# MODELING THE SPREAD OF *PSEUDOGYMNOASCUS DESTRUCTANS* IN TEXAS AND MEXICAN KARST REGIONS

A Thesis

by

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## ABSTRACT

White-nose Syndrome (WNS) is caused by a fungus that has led to deaths of millions of North American bats since it was first documented in New York 2006. Since the first cases were recorded, WNS has spread rapidly across North America, and is now present in 34 US states and 7 Canadian provinces. The disease is caused by the introduced fungal pathogen *Pseudogymnoascus destructans*. Often, the presence of *P. destructans* is detected in a cave environment before signs of WNS manifest in the resident bat population – making expansion of the fungus a more reliable assessment of epidemic spread than expansion of manifested WNS. We generated a predictive model to assess the potential spread of *P. destructans*, the fungal causal agent of WNS, through Texas karst systems based on external features that correlate with suitable internal microclimates for fungal growth. An analysis of 43 cave microclimates across the state of Texas reveals a pattern of thermal suitability for *P. destructans* that correlates significantly with landscape (elevation, lithology) and external climate (mean surface temperature and precipitation). Applications of this model to external climatic variables from 2019 show seasonally varying patterns of suitability for fungal growth in select regions of Texas karst systems. Similar work conducted in Mexico surveyed 4 caves in 2 areas of varying climate and elevation. Results from these surveys show that microclimates of Mexican caves are likely able to sustain the growth of *P. destructans* and could act as stepping stones for the fungus, allowing it to travel southward. The resulting work will inform researchers and natural resource managers of areas of significant concern while monitoring the spread of WNS.

## ACKNOWLEDGEMENTS

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# CONTRIBUTORS AND FUNDING SOURCES


**Contributors**

This work was supervised by a thesis (or) dissertation committee consisting of Professor Thomas Lacher [advisor], Michael Morrison [co-adviser] and David Cairns of the Department of Geography.

The data analyzed for Chapter 1 was collected during my time as an employee of the Natural Resources Institute at Texas A&M University, where I worked with Dr. Melissa Meierhofer. Other data collected during these efforts were part of Dr. Meierhofer's PhD dissertation. All other work conducted for the thesis was completed by myself independently.

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# NOMENCLATURE

| | |
|---|---|
| WNS | white-nose syndrome |
| *P. destructans* | *Pseudogymnoascus destructans* |

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# CHAPTER I

# INTRODUCTION

Emerging infectious diseases in wildlife populations have led to steep declines in taxa of concern and present a substantial risk to biodiversity (Daszak et al., 2000; Kolby and Daszak, 2016; Cunningham et al., 2017). The increase in prevalence of wildlife diseases in the later 20th and present 21st century has been driven by a suite of causal factors: humans and livestock are increasingly encroaching into wild areas; shifts in climate and weather patterns brought on by climate change extend the range of pathogens to intersect with new hosts; and increasing movement of people, livestock, and goods creates a conduit for pathogens to cross previous geographic barriers and other range boundaries (Daszak et. al, 2001; Thompkins et al., 2015; Cunningham et al., 2017). Such cases of emerging infectious diseases of conservation concern include the deadly amphibian chytrid fungal disease caused by the introduced *Batrachochytrium dendrobatidis* fungus (Daszak et al. 1999; Rödder et al. 2010; Rosenblum et al. 2010), introduced West Nile encephalitis virus which continues to cause massive die offs of American birds (Lim et al. 2015; Reisen, 2013), and sea star wasting disease which is thought to be exacerbated by the effects of climate change (Maynard et al. 2015). As wildlife disease outbreaks increase in frequency and severity, conservationists scramble to address them quickly, but often lack the tools to do so effectively and efficiently. In particular, predictive modelling of disease spread is crucial to gain an edge against quickly spreading wildlife diseases. In this vein, suitability assessments for disease presence and infection potential are needed, but unfortunately rare.

One such pathogenic agent of concern is *Pseudogymnoascus destructans,* a virulent fungus which causes the disease white-nose syndrome (WNS) in hibernating North American bats. WNS has led to a steep decline in North American bat populations since it was first documented in New York in 2006 (Blehert et al., 2009), nearly extirpating once common species of microchiroptera in the northeastern regions of the United States and adjacent regions in Canada. The strain of *P. destructans* causing die-offs in North America is most similar to that of *P. destructans* in Europe, and it is believed that the fungus was introduced to North America from Europe (Leopardi et. al, 2015). Once introduced to a hibernating bat, fungal spores of *P. destructans* invade and destroy the skin of the host while developing fruiting growths on its wings, ears, and muzzle. The progression of this infection makes the nose of the infected bat host appear whitish with fungal growth - the characteristic physical manifestation which the disease is named for. The fungus irritates the hibernating bat host, causing it to arouse frequently from torpor, dehydrate, and accelerate the depletion of its fat stores necessary to survive winter hibernation (Blehert et al. 2009; Cryan et al. 2013; Warnecke et al. 2013). WNS kills by either causing bats to starve inside of caves, dehydrate from frequent arousal, or by leading them to become so hungry that they fly out in search of food in harsh winter conditions and freeze to death (Janicki, 2010; Willis et. al 2011; Reeder et. al 2012; Cheng et al., 2019; McGuire et al., 2019).

*P. destructans* is a cold-adapted fungus best suited to cool, static climates found within caves. Without the appropriate environment, the fungal spores of *P. destructans* may be able to survive, but not grow and propagate and become infectious and be able to spread (Verant et al. 2012; Raudabaugh and Miller 2013; Marroquin et al. 2017). As such, the suitability of a cave environment for growing *P. destructans* is best described by that cave's internal temperature

(Verant et al., 2012, Langwig et al., 2012). *P. destructans* can thrive in temperatures between 0 and 19°C, and the optimal temperature for *P. destructans* to grow and reproduce is between 12.5 and 15.8°C (Verant et al. 2012). Laboratory experiments have suggested that *P. destructans* spores can persist in an environment for 5 or more years without a bat host (Lorch et al. 2013, Hoyt et al. 2015). Since subterranean cave environments are relatively static compared to the surrounding above-ground landscape (Poulson and White, 1969), the introduction of *P. destructans* to a cave may permanently infect host caves and create a nexus of dispersal for the fungus even if the resident bats themselves do not contract WNS (Raudabaugh and Miller 2013; Hoyt et al. 2015).

Since the introduction of *P. destructans* and subsequent WNS to North America, the disease has spread rapidly in all directions. WNS is now present in 34 states in the United States, and 7 Canadian provinces (WNS, 2019). Further, *P. destructans* has been documented but not yet observed to be infectious in 5 additional states in the United States. In the state of Texas, *P. destructans* was first observed in the winter of 2017 (TPWD 2017a). During this season, PCR's of swabs collected from bats in the Texas panhandle returned positive results for the presence of *P. destructans* (M. Meierhofer, pers. comm.). In the following three years, the presence of the fungus was moving farther and farther south through the state every season (TPWD 2017a, 2018, 2019). It was initially thought that perhaps Texas had a climate that was too mild for bats to hibernate for the length of time necessary to be infected with *P. destructans* and develop WNS, but in the winter of 2020 an individual of *Myotis velifer* was confirmed dead from the disease in Gillespie County of Texas (TPWD 2020). The future progression of WNS in Texas remains uncertain.

The objective of this study was to build a model predicting internal microclimates of caves in areas where this information will have application in predicting the likely spread of WNS. This model consolidated internal microclimate data collected in Texas with available external climatic and geographic data to determine what external features suggest a specific region's propensity for sustaining the growth of *P. destructans* (thereby causing a cave to be a nexus of dispersal). In order to determine the ability of karst regions to become nexuses of dispersal for *P. destructans,* available information on external features were used to extrapolate findings and determine on a landscape scale where *P. destructans* is likely to persist in Texan karst regions.

# CHAPTER II

# MODELING SUITABILITY FOR *PSEUDOGYMNOASCUS DESTRUCTANS* IN TEXAS KARST REGIONS

The fungal causal agent of white-nose syndrome (WNS), *Pseudogymnoascus destructans* (*Pd*) was first detected in the state of Texas in the winter of 2017 (TPWD 2017a), and each subsequent year the fungus has been detected further and further south (TPWD 2017a, 2018, 2019). A case of WNS disease itself was recently reported for the first time in a central Texas county earlier this spring (TPWD 2020). This disease kills hibernating bats, and has led to a precipitous decline in hibernacula populations since it was introduced to North America in the early 2000's (Blehert et al. 2009; Cryan et al. 2013; Warnecke et al. 2013). The fungal spores of *Pd* infect bats when they are hibernating and their immune response is low. The spores invade the thin flesh of the bat in areas around the muzzle, ears, and wings. This causes irritation and forces the bat to arouse frequently – depleting fat stores and causing dehydration which ultimately leads to the bat host's death (Janicki, 2010; Willis et. al 2011; Reeder et. al 2012; Cheng et al., 2019; McGuire et al., 2019). Bats are a taxa of particular value in Texas. They are valued in the billions of dollars for ecosystem services they offer in the form of pest control and pollination (Cleveland et al, 2006; Boyles et al. 2013). Further, bat die-off as a function of WNS can be attributed to an increase in public health issues that stem from increased pesticide use (Frank et al. 2017). It is paramount at this juncture that unique tools be developed to assess the threat of WNS in Texas. The objective of this study was to utililze internal microclimate recordings of caves in Texas in order to build a model of *Pd* growth suitability in Texas karst regions. This model consolidated internal microclimate data collected in Texas with available external climatic and geographic data to determine what external features suggest a specific region's propensity for sustaining the growth of *P. destructans* (thereby causing a cave to be a nexus of dispersal). Findings were extrapolated to a landscape scale to describe which areas of Texas should be considered highest concern when managing the spread of *Pd* and subsequent WNS.

## MATERIALS AND METHODS

### *STUDY AREA*

Texas is the largest state in the continental United States - covering 695,621 square kilometers. The state encompasses twelve distinct level III ecoregions and three major karst types (Griffith et al. 2007). Karst systems cover approximately one-third of the total Texas territory (Fig. 2), with the majority of caves located in the central limestone deposit area, encompassing the Edwards Plateau ecoregion (TSS, 2007). Elevation in Texas varies from sea level at the coastline to 8,751m at Guadalupe Peak in West Texas (Fig. 1). Areas in the northern and southern parts of the state are generally low elevation and low relief, ranging from approximately 0 to 1,000m. The central area of the state is characterized by low rolling hills, not reaching above 500m in elevation.

