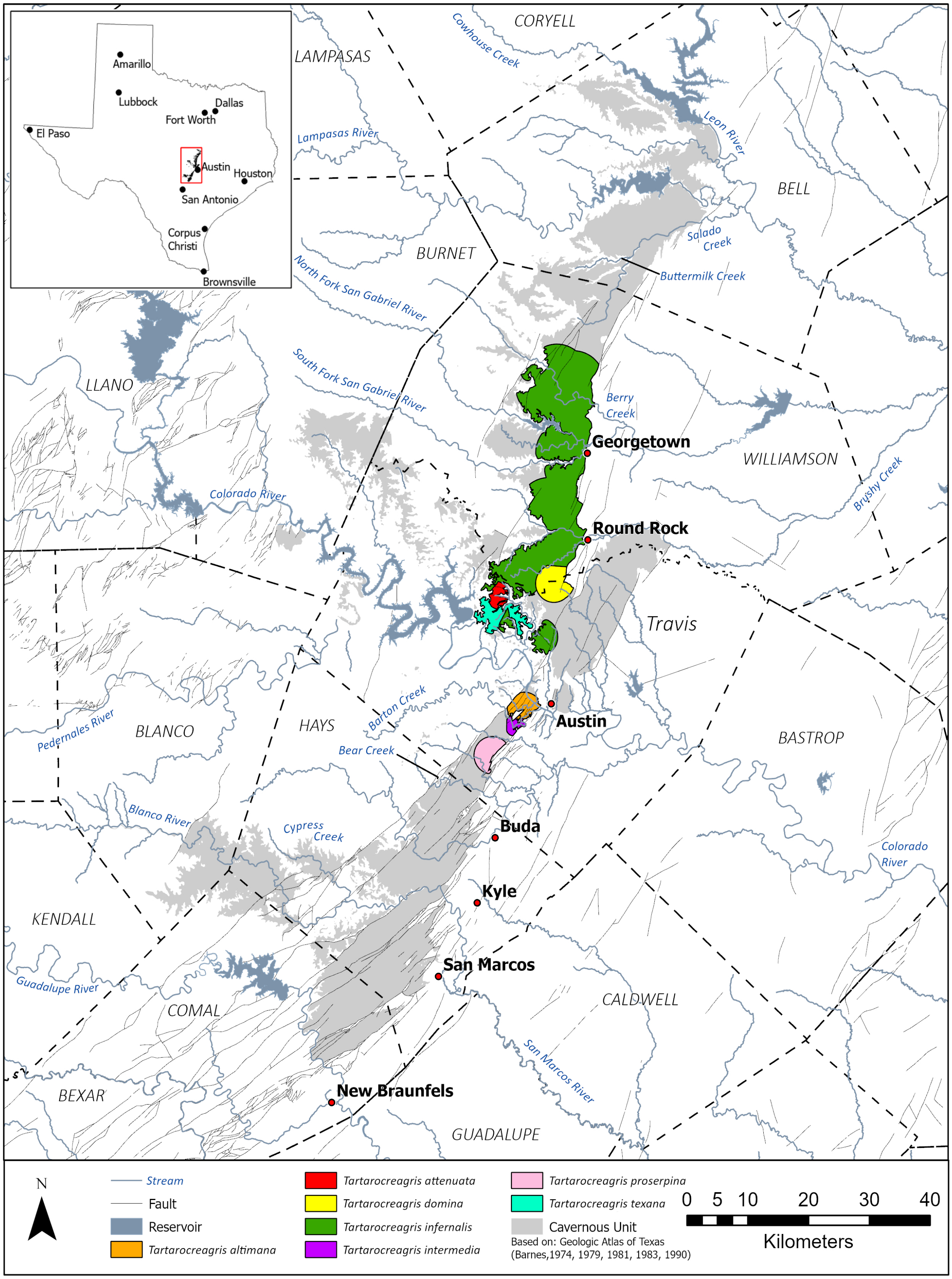

Figure 10. *Ranges of* Tartarocreagris *species.*

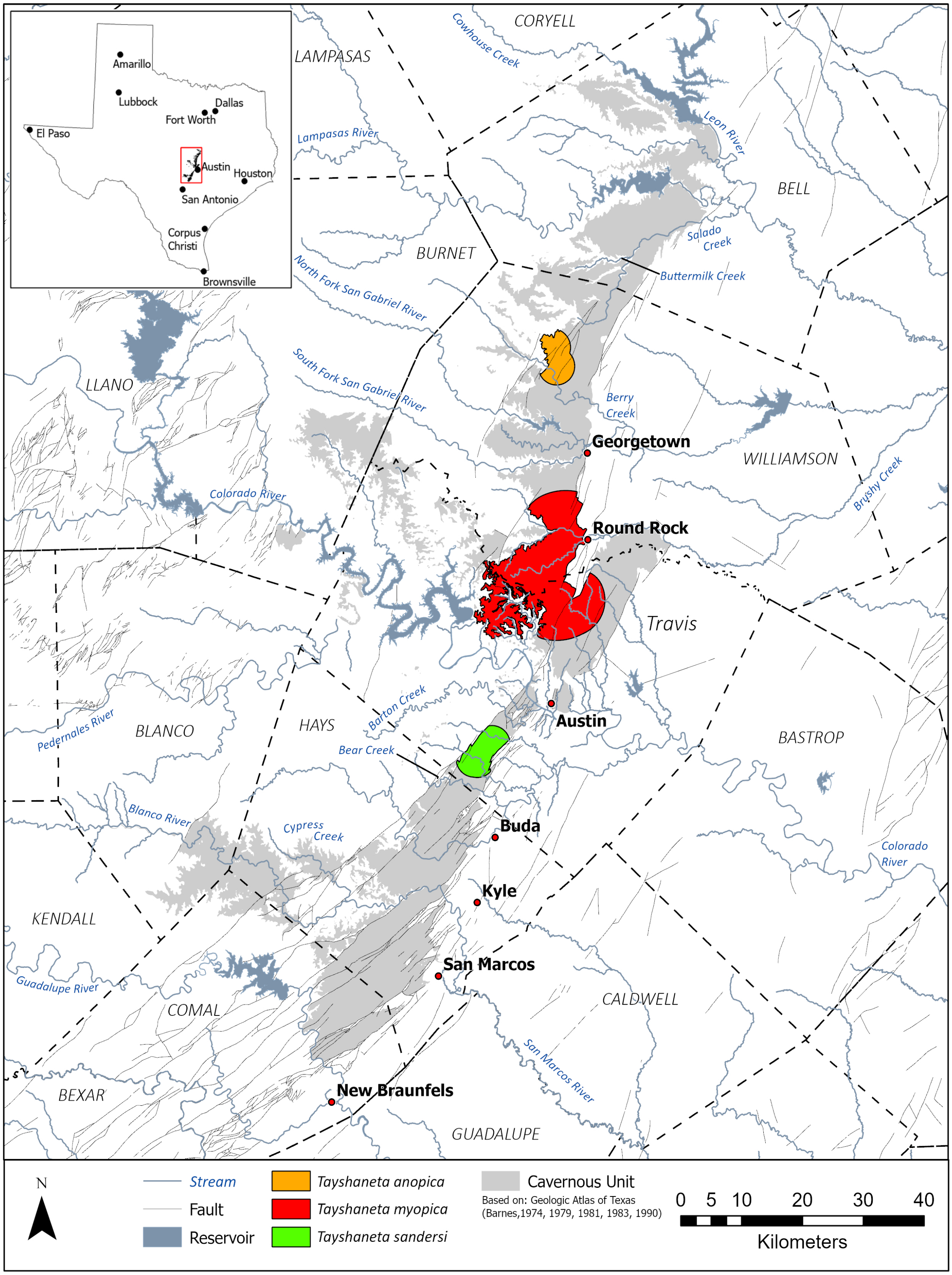

Figure 11. *Ranges of* Tayshaneta *species.*

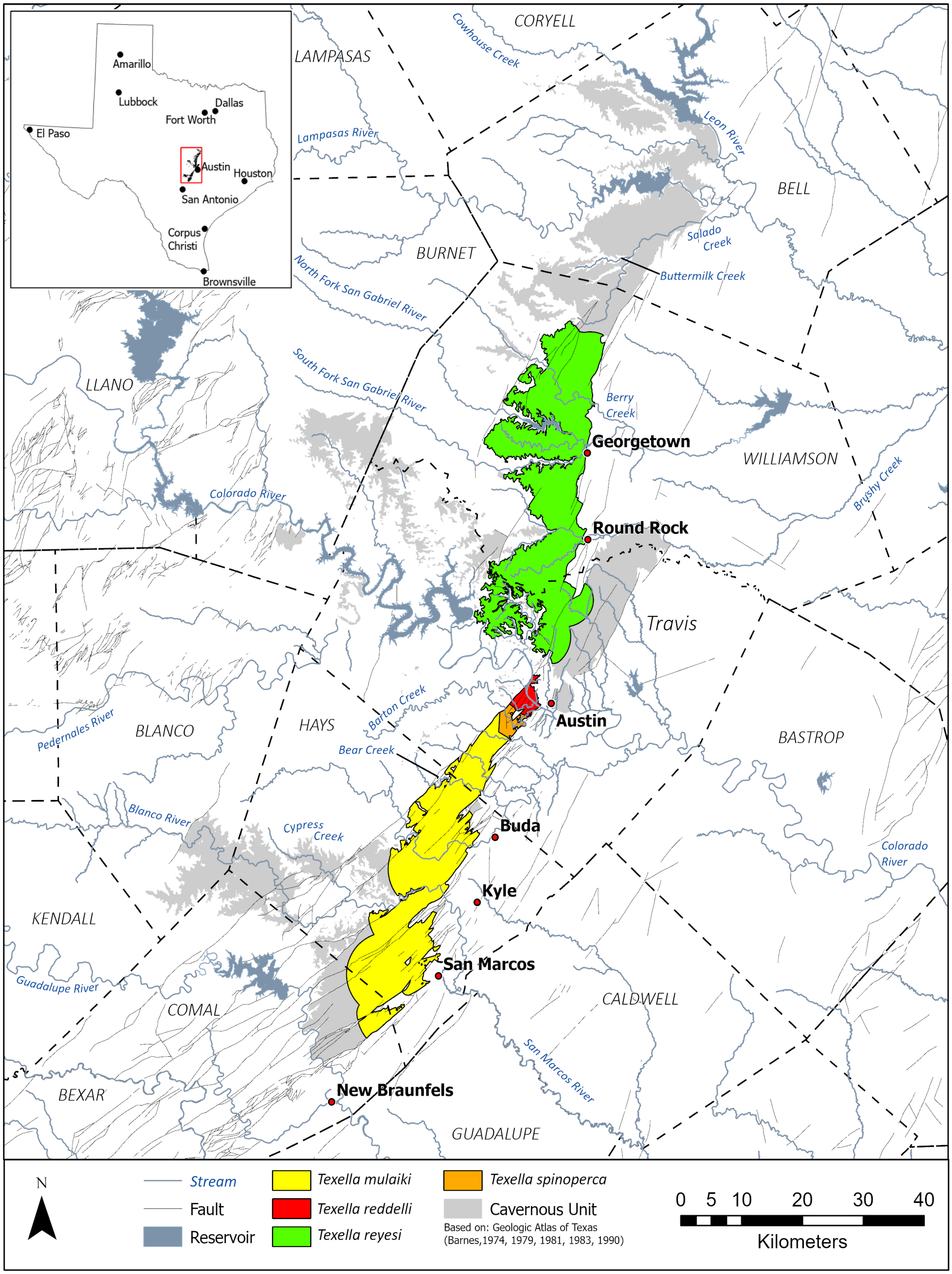

Figure 12. *Ranges of* Texella *species.*

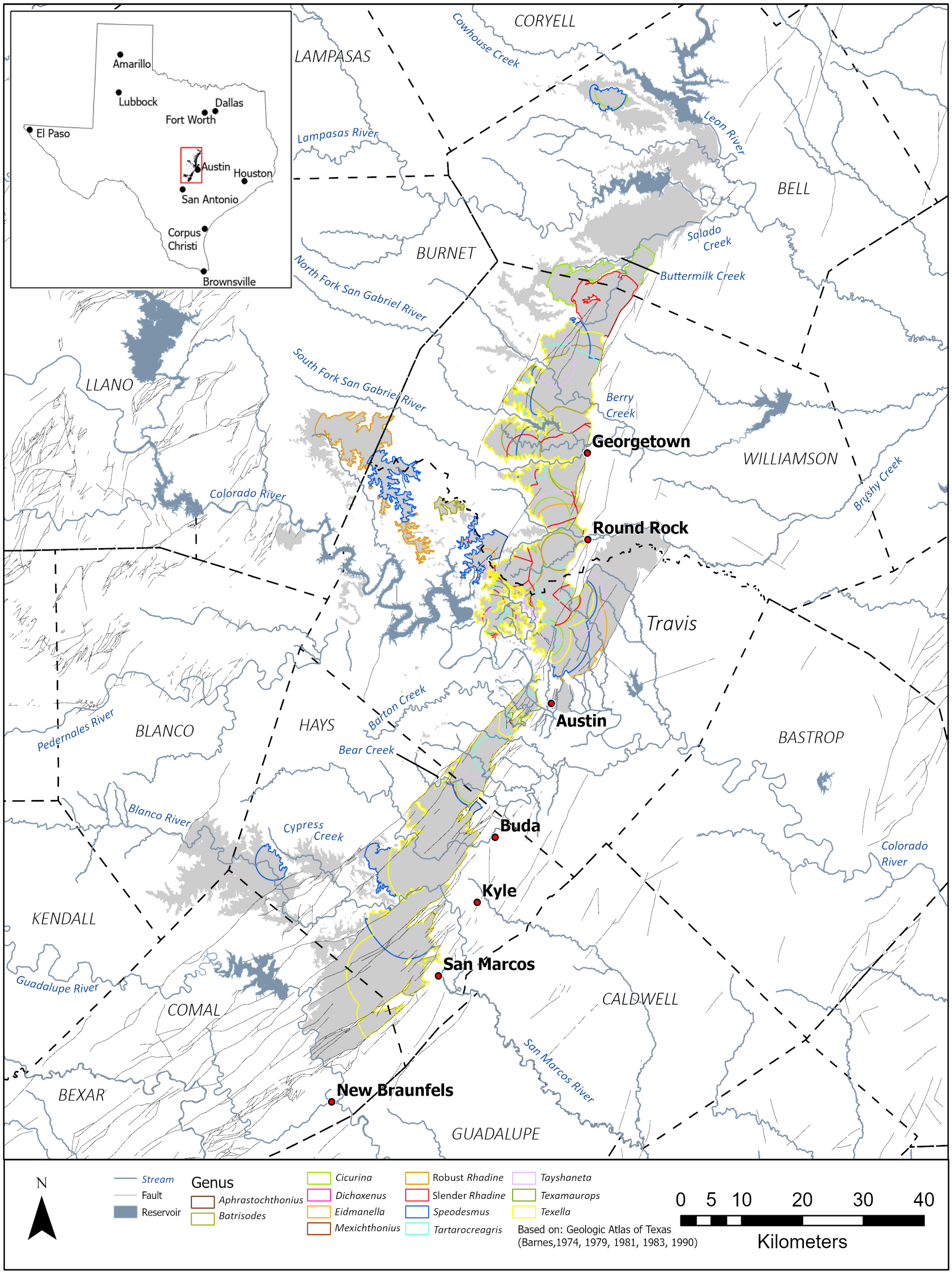

Figure 13. *Combined ranges of all species.*

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 a feature or features account for the cluster. If so, a KFR boundary is drawn along that feature. The KFR boundary is required to occur 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 and 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, this evaluation is conducted without any consideration given to 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 does not 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 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

The most critical of the karst zones is Zone 1, where the endangered species are known to occur. When the existing maps were first drafted in 1992, only 43 caves were known to contain federally listed endangered karst species in the study area. When Veni and Martinez (2007) updated the karst zones, 249 caves were known or reported to contain listed species. That study, and a revision of similar karst zones in the San Antonio, Texas, area (Veni, 2003), found that wherever caves with habitat appropriate for the listed species were found in Zone 2, that the endangered species were often found—confirming Zone 2 as an area of high probability for containing the federally listed species.

For this study, a total of 291 caves are known to contain (255) or are reported as potentially containing (36) the endangered karst species. This increase in the number of localities requires additional revision of Zone 1 for more effective species management, study, and protection. The need for revision is not limited to the discovery of new species localities but also due to better understanding of their ranges through this report's KFR boundary analyses.

Additionally, the remaining two zones are revised as needed with two notable related changes from the earlier zone maps. Previously, Zone 3 was defined as "areas that probably do not contain endangered cave fauna" and Zone 4 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 troglobite species but which have a low probability of containing endangered karst species because the habitat is occupied by other troglobite species;
- Zone 3b: areas which have a low probability of containing endangered karst species because they are poorly suited for troglobite species;
- Zone 4a: areas suitable for troglobite species but which do not contain endangered karst species because the habitat is occupied by other troglobite species;
- Zone 4b: areas which do not contain troglobite species.

The karst zones are revised based on the GIS karst zone files developed by Veni and Martinez (2007). Any issues resulting from the software advance of ArcGIS – ArcInfo 9.1, state-of-the-art in 2007, to the currently most advanced software version, ArcPro 2.6.0, are addressed before further work is conducted.

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 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 Bee Cave Marl, Cedar Park Limestone and Comanche Peak Limestone, Georgetown Formation, and undivided Georgetown Formation and Del Rio Clay, where the potential for collapse into caves in the underlying cavernous unit occurs; additionally Zone 3b occurs in the Austin Chalk, because it is poorly cavernous in the study area, and in the Comanche Peak Limestone where it interfingers with the Edwards Limestone and could contain small caves.
- Zone 4a is in areas of the cavernous unit which are sufficiently distant from the endangered karst species to preclude their presence, and where a

different suite of troglobites are 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 and 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) and specifically for the study area (summarized by Stafford and Arens, 2014), and on biological information and the KFR modeling on the distribution of endangered and non-endangered troglobite species. The principles used to delineate specific zone boundaries are to identify hydrogeologic and/or topographic features that may restrict the distribution of the endangered species, and examine the KFR modeling's distribution of endangered and non-endangered troglobite species for indications that the zone boundaries are valid. Contacts between geologic units where caves are common, versus units where caves are rare or absent, are the most reliable factors in delimiting Zone 1 boundaries. These sometimes occur in valleys where erosion has removed one unit and exposed another. They can also occur along faults where one unit may be juxtaposed against another.

Many Zone 1 boundaries are not simple to define. Except for newly added factors 5 and 6 below, the following zone delineation methodology follows that established by Veni and Martinez (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. Comparison of the lowest known cave elevation 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. Examination of the distribution of federally listed and non-listed troglobites in different caves. If the troglobite and especially the endangered troglobite fauna are similar, the caves may warrant grouping into a single zone. The quality of the collections is weighed as well. Collections conducted only once, under poor conditions, cursorily, and/or by non-specialists in the collection of cave species, are given greater weight for similarity of species, since more detailed studies would likely yield more similarities.
3. The type and extent of cave development in the area will indicate 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 federally listed species, demonstrates the presence of potential habitat for the species, unless the caves have been carefully surveyed and the species were not found
5. The GIS-modeled ranges of the endangered karst species, primarily, with some consideration of the non-endangered 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, but their presence, especially if high confidence exists in the tentative identification, may assist in refining boundary details.

These 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 were applied to other zones if additional considerations were needed beyond lithology and the species present.

Karst Fauna Region Boundary Analysis

The following subsections use the GIS modeling to evaluate the boundaries between all previously established KFRs 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 evaluations occur in a general south-to-north order, with a westward detour midway to the Cedar Park, Jollyville Plateau, and Post Oak Ridge KFRs. The conclusions of this report provide summary descriptions of all KFRs based on this following assessment.

North Hays County – South Travis KFR Boundary

George Veni and Associates (1992) described the bed of Bear Creek through the Edwards Limestone as the boundary between the North Hays County and the South Travis County KFRs. The creek approximately straddles the Hays-Travis County line in that area. Both KFRs are delimited by erosion and faults along their northwest and southeast edges, perpendicular to the creek, which mark the end of the cavernous unit in those directions (Figure 1).

Figure 13 illustrates a cluster of four range margins in the Bear Creek area:

1. *Cicurina bandida* (Figure 5),
2. *Rhadine austinica* (Figure 8),
3. *Speodesmus bicornourus* (Figure 9), and
3. *Tayshaneta sandersi* (Figure 11).