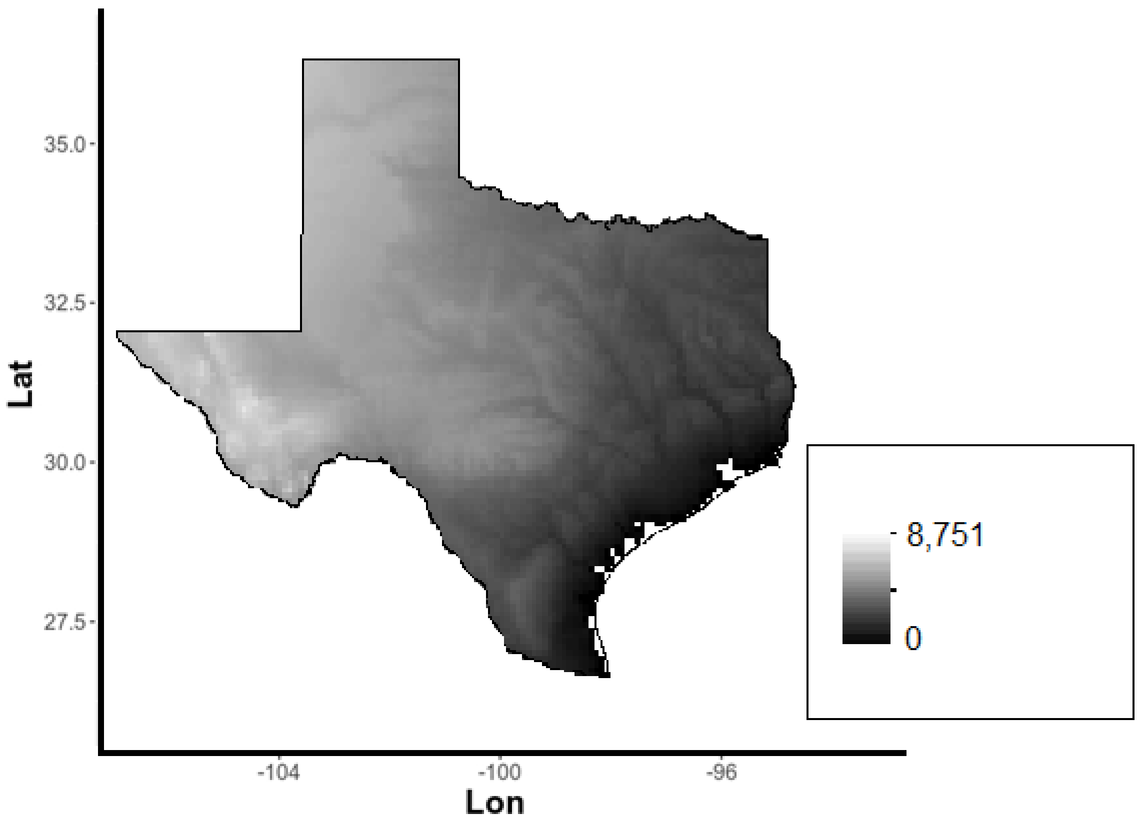


Figure 1. Elevation across the state of Texas. Coastal elevation is at sea level, and increases westward throughout the state. The highest point in the state is Guadalupe Peak in West Texas, at 8,751 meters above sea level.

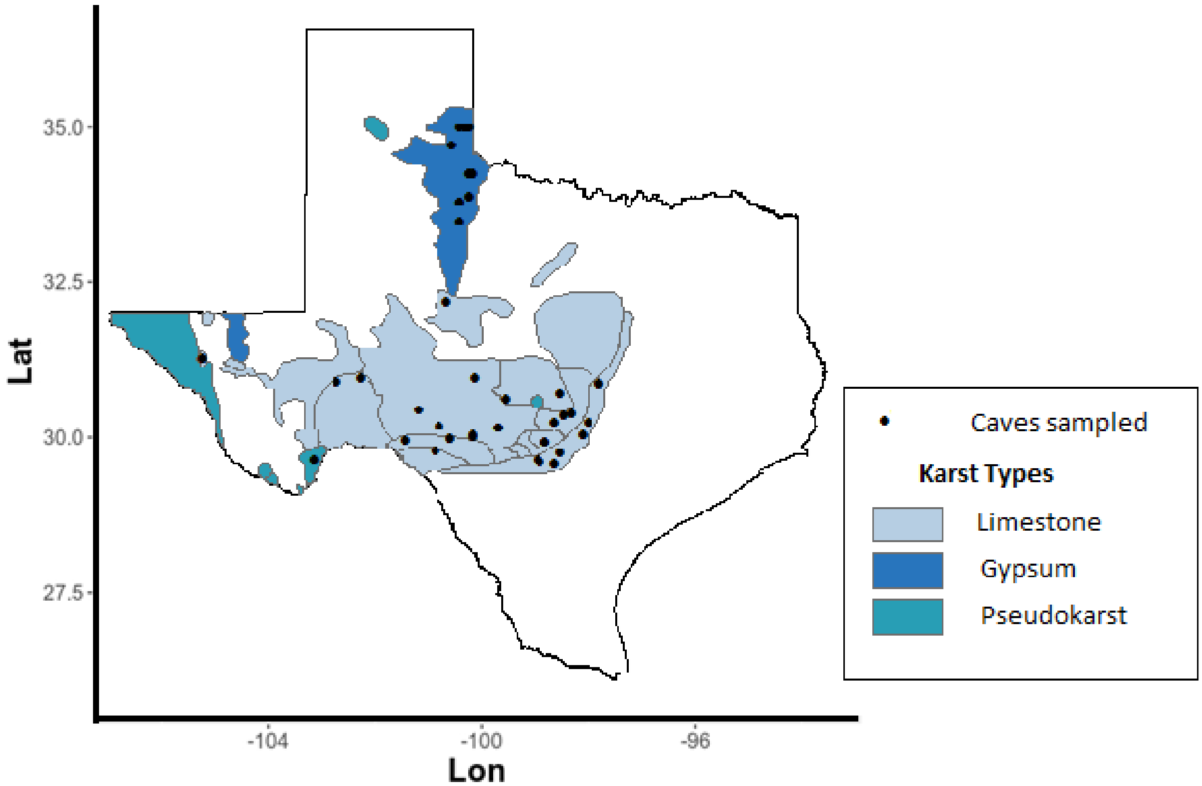


Figure 2. Map of the sampling sites where data loggers were deployed to record microclimatic temperatures in caves distributed along Texas karst systems.

Seasonality in Texas is highly marked with temperatures ranging from -8 °C during the winter to 44 °C in the summer – with regional and latitudinal variations in average temperature (Runkle et al. 2017). The mean annual precipitation varies regionally as well, ranging between 1200mm and 300 mm a year, with rainfall events distributed all over the year, but more concentrated between the months of May and September in west Texas, and September and April in eastern and central Texas (Runkle et al. 2017).

Thirty-three bat species are present within the state of Texas, of which fifteen species are known to inhabit caves (Schmidly and Bradley, 2016). The size of populations of cave-dwelling bats in Texas make this state particularly relevant for study. Texas is a major throughway for bat migrations between Central and North America and large numbers of migratory bats alternate seasons in the state (Russell et al. 2005).

Texas karst is divided into three categories: limestone, gypsum, and pseudokarst (TSS, 2007) (Fig. 2). Pseudokarst areas contain caves that are formed from a process other than dissolution, such as wind. For the purposes of this study, pseudokarst is broken into two subcategories (quartz sand and alluvium) to account for notable regional and geological differences between those caves.

### *DATA SAMPLING*

43 caves were sampled for internal microclimatic temperature in Texas. Caves were selected from a pool of cave records obtained from the Texas Speleological Society and interviews with Texas landowners. For selection, all caves were visited to inspect for qualifying criteria for the study, which included: (i) potential to sustain a wintering bat population, indicated by evidence of bat presence during the winter season (e.g., presence of an individual, guano); (ii) low levels of human disturbance, avoiding interferences for the deployed equipment; (iii) representativeness of gradients of external factors such as elevation, climate, lithology, and spatial distribution. Selected caves were widely distributed among Texas karst systems, covering karstic geologies of limestone (n = 28), gypsum (n =12), quartz sand (n = 2), and alluvium (n = 1) (Fig. 2). With this sampling scheme, the geographic position of the caves reflected a wide gradient of external temperature, annual precipitation, lithology, and elevation. EasyLog EL-USB-2 data loggers were deployed in each cave deemed to be suitable for data collection. These data loggers recorded microclimate temperature at one-hour intervals throughout the course of their deployment. Data loggers were deployed in the coolest room of each cave, which typically

was the room furthest from the entrance of the cave. Each data logger was attached to the wall of a cave, far enough off the floor of the cave to be near an area where an overwintering bat might roost, in an area where the equipment would be safe from disturbance throughout the time of its deployment. Each data logger was left to record data for at least one winter season, and occasionally data loggers were left for longer until they could be collected. Once the equipment was retrieved, the resulting information was downloaded using EasyLog system software. All data loggers were deployed and retrieved within the period between June 2016 and February 2019.

### *MICROCLIMATE DATA STANDARDIZATION*

Raw temperature data consisted of hourly measurements of temperature throughout the time of equipment deployment. Temperature data were standardized by determining the mean temperature for each day of each cave. As intraday variation of temperature within caves is slight (mean CV = 0.03, Table S1), daily average temperature was deemed an appropriate measurement.

External data were obtained from open source online repositories. Elevation was obtained from a DEM with a resolution of 1 meter provided by the USGS National Map. External temperature data were described by monthly mean land surface temperature obtained from rasters provided by NASA Earth Observations (NEO). Precipitation was described by monthly accumulated rainfall, which was obtained from 0.5° resolution rasters provided by NOAA Climate Prediction Center. Lithology was obtained from geological maps provided by the USGS Mineral Resources database. Databases utilized for external data collection included the USGS Mineral Resources database, the TNRIS DataHub, the NOAA Climate Prediction Center, and

BIOCLIM.