The range margins have an average length of 5.1 km and occur within a 3.2-km width, qualifying as a cluster. Two additional species also occur through this area: *Speodesmus* n. sp. millipedes (Figure 9) and *Texella mulaiki* harvestmen (Figure 12). With four of the six species in the area (67%) occurring at their range margins, and no modeling artifacts observed in the ranges, the cluster suggests a potential KFR boundary.

While the cavernous unit was based on the 1:250,000 scale Geologic Atlas of Texas for uniform application across the study area, Small et al. (1996) provide a more detailed 1:24,000 geologic map of the Edwards Aquifer area south of the Colorado River, which offers additional insight to geologic factors that might affect species distribution. Faults and lithology are evaluated and neither have any influence on the species' ranges. The range margins are perpendicular to the faults and five of the six species occur on each side of the major faults within both the Kainer and Person formations of the Edwards Limestone Group.

Following additional study, the bed of Bear Creek remains as the KFR boundary in this area:

- The creek occurs within the range cluster.
- None of the localities for the three species whose ranges create this cluster are known to extend southwest across the creek, and neither does *Speodesmus bicornourus* whose range ends 3 km further southwest of the cluster.
- Bear Creek cuts through the cavernous unit along much of its length, reducing the width of the cavernous unit almost in half to about 4.2 km with only the basal portion of the cavernous unit (Kainer Formation) present for all but approximately 300 m.
- As the elevation of the creek bed descends from 240–215 m in that area, the water table descends from about 229–168 m (e.g. Scanlon et al, 2001) downstream, leaving only an 11–47-m vadose zone that the species could potentially cross, except that the vadose zone at creek level is periodically flooded and otherwise often too moist for the species' habitat preferences.

This KFR boundary along Bear Creek is a restriction to species distribution because it limits but does not absolutely prevent troglobitic species from crossing the boundary.

South Travis – Rollingwood KFR Boundary

George Veni and Associates (1992) described the bed of Barton Creek through the Edwards Limestone as the boundary between the South Travis County and Rollingwood KFRs. Both KFRs are delimited by erosion and faults along their northwest and southeast edges, perpendicular to the upstream portion of the creek, which mark the end of the cavernous unit in those directions (Figure 1).

Figure 13 illustrates a cluster of seven range margins in the Barton Creek area:

1. *Mexichthonius exoticus* (Figure 3),
2. *Tartarocreagris altimana* (Figure 10),
3. *Tartarocreagris intermedia* (Figure 10),
4. *Tayshaneta sandersi* (Figure 11),
5. *Texella mulaiki* (Figure 12),
6. *Texella reddelli* (Figure 12), and
7. *Texella spinoperca* (Figure 12).

The range margins have an average length of 4.1 km and occur within a 3.9-km width, qualifying as a cluster. Four additional species also occur through this area:

1. *Cicurina bandida* (Figure 5),
2. *Rhadine austinica* (Figure 8),
3. *Speodesmus bicornourus* (Figure 9), and
4. *Speodesmus* n. sp. (Figure 9).

Three of the list of seven species are single-site endemic pseudoscorpions, *Mexichthonius exoticus*, *Tartarocreagris altimana* and *Tartarocreagris intermedia*, which could potentially introduce minor modeling artifacts, but none are apparent. Therefore, with seven of the eleven species in the area (63.7%) occurring at their range margins, the cluster suggests a potential KFR boundary.

Using the geologic map of Small et al, (1996), faults and lithology were evaluated and neither have any influence on the species' ranges. The range margins are perpendicular to the faults and three of the four non-site endemic species are present on each side of the major faults, occurring within both the Kainer and Person formations.

Following additional study, the bed of Barton Creek remains as the KFR boundary from where the creek flows onto the cavernous unit to where non-cavernous rock occurs in its valley about 250 m southeast of the Barton Springs Fault. Contrary to the initial definition of the boundary by George Veni and Associates (1992), rather than follow the creek northeast to the Colorado River, the boundary follows the edge of the cavernous unit east of Barton Creek on the northwest side of the Barton Springs Fault. While no biologically surveyed caves are known within the 2.3-km long by up to 750-m wide area between the fault and that lower section of the creek, it occurs within the modeled ranges of the species limited to the Rollingwood KFR (*Mexichthonius exoticus*, *Tartarocreagris altimana*, and *Texella reddelli*), as well the other four troglobites known from that KFR.

The justification for the northwest to southeast section of Barton Creek as the KFR boundary starts with it occurring centrally within the range cluster. Additionally:

- None of the seven species whose ranges create this cluster have localities on the opposite sides of the creek from where their known localities occur.
- The range of *Tartarocreagris proserpina*, another single-site endemic pseudoscorpion not included in the cluster, extends northeast to within 700 m of the cluster and potentially also reflects this boundary.
- Barton Creek cuts through most of the cavernous unit along this 6.4-km path, with only the basal portion of the cavernous unit (Kainer Formation) present for all but approximately 850 m.
- As the elevation of Barton Creek's bed descends from 209–148 m in that area, the water table descends from approximately 160 m to the aquifer's water table at 134 m at Barton Spring (e.g. Scanlon et al, 2001) about 2.4 km downstream, leaving a 14–49-m vadose zone that the species can potentially cross, except that the vadose zone at creek level is periodically flooded and otherwise often too moist for the species' habitat preferences.

This KFR boundary along Barton Creek is a restriction to species distribution because it limits but does not absolutely prevent troglobitic species from crossing the boundary.

Rollingwood – Central Austin KFR Boundary

George Veni and Associates (1992) described the bed of the Colorado River through the Edwards Limestone as the boundary between the Rollingwood and Central Austin KFRs. Both KFRs are delimited by erosion and faults along their northwest and southeast edges, perpendicular to the river, which mark the end of the cavernous unit in those directions (Figure 1).

The midline of the Colorado River was initially established as the simplified and practical boundary between the two KFRs. The Edwards Limestone portion of the cavernous unit extends from Rollingwood to the north side of the river where it has minor exposures. Non-cavernous rocks separate it from the Austin Chalk portion of the cavernous unit by about 2.5 km. Based on unpublished data from the Texas Speleological Survey, only nine caves are known in this continuation of the Edwards Limestone immediately north of the river. Six are small, in a cliff, have not been investigated biologically, and do not seem likely to contain troglobites based on their descriptions. Two have been destroyed from overlying development of downtown Austin. The remaining cave, Austin Caverns, was surveyed biologically with no troglobites found; it is structurally unstable, generally inaccessible, and unlikely to be surveyed further. Consequently, there is insufficient information about troglobite species in the Edwards Limestone immediately north of the river to postulate on its biological status, which is partly why the river was designated the KFR boundary.

Figure 13 illustrates six species ranges extending beyond the Rollingwood KFR, as much as 2.7 km into the Edwards Limestone on the north side of the Colorado River, although they have not been found north of the river:

1. *Cicurina bandida* (Figure 5),
2. *Mexichthonius exoticus* (Figure 3),
3. *Rhadine austinica* (Figure 8),
4. *Speodesmus* n. sp. (Figure 9),
5. *Tartarocreagris altimana* (Figure 10), and
6. *Texella reddelli* (Figure 12).

It also shows six species ranges extending south in the Central Austin KFR toward the south end of the cavernous unit closest to the river:

1. *Cicurina travisae* (Figure 5),
2. *Eidmannella reclusa* (Figure 6),
3. *Rhadine subterranea subterranea* (Figure 8),
4. *Tartarocreagris infernalis* (Figure 10),
5. *Tayshaneta myopica* (Figure 11), and
6. *Texella reyesi* (Figure 12).

Of these, *Tayshaneta myopica* is excluded from consideration because while the modeled range margin for the spider is near the southern edge of the Central Austin KFR, the nearest known localities are 11.5 km from that edge so this species may not be a reliable indicator of boundary conditions. Only one of the

39 species examined by this study is known to occur on both sides of the river: *Speodesmus bicornourus* (Figure 9). Therefore, with 10 of the 11 species in the area (90.9%) occurring no further than the Colorado River, this clustering suggests the river is a potential KFR boundary.

The geology of central and western Austin is mapped in more detail than the Geologic Atlas of Texas, at a scale of 1:62,500, by Garner and Young (1976) and that map is used for additional insight to geologic factors that might affect species distribution. Faults are not an influence since the range margins are perpendicular to the faults and the species occur in different faults blocks in the Rollingwood KFR. Lithology is partially examined and found to have no effect on species distribution. South of the river the species occur in both the Kainer and Person formations of the Edwards Limestone Group. Lithology was not examined north of the river because all the caves are in the Edwards Limestone, which is mapped as one unit and not divided into two formations.

Although the Edwards Limestone crops out on the north side of the river and the modeling extends the ranges of six species there, none of these species occur in this area to link it to the Rollingwood or Central Austin KFRs. Therefore, the bed of the Colorado River remains as the KFR boundary in this area. The river has flowed continuously since Austin's settlement in the 1830s, demonstrating that any potential terrestrial troglobite habitat below the river has been submerged and inaccessible to the 39 species for at least about 190 years. This would suggest the river is a barrier to species distribution, except that *Speodesmus bicornourus* occurs on both sides of the river. The species is peripatetic and an older troglobite than some other millipede species (Elliott, 1976) and possibly crossed the river during unrecorded prehistoric droughts. This KFR boundary along the Colorado River is therefore identified as a modern barrier but former restriction to species distribution. It currently prevents troglobitic species from crossing that area, but at some undetermined point in the past it likely allowed some species to cross.

Central Austin – McNeil-Round Rock KFR Boundary

George Veni and Associates (1992) described an area with a thin and narrow section of Edwards Limestone south of the McNeil area as the boundary between the north end of the Central Austin and southeast end of the then McNeil (later McNeil-Round Rock) KFRs. The Central Austin KFR is additionally delimited by the eroded end of the cavernous unit along its western and southern edges and faulting that truncates the cavernous unit to the east. The McNeil-Round Rock KFR is also defined by the same faulting to the east, Brushy Creek to the north, the eroded end of the cavernous unit to the northwest, and the boundary with the Cedar Park KFR to the west (Figure 1).

Figure 13 illustrates the most complex cluster of species ranges in this study in the Central Austin KFR area. Close examination shows they are two clusters, one extends generally south-to-north and the other heads predominantly west from that north end. The south-to-north cluster is discussed below first.
The south-to-north cluster follows the fault along the east edge of the Central Austin KFR. The cavernous unit occurs on both sides of the fault, with Edwards Limestone on the west and Austin Chalk on the east side. When the Central Austin KFR was initially delineated, no caves were known in that section of the Austin Chalk. Although named a chalk, its beds vary from highly cavernous limestone to clay-rich non-cavernous marls. The most extensive Austin Chalk caves occur about 125 km to the southwest in San Antonio, while only one small cave is known in Travis County, about 20 km south of the Central Austin KFR. However, small, humanly impassible karst conduits are known in the Austin Chalk in parts of its exposure in Travis County, which explains the presence of *Texella* sp. troglobites in Stark's North Mine (a historical dug tunnel) found since George Veni and Associates' 1992 KFR delineation. Originally described as the endangered *Texella reddelli* harvestman by Ubick and Briggs (2004), genetic studies by Hedin and Derkarabetian (2020) strongly indicate that species occurs only south of the Colorado River. USFWS conferred with Darrell Ubick regarding the Stark's North Mine locality and, for purposes of this study, the *Texella reddelli* specimen from that location will be considered a tentative locality for that species and not included in the species range until it can be genetically examined (Jenny Wilson, USFWS, personal communication, 2020).

While no troglobites from the Austin Chalk could be included in the analysis of species ranges, the Austin Chalk was included as a part of the cavernous unit. Nine species ranges comprise the south-to-north cluster in that Austin Chalk-Edwards Limestone area:

1. *Cicurina buwata* (Figure 5),
2. *Cicurina travisae* (Figure 5),
3. *Eidmannella reclusa* (Figure 6),
4. *Rhadine subterranea mitchelli* (Figure 8),
5. *Rhadine subterranea subterranea* (Figure 8),

6. *Speodesmus bicornourus* (Figure 9),
7. *Tartarocreagris infernalis* (Figure 10),
8. *Tayshaneta myopica* (Figure 11), and
9. *Texella reyesi* (Figure 12).

The range margins have an average length of 9.4 km and occur within an 8.1-km width, qualifying as a cluster. With no modeling anomalies detected and no other species extending beyond the cluster, the presence of all nine species in the area (100%) occurring at their range margins suggests the cluster is a potential KFR boundary.

Examination of the Geologic Atlas of Texas and Garner and Young's (1976) geologic map reveals that all nine species occur in the Edwards Limestone. What is not clear is if this represents a sampling bias, because caves are known only in the Edwards to access and collect troglobites. Additionally, without more species for analysis from the Austin Chalk, it is unknown if its conduits (and associated differences in nutrient and moisture inputs) create different habitat conditions that result in a different suite of troglobite species. There is no evidence that the fault between the Austin Chalk and Edwards Limestone creates any restrictions to species distribution beyond that resulting from the different lithologies, but the fault's alignment with the range margins and as the border between the lithologies reaffirms it as the eastern boundary of the Central Austin KFR.

The distribution of *Cicurina travisae* spiders as discussed above and below, requires special note. Figure 5 shows its range occurs in the Central Austin and Jollyville Plateau KFRs, divided by Bull Creek. Hedin (2015) shows the population of *Cicurina travisae* in Central Austin in a different subclade from *Cicurina travisae* on the Jollyville Plateau. This genetic drift is likely the result of Bull Creek cutting through the Edwards Limestone and separating the populations, although the possibility that the population was once connected via the contiguous limestone that wraps around Bull Creek to the north cannot be discounted. In either case, the populations of *Cicurina travisae* in both KFRs seem genetically distinct and their ranges in each KFR are evaluated separately.

From the approximate north end of the Austin Chalk-Edwards Limestone fault, the second cluster of range margins extends west for 7.5 km and 1 km to the east. Seven species range margins comprise this cluster:

1. *Cicurina buwata* (Figure 5),
2. *Cicurina travisae* (Figure 5),
3. *Rhadine subterranea mitchelli* (Figure 8),
4. *Tartarocreagris domina* (Figure 10),
5. *Tartarocreagris infernalis* (Figure 10), and
6. *Tayshaneta myopica* (Figure 11).

The remaining seven range margins have an average length of 6.8 km and occur within a 6.1-km width, qualifying as a cluster.

This cluster marks the northern limit of *Cicurina travisae* and *Tartarocreagris infernalis* and the southern limit for *Cicurina buwata*, *Rhadine subterranea mitchelli*, *Tartarocreagris domina*, and *Tayshaneta myopica*. Additionally, four other species occur through the cluster area, but their margins are not part of the cluster:

1. *Eidmannella reclusa* (Figure 6),
2. *Rhadine subterranea subterranea* (Figure 8),
3. *Speodesmus bicornourus* (Figure 9), and
4. *Texella reyesi* (Figure 12)

With six of the ten species in the area (60%) occurring within the cluster, the cluster suggests a potential KFR boundary.

Examination of the Geologic Atlas of Texas and Garner and Young's (1976) geologic map reveals that faults are not an influence since the range margins are perpendicular to faulting and the one mapped fault ends north of the cluster. The existing KFR boundary in this area was drawn in 1992 across a peninsular outcrop of Edwards Limestone where the limestone was narrowest, about 1 km, and thinnest, no more than approximately 30 m. A contributing possible influence is the non-cavernous to poorly cavernous Comanche Peak Limestone, which interfingers with the Edwards Limestone in that area. Garner and Young (1976) show it pinches out about 300 m north of the KFR boundary, but it likely extends south to the boundary and could not be illustrated at Garner and Young's map scale. If so, it could restrict cave development at the boundary to an even thinner area.

Few caves had been surveyed biologically in this area during the 1992 study. Currently, the Texas Speleological Survey (unpublished data, 2020) shows at least 13 caves have been surveyed within about 4 km of the 1992 KFR boundary, seven to the south and six to the north; the species evaluated in this study have not been found in all 13 caves. Of the six species whose range margins occur in this area, none of the southern species' localities occur north of that KFR boundary and none of the northern species' location occur south of the boundary. All these factors affirm the validity of the original 1992 KFR boundary, which is a restriction to species distribution because it limits but does not absolutely prevent troglobite species from crossing the boundary.

McNeil-Round Rock – Cedar Park KFR Boundary

Veni and Martinez (2007) described the McNeil-Round Rock KFR as bounded by the Central Austin KFR to the southeast, a major fault that marks the limit of the cavernous unit to the east, Brushy Creek to the north, the eroded limits of the cavernous unit to the northwest along the Brushy Creek valley and to the south along the Bull Creek valley, and along the Cedar Park KFR boundary to the west (Figure 1). The boundary with the Cedar Park KFR was based on species distribution since no geological or hydrological features were found along which to align the boundary.

Figure 13 illustrates seven species ranges in the vicinity of the McNeil-Round Rock – Cedar Park KFR boundary:

1. *Batrisodes reyesi* (Figure 4),
2. *Rhadine persephone* (Figure 7),
3. *Rhadine* n. sp. 1 (Figure 8),
4. *Rhadine* n. sp. 2 (Figure 8),
5. *Rhadine subterranea subterranea* (Figure 8),
6. *Tartarocreagris domina* (Figure 10), and
7. *Tartarocreagris infernalis* (Figure 10).

Of these, *Batrisodes reyesi* is excluded from consideration because the nearest known locality of the beetle is 7 km from the cluster so this species may not be a reliable indicator of cluster or boundary conditions. Additionally, *Tartarocreagris infernalis* is credited for half a range because its range is limited in the southern half of the cluster but not the northern half.

The remaining six range margins have an average length of 6.0 km and occur within a 2.2-km width, qualifying as a cluster. Five other species occur through the cluster area, but their margins are not part of the cluster:

1. *Cicurina buwata* (Figure 5),
2. *Eidmannella reclusa* (Figure 6),
3. *Speodesmus bicornourus* (Figure 9),
4. *Tayshaneta myopica* (Figure 11), and
5. *Texella reyesi* (Figure 12).

Tartarocreagris infernalis is also half-credited as crossing the cluster. With 5.5 of the 11 species in the area (50%) occurring within the cluster and no other modeling artifacts observed, the cluster suggests a potential KFR boundary.

Garner and Young's (1976) geologic map shows a short southwest-trending fault near the northwest end of the cluster, but it cuts through the middle of the range of *Rhadine* n. sp. 1 with no effects on its distribution. No lithologic factors affecting species distribution were identified from that map or the Geologic Atlas of Texas.

An important factor affecting species distribution is observed in unpublished data from the Texas Speleological Survey (2020), which show a 3-km wide north-south area, with no known caves, aligned with the cluster. Twenty-seven caves are recorded within 1 km of this area, with 16 to the east and 11 to the west. Mike Warton (personal communication, 2020) reports most of this area has been searched professionally for caves and none were found. Potential karst features were found but when excavated most led to unfractured limestone beds and the rest ended in hard-packed clay. He further comments that none of the geotechnical borings in this area, averaging about 6 m deep, encountered notable voids or solutioned zones and may suggest a thinning and/or base of the Edwards Limestone with the interfingered and poorly cavernous Comanche Peak Limestone. These observations suggest an unmapped change in the geology that prevents cave development, at least near the surface if not the entire thickness of the Edwards, to create the range cluster. If cave development occurs at depth, the presence of the range cluster indicates that moisture and nutrient input from the surface may restrict species distribution.

Two final factors in evaluating this cluster are Hedin's (2015) genetic study of *Cicurina* and Hedin and Derkarabetian's (2020) genetic study of *Texella*. The former study found two distinct subclades of *Cicurina buwata*, one extending to within 800 m of the west side of the cluster and the other within 2.4 km of its east side. The latter study similarly found different subclades of *Texella reyesi* on either side of the cluster. Along with the tightly clustered ranges, these results support the presence of the Cedar Park – McNeil-Round Rock KFR boundary but redrawn from its original position. The new boundary is 3 km eastward and established as a nearly north-south 9.3-km long line down the axis of the cluster at the narrowest point in that area, between tributaries of Brushy and Bull creeks. This KFR boundary is a restriction to species distribution because it limits but does not absolutely prevent troglobitic species from crossing the boundary.