### *MODEL DEVELOPMENT*

A generalized least squares model (GLS) was fit to evaluate changes in internal microclimates of caves (Zuur 2007: Zuur 2009). We modeled internal microclimatic temperature as a function of external temperature, latitude, longitude, annual precipitation, lithology, and elevation. In order to account for temporal dependence in measures of internal microclimatic temperature, we used an autoregressive process of order 1 (corAR1) with Julian day of samples as the autocorrelation structure. Because all the explanatory variables are linked with potential mechanisms that can explain variation in internal microclimatic temperature, we used model selection with the all subset approach in order to determine the best model explaining the data. We used Akaike Information Criterion for model selection, and we assumed a ΔAIC of 2 to determine the best competitor models in the model collection (Burnham and Anderson 2003). We used likelihood-ratio pseudo $R^2$ to evaluate model goodness-of-fit and $\chi^2$ tests to assess for significance of model parameters. Analyses were conducted in R environment using *car* (Fox et al. 2017), *nlme* (Pinheiro et al. 2019) and *MuMIn* (Barton and Barton, 2019) packages. (Fig. 3)

### *MODEL PROJECTIONS*

After fitting the model, we applied data on external temperature, latitude, longitude, annual precipitation, lithology, and elevation to predict internal microclimatic temperature of other caves across Texas. For this, we first generated a grid of 10,000 equidistant, evenly distributed points contained within the limits of Texas karst systems. Then, we obtained external temperature, latitude, longitude, annual precipitation, lithology, and elevation for each point coordinate and used the fitted model to predict internal microclimatic temperature. Because we were interested in modeling habitat conditions for *P. destructans,* we converted the predictions of internal microclimatic temperature into suitability scores for fungal growth. For this, we used a growth model fitted in the laboratory to obtain the temperature equivalence for growth condition of *P. destructans* (Verant et al. 2012). Resulting growth rates were rescaled to an interval between 0 and 1, indicating growth conditions from worst (0) to optimum (1) for the fungus *P. destructans*. This final step resulted in a unit of fungal growth suitability for each generated point. (Fig. 3)

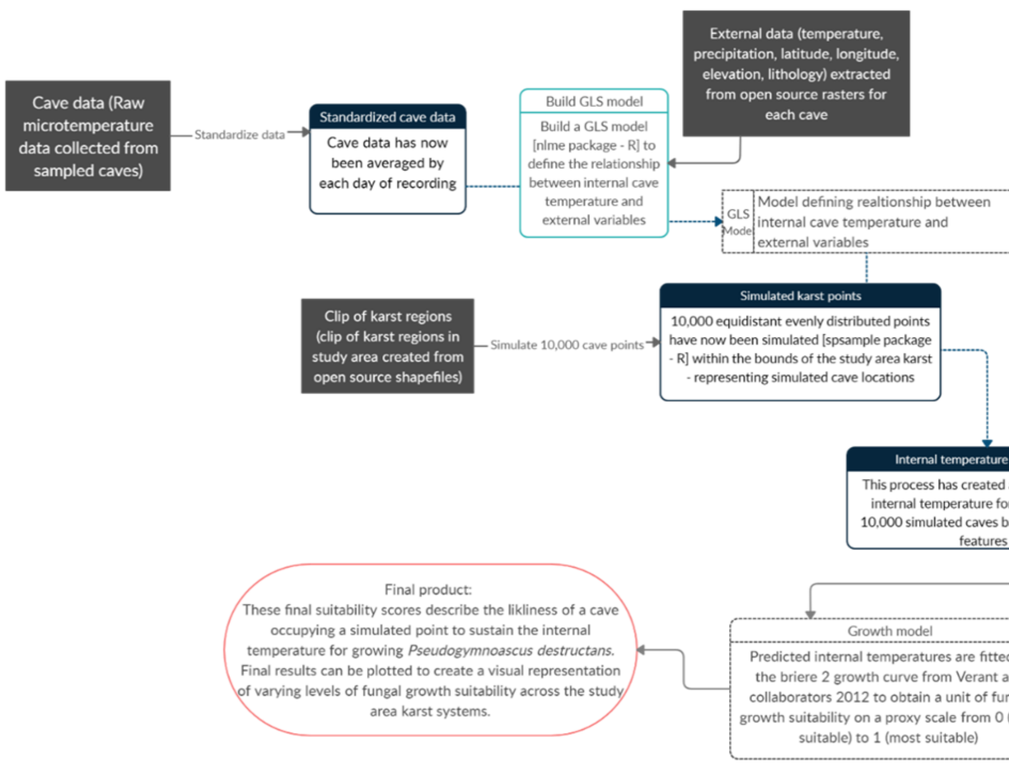


Figure 3. Data flow diagram describing the process of digesting internal cave micro-temperature data to predict suitability for *P. destructans* growth across study area karst

## RESULTS

Caves sampled in Texas covered a broad area and a wide range of external features. These points where caves were sampled included elevation ranges between 108m and 1,867m (mean =525, SD = 253m). External temperatures varied from 8.0°C in 44.7°C (mean=27.4°C, SD=8.26°C), and external precipitation varied in the interval between 0.30mm and 326.20mm (mean=54.3, SD=50.8) during the sample period. The microclimatic temperatures recorded within the caves varied within the interval between -8°C in January 2017 to 29°C during July 2019.

### *MODEL RESULTS*

The best model explaining variation in microclimatic temperature contained all the explanatory variables (Table 1; Table S2) and accounted for 43% of the total variation in data ($R^2 = 0.43$). Mean land surface temperature was the most important variable to explain variation in microclimatic temperature ($\chi^2 = 6238.33$; $p < 0.001$). The second most important variable to explain microclimatic temperature was latitude ($\chi^2 = 1273.50$; $p < 0.001$), followed by longitude ($\chi^2 = 126.08$; $p < 0.001$), monthly precipitation ($\chi^2 = 148.97$; $p < 0.001$), elevation ($\chi^2 = 99.37$; $p < 0.001$) and lithology ($\chi^2 = 17.21$; $p < 0.001$).

Table 1. Estimated parameters for the most parsimonious model created to explain variation in cave's internal microclimate temperature in response to external climatic and geographic data in Texas karst system.

| | Parameter estimates | | | | |
|---|---|---|---|---|---|
| **Parameter** | **Mean estimate** | **SE** | **95% upper CI** | **95% lower CI** | **Relative Importance** |
| Intercept | -38.62430 | 7.198544 | -24.515400 | -52.733100 | - |
| Mean monthly temperature | 0.29185 | 0.003695 | 0.299091 | 0.284606 | 1.000 |
| Latitude | -1.27951 | 0.035855 | -1.209230 | -1.349780 | 0.974 |
| Longitude | -0.85833 | 0.076441 | -0.708510 | -1.008150 | 0.611 |
| Elevation | -0.00234 | 0.000235 | -0.001880 | -0.002800 | 0.266 |
| Lithology | 0.30667 | 0.073921 | 0.451554 | 0.161790 | 0.086 |
| Mean monthly precipitation | 0.08423 | 0.006901 | 0.097755 | 0.070703 | 0.496 |

Suitability for *P. destructans* varied between 0 and 1 within the sampling interval, indicating a large range of temperature conditions for the growth of fungus (Fig. 4). Projections for the entirety of Texas karst systems indicated that reasonable conditions for fungus development (suitability > 0.65) were expected for 75% of the karst systems. Further, the most suitable conditions for fungal growth (suitability > 0.89) were expected in 50% of the region covered by Texas karst features (Fig. 4). Geographically, areas of Texas karst sustaining thermal conditions most suitable for the growth of *P. destructans* are in the northern areas of limestone deposits in central Texas, the southern areas of the gypsum karst in the northern Texas panhandle, and in some smaller karst areas near high altitude mountainous karst regions in West Texas. Thermal suitability decreases in the northern regions of gypsum karst in the Texas panhandle, southern regions of the central Texas limestone karst, and smaller areas near low elevation karst regions near the southern border in West Texas.

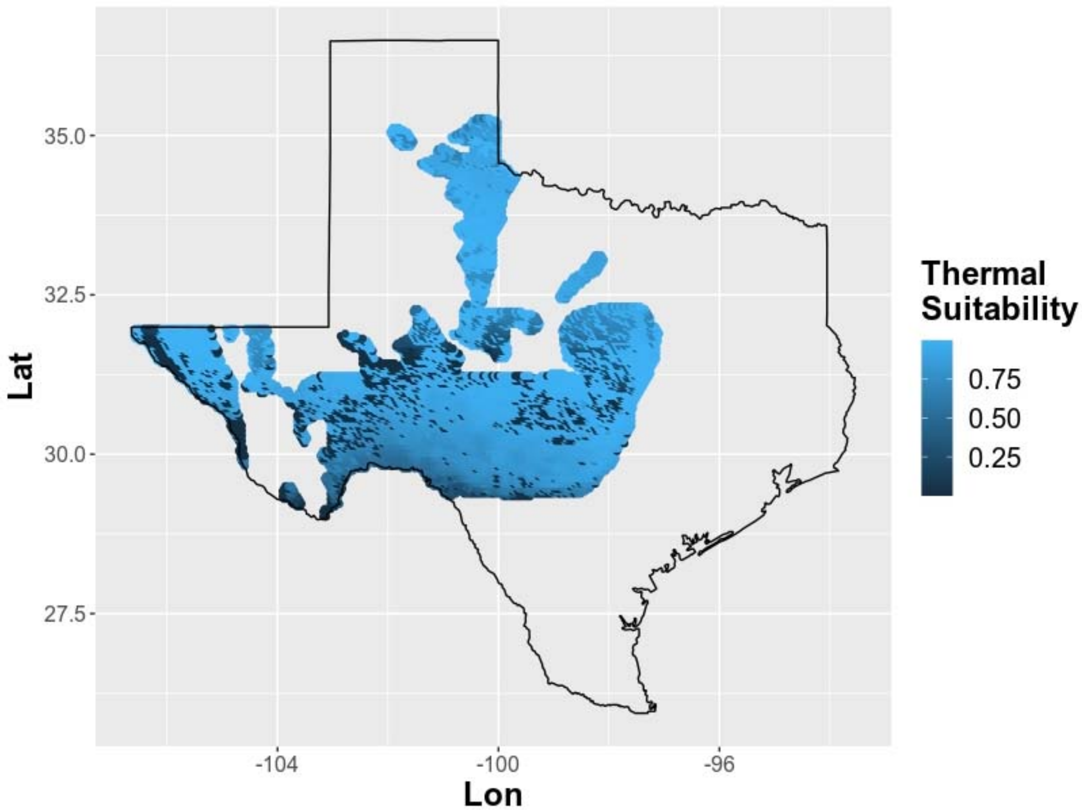


Figure 4. Suitability predictions for *P. destructans* in response to monthly temperature, monthly precipitation, latitude, longitude, elevation and lithology for mean annual conditions in 2019. See methodological details in the '*Model Development*' section.

For the predictions including seasonal variation in suitability for *P. destructans*, model predictions indicated that karst areas supporting thermal suitability increases in warmer months (April-October) and decreases in cooler months (November-March) (Fig. 5). Suitability for fungal growth expands spatially as months become cooler - beginning in the northern regions of gypsum karst in the Texas panhandle, and spreading southward, then westward into central Texas limestone karst and west Texas karst regions. Even for areas showing low suitability during most of the year, conditions for *P. destructans* growth exceeded sub optimal thresholds during winter months.