Cedar Park – Jollyville Plateau KFR Boundary

George Veni and Associates (1992) described the Jollyville Plateau KFR as connecting at its north end to the Cedar Park KFR through a narrow, winding, section of the cavernous unit at the head of Cypress Creek. They also connected the Jollyville Plateau's KFR to the McNeil-

Round Rock KFR in two locations, mostly at the northeast end and through another narrow, winding section of the cavernous unit, this one along the north side of the Bull Creek valley (Figure 1) in areas now occupied by the eastward-expanded Cedar Park KFR per the previous subsection.

Figure 13 illustrates six species ranges in the area of the former northeast Jollyville – McNeil-Round Rock boundary:

1. *Texamaurops reddelli* (Figure 4),
2. *Cicurina buwata* (Figure 5),
3. *Cicurina travisae* (Figure 5),
4. *Rhadine* n. sp. 2 (Figure 8),
5. *Tartarocreagris attenuata* (Figure 10), and
6. *Tartarocreagris infernalis* (Figure 10).

These range margins have an average length of 1.8 km and occur within an 0.8-km width, qualifying as a cluster. Five other species occur through the cluster area, but their margins are not part of the cluster:

1. *Eidmannella reclusa* (Figure 6),
2. *Rhadine persephone* (Figure 7),
3. *Speodesmus bicornourus* (Figure 9),
4. *Tayshaneta myopica* (Figure 11), and
5. *Texella reyesi* (Figure 12).

With six of the 11 species in the area (58.3%) occurring within the cluster, the cluster suggests a potential KFR boundary. Supporting this result, Hedin and Derkarabetian (2020) found two distinct genetic subclades of *Texella reyesi* on either side of the cluster, and the range of *Rhadine subterranea mitchelli* is within 600 m to the south of qualifying as part of the cluster.

The Geologic Atlas of Texas and Garner and Young's (1976) geologic map show no faults in the area. The only geologic constraints are the thinning of the cavernous unit from the interfingering of the Comanche Peak Limestone with the Edwards Limestone and the thinning and narrowing of the cavernous unit from headward erosion from the east by Bull Creek and from the west by Cypress Creek.

Four major constrictions in the cavernous unit occur in the cluster area that could represent a KFR boundary. The southernmost was eliminated as two localities for *Cicurina travisae* spiders occur north of this constriction. *Tartarocreagris infernalis* pseudoscorpions are also present in the western of those localities, McDonald Cave. The localities for *Texamaurops reddelli*, *Cicurina buwata*, *Rhadine* n. sp. 2, *Rhadine subterranea mitchelli*, and *Tartarocreagris attenuata* are too distant from the potential boundaries to provide any insights. However, while *Rhadine persephone* carabid beetles and *Speodesmus bicornourus* millipedes are distributed well beyond these potential boundaries, their localities suggest distribution through the narrow section of the cavernous unit to the northern Jollyville Plateau – Cedar Park KFR boundary described at the start of this subsection. The most equitable accounting for the distribution of all these species requires the Jollyville Plateau – Cedar Park KFR boundary be redrawn, not at one of the four constrictions but at a slightly wider area about 1 km south of the former Jollyville – McNeil-Round Rock KFR boundary. While the Geologic Atlas of Texas basemap shows this boundary as 2.5 km long, it measures as only 1.8 km on the more detailed map of Garner and Young (1976). This KFR boundary is a restriction to species distribution because it limits but does not absolutely prevent troglobitic species from crossing the boundary.

The second KFR boundary must occur within the narrow outcrop at the north end of Bull Creek. While the margins of the four species in that area (*Texamaurops reddelli*, *Cicurina travisae*, *Rhadine persephone*, and *Tartarocreagris attenuata*) are distributed only 2.4 km apart, the average 200 m width of the area prevents the range margins from strictly meeting the cluster guidelines established in this study's methodology. Using instead the methodology's guidance on karst zone boundaries, this KFR boundary remains unchanged from Veni and Martinez (2007) and follows the bed of a short creek where the cavernous unit is thinnest, averaging about 3–5 m.

Figure 13 shows other range clusters near the south and southeast ends of the Jollyville Plateau, but they are not considered KFR boundary candidates. They mark the short gaps to the ends of the cavernous unit where caves have not been found or biologically investigated, and where further study would almost certainly extend those ranges to the edges of the cavernous unit.

Cedar Park KFR Boundary

The Cedar Park KFR was established by George Veni and Associates (1992) based on biological affinities between two cavernous areas. They are separated by a non-cavernous area, as much as 1.6 km wide, that trends southwest along South Brushy Creek to include the downstream 2.3-km of Buttercup Creek. It then meanders south 3.1 km as the 100- to 300-m wide outcrop of the poorly cavernous Comanche Peak Limestone (Figure 1). Following additional biological surveys in the Cedar Park KFR by many investigators, Veni and Martinez (2007) recommended:

> *The Cedar Park Karst Fauna Region should probably be managed as two distinct karst*

fauna regions, as indicated by the new Zone 1 boundaries, distribution of listed and non-listed troglobites, and the geological and topographical features that affect karst species distribution. Analysis of troglobites in these zones and the adjoining karst fauna regions, per recommendation #1 above, is especially warranted.

Recommendation #1 is the study now conducted as this report, and the specific recommendation for the Cedar Park KFR is evaluated here.

Figure 13 illustrates the margins of five species ranges which end where the cavernous unit contacts the eastern edge of the intervening non-cavernous rocks:

1. *Rhadine* n. sp. 2 (Figure 8),
2. *Tartarocreagris attenuata* (Figure 10),
3. *Tartarocreagris infernalis* (Figure 10),
4. *Tayshaneta myopica* (Figure 11), and
5. *Texella reyesi* (Figure 12).

None of the species in this study are limited to the area west of the non-cavernous rocks. The ranges of the following seven species occur on both sides of the non-cavernous area:

1. *Batrisodes reyesi* (Figure 4),
2. *Cicurina buwata* (Figure 5),
3. *Eidmannella reclusa* (Figure 6),
4. *Rhadine persephone* (Figure 7),
5. *Rhadine* n. sp. 1 (Figure 8),
6. *Speodesmus bicornourus* (Figure 9), and
7. *Texella reyesi* (Figure 12)

However, *Batrisodes reyesi* and *Eidmannella reclusa* are excluded from further consideration. Although *Batrisodes reyesi* is found on each side of the non-cavernous area, its nearest locality to the east is 7.2 km away and to the west it is 10 km distant. Given the extensive biological studies in the Cedar Park area, the absence of this mold beetle from those collections indicates it is not locally present and thus not a good indicator of potential boundary conditions. Similarly, while *Eidmannella reclusa* has a modeled range that occurs on both sides of the non-cavernous area, this spider is only known from the east side, with the nearest locality and about 6 km distant, and may also be an unreliable indicator of boundary conditions.

Rhadine n. sp. 1, which occurs on both sides of the non-cavernous area requires additional mention. It seems partly segregated by the non-cavernous unit but is interpreted as once having a contiguous extent on both sides until extirpated from part of its eastern range by *Rhadine* n. sp. 2. With five of the 10 species in the area (50%) occurring east of the non-cavernous area, a potential KFR boundary is indicated by the minimum standard of this study.

The boundary between the east and west parts of the Cedar Park KFR is primarily the non-cavernous rocks between them and thus a barrier to species distribution. The location of the boundary is less clear for the narrow section of the cavernous unit along the head of the Cypress Creek valley, between the south-trending section of the Comanche Peak Limestone and the eroded edge of the cavernous unit about 500 m to the west. Garner and Young (1976) provide the most detailed geologic map of that area and identify only one short southwest-trending and low-displacement fault that ends within that narrow outcrop at its north end, but the occurrence of the same endangered species in caves on either side of the fault shows it does not affect species distribution. No other caves are known in that outcrop for any species evaluated in this report. The boundary between what is now designated the East Cedar Park and West Cedar Park KFRs is the area where the cavernous unit is thinnest on average and among the narrowest locations at about 110 m. It is a restriction to species distribution because it limits but does not absolutely prevent troglobitic species from crossing the boundary. This boundary location is also supported as the approximate center of the modeled range margins for *Rhadine* n. sp. 1, *Tartarocreagris infernalis*, *Tayshaneta myopica*, and *Texella reyesi*.

While the splitting of the Cedar Park KFR into two KFRs is supported by the minimum standards of this study, continued study of the area's karst fauna, especially in the West Cedar Park KFR, may provide additional support. *Batrisodes reyesi* is modeled as widely and discontinuously dispersed throughout four KFRs (Figure 4), including three localities at the northwest end of the West Cedar Park KFR. Further investigation could determine if it is in fact one or multiple mold beetle species. The West Cedar Park localities for this species, along a long, narrow, peninsular outcrop of the cavernous unit, are more prone to speciation than areas where the unit is broadly expansive.

Additionally, Sinkhole de Mayo was initially identified as containing the endangered *Texella reddelli* harvestmen, until Hedin and Derkarabetian (2020) found that species appears to be limited to south of the Colorado River putting that locality's *Texella reddelli* identification in doubt. While *Texella reyesi* is distributed broadly north of the river, it is not known in the West Cedar Park KFR. The core of that KFR, along the cavernous reach of Buttercup Creek, contains at least 41 biologically surveyed caves and karst features

(Texas Speleological Survey, unpublished data, 2020) where *Texella reyesi* should occur if its range extends through that area to Sinkhole de Mayo. The *Texella* from Sinkhole de Mayo requires more study.

Cedar Park – Post Oak Ridge KFR Boundary

George Veni and Associates (1992) described the Post Oak Ridge KFR as an isolated 33-km long ridge of Edwards Limestone and a cavernous horizon of the Walnut Formation. It extends northwest from the Cedar Park (now West Cedar Park) KFR, across the Sandy Creek tributary of the Colorado River (Figure 1). No endangered karst species were known in that KFR, which was reaffirmed by Veni and Martinez (2007) following additional biological surveys in the region by many investigators. Post Oak Ridge is included in this study for modeling purposes as a constraint on the distribution of the endangered karst species.

Figure 13 illustrates four species ranges extending northwest in the West Cedar Park KFR toward Post Oak Ridge:

1. *Cicurina buwata* (Figure 5),
2. *Eidmannella reclusa* (Figure 6),
3. *Rhadine persephone* (Figure 7), and
4. *Rhadine* n. sp. 1 (Figure 8)

Only one species is limited to Post Oak Ridge, *Rhadine russelli* (Figure 7), and two species occur in both KFRs, *Batrisodes reyesi* (Figure 4) and *Speodesmus bicornourus* (Figure 9). Of the four species, *Eidmannella reclusa* is excluded from further consideration because while its modeled range margin ends in West Cedar Park, the spider's nearest known locality is in the East Cedar Park KFR and it may not be a reliable indicator of boundary conditions. With the margin of three of the five species (60%) in either the Post Oak Ridge or West Cedar Park KFRs this distribution suggests a potential KFR boundary.

The Geologic Atlas of Texas does not show any faults or other geologic factors that might affect species distribution. Neither does the mapped facies change on Post Oak Ridge from Edwards Limestone to the Walnut Formation, which is cavernous in that area. The only observed factor affecting species distribution is the absence of cavernous rock in the Sandy Creek valley between the KFRs, which indicates the boundary is a barrier to species distribution. Although the presence of *Batrisodes reyesi* and *Speodesmus bicornourus* in both KFRs may suggest a connection between the KFRs, they more likely represent a geologically recent severing of the KFRs by erosion removing the Edwards Limestone at the head of Sandy Creek. This might be confirmed by genetic study of these species, as suggested for some other species in the region.

McNeil-Round Rock – Georgetown KFR Boundary

George Veni and Associates (1992) described the bed of Brushy Creek through the Edwards Limestone as the boundary between the McNeil-Round Rock and Georgetown KFRs (Figure 1). This boundary is the southern margin of the Georgetown KFR; its west and east margins extend from the eroded western end of the cavernous unit to where the unit is truncated by faulting to the east.

Figure 13 illustrates nine species ranges occur at and north of Brushy Creek:

1. *Batrisodes reyesi* (Figure 4),
2. *Batrisodes texanus* (Figure 4),
3. *Cicurina browni* (Figure 5),
4. *Cicurina buwata* (Figure 5),
5. *Cicurina vibora* (Figure 5),
6. *Eidmannella reclusa* (Figure 6),
7. *Rhadine subterranea mitchelli* (Figure 8),
8. *Rhadine subterranea subterranea* (Figure 8), and
9. *Tayshaneta myopica* (Figure 11).

Of these, *Batrisodes texanus* and *Cicurina vibora* are excluded from further consideration because only small portions of their modeled range margins extend into the cluster. Also, their nearest known localities are about 11 km and 15 km north of Brushy Creek and are probably not reliable indicators of boundary conditions along the creek. (It is noted that *Rhadine subterranea mitchelli* occurs in discontinuous ranges 10 km to the south and 17 km southwest, interpreted as the result of former bio-geologic conditions, and only modern ranges are considered in this analysis.)

The seven remaining range margins have an average length of 6.2 km and occur within a 6.4-km width, which does not qualify as a cluster. However, excluding the most distant margin, *Tayshaneta myopica*, produces a six-species cluster with an average length of 5.8 km and within a 5.4-km width, which does qualify as a cluster. Three other species occur within the cluster area, but their margins are not part of the cluster: *Speodesmus bicornourus* (Figure 9), *Tartarocreagris infernalis* (Figure 10), and *Texella reyesi* (Figure 12). With six of the ten species in the area (60%) occurring within the cluster and no other modeling artifacts observed, the cluster suggests a potential KFR boundary. Supporting this result, Hedin and Derkarabetian (2020) found distinct genetic subclades of *Texella reyesi* occur on either side of the cluster.

Examination of the Geologic Atlas of Texas and an earlier detailed geologic map of the Brushy Creek area (Atchison, 1954) shows faults are not an influence in species distribution since the range margins are perpendicular to the faults and two of the species in the areas occur on each side of the faults; the rest of the species are located away from the small faulted area. There were no differences in lithology; all the caves are in the Edwards Limestone.

The only remaining hydrogeologic constraint is Brushy Creek which narrows the cavernous unit to 2.8 km and reduces its thickness. While the available Edwards Limestone increases eastward to nearly its full thickness at the eastern KFR fault boundary, the almost perennial flow of Brushy Creek keeps the Edwards saturated and inaccessible to terrestrial troglobites except during droughts. The presence of this boundary is also supported by the locations of the six species in the cluster. *Cicurina browni* is only known north of the creek, and the northern subrange of *Rhadine subterranea mitchelli* also stays north of the creek. In contrast, while the modeled ranges of the four remaining species extend from 0.8-3.9 km north of Brushy Creek, none of the species are found north of the creek. Additionally, although *Tayshaneta myopica* was not included in the cluster because it is 650 m too far north, it is also known only from the area south of Brushy Creek. This KFR boundary along Brushy Creek is a restriction to species distribution because it limits but does not absolutely prevent troglobitic species from crossing the boundary.

Georgetown – North Williamson KFR Boundary

George Veni and Associates (1992) described the bed of the South Fork of the San Gabriel River through the Edwards Limestone as the boundary between the Georgetown and North Williamson County KFRs (Figure 1). While the river was defined as the southern boundary of the North Williamson County KFR, its east and west boundaries are fault-bounded from the South Fork of the San Gabriel River north to near Berry Creek; further north, it is bounded by faulting to the east and by the eroded edge of the cavernous unit to the west.

Figure 13 illustrates five widely separated species ranges relative to the South Fork of the San Gabriel River:

1. *Batrisodes cryptotexanus* (Figure 4),
2. *Batrisodes texanus* (Figure 4),
3. *Cicurina vibora* (Figure 5),
4. *Rhadine noctivaga* (Figure 8), and
5. *Rhadine subterranea mitchelli* (Figure 8).

These range margins have an average length of 4.2 km and occur within a narrowest width of 13 km, thus not qualifying as a cluster.

However, *Batrisodes cryptotexanus Batrisodes texanus*, *Rhadine noctivaga*, and *Rhadine subterranea mitchelli* have an average length of 7.5 km and occur in a much narrower average width of 3 km, qualifying as a cluster. But this cluster is centered just north of the North Fork of the San Gabriel River, not the South Fork. (It is noted that *Batrisodes texanus* occurs in a discontinuous range 8.3 km north of the cluster, interpreted as the result of former bio-geologic conditions, and only modern ranges are considered in this analysis.) Four other species occur through the cluster area, but their margins are not part of the cluster:

1. *Cicurina vibora* (Figure 5),
2. *Speodesmus bicornourus* (Figure 9),
3. *Tartarocreagris infernalis* (Figure 10), and
4. *Texella reyesi* (Figure 12).

With four of the eight species in the area (50%) occurring within the cluster, the cluster suggests a potential KFR boundary.

Examination of the Geologic Atlas of Texas basemap and an earlier detailed geologic map of the central Williamson County area (Evans, 1965) reveals no differences in lithology that might affect species distribution; all the caves are in the Edwards Limestone. Faults were evaluated and are not an influence since the range margins are perpendicular to the trend of faulting at the edge of the cavernous unit and no faults are mapped within that part of the unit. An additional cluster of range margins is apparent in Figure 13 in the western half of area, extending north from the South Fork to the North Fork of the San Gabriel River. This cluster occurs parallel to the major direction of faulting, but the geologic maps do not show faults in that area. Instead, close examination shows this cluster is a modeling artifact resulting from fewer species localities in that area and that the actual margins of the species ranges have probably not been reached or at least not demonstrated; it does not suggest the presence of a KFR boundary.

The only remaining hydrogeologic constraint is the North Fork of the San Gabriel River, which narrows the cavernous unit to 3.5 km and reduces its thickness. While the available Edwards Limestone increases eastward to nearly its full thickness at the eastern KFR fault boundary, the almost perennial flow of the river keeps the Edwards saturated and inaccessible to terrestrial troglobites except during droughts. The presence of this boundary is also supported by the locations of three of the four species in the cluster. While the modeled margins of the clusters extend as far as 5 km north of the river, three of the species do not cross the river.

The genetic study by Hedin and Derkarabetian (2020) lends mixed support to this cluster analysis. They found two distinct subclades of *Texella reyesi* on either side of the original KFR boundary along the South Fork of the San Gabriel River, but also show a less deep genetic divide along the North Fork, supporting the river as a potential KFR boundary. For consistency and reproducibility of the methodology, these and other genetic results discussed in this report are noted but not heavily factored into the KFR boundary evaluation.

The bed of the North Fork of the San Gabriel River through the Edwards Limestone replaces the original KFR boundary between the Georgetown and North Williamson KFRs. It is a restriction to species distribution because it limits but does not absolutely prevent troglobitic species from crossing the boundary.

North Williamson – Bell County KFR Boundary
George Veni and Associates (1992) set the northern boundary of the North Williamson County KFR where the Williamson-Bell County line crosses the Edwards Limestone (Figure 1). No caves with federally listed karst species, or non-listed karst species in that study's analysis, were known within 11 km of that border while the cavernous Edwards Limestone continued north to and beyond that border with no obvious limit on species distribution. The KFR boundary was selected as a clearly identifiable boundary within the potential range of the species known at that time.

The cavernous unit in Bell County narrows gradually from nearly 17 km at the county line to 4 km along the Lampasas River 19 km to the northeast. Its western edge is the eroded limit of the cavernous unit and its eastern edge occurs where the cavernous unit dips under younger, non-cavernous formations. Clays become more prevalent northward in the cavernous unit; if they restrict cave development it is not evident because the area has not been searched well for caves. Ten caves are known and only two have been biologically surveyed (Texas Speleological Survey, unpublished data, 2020). Neither of those caves have troglobites relevant to this study. The nearest such caves are along the southern edge of Fort Hood 18 km further northwest. Those caves were included in this study's analysis to constrain the boundaries of the endangered karst species, but because of their 35-km distance from the nearest other cave in this analysis, they are not useful in establishing a more realistic boundary for the North Williamson County KFR.

Figure 13 illustrates a group of six species ranges mid-way along the length of the North Williamson County KFR:

1. *Batrisodes cryptotexanus* (Figure 4),
2. *Batrisodes texanus* (Figure 4),
3. *Speodesmus bicornourus* (Figure 9),
4. *Tartarocreagris infernalis* (Figure 10),
5. *Tayshaneta anopica* (Figure 11), and
6. *Texella reyesi* (Figure 12).

These range margins have an average length of 7.8 km and occur within a 3.8-km width, thus qualifying as a cluster. Two other species occur within the cluster area, but their margins are not part of the cluster: *Cicurina vibora* (Figure 5) and *Rhadine noctivaga* (Figure 8). With six of the eight species in the area (75%) occurring within the cluster, the cluster suggests a potential KFR boundary.

The Geologic Atlas of Texas shows no differences in lithology that might affect species distribution; all the caves are in the Edwards Limestone. Faults are not an influence since the range margins are perpendicular or sub-perpendicular to the trend of faulting and all eight species in the area occur in caves in different fault blocks. Like the evaluations of other KFR boundaries, the narrowing and thinning of limestone along streams cutting through the cluster area was considered, but unlike those evaluations, such a boundary was rejected near the cluster although applied further north.

A close examination of this cluster suggests it is a modeling artifact resulting from decreasing known species localities northward and no ranges from other species to constrain their extent. Many species localities occur in the well-studied Sun City area immediately south of US Highway 195, but few are known, and few properties have been searched for caves and species north of the highway. The major exceptions are Cobb Cavern and Coffin Cave, located respectively near the west and east margins of the cavernous unit. Both contain rich faunas, suggesting favorable habitat for troglobite species exists further north.

Recognizing that the modeled species ranges are not exact predictions of species distribution, the fact that the modeled ranges of *Cicurina vibora* and *Rhadine noctivaga*, which occur widely through the KFR, align with substantial portions of the Buttermilk Creek valley, the North Williamson County KFR boundary is defined as the limit of the cavernous unit along that valley and where the bed of the creek crosses the cavernous unit. This boundary is hydrologically and biologically more realistic than the county line. The cavernous unit is only 4.9 km wide, at its thinnest along the creek, and often saturated by stream flows which further limits the distribution of terrestrial troglobites. This KFR boundary is a restriction to species distribution because it limits but does not absolutely prevent troglobitic species from crossing the boundary.

Karst Zone Revision

Figure 14 illustrates the karst zones as defined by Veni and Martinez (2007). The following analysis focuses on the distribution of Zone 1, which has increased in size since 2007 based on new localities. In turn, Zone 2, where there was a high probability for endangered species but not known until this revision, has reduced in size. Zones 3 and 4 are expanded substantially beyond the limits of Veni and Martinez (2007) because the study area for this investigation was expanded. They were divided into two sub-zones, each based on their potential for endangered karst species in cavernous or poorly cavernous or non-cavernous rock.

It is beyond the scope of this report to describe the rationale for each specific zone boundary in detail. However, a general description of and explanation for the zone boundaries follows below in roughly south to north order by KFR. The KFRs which are not part of the above KFR boundary analysis are not proposed formally, but only as a mechanism to describe those areas where species in Table 1 (available online) occur beyond the KFRs evaluated above. It is beyond the scope of this report to fully analyze, and thus describe or define those informal KFR areas. Their boundaries, as approximated below, are shown on Figure 15 with the updated KFR boundaries described in the previous section.

Blanco-Cypress Karst Fauna Region

This KFR is informally designated as the outcrop of the Lower Member of the Glen Rose Limestone along the Blanco River, and its Cypress Creek tributary, in southern Blanco, northern Comal, and western Hays counties. Except for its southwest section, it is surrounded by the Upper Member of the Glen Rose, which is not cavernous in that area. The Lower Glen Rose outcrop continues south in the southwest part of the KFR, but the KFR is terminated at its 3-km long exposure along the surface water drainage divide between the Blanco and Guadalupe rivers.

No endangered karst species occur in this KFR. It was included in this study to constrain the distribution of the endangered karst species. Of the species listed in Table 1 (available online), only *Speodesmus* n. sp. (Figure 9) is confirmed here from one cave and *Cicurina bandida* is tentatively identified from three localities. As a result of being a cavernous area but with a different group of species, as established by the species list of Reddell et al. (1999), this KFR is classified as Zone 4a.

Hays County Karst Fauna Region

This KFR is informally designated as the contiguous cavernous unit south of Bear Creek, located near the Travis County line. It is predominantly in Hays County, within the outcrops of the Edwards Limestone, and extends south to the Guadalupe River in Comal County. For the purposes of karst zone mapping, it is expanded from the North Hays County KFR discussed previously in this report since it is beyond the scope of this study to distinguish between the different faunal groups in this area.

No endangered karst species occur in this KFR. It was included in this study to constrain the distribution of the endangered karst species. Of the species listed in Table 1 (available online), only *Speodesmus* n. sp. (Figure 9) and *Texella mulaiki* (Figure 12) are confirmed here from multiple caves; *Cicurina bandida* spiders and *Rhadine austinica* carabid beetles are tentatively identified from several localities. As a result of being a cavernous area but with a different group of species, as established by Zara Environmental (2010b), this KFR is classified as Zone 4a.

South Travis County Karst Fauna Region

No karst zone boundary changes were made in the South Travis County KFR from the previous delineation by Veni and Martinez (2007). No endangered karst species are known and, based on the karst species distribution modeling and KFR boundary analyses conducted in this report, it is unlikely that the endangered troglobites will occur in this KFR. The only change is a reclassification, per the new zone categories of this report, from Zone 3 to Zone 3a, where troglobites are present but the probability of federally listed troglobites is low.