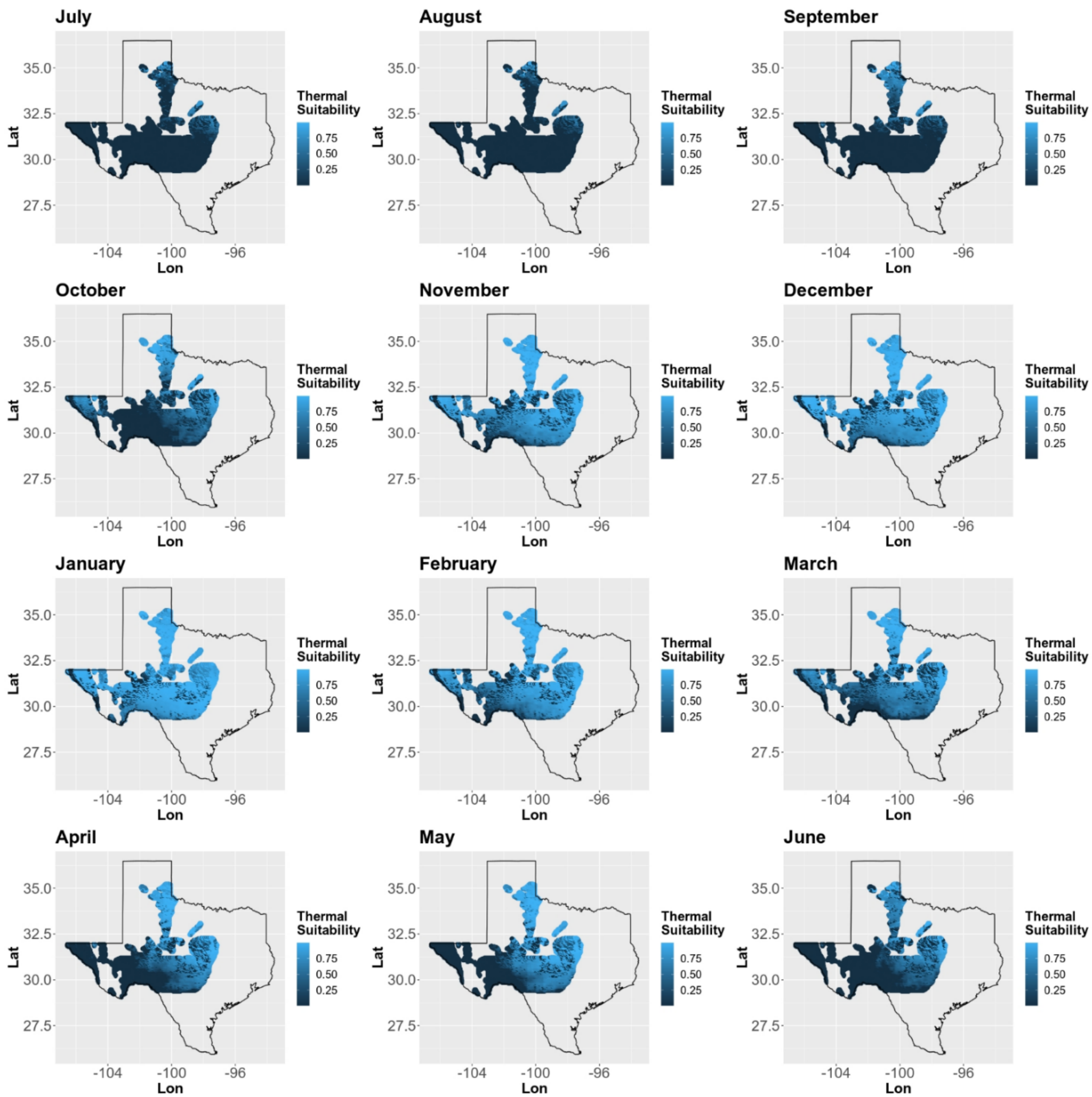


Figure 5. Suitability predictions for *P. destructans* in response to monthly temperature, monthly precipitation, latitude, longitude, elevation and lithology for all months in 2019. See methodological details in the '*Model Development*' section.

## DISCUSSION

A GLS model fed with internal cave micro temperature data indicated that, among the explanatory variables, external temperature and latitude are the most important factors driving microclimatic temperature conditions in Texas caves. Suitability forecasts based on average annual climatic data obtained with model predictions indicated that 50% of the Texas karst system is in the upper bounds (suitability > 0.89) of likelihood to sustain populations of *P. destructans*. This indicates that Texas karst supports cave environments which can be critical for further expansion of *P. destructans* and WNS towards Mexico and Central America.

Optimal suitability conditions for *P. destructans* growth in Texas concentrate in the northern karst zones of the Edwards Plateau, northern zones of gypsum karst in the Texas panhandle, and the Guadalupe Mountains area of west Texas, indicating that these areas require priority in terms of management strategies. In accordance with this analysis, I recommend that these areas be closely monitored for the development of white-nose syndrome, and be targets of interest if a treatment is developed in the future.

Currently, microclimate data is expensive and labor-intensive to obtain (M. Meierhofer, pers. comm). Researchers must use their resources for travel to locations with unknown microclimates twice: once to deploy equipment and once to collect it. Prior to this research, there was no way to target caves which are more likely than others to sustain a microclimate suitable for the sustainment and growth of *P. destructans* on a landscape scale. The product of this research allows researchers to target areas on a landscape most likely to sustain the microclimate which supports the fungus. This way, researchers and managers will be able to allocate their resources to most effectively monitor their region for the arrival of the fungus. Based on these findings, I would recommend the northern areas of the gypsum karst in the Texas panhandle, the northeastern section of the Edwards Plateau, and the Guadalupe Mountains area of west Texas be closely monitored for the development of white-nose syndrome, and be targets of interest if a treatment is developed in the future.

The first recorded case of WNS in Texas this year (TPWD, 2020) underlines the crucial need for tools such as this one to understand and attempt to stifle the spread of the disease. Six species occurring in Texas have been documented as carriers for *P. destructans,* three of which are known to be susceptible to WNS (TPWD 2017b). It was once supposed that resident bat populations in more temperate climates might not be able to become infected as they don't enter extended periods of deep torpor. Infections and die-offs in South Carolina, Tennessee, Georgia, and Alabama soon dispelled this idea, and showed the aggressiveness of WNS even in regions with more temperate winters (Kindell 2019; O'Keefe et al., 2019; WNS 2019; ). As a consequence of WNS in southeastern states, *Perimyotis subflavus,* a previously common species of bat is currently petitioned for listing under the Endangered Species Act (USFW 2017). As the southward movement of WNS progresses, we may see similar threats to conservation – especially in species-rich areas of Mexico and Central America. Further, the value of bats in an ecosystem go beyond the mission of biodiversity conservation. Bats are a taxa of significant economic value in North America, and ecosystem services offered by bats are valued in the billions of dollars they provide to agriculture (Cleveland et al., 2006; Trejo-Salazar et al., 2006; Boyles et al., 2011; Kunz et al., 2011; Kasso and Balakrishnan, 2013). Further, the indirect effects of WNS on human public health have already become evident. As a consequence of increased pesticide use, infant mortalities have experienced an increase of 14.5% relative to the mean in areas hardest hit by WNS (Frank 2017). There are multiple different stakeholders in the fight against the spread of WNS, and novel tools are crucially needed to anticipate the movement and future activity of the disease.

In conclusion, this study provides important information that builds on the understanding of the potential spread of *P. destructans* along Texas karst systems. Besides providing a useful tool for predicting the microclimatic suitability for *P. destructans*, the major findings of this study suggest that, with the highly suitable conditions for persistence of major findings, caves within Texas karst can become nexuses of dispersal and may facilitate the spread of the disease to karst systems in Central and South America. Such findings raise concerns, particularly for bat species of conservation concern, as Central America is considered a hot spot for bat biodiversity as well as an area that is already under increasing anthropogenic pressure - further imperiling native bat species. In addition, the projections presented here set the stage for future conservation strategies, suggesting priority areas for management actions in order to monitor and possibly control the spread of the white-nose syndrome. Future studies should include (i) matching the occurrence of *P. destructans* with suitability estimates in order to improve the prediction power of the model; and (ii) estimations of future suitability projections for *P. destructans* in order to anticipate potential future responses of the disease to different climate change scenarios.

CHAPTER III

SUITABILITY FOR GROWTH OF *PSEUDOGYMNOASCUS DESTRUCTANS* IN VARYING REGIONS OF MEXICAN KARST

## INTRODUCTION

White-nose syndrome (WNS) has led to the deaths of millions of bats in North America since its first documentation in 2006 (Blehert et al., 2009; Turner et al. 2011; USFW, 2012). Since its initial discovery, the disease, and the fungus that causes it, *Psuedogymnoascus destructans,* has radiated across North America (WNS, 2019). WNS and *P. destructans* are now present in 34 states in the United States, and 7 Canadian provinces (WNS, 2019). While it is believed that *P. destructans* was initially introduced to North America through anthropogenic activity, bats are believed to be the primary vector introducing *P. destructans* to new caves in North America, and WNS spread in the early years of the pandemic was a product of spatially diffusive mechanisms (seasonal bat movements introducing the fungus to new caves) and network spread (hibernacula cluster presence and size weighting the ability of a fungus to spread to a particular region) (Maher at al., 2012).

Most concerningly, 18 *Tadarida brasiliensis* bats have tested positive for the fungus (Batcon, 2019). *T. brasiliensis* have a broad migratory range, from as far north as Kansas in the United States to as far south as Bolivia, with a major migratory pathway between central Texas and Central Mexico (Russell et al. 2005). Studies have shown the ability of *P. destructans* conidia to survive on bat fur at temperatures as high as 37°C (Campbell et al. 2020). *T.* brasiliensis are not believed to be highly susceptible to WNS but ostensibly, this species could serve as a highly dispersive vector, traveling long distances and introducing *P. destructans* spores to novel caves in Mexico, and Central and South America (Verant et al., 2018).

As a whole, Mexico and Central America experience a subtropical climate, but high elevation karst areas remain relatively cooler year-round (Escoto and Antonio, 1964; Taylor and Alfaro, 2005; Parks et al., 2020), potentially resulting in optimum conditions for the growth of *P. destructans.* Southern South America has a temperate climate and can experience harsh cold winters, similar to those in the northern United States, where the WNS epidemic began (Escobar et al., 2014). Further, external climatic suitability modeling for *P. destructans* shows suitability for the fungus in ranges that overlap with several endemic bat species (Escobar et al. 2014). Even if *P. destructans* does not manifest as WNS in warmer subtropical regions, ostensibly, if *P. destructans* gains a foothold in Mexican caves, it could spread bat-to-bat, cave-to-cave southward along mountainous karst regions. The virility of *P. destructans* in these more equatorial environments is as of yet unknown, but the recent cases of WNS indicate that cave bats in warmer temperate climates may be at higher risk than previously thought (TPWD, 2020). Further, southern regions of South America are home to cave hibernating bat species such as the Chilean Myotis (*Myotis chiloensis)* which may be susceptible to WNS (Lilley et al. 2020). The hardiness of this fungus, coupled with the migratory patterns of *T. brasiliensis,* makes it plausible that *P. destructans* could travel as an innocuous fungus into Mexico and southward through Central and South American karst systems, until it reaches an area with winters harsh enough for the fungus to become virulent. This remarkable expansion in *P. destructans* distribution is a matter of considerable interest to conservation – Mexico, Central, and South America are home to the most species-rich hotspot regions for bat biodiversity in the world (Alves et al. 2018), and exposure of these areas to a fatal bat disease could lead to extirpation of local populations of several bat species.