Rollingwood Karst Fauna Region

No new endangered species localities have been found in the Rollingwood KFR since the previous karst zone delineation by Veni and Martinez (2007), but one zone change is made by this study. The entire outcrop of the Edwards Limestone Group had been designated as Zone 1 but following this study's karst species

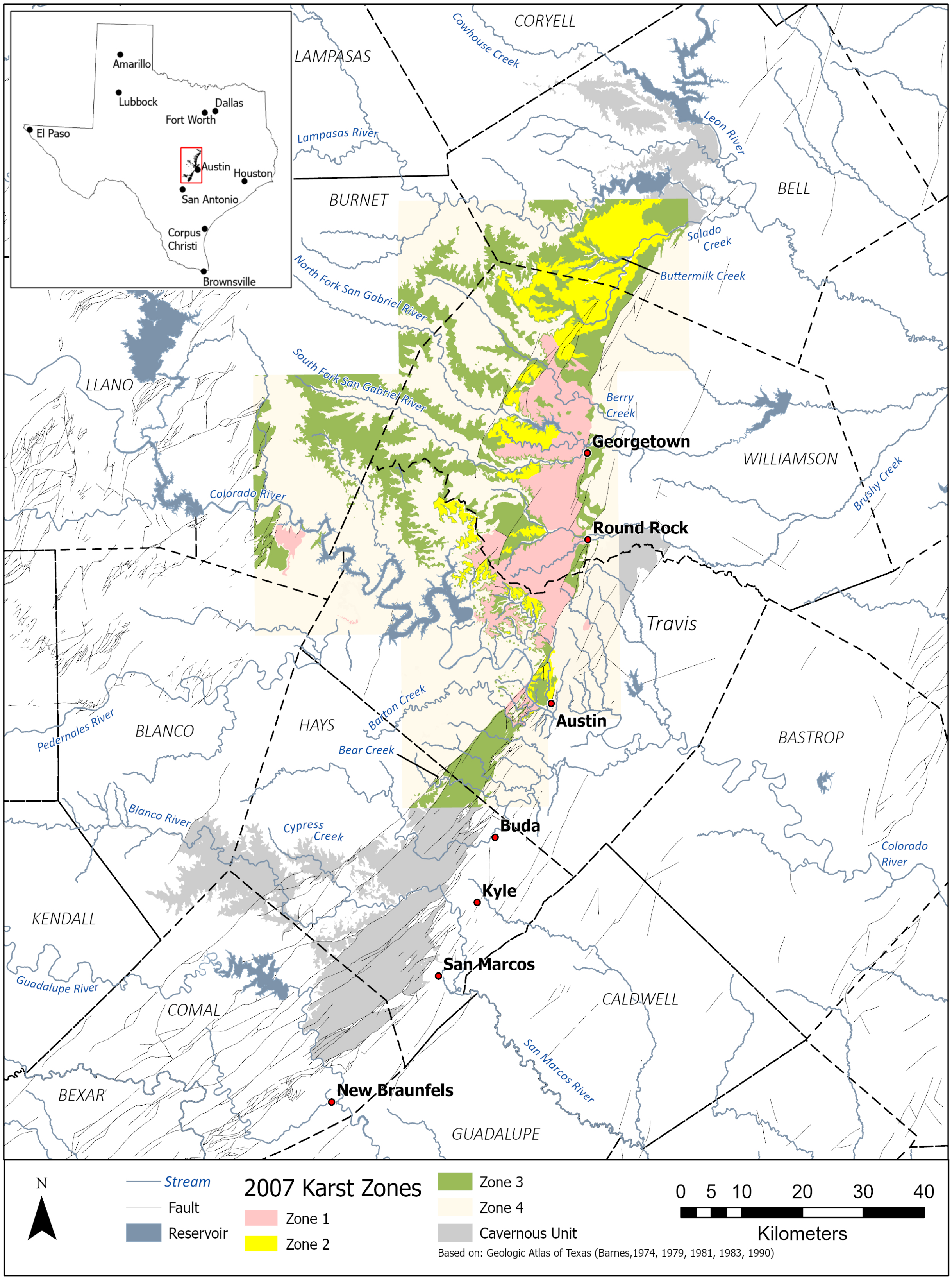

Figure 14. *2007 karst zones per Veni and Martinez (2007).*

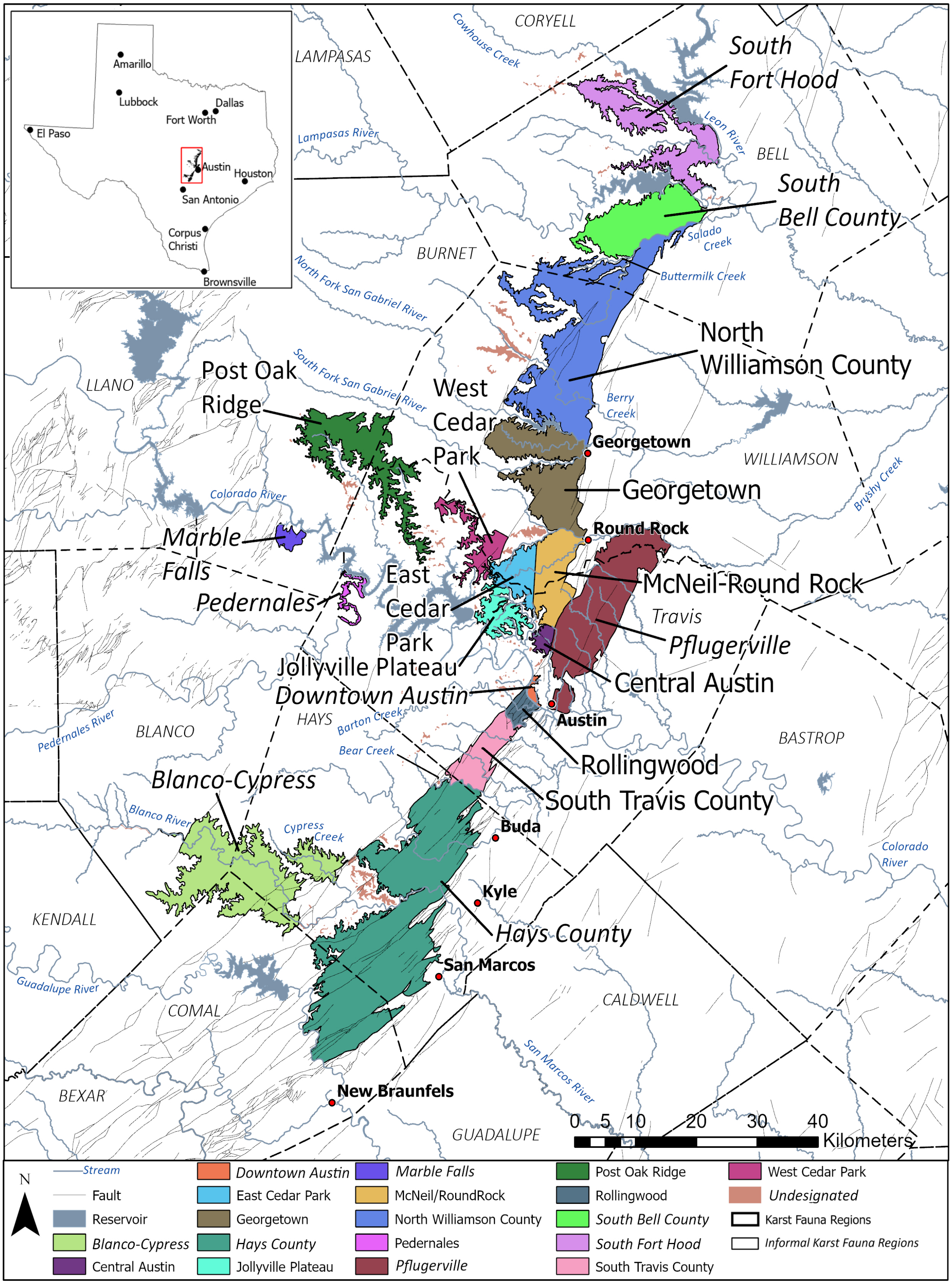

Figure 15. *Karst fauna regions as revised by this study.*

distribution modeling that zone is divided into Zone 1, in the northeast half of the KFR, and Zone 2 in the southwest half. This coincides with the modeled range for the endangered species (Figure 12), and with two tributaries to Barton Creek where the cavernous unit is thinner and may restrict the species' distribution.

Downtown Austin Karst Fauna Region

This KFR is informally designated as the outcrop of the cavernous unit north of the bed of the Colorado River and south of the Central Austin KFR. It could be biologically distinct, but the degree of urban development makes it difficult to evaluate. Of the few caves reported in this area, they either do not appear likely to contain habitat for troglobites, are buried by urbanization, or have been biologically surveyed with no troglobites found. Until more is known, this section of the cavernous unit is assigned to Zone 3a, a cavernous area with presumably low potential to contain the endangered karst species. The area of the cavernous unit under the Colorado River is classified as Zone 4a, because it is cavernous Edward Limestone but in historic time is underwater and not habitat for the endangered terrestrial invertebrate karst species.

Central Austin Karst Fauna Region

There is one less endangered species locality in the Central Austin KFR since the previous karst zone delineation by Veni and Martinez (2007). Moonmilk Cave was listed as containing *Tayshaneta* (then *Neoleptoneta*) *myopica*, which was since discovered to be an error. However, because this cave is only a few hundred meters from the Central Austin KFR's two other known endangered karst species localities (Cotterell Cave and West Rim Cave), its exclusion does not affect the local karst zone. In fact, Zone 1 is expanded slightly to include the entire outcrop of the cavernous unit in the Central Austin KFR based on this study's karst species distribution modeling results.

Pflugerville Karst Fauna Region

This KFR is informally designated as the contiguous exposure of the Austin Chalk east of the fault that marks the boundary with the Central Austin KFR and the Edwards Limestone. No caves are known in this section of the Austin Chalk.

No endangered karst species occur in this KFR. It was included in this study because of the initially reported occurrence of the endangered troglobite, *Texella reddelli*, in Stark's North Mine, although as discussed previously in the report, recent genetic research by Hedin and Derkarabetian (2020) demonstrate that identification needs further investigation. Nonetheless, the presence of troglobites in this poorly cavernous area is demonstrated, and the area's adjacency to Zone 1 requires classifying this KFR as Zone 3b.

McNeil-Round Rock Karst Fauna Region

Veni and Martinez (2007) reported 11 caves with endangered karst species in the McNeil-Round Rock KFR and designated the entire cavernous outcrop as Zone 1, except for the southwest margin along the Bull Creek valley. In this report, 66 caves are now known in this KFR to contain *Texella reyesi* (Figure 12), two of which also contain *Tayshaneta myopica* (Figure 11). *Texella reyesi* is also tentatively reported from eight new localities.

Despite this significant increase in known endangered species localities, and this study's range modeling which indicates the species occur throughout the entire KFR, the previously designated Zone 2 areas at the southwest end of the KFR are mostly maintained. However, with the change in the location of the boundary between McNeil-Round Rock and the East Cedar Park KFR, this Zone 2 area now occurs in both KFRs.

Veni and Martinez (2007) justified Zone 2 designation because of the narrow band of Edwards Limestone that extends northwest through that area to the Jollyville Plateau KFR. This section of Edwards is sandwiched between two poorly cavernous units, the overlying Comanche Peak Limestone and the underlying Bee Creek Marl Member of the Walnut Formation (Barnes 1974; Garner and Young, 1976). Veni and Martinez felt that unmapped details of that area's stratigraphy may restrict cave development and karst species distribution. While surveys for the endangered karst species often occur in newly urbanizing areas, creating a bias in the localities, the addition of only one new locality among the 14 closest to this southern margin may reflect a limit on cave development in that part of the McNeil-Round Rock KFR. Additional biological and geological surveys are needed to test this hypothesis.

The one change from Veni and Martinez's (2007) Zone 2 designation occurs at the west end of the narrow section of the cavernous unit. An endangered species locality near that area in the Jollyville Plateau KFR, and the associated KFR modeling discussed above, extends Zone 1 through that narrow area to the boundary with the East Cedar Park KFR.

East Cedar Park Karst Fauna Region

No new endangered karst species localities have been found in what is now the East Cedar Park KFR since Veni and Martinez (2007) designated most of its cavernous outcrop as Zone 1. *Rhadine persephone* (Figure 7), *Tayshaneta myopica* (Figure 11), and *Texella reyesi* (Figure 12) each occur in at least one of five caves and a well.

Although the species' range modeling from this study indicates these federally listed troglobites occur throughout the cavernous unit in this KFR, following the rationale for the narrow Zone 2 area that connects with the McNeil-Round Rock Zone 2 along the northern edge of the Bull Creek valley, it is maintained as Zone 2 by this investigation.

Jollyville Plateau Karst Fauna Region

Seven new endangered karst species localities have been found in the Jollyville Plateau KFR since Veni and Martinez's (2007) zone delineation, increasing the total to 32. They designated nearly the entire KFR as Zone 1, except for some lower elevation areas listed as Zone 2 based on work by George Veni and Associates (1988), which identified a dolomitic chert horizon below which cave development was not widely known.

Caves are now known throughout the thickness and areal extent of the cavernous unit on the Jollyville Plateau, including caves with endangered species, demonstrating that the dolomitic horizon does not impede troglobite distribution. The species range modeling from this study also indicates the federally listed troglobites occur throughout the cavernous unit in this KFR, therefore, all the Jollyville Plateau KFR is designated as Zone 1.

West Cedar Park Karst Fauna Region

The number of endangered karst species localities in what is now the West Cedar Park KFR has seen additions and deletions since Veni and Martinez (2007) delineated its karst zones. Species identified in Convoluted Canyon Cave and Whitewater Cave were reexamined and found to not be among the federally listed troglobites. Their exclusion from this study had no effect on delineation of Zone 1 because they were near other caves with confirmed endangered karst species. Also, Ilex Cave was excluded because it was connected into Buttercup Creek Cave to create the Buttercup Creek Cave System; excluding Ilex Cave prevented double-counting the newly recognized combined cave.

Four caves with endangered karst species were added to the West Cedar Park KFR, raising the total number of localities to 29. Hunter's Lane Cave occurs near known localities. Broken Arrow Cave extends the range of localities 700 m northwest. Dies Ranch Treasure Cave extends the range of localities 1 km south. Rolling Rock Cave extends the range of localities 1.2 km west.

Based on an examination of the caves and karst features in the area (Texas Speleological Survey, unpublished data, 2020), the distribution of the new localities, and the modeled range for the one endangered species known in this KFR (*Rhadine persephone*), Zone 1 was extended to the modeled margins of that species. Lending confidence to this determination was the location of Dies Ranch Treasure Cave. It occurs at the west end of the narrow outcrop connecting to the East Cedar Park KFR, and south of a fault that Veni and Martinez (2007) used as a Zone 1 boundary, which demonstrates that this fault, like others examined above in the KFR boundary analysis, does not restrict distribution of the endangered troglobites.

Post Oak Ridge Karst Fauna Region

This KFR was designated by George Veni and Associates (1992) in the initial analysis of endangered karst species distribution in the region. They established the KFR as the outcrop of the Walnut Formation and equivalent basal Edwards Limestone. The Post Oak Ridge KFR extends 33 km northwest from its southern end to a 1.3-km narrowing of the outcrop at the head of Oatmeal Creek.

Oatmeal Creek is used as the northwest boundary of this KFR because even though the Walnut Formation continues north for about 240 km, it is predominantly non-cavernous and poorly studied relative to karst development in this area. Although three small caves are known approximately 2–4 km north of the creek, they have not been biologically studied. Only one species range occurs in this area, *Batrisodes reyesi*; however, the nearest known locality is more than 7 km to the southeast making it an unreliable indicator of boundary conditions in this area.

No endangered karst species occur in this KFR, but it was included in this study to constrain the distribution of the endangered karst species. Of the species listed in Table 1 (available online), only *Batrisodes reyesi* mold beetles (Figure 4), *Rhadine russelli* carabid beetles (Figure 7), and *Speodesmus bicornourus* millipedes (Figure 9) are confirmed here from multiple caves. As a result of being a cavernous area but with a different group of species, as further established by the species listed by Atkinson (2002), this KFR is classified as Zone 4a.

Marble Falls Karst Fauna Region

This KFR is informally designated as the contiguous exposure of the Marble Falls Limestone, south of the Colorado River, where troglobitic *Texella* harvestmen were found in two caves and two shallow excavations. While the Marble Falls Limestone extends discontinuously in fault blocks up to 15 km from this location, *Texella* sp. are not known from those blocks and they are not included in this informal KFR.

No endangered karst species occur in this KFR. It was included in this study because of the initially reported occurrence of the endangered troglobite *Texella reddelli*. For the purposes of this study, this record was classified as tentative as recent genetic research by Hedin and Derkarabetian (2020) suggest that additional work is necessary to determine whether these specimens, although south of the Colorado River, will place within the *T. reddelli* clade. As a result of being a cavernous area but likely with a different group of species, as further established by the species listed by Atkinson (2002), this KFR is classified as Zone 4a.

Pedernales Karst Fauna Region

This KFR is informally designated as the contiguous exposure of the cavernous Cow Creek Limestone, which is mapped as undivided from the non-cavernous overlying Hensel Formation at the Colorado River where it extends southwest along the Pedernales River for 22 km. *Texella* harvestmen were found in a shallow excavation in this area.

No endangered karst species occur in this KFR. It was included in this study because of the initially reported occurrence of the endangered troglobite *Texella reddelli*, although recent genetic research by Hedin and Derkarabetian (2020) suggest that identification is unlikely and additional work is necessary to determine whether it will place within the *T. reddelli* clade. Few and only small caves with limited habitat for troglobites are known in this KFR; none have been surveyed biologically (Texas Speleological Survey, unpublished data, 2020). However, considering its geologic isolation from other parts of the cavernous unit, and that this karst area is most likely occupied by a different group of species than those occurring with the federally listed troglobites based on a review of information of cave, karst, and biological data for the surrounding area (Atkinson, 2002; Texas Speleological Survey, unpublished data, 2020), this KFR is classified as Zone 4a.

Georgetown Karst Fauna Region

The Georgetown KFR was expanded north by this study from the South Fork of the San Gabriel River to a new KFR boundary at the North Fork of the river. Since 2007, when Veni and Martinez delineated karst zones in these areas, 11 new endangered karst species localities have been found in the original KFR area south of the South Fork. All occur in or between previously known endangered species localities. However, the modeled range of *Texella reyesi* encompasses all the area. Although the earlier zone mapping identified the northwest corner of the area as Zone 2, it is now assigned as Zone 1 based on the modeling results plus the presence of three known caves that have not been biologically surveyed but have potentially suitable habitat based on their descriptions (Texas Speleological Survey, unpublished data, 2020).

The new section of the Georgetown KFR, located between the South Fork and North Fork of the San Gabriel River, was previously delineated as Zone 1 in the eastern third of the area and extended along the southern edge of the area to the west end of the KFR to encompass Stalagroot Cave. The location of Stalagroot Cave was discovered during this study as mis-located 3.4 km too far west. However, 12 new endangered species localities have since been found, with seven occurring in the western half of the area. Considering their distribution and the modeled range of *Texella reyesi* encompasses all the area between the South Fork and North Fork of the San Gabriel River, all this area is now designated as Zone 1.

North Williamson County Karst Fauna Region

The south end of the North Williamson County KFR was shortened by this study, moving its southern boundary to the North Fork of the San Gabriel River, while expanding its north end beyond the Williamson-Bell County line to Buttermilk Creek. As a result, the approximate area of the KFR remains about the same although no new caves with endangered species were added through the northward expansion.

Since 2007, when Veni and Martinez delineated karst zones in this area, 11 new endangered karst species localities have been found in the North Williamson County KFR. Most occur within areas previously known to contain the species. Exceptions are:

- Highway 195 Cave F-3, which extends the range of localities 1 km west to the edge of the KFR and cavernous unit;
- Twin Springs Cave, which extends the range of localities 1 km southwest to the edge of the KFR and cavernous unit;
- Willow the Wisp Cave, which extends the range of

localities 1.2 km northeast to within 900 m of the edge of the KFR and cavernous unit; and
- Blowhole Cave, an important northern locality, occurring between Cobb Cavern and Coffin Cave where few caves are presently known.

Additionally, dozens of cave locations recorded in the Texas Speleological Survey files were improved as part of this study. Notably for the North Williamson KFR, the improved coordinates for Coffin Cave, Duckworth Bat Cave, Rattlesnake Inn Cave, and Sore-Ped Cave place them into the Georgetown Formation of the cavernous unit, with Coffin Cave now situated further north and east in the poorly studied part of the KFR. Based primarily on the new and corrected localities and range modeling of this study, with minor consideration of newly discovered caves with likely or potential endangered karst species habitat near or within areas previously mapped as Zone 2, the following zone revisions are made:

1. Zone 1 is expanded into the two small Zone 2 areas at the southwest side of the KFR;
2. Zone 1 is expended north to the modeled range limit of the two endangered species known in the KFR, *Batrisodes texanus* (Figure 4) and *Texella reyesi* (Figure 12), in the Edwards Limestone portion of the cavernous unit, beyond which the cavernous unit continues as Zone 2;
3. The 3-km long by up to 1-km wide area of the Georgetown Formation in the south-central part of the KFR is changed from Zone 3 to Zone 1;
4. The southeast 1 km of the Georgetown Formation between Berry Creek and the Smalley Branch of Dry Berry Creek is changed from Zone 3 to Zone 1;
5. The northwest 3.2 km of the Georgetown Formation between Berry Creek and Dry Berry Creek is changed from Zone 3 to Zone 1;
6. Zone 1 is expanded north and east to include the Georgetown Formation portion of the cavernous unit between the Smalley Branch and Cobbs Springs Branch tributaries of Dry Berry Creek; and
7. The remaining portions of the Georgetown outcrop are designated as Zone 3b.

The northward extension of Zone 1, of 5–6 km beyond the closest known endangered karst species localities, is additionally supported by the large number of caves (58) with endangered species in this KFR. Their concentration in the well-studied area south of US Highway 195 indicates that detailed study of the area north of the highway will discover many new localities. Further, caves containing troglobite habitat, including two species examined in this study (*Cicurina vibora* and *Rhadine noctivaga*), occur in the few caves known north of this new Zone 1, supporting this Zone 1 boundary for that mostly biologically unsurveyed area.

South Bell County Karst Fauna Region

This KFR is informally designated as the contiguous exposure of the cavernous unit north of the North Williamson County KFR to the Lampasas River. No endangered karst species, or any of the 39 species evaluated in this study, occur in this KFR. Only 10 and mostly biologically unstudied caves are known (Reddell, 2001).

While the cavernous unit becomes marlier to the north, the impact on cave development and endangered karst species distribution is unknown. This KFR could potentially be part of the North Williamson County KFR but until more information is available, it is known only as a cavernous area with a low estimated probability of containing the federally listed troglobites. It is thus classified as Zone 3a.

South Fort Hood Karst Fauna Region

This KFR is informally designated as the contiguous portion of the cavernous unit comprised of the undivided Denton Clay, Fort Worth Limestone, Duck Creek Limestone, Kiamichi Clay, and Edwards Limestone that is exposed from Cowhouse Creek and the Leon River south to the Lampasas River. Most of the karst research in this area has occurred in the southern part of Fort Hood.

No endangered karst species occur in this KFR. It was included in this study to constrain the distribution of the endangered karst species. Of the species listed in Table 1 (available online), only *Aphrastochthonius muchmoreum* (Figure 3), *Cicurina coryelli* (Figure 5), and *Speodesmus castellanus* (Figure 9) are confirmed here from two caves. As a result of being a cavernous area but with a different group of species, as established by research on Fort Hood (Reddell, 2004a), this KFR is classified as Zone 4a.

Undesignated Karst Fauna Region

Several KFRs have nearby “islands” of cavernous rock, surrounded by non-cavernous rock and thus separated from the above designated KFRs. Where these islands are unstudied for caves and/or karst invertebrates, it is impossible to justify including them with the designated KFRs at this time. They are therefore grouped as part of a physically unconnected collection of karst areas awaiting study to determine their biological status and if they should be included as part of a designated KFR.

In the earlier studies by George Veni and Associates (1992) and Veni and Martinez (2007), these island-like outcrops of karst were mostly included in the KFRs because the KFRs were broader in some areas to include rock units that might contain caves. Since those units are now known as non-cavernous and removed from the KFRs, the karst outcrops they encircled became isolated. Although these island-like outcrops are now excluded from the KFRs, this study follows the methodology of the earlier studies and generally designates their karst zones as one rank below the zone in the nearest designated KFR, down no further than Zone 3a or 3b. For example, if the area of the closest designated KFR was Zone 1, the karst island would be Zone 2.

Conclusions

Karst Fauna Regions

The GIS analysis of 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 model. The results support the initial hypothesis from 1992, used conceptually to define Karst Zone 2, that if cavernous rock is present and appropriate habitat conditions exist, then its caves will contain troglobitic species. KFR boundaries occur where cavernous rock is absent, thin and/or narrow, and filled at least periodically with water. Faults create boundaries only where they juxtapose cavernous and non-cavernous rock. While some faults and other geologic factors may have local effects, no effects are seen at the scale of the KFRs.

Most of the KFR boundaries are restrictions, not barriers to 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 the endangered karst 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 15 illustrates the KFRs of the study area as defined or redefined by this study, including the informally designated and undesignated KFRs. The most significant difference between Figure 15 and the 1992 boundaries of Figure 1 is that the new boundaries are as precise as possible in all respects. The initial, pre-GIS, boundaries were hand-drawn and limited to the precision of manually interpolating information from various maps onto 1:24,000 scale topographic quadrangles. Following Veni and Martinez's (2007) karst zone update and conversion into GIS, USFWS schematically illustrated the KFRs in various mapping applications, including areas now recognized as non-cavernous on the chance that 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 KFRs with endangered karst species, KFRs defined in previous studies, and the Undesignated KFR. The informally defined KFRs in the karst zone analysis of this report are not included because their boundaries are only approximated.

<u>North Hays County Karst Fauna Region</u>
Bounded to the northeast by Bear Creek, the North Hays County KFR's northwest and southeast boundaries are delineated by the edges of the cavernous unit along erosional contacts, predominantly to the northwest, and fault contacts predominantly to the southeast. Its southwest boundary is beyond the scope of this study to determine, but Zara Environmental (2010b) provides boundary recommendations and additional insights for this KFR. Figure 15 illustrates the informally designated Hays County KFR in its place. No endangered, federally listed, terrestrial karst invertebrates occur or are likely to occur in this KFR.

<u>South Travis County Karst Fauna Region</u>
Bounded to the northeast by Barton Creek and to the southwest by Bear Creek, South Travis County's northwest and southeast boundaries are delineated by the edges of the cavernous unit along erosional contacts, predominantly to the northwest, and fault contacts predominantly to the southeast. No endangered, federally listed, terrestrial karst invertebrates are known to occur in this KFR, but the boundary with the Rollingwood KFR is a restriction which does not absolutely prevent listed species from occurring in the South Travis County KFR.

<u>Rollingwood Karst Fauna Region</u>
Rollingwood is bounded to the northwest by the Mount Bonnell Fault, which marks the end of the cavernous unit in that direction, to the northeast by the Colorado River, and to the south and southwest by Barton Creek. Its southeast margin follows the edge of the cavernous

unit on the northwest side of the Barton Springs Fault. One federally listed endangered karst invertebrate species occurs in this KFR: *Texella reddelli*.

Central Austin Karst Fauna Region

The eroded edge of the cavernous unit delimits the Central Austin KFR to the west and south. The east side of this KFR is bounded by a fault that juxtaposes the Edwards Limestone with the Austin Chalk. The north end of the KFR is the narrowest and thinnest exposure of the Edwards Limestone in that area, which spans between the head of the valley at the east of the Capitol of Texas Highway and the head of Shoal Creek about 1 km to the east. One federally listed endangered karst invertebrate species occurs in this KFR: *Texella reyesi*.