Presumably, whether or not Mexican bat species are susceptible to WNS, karst regions in Mexico could be utilized by the fungus as a stepping stone as its range expands southward into Central and South America. This project aimed to assess microclimate suitability within caves in Mexican karst systems in order to characterize the region's susceptibility to WNS, and ability of mexican caves to act as a dispersive agent for *P. destructans.*

## MATERIALS AND METHODS

### *STUDY AREA*

The country of Mexico encompasses a diversity of land surface and biological features. Mexico is bordered by the Gulf of Mexico and the Pacific Ocean, and characterized by broad, temperate, arid desert regions in the central north part of the country, and lowland tropical forests in the south. Temperatures in Mexico vary considerably and are highly variable depending on elevation (Parks et al., 2020). La Rosilla, the city in Mexico which experiences the coldest average temperatures sees average daily summer temperatures ranging from 10.5 and 21°C (Weatherspark, 2020). Conversely, the warmest city in Mexico - Hermosillo, Sonora - sees average daily summer temperatures ranging between 25 and 40.5°C (Weatherspark, 2020). Elevation in the country varies from 0 m at sea level, to 5,636 meters at the peak of Pico de Orizaba in Veracruz state in southeastern Mexico (Parks et al., 2020).

The country contains seven ecoregions of distinct location, climate, vegetation, hydrology, terrain, wildlife, and land use/human activities (Rios and Raga, 2018). These ecoregions include North American deserts, temperate sierras, tropical dry forests, tropical humid forests, southern semiarid highlands, Great Plains, and Mediterranean California (Fig. 6). This wide range in biomes has made Mexico a key spot for biodiversity conservation. It is estimated that Mexico contains 10-12% of the world's biodiversity, containing approximately 11% of the world's mammals - 544 species, of which 161 are endemic (Ordonez and Carrera, 2015; Ceballos, 2014). Mexico is home to 138 species of bats, half of which are cave roosters (Arita, 1993; Tuttle and Moreno, 2005). The karst regions in Mexico are concentrated along high elevation limestone and volcanic deposits in central mountainous regions, and coastal limestone deposits in the Yucatan Penninsula. For the purposes of this study, data loggers were deployed in six states and two mountain ranges: The Sierra Madre Oriental which runs longitudinally through six states in the central eastern part of the country, and the Eje Volcanico Transversal, a seismically active volcanic belt which runs latitudinal through twelve states in south central Mexico (Quinn and Woodward, 2015).

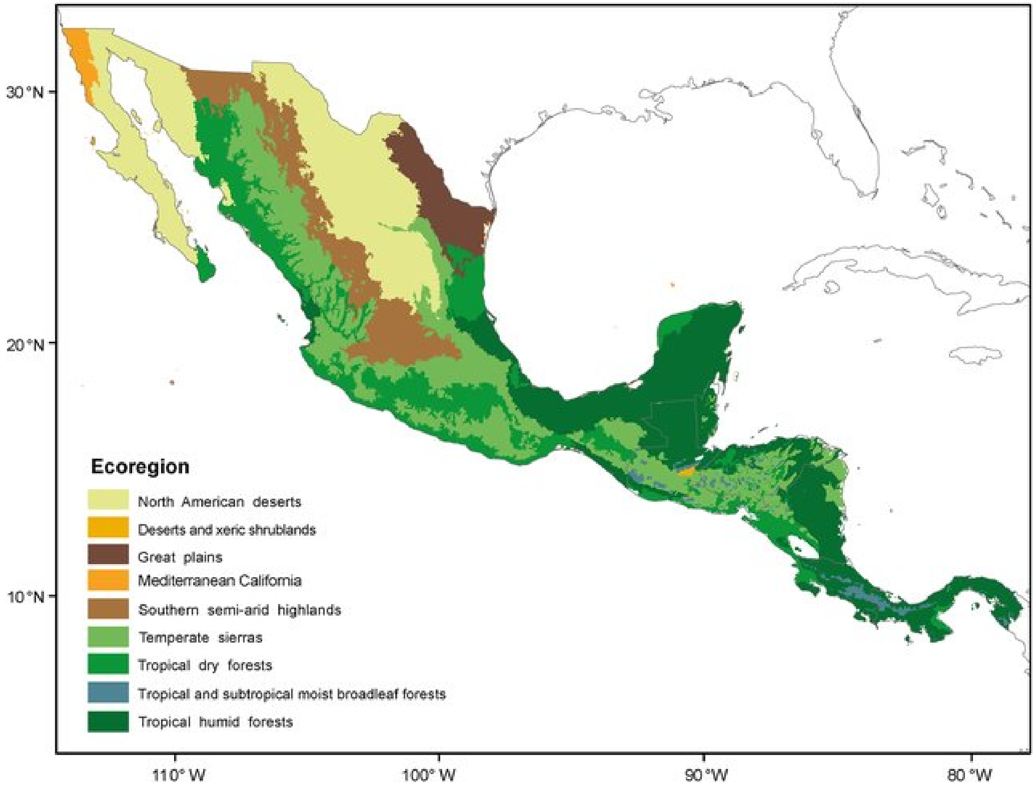


Figure 6. Map of ecoregions in Mexico and Central America. Adapted from Rios and Raga (2019).

### *DATA SAMPLING*

For Mexico, the majority of caves were located from existing records provided by collaborating biologists. Two caves sampled in Nuevo Leon were new to science, and first documented during an expedition survey in the summer of 2019. For these caves, data loggers were deployed at the time of the initial survey. In total, 24 data loggers were deployed in 6 states in the country of Mexico (Fig. 7). Due to complications (Appendix A), only 4 of those data loggers were collected and provided data for this thesis (Fig. 7). With this sampling scheme, the geographic position of the caves reflected a wide gradient of external temperature, annual precipitation, lithology, and elevation. All caves were visited to inspect for qualifying criteria for the study, which included: (i) potential to sustain a wintering bat population, indicated by evidence of bat presence during the winter season (e.g., presence of an individual, guano); (ii) low levels of human disturbance, avoiding interferences for the deployed equipment; (iii) representativeness of gradients of external factors such as elevation, climate, lithology, and spatial distribution.

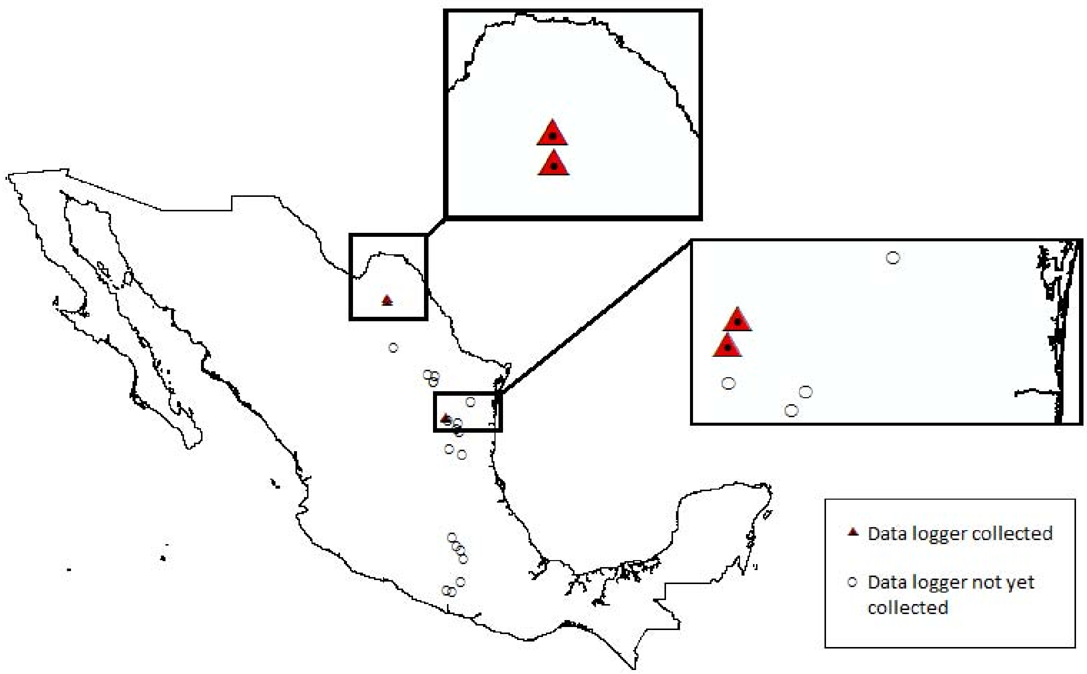


Figure 7. Map of the sampling sites where data loggers were deployed to record microclimatic temperatures in caves distributed amongst Mexican caves. Only data from 4 caves (marked on the map with △) were collected (Appendix A). Data loggers from 20 other caves (marked on the map with ○) remain in the field and will be collected once travel in Mexico is possible.

EasyLog EL-USB-2 data loggers were deployed in each cave deemed to be suitable for data collection. These data logger recorded microclimate temperature at one-hour intervals throughout the course of their deployment. Data loggers were deployed in the coolest room of each cave, which typically was the room furthest from the entrance of the cave. Each data logger was attached to the wall of a cave, far enough off the floor of the cave to be near an area where an overwintering bat might roost, in an area where the equipment would be safe from disturbance throughout the time of its deployment. Each data logger was left to record data for at least one winter season. Due to unforeseen restrictions on travel (Appendix A) only 4 of the 24 deployed data loggers were collected for review. The recorded data was downloaded using EasyLog system software. The 4 data loggers retrieved for analysis in this thesis were deployed and retrieved within the period between November 2018 and February 2020.

### *MICROCLIMATE DATA STANDARDIZATION*

Internal micro-temperature data was analyzed following that same protocol used for Texas data. Raw temperature data consisted of hourly measurements of temperature throughout the time of equipment deployment. Temperature data were standardized by determining the mean temperature for each day of each cave - this was our time unit of measurement.

Because we were interested in modeling habitat conditions for *P. destructans,* we converted the predictions of internal microclimatic temperature into habitat suitability. For this, we used a growth model fitted in the laboratory to obtain the temperature equivalence for growth condition of *P. destructans* (Verant et al. 2012). Resulting growth rates were rescaled to an interval between 0 and 1, indicating growth conditions from worst (0) to optimum (1) for the fungus *P. destructans*.

## RESULTS

Out of the 24 caves sampled with data loggers in 6 states of Mexico, 4 data loggers - 2 from the state of Coahuila, and 2 from the state of Nuevo Leon- were retrieved with usable data.

These caves, their microclimates, and their predicted suitability for sustaining the growth of *P. destructans* are described below.

***MEXICO 1 - COAHUILA***

Mexico 1 was first documented during a caving survey expedition in the Muzquiz municipality of Coahuila in November of 2018. The cave resembles a pit - a steep 30-meter drop with no branching tunnels. At the time of deployment, one bat, believed to be a *Corynorhinus townsendii,* was present.

The area of Muzquiz municipality is situated in the central northern area of Coahuila state. Muzquiz is contained within the Coahuila desert, which is characterized by a hot, arid climate. Rainfall in Coahuila state varies seasonally. The area sees little rainfall for the majority of the year, but a rainy monsoon season in the early summer and smaller rain events throughout the winter season bring nearly all the yearly precipitation to the state. Muzquiz experiences daily average temperatures ranging between 25° C and 37°C in summer months, and 8° C and 20° C in winter months.

All caves surveyed in Muzquiz for this project were formed from limestone karst. Caves in Muzquiz are generally accessible from the tops of mesas - isolated flat-topped landforms on otherwise flat landscapes. Mesas in the Muzquiz survey area rarely extend more than 200 meters above their surrounding landscape and their flat tops do not experience differences in daily temperatures compared to the surrounding lower areas. The entrance to Mexico 1 was determined to be at an elevation 1361 meters above sea level.

The data logger deployed in this cave was placed near the sighted bat, approximately 30 meters from the entrance, and collected the following year. The recorded data from this cave returns a thermal suitability of 0.79 (Fig. 8).

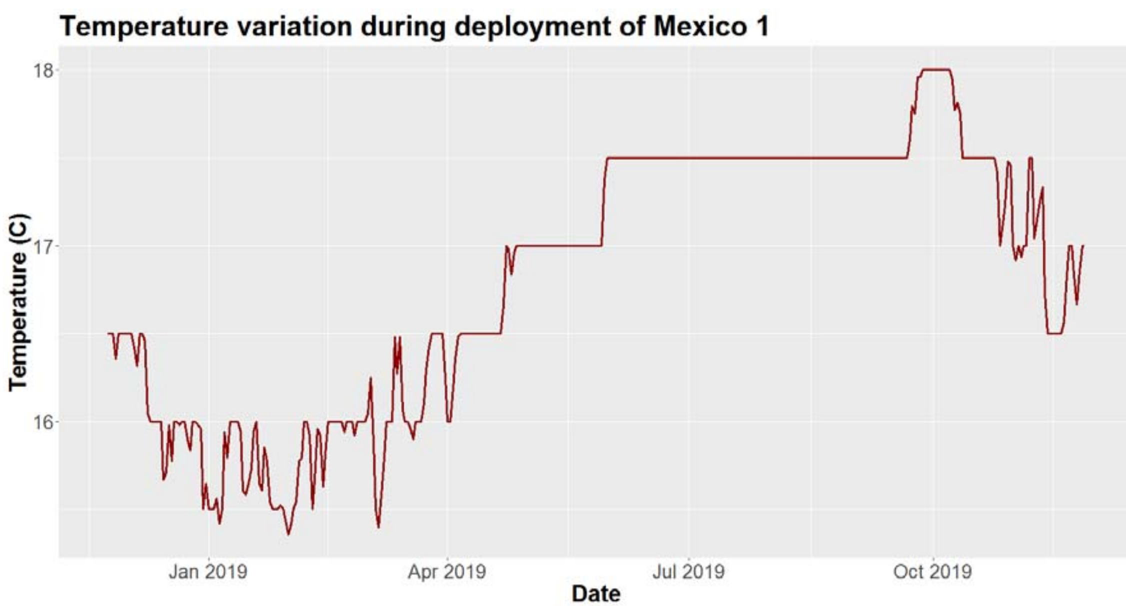


Figure 8. Temperature variation of Mexico 1 over the course of data logger deployment. This cave returned a *P. destructans* growth thermal suitability score of 0.79.

***MEXICO 2 - COAHUILA***

Mexico 2 was first documented during the same caving survey expedition as Mexico 1 - in the Muzquiz municipality of Coahuila in November of 2018. The entrance to Mexico 2 was located approximately 6.5 kilometers from Mexico 1, also at the top of a low mesa, at an elevation of 1005 meters. The same climatic conditions characterizing the areas around Mexico 1 were present at Mexico 2. This cave was also pit-like, with a depth of approximately 55 meters. One bat was present the time of data logger deployment, also believed to be a *Corynorhinus townsendii*. The data logger was deployed near this bat, approximately 20 meters from the cave entrance.  The recorded data from this cave returns a thermal suitability of 0.74 (Fig. 9).

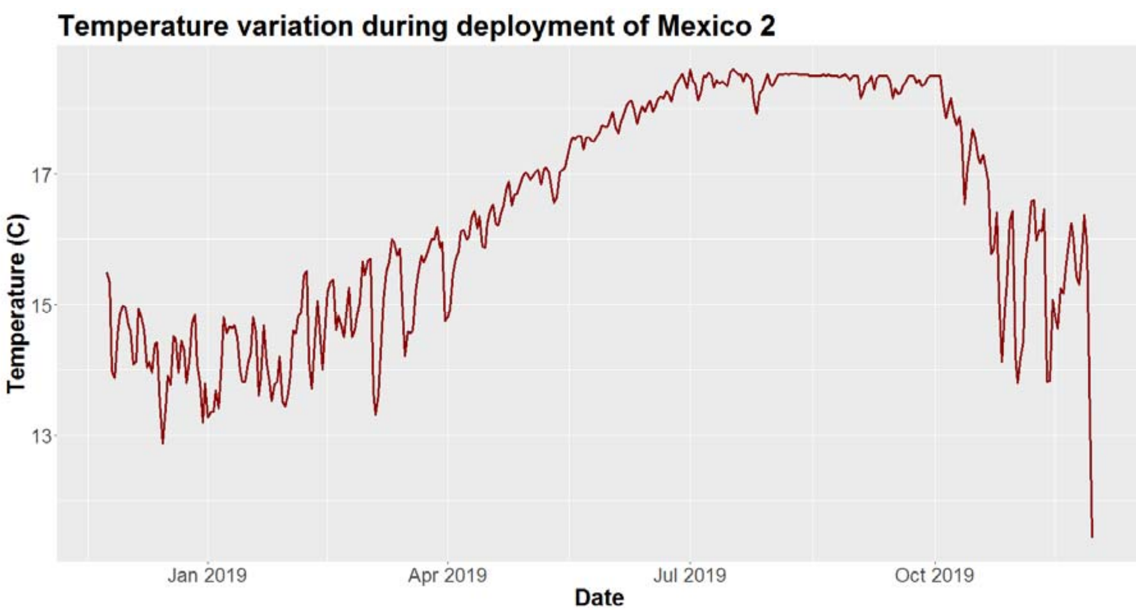


Figure 9. Temperature variation of Mexico 2 over the course of data logger deployment. This cave returned a *P. destructans* growth thermal suitability score of 0.74.

### *MEXICO 3 - NUEVO LEON*

Mexico 3 exists in the mountains east of the town of Zaragoza in southeastern Nuevo Leon state. This cave region exists in the high elevation karst region of the Sierra Madre Oriental mountain range, and its elevation is 2535 meters above sea level. This high elevation area experiences a relatively moderate climate. Average daily temperatures in the summer months range between 20.5°C and 35°C, and winter month temperatures range from 9.5°C and 21.5°C. Rainfall in this region is variable throughout the year, with the most precipitation occurring during the summer-autumn monsoon season. The region is characterized by a diversity of flora, including coniferous forests, oak forests, and agave. This cave has been well known to local ranchers for at least the past 60 years, but its location was first documented for scientific purposes during a caving survey trip in July of 2019. Mexico 3 is a horizontal limestone cave with two large rooms - each approximately 10 meters in length, and 2.5 meters in height - and a third smaller, highly decorated side room of approximately 8 meters in length and 1 meter in height. At the time of data logger deployment, 4 Choeronycteris mexicana were present in the first room of the cave, near the entrance. A data logger was deployed in the second large room, which was the coolest room in the cave. The recorded data from this cave returns a thermal suitability of 0.85 on an interval between 0 and 1 (Fig. 10).

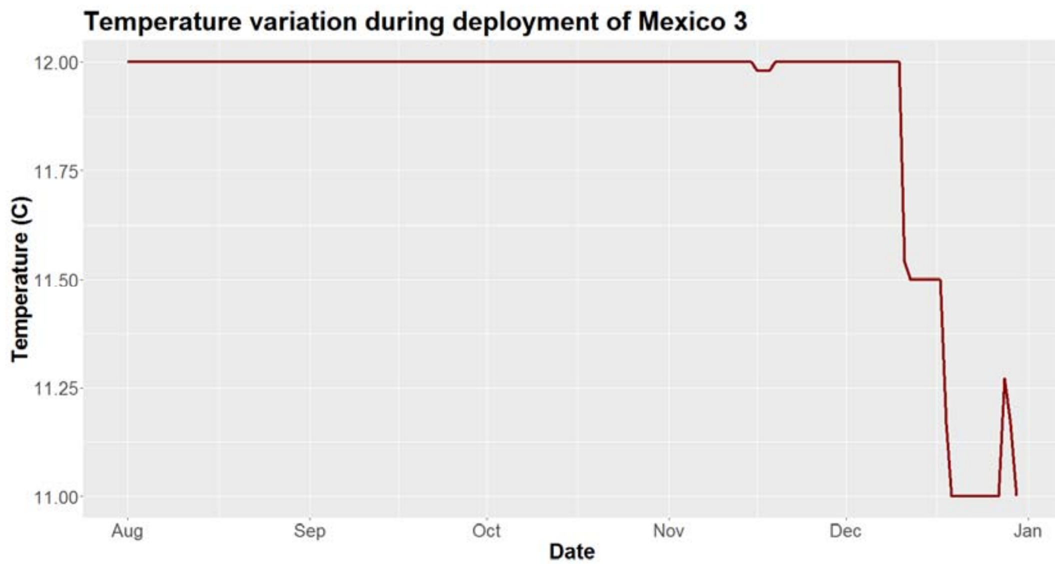


Figure 10. Temperature variation of Mexico 3 over the course of data logger deployment. This cave returned a *P. destructans* growth thermal suitability score of 0.85.

### *MEXICO 4 - NUEVO LEON*

Mexico 4 exists in the mountains east of the town of Zaragoza in southeastern Nuevo Leon state - just 1 kilometer from Mexico 3. Similar to Mexico 3, this cave is also part of the high altitude karst region of the Sierra Madre Oriental Mountain range. Its elevation 2459 meters above sea level. This limestone cave consists of two vertical drops - one 15 meter, and one 10 meter drop - and a floor room of approximately 10 meters in length and 5 meters in width with a high ceiling extending 15 meters off of the cave floor. The data logger was deployed in this floor room. At the time of deployment, 2 bats of an unknown species were sighted near the entrance to the cave. Although there were no bats seen roosting during the day further within the cave, the area where the data logger was deployed (Fig. 11) showed signs of old guano. The recorded data from this cave returns a thermal suitability of 0.84 (Fig. 12).