McNeil-Round Rock Karst Fauna Region

Bounded to the southeast by the Central Austin KFR and to the east by a fault that marks the eastern edge of the cavernous unit, the McNeil-Round Rock KFR is further bounded to the northeast where the bed of Brushy Creek crosses the cavernous unit, and by the eroded limits of the cavernous unit to the northwest along the Brushy Creek valley and to the south by the Bull Creek valley. The western end of the McNeil-Round Rock KFR is redefined as 3 km eastward along the north-south axis of a species range cluster. Two federally listed endangered karst invertebrate species occur in this KFR: *Tayshaneta myopica* and *Texella reyesi*.

East Cedar Park Karst Fauna Region

The former Cedar Park KFR is divided into two new KFRs: East Cedar Park and West Cedar Park. The names were selected to eliminate the original name to prevent confusion, but reference that name for orientation. The East Cedar Park KFR is bounded to the east along the north-south axis of the species range cluster that marks the boundary with the McNeil-Round Rock KFR. The boundaries to the north, west, and south follow the eroded edge of the cavernous unit along the valleys of Brushy Creek, South Brushy Creek, Buttercup Creek, and Bull Creek, respectively. The southwest boundaries are at thin and narrow sections of the cavernous unit that mark the boundaries with the Jollyville Plateau and West Cedar Park KFRs. Two federally listed endangered karst invertebrate species occur in this KFR: *Rhadine persephone* and *Texella reyesi*.

Jollyville Plateau Karst Fauna Region

Nearly the entire Jollyville Plateau KFR is bounded by the edge of the cavernous unit where it is eroded along the valley margins of Bull and Cypress creeks and the Colorado River. Its original boundaries with the Cedar Park and McNeil-Round Rock KFRs were moved south about 4.5 km and 1 km respectively, to a new common boundary with the newly designed East Cedar Park KFR. This boundary occurs across a narrow section of the plateau. A short boundary along another narrow section of the cavernous unit at the north end of the Bull Creek valley remains unchanged, except that it is now with the East Cedar Park KFR and not McNeil-Round Rock. Five federally listed endangered karst invertebrate species occur in the Jollyville Plateau KFR: *Rhadine persephone*, *Tartarocreagris texana*, *Tayshaneta myopica*, *Texamaurops reddelli*, and *Texella reyesi*.

West Cedar Park Karst Fauna Region

The western and southern sides of the West Cedar Park KFR are bounded by the eroded edge of the cavernous unit in the Colorado River and South Brushy and Buttercup Creek valleys. The eastern side is similarly bounded, except that erosion is not as deep before exposing non-cavernous units that do not occur further south and east. The West Cedar Park KFR connects at its southernmost point to the East Cedar Park KFR at a narrow and thin section of the cavernous unit. One federally listed endangered karst invertebrate species occurs in this KFR: *Rhadine persephone*.

Post Oak Ridge Karst Fauna Region

This isolated ridgetop exposure of Edwards Limestone and the Walnut Formation defines Post Oak Ridge. It is separated from the West Cedar Park KFR by an absence of cavernous rock in the Sandy Creek valley. It's northwest end is truncated at the upper end of Oatmeal Creek where the limestone is locally thin and narrow, and starts to becomes less cavernous. No endangered, federally listed, terrestrial karst invertebrates occur or are likely to occur in this KFR.

Georgetown Karst Fauna Region

This KFR is redefined by setting its northern boundary along the crossing of the Edwards Limestone by the bed of the North Fork, instead of the South Fork, of the San Gabriel River. Its southern boundary is located where the bed of Brushy Creek crosses the Edwards Limestone. Between the North and South Fork, the east and west KFR boundaries are delineated by faults that truncate the exposure of the cavernous unit. South of the South Fork, the eastern boundary continues to be delineated along a fault at the edge of the cavernous unit and the west boundary is where the cavernous unit is removed by erosion. Two federally listed endangered karst invertebrate species occur in this

KFR: *Batrisodes texanus* and *Texella reyesi*.

North Williamson County Karst Fauna Region
This KFR is redefined as extending north from the North Fork of the San Gabriel River to where the cavernous unit is crossed by Buttermilk Creek. Its eastern boundary is delineated along a fault at the edge of the cavernous unit, and the west boundary is located where the cavernous unit is removed by erosion. Two federally listed endangered karst invertebrate species occur in this KFR: *Batrisodes texanus* and *Texella reyesi*.

Extensions of the cavernous unit north of the North Williamson County KFR comprise other KFRs but are outside the scope of this study to define formally. If new localities for the endangered karst species are discovered near the northern limit of the North Williamson County KFR, the area north of Buttermilk Creek should be evaluated to determine its potential to contain the species.

Undesignated Karst Fauna Region
Over 100 small, geologically isolated karst areas comprise this KFR. They occur throughout the length of the study area, but predominantly on the west side of the formal and informally designated KFRs. Caves and karst features are not known in most of these areas, and none have been studied biologically to determine if they are part of a designated KFR.

Karst Zones

The karst zones were expanded from the four previous zones to include two subzones for Zone 3 and 4 to better identify their biological status and manage their ecosystems. The troglobite distribution modeling, especially for the endangered species, proved a valuable tool in revising the karst zones, in addition to the new localities, the improvement of cave location precisions, and associated updates and information.

Figure 16 illustrates the karst zones of the study area following the results of this study. It includes zone determinations for the informally designated KFRs, described to constrain and describe the likely distribution of the endangered karst species. Also included is the Undesignated KFR, comprised of small, isolated areas of the cavernous unit outside of the formal and informal KFR boundaries. These areas have not been studied for caves or karst fauna, but their potential for endangered karst fauna, shown in Figure 16, is assigned one zone rank lower than the nearest zone in a designated KFR, down no further than Zone 3a or 3b. Additionally, due to the size and geologic complexity of the area in Figure 16, it is beyond the scope of this study to show all Zone 4a areas, thus Zone 4b as shown includes some 4a areas with the intent that only areas adjacent to the formally designated KFRs with endangered karst species are definitely Zone 4b.

The following summarizes the notable karst zone changes, with a focus on the formal and previously designated KFRs which contain the federally listed species:

- North Hays County and Post Oak Ridge KFRs were designated as Zone 4a, where the endangered karst species will not occur.
- South Travis County KFR was confirmed as Zone 3a, where the potential for endangered karst species is low.
- Zone 1 was downgraded to Zone 2 in the southwest portion of the Rollingwood KFR.
- Zone 4a was added where the cavernous unit is below the Colorado River.
- Zone 1 was expanded to fill all the Central Austin, Georgetown, and Jollyville Plateau KFRs.
- No zone changes were made in the East Cedar Park and McNeil-Round Rock KFRs.
- Zone 1 was expanded to fill the south and southwest sections of the North Williamson County and West Cedar Park KFRs.
- Zone 1 was expanded into certain areas previously mapped as Zone 3 in the North Williamson County KFR.
- Zone 1 in the North Williamson County KFR was expanded to Salado Creek, and north beyond that Zone 2 and 3a were expanded into Bell County.

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 were recognized as supporting and one refuting the modeling results, but those data are not considered in this study's GIS analyses, which are based on named species and subspecies. 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 12 genera examined in this report, the next update of this analysis should establish standards for what level of genetic differentiation, *irrespective of species name*, suggests the presence of a KFR boundary. That

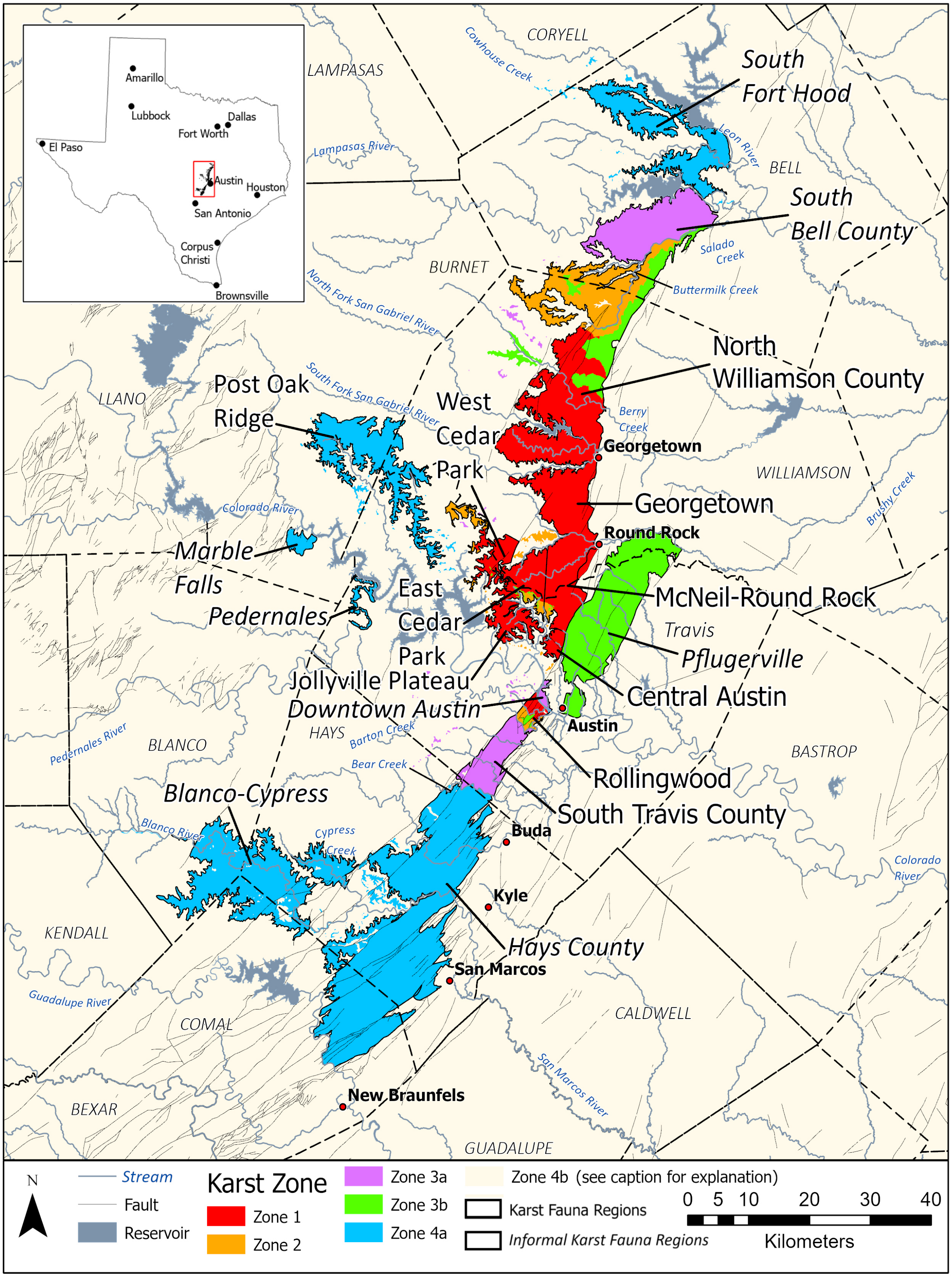

Figure 16. *Karst zones as revised by this study. Due to the broad area and its complexity, Zone 4b as shown includes some Zone 4a areas with the intent that only areas adjacent to the KFRs with endangered karst species are Zone 4b.*

information should be included in the analysis.
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 ecological communities of their caves. Consequently, less information was available for understanding the ecological conditions of the species, and for studies like this that would benefit from a richer data set. USFWS should require thorough biological surveys of all caves.
3. Additional searches for and study of caves north of US Highway 195 into Bell County is needed to better evaluate the potential for endangered karst species and their distribution in that area.
4. Further detailed biological surveys are needed for troglobites at Stark's North Mine, especially genetic study of its *Texella* sp., to better evaluate the potential biological status of this section of the Austin Chalk relative to the Central Austin KFR, and other KFRs in general. If new caves or related potential troglobite habitat are discovered in the Austin Chalk, they should also be sampled for troglobites.
5. Genetic study is needed of the *Texella* sp. in the Marble Falls, Pedernales, and West Cedar Park KFRs to determine their relationship with the endangered *Texella* species.
6. Caves and karst features in the Undesignated KFR require investigation and biological study. Based on the results of such studies, the individual isolated karst areas of this KFR could be assigned to a designated KFR or new KFRs, unrelated to the endangered karst species, and classified as Karst Zone 4a.
7. *Batrisodes reyesi* and *Speodesmus bicornourus* are broadly distributed across multiple KFRs and warrant genetic study to determine if this distribution is accurate or if they are multiple species or species subclades. While these species are not listed as endangered, better understanding their distribution is valuable in better defining KFR boundaries.
8. Detailed mapping of the geology is extraordinarily helpful in evaluating species distribution in KFR and karst zone mapping, as seen in this study, in addition to delineating critical habitat and developing effective management plans for the species (e.g. Veni, 2003). Presently, detailed geologic mapping is only available for the Edwards Limestone south of the Colorado River. Observable changes in patterns of cave development occur north of the river but cannot be adequately assessed with the current level of geologic mapping. Two areas noted in this report that would especially benefit from better geologic mapping are the boundary between the East Cedar Park and McNeil-Round Rock KFRs, and the north end of the study area to better predict the likelihood and degree that the endangered species may extend into Bell County.
9. As a related recommendation, the use of genetics to determine the timing of species division would be important in evaluating species evolution relative to changing geological factors and the development of new species that invade and fragment the ranges of older species.

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