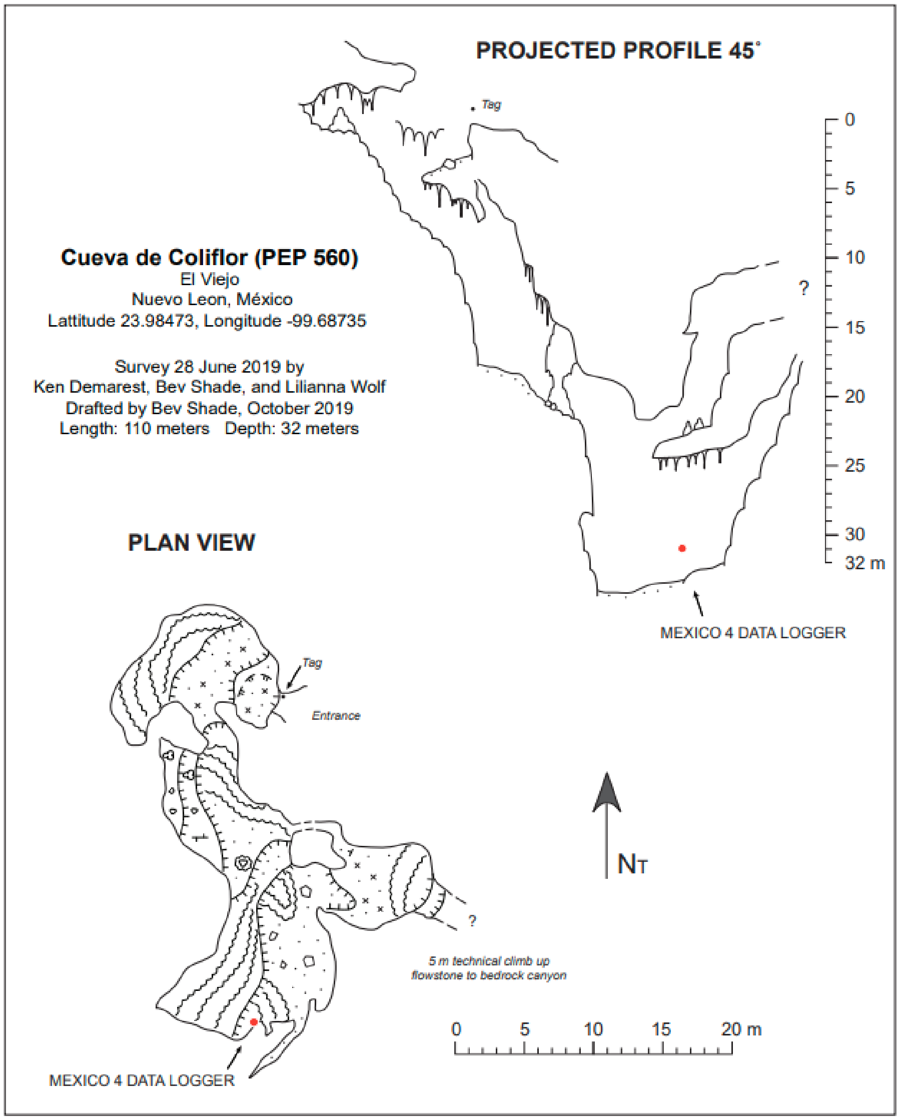


Figure 11. Cave Map of Mexico 4, drawn by Beverly Shade. This cave was newly discovered to science in July of 2019. A data logger for this project was deployed on the day of the cave's initial survey. The deployment site for the data logger is labeled.

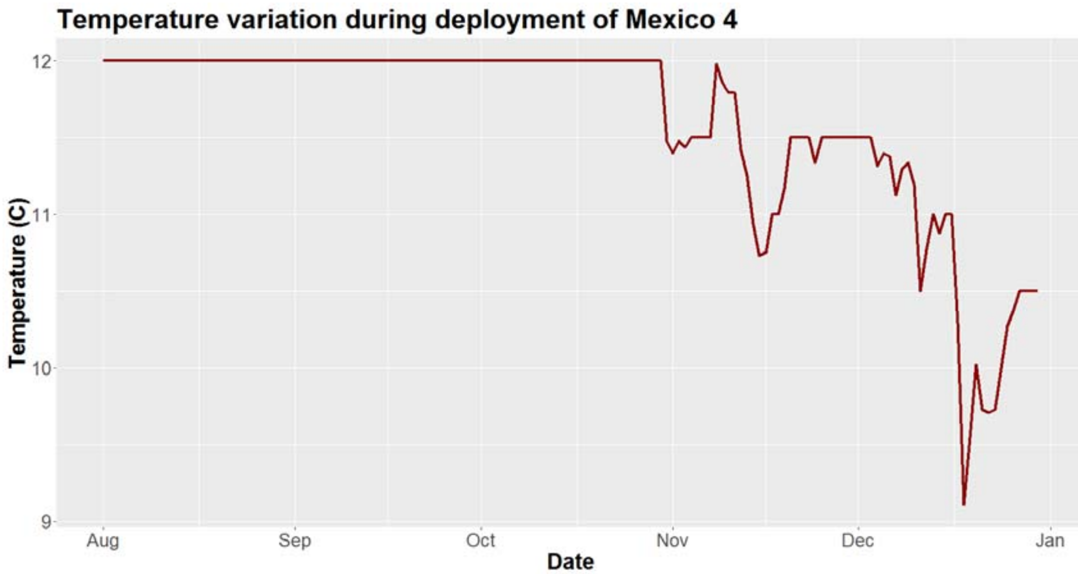

Figure 12. Temperature variation of Mexico 4 over the course of data logger deployment. This cave returned a *P. destructans* growth thermal suitability score of 0.84.

## DISCUSSION

The detection of *Psuedogymnoascus destructans* on 18 *Tadarida brasiliensis* in Texas has raised concerns that the virulent fungus may soon be introduced to caves in Mexico. The microclimate of 4 sampled Mexican caves in regions of varying climate and elevation suggest that karst regions in Mexico are likely able to sustain the growth of *P. destructans*, contributing to the continued spread of this pathogen. While the microclimates of all 4 sampled caves are in the upper bounds (suitability > 0.5) of suitability for fungal growth, differences in levels of suitability between the caves may be partially explained by differences in their surrounding regions.

The karst area where Mexico 1 and 2 were deployed experiences higher average annual temperatures than the high elevation area where Mexico 3 and 4 were deployed. Since there is much higher elevational diversity in Mexico compared to Texas, it is possible elevation will explain more variation in cave thermal suitability for fungal growth when modeling Mexican cave microclimate as a function of external variables. This would be considerable, as areas of steep karst in the Sierra Madre Oriental lead to a patchwork of elevation suitability for flora and fauna (Sánchez-González and López-Mata, 2005) and could support different fungal growth suitabilities between caves of different elevations who otherwise share similar attributes and are spatially near each other. Further, Mexico 3 and 4 are in regions where there exist known migration colonies of *Leptonycteris nivalis,* an endangered species of nectar-feeding bat (Gomez and Lacher, 2017). This keystone species is a critical component of high altitude Mexican ecosystems as it is the principal pollinator for multiple species of agave (Moreno-Valdez et al. 2004). The relationship between these pollinating bats and agave plants is so strong, that it has been said that one may not be able to survive without the other (Arita and Wilson, 1987; Trejo-Salazar et al., 2016; Ratto et al., 2018; Frick et al., 2019). *L. nivalis* is already imperiled by loss of habitat and anthropogenic disturbance (Medellin, 2016). If WNS were to develop in their colonies, it could have the potential to be catastrophic.

*Pseudogymnoacus destructans* will likely be introduced to Mexican karst regions in the near future by migrating *Tadarida brasiliensis*, and understanding the way that the fungus will behave is a crucial first step for developing management plans. Applications of a completed model (Appendix A) will allow me to recommend certain regions of Mexican karst to be closely monitored for the development of white-nose syndrome, and be targets of interest if a treatment is developed in the future, but for now, it is notable that all 4 caves surveyed in the regions of limestone karst in Muzquiz, Coahuila and high elevation karst regions of the Sierra Madre Oriental contain caves that maintain suitable thermal conditions for *P. destructans* growth. These data suggest that *P. destructans* could gain a foothold in Mexican karst regions - a crucial first step in a potential expansion into Central and South America. Future research efforts will include obtaining data from 20 other caves in Mexico – sampling the karst regions of the Sierra Madre Oriental and the Eje Volcanico Transversal – and applying the modeling approach described in chapter 1 to assess microclimate suitability for fungal growth across Mexican karst regions.

# CHAPTER IV

# CONCLUSIONS

The tool built for my thesis uses microclimate as a base variable for developing models to understand *Pd* spread, and can be very useful at targeting areas of concern on a landscape. Previous attempts to model regional suitability for *Pd* have relied on an ecological niche modeling approach. This is useful when little information is available, but does not encompass microscale variation which is necessary to understand fungal growth differences on a variable landscape. Further, incorporating real microscale measurements in model development facilitates a bottom-up build that is more reliable in terms of predictability of suitable conditions. All in all, thermal microclimate is a very descriptive variable when modeling suitability for *Pd*.

In the future, it would be useful for internal microclimate collection to be expanded across all areas of the Americas where WNS may spread. In the early days of scrambling to prepare for and manage WNS spread, the only option was to take a blanket approach to surveys and check and swab as many caves as a biologist or land manager could get access to. This is tough on resources, and often difficult in areas like Texas and Mexico where many caves are either on private property or in areas that are difficult to access. This tool has the potential to target areas of high concern on a landscape, and therefore offer recommendations that allow managers to save time and resources and offer a better more streamlined response to combat the spread of WNS.

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# APPENDIX A

I planned to build a model predicting thermal suitability for *Pseudogymnoascus destructans* in Mexican karst systems in 6 Mexican states where 24 data loggers were deployed for my project. These data loggers were scheduled to be collected in late March of 2020. On March 20th, 2020, the Covid-19 pandemic caused the closure of the border between the United States and Mexico to non-essential travel. Shortly after, Mexican states began encouraging residents to stay home and increasingly issued stronger stay-at-home orders which prevented my mexican colleagues (Dr. Emma Gomez, Universidad Autonoma de Nuevo Leon; Dr. Arnulfo Moreno and Luis Humberto Velez Horta, Comisión de Parques y Biodiversidad de Tamaulipas; and Daniel Ramos, Universidad Nacional Autónoma de México) from traveling to the field and accessing their university offices. Two data loggers had been collected before the shutdown, but as per university policy, they were left in the university office and my colleague at UNAM has since been unable to upload the data to send to me. For these reasons, sufficient data from Mexico was not collected in time to build a model of thermal suitability for fungal growth across Mexican karst systems for my thesis defense. Before the pandemic restricted travel, I was able to retrieve data from 4 points of deployment in Mexico. I will describe the retrieved data from these caves in the results section.

## SUPPLEMENTARY MATERIALS

Table S1. Mean Coefficient of Variation of daily temperature in Texas caves

| Cave | Mean Coefficient of Variance |
|---|---|
| 1 | 0.078651028 |
| 2 | 0.00757964 |
| 3 | 0.042489911 |
| 4 | 0.00331515 |
| 5 | 0.02242742 |
| 6 | 0.009712665 |
| 7 | 0.009341536 |
| 8 | 0.046967209 |
| 9 | 0.005047125 |
| 10 | 0.030498804 |
| 11 | 0.011411884 |
| 12 | 0.005744881 |
| 13 | 0.061622664 |
| 14 | 0.051461484 |
| 15 | 0.010920313 |
| 16 | 0.013385986 |
| 17 | 0.015780186 |
| 18 | 0.006781737 |
| 19 | 0.008576449 |
| 20 | 0.019216827 |
| 21 | 0.003182585 |
| 22 | 0.029347209 |
| 23 | 0.048936759 |
| 24 | 0.001289997 |
| 25 | 0.011119974 |

Table S1. continued

| Cave | Mean Coefficient of Variance |
|---|---|
| 26 | 0.049290343 |
| 27 | 0.000731423 |
| 28 | 0.00315884 |
| 29 | 0.066927866 |
| 30 | 0.005283012 |
| 31 | 0.024586177 |
| 32 | 0.014170829 |
| 33 | 0.05199554 |
| 34 | 0.032475519 |
| 35 | 0.053724207 |
| 36 | 0.008783256 |
| 37 | 0.024076384 |
| 38 | 0.067592589 |
| 39 | 0.035563952 |
| 40 | 0.018853066 |
| 41 | 0.002342348 |
| 42 | 0.047139525 |

Table S2. Models created to explain variation in cave's internal microclimate temperature in response to external climatic and geographic data in Texas karst system.

| Model parameters | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | Elevation | Latitude | Lithology | Longitude | Mean Monthly Precipitation | Mean Monthly Temperature | df | logLik | AICc | ΔAICc | weight |
| -38.62 | -0.00234 | -1.28 | 0.3067 | -0.8583 | 0.08423 | 0.2918 | 9 | -44590.4 | 89198.9 | 0 | 0.997 |
| -22.45 | -0.00208 | -1.31 | | -0.7145 | 0.0799 | 0.2913 | 8 | -44597.2 | 89210.4 | 11.58 | 0.003 |
| 24.46 | | -1.145 | | -0.1963 | 0.04344 | 0.293 | 7 | -44630.5 | 89275 | 76.19 | 0 |
| 20.65 | | -1.126 | 0.1135 | -0.2255 | 0.04335 | 0.2933 | 8 | -44631 | 89278 | 79.13 | 0 |
| 41.51 | | -1.031 | | | 0.01882 | 0.2933 | 6 | -44639.7 | 89291.4 | 92.52 | 0 |
| 41.9 | | -1.043 | -0.03497 | | 0.01998 | 0.2932 | 7 | -44641.4 | 89296.7 | 97.85 | 0 |
| 41.35 | -0.00018 | -1.02 | | | 0.01635 | 0.2932 | 7 | -44646.8 | 89307.6 | 108.72 | 0 |
| 41.94 | -0.0002 | -1.036 | -0.05432 | | 0.01785 | 0.293 | 8 | -44648.2 | 89312.5 | 113.63 | 0 |
| 48.87 | | -0.9507 | | 0.09085 | | 0.2922 | 6 | -44655.8 | 89323.5 | 124.67 | 0 |
| 37.99 | | -0.9131 | 0.2441 | | | 0.2923 | 6 | -44656.1 | 89324.2 | 125.31 | 0 |
| 40.21 | -0.00064 | -0.9519 | | | | 0.2913 | 6 | -44657 | 89325.9 | 127.07 | 0 |
| 44.82 | | -0.9311 | 0.1188 | 0.05958 | | 0.2925 | 7 | -44656.1 | 89326.2 | 127.38 | 0 |
| 39.09 | -0.00049 | -0.9297 | 0.1253 | | | 0.2921 | 7 | -44656.5 | 89327 | 128.12 | 0 |
| 34.93 | -0.00063 | -0.9229 | 0.1721 | -0.03909 | | 0.2919 | 8 | -44658.3 | 89332.7 | 133.79 | 0 |
| 42.06 | -0.00054 | -0.9512 | | 0.01933 | | 0.2916 | 7 | -44659.4 | 89332.7 | 133.84 | 0 |
| 40.14 | | -0.9597 | | | | 0.2903 | 5 | -44666.8 | 89343.6 | 144.78 | 0 |
| 101.4 | 0.00139 | | 0.8526 | 0.8958 | -0.1231 | 0.2991 | 8 | -45199.8 | 90415.6 | 1216.72 | 0 |
| 70.2 | | | 1.041 | 0.5857 | -0.1116 | 0.2986 | 7 | -45211.9 | 90437.9 | 1239.01 | 0 |
| 157.8 | 0.002387 | | | 1.433 | -0.1497 | 0.2981 | 7 | -45262.1 | 90538.2 | 1339.35 | 0 |
| 9.292 | -0.00105 | | 1.646 | | -0.07815 | 0.2994 | 7 | -45296.9 | 90607.8 | 1408.94 | 0 |
| 7.924 | | | 1.814 | | -0.07034 | 0.3005 | 6 | -45317.1 | 90646.3 | 1447.44 | 0 |
| 119.4 | | | | 1.04 | -0.1381 | 0.2967 | 6 | -45322.6 | 90657.3 | 1458.41 | 0 |
| -60.05 | -0.00171 | | 2.216 | -0.6478 | | 0.3064 | 7 | -45659.9 | 91333.8 | 2134.9 | 0 |
| -34.78 | | | 2.117 | -0.3874 | | 0.3082 | 6 | -45687.4 | 91386.8 | 2187.99 | 0 |

| Model parameters | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | Elevation | Latitude | Lithology | Longitude | Mean Monthly Precipitation | Mean Monthly Temperature | df | logLik | AICc | ΔAICc | weight |
| 4.583 | 0.000837 | | 1.628 | | | 0.3116 | 6 | -45786.9 | 91585.7 | 2386.88 | 0 |
| 5.45 | | | 1.463 | | | 0.3119 | 5 | -45799.3 | 91608.6 | 2409.7 | 0 |
| 14.58 | -0.00303 | | | | -0.0774 | 0.2977 | 6 | -45803 | 91618 | 2419.11 | 0 |
| 11.63 | | | | | -0.04931 | 0.3005 | 5 | -46072.5 | 92155 | 2956.15 | 0 |
| 30.48 | | | | 0.2128 | | 0.3093 | 5 | -46247.8 | 92505.5 | 3306.64 | 0 |
| 25.68 | -0.00037 | | | 0.1626 | | 0.309 | 6 | -46253.8 | 92519.5 | 3320.69 | 0 |
| 9.934 | -0.00118 | | | | | 0.3076 | 5 | -46262.4 | 92534.8 | 3335.93 | 0 |
| 9.313 | | | | | | 0.3068 | 4 | -46305.7 | 92619.3 | 3420.45 | 0 |
| -3.959 | -0.002 | -1.338 | | -0.6326 | 0.0471 | | 7 | -46358.8 | 92731.6 | 3532.74 | 0 |
| 2.601 | -0.0019 | -1.353 | -0.1264 | -0.5751 | 0.04544 | | 8 | -46359.1 | 92734.2 | 3535.37 | 0 |
| 41.94 | -0.00106 | -1.162 | -0.1884 | -0.1372 | | | 7 | -46373.2 | 92760.3 | 3561.45 | 0 |
| 34.16 | -0.00117 | -1.128 | | -0.2002 | | | 6 | -46374.5 | 92761 | 3562.18 | 0 |
| 55.25 | | -1.165 | -0.2259 | | | | 5 | -46377 | 92764 | 3565.11 | 0 |
| 56.41 | -0.00055 | -1.182 | -0.3521 | | | | 6 | -46376.6 | 92765.2 | 3566.31 | 0 |
| 57.71 | | -1.171 | -0.2704 | 0.02174 | | | 6 | -46379.4 | 92770.7 | 3571.85 | 0 |
| 56.33 | | -1.2 | -0.3072 | | 0.005752 | | 6 | -46380.3 | 92772.5 | 3573.69 | 0 |
| 56.39 | -0.00055 | -1.181 | -0.3507 | | -0.00014 | | 7 | -46381.3 | 92776.5 | 3577.69 | 0 |
| 50.43 | | -1.224 | -0.2711 | -0.0629 | 0.0123 | | 7 | -46381.6 | 92777.1 | 3578.28 | 0 |
| 52.92 | | -1.109 | | | | | 4 | -46384.8 | 92777.5 | 3578.65 | 0 |
| 48.33 | | -1.121 | | -0.04975 | | | 5 | -46384.2 | 92778.3 | 3579.44 | 0 |
| 41.08 | | -1.174 | | -0.1339 | 0.0122 | | 6 | -46386.4 | 92784.8 | 3585.94 | 0 |
| 52.74 | | -1.098 | | | -0.00423 | | 5 | -46388.4 | 92786.7 | 3587.84 | 0 |
| 52.88 | -0.00014 | -1.106 | | | | | 5 | -46392.2 | 92794.3 | 3595.49 | 0 |
| 52.40 | -0.00043 | -1.072 | | | -0.0099 | | 6 | -46392 | 92796 | 3597.14 | 0 |
| 144.90 | 0.001644 | | 0.5154 | 1.224 | -0.1638 | | 7 | -46927.3 | 93868.7 | 4669.81 | 0 |
| | | | 0.7317 | 0.8658 | -0.15 | | 6 | -46945.1 | 93902.3 | 4703.43 | 0 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 108.90 | | | | | | | | | |
| 180.10 | 0.002235 | | 1.559 | -0.181 | 6 | -46947.6 | 93907.1 | 4708.28 | 0 |
| 146.10 | | | 1.211 | -0.1705 | 5 | -46994.9 | 93999.8 | 4800.93 | 0 |
| 18.78 | -0.00153 | 1.597 | | -0.09749 | 6 | -47089.2 | 94190.4 | 4991.57 | 0 |
| 16.87 | | 1.812 | | -0.08539 | 5 | -47129.8 | 94269.6 | 5070.7 | 0 |
| -55.12 | -0.00187 | 2.12 | -0.6863 | | 6 | -47534.9 | 95081.7 | 5882.85 | 0 |
| 23.64 | -0.00353 | | | -0.0912 | 5 | -47544.7 | 95099.4 | 5900.51 | 0 |
| -28.35 | | 2.004 | -0.4109 | | 5 | -47563.2 | 95136.4 | 5937.5 | 0 |
| 13.62 | 0.000804 | 1.457 | | | 5 | -47660.1 | 95330.1 | 6131.27 | 0 |
| 14.44 | | 1.305 | | | 4 | -47667.6 | 95343.2 | 6144.37 | 0 |
| 20.14 | | | | -0.05508 | 4 | -47827.9 | 95663.8 | 6464.91 | 0 |
| 37.49 | | | 0.1979 | | 4 | -48009.7 | 96027.5 | 6828.62 | 0 |
| 31.55 | -0.00048 | | 0.1356 | | 5 | -48014.9 | 96039.8 | 6840.91 | 0 |
| 18.39 | -0.00119 | | | | 4 | -48019.9 | 96047.8 | 6848.95 | 0 |
| 17.74 | | | | | 3 | -48054.9 | 96115.7 | 6916.87 | 0 |