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The Bees of Two Sites in the Big Thicket National Preserve, Texas, with a Consideration of the Effects of a Rare Flooding Event

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The Bees of Two Sites in the Big Thicket National Preserve, Texas, with a Consideration of the Effects of a Rare Flooding Event

The Bees of Two Sites in the Big Thicket National Preserve, Texas, with a Consideration of the Effects of a Rare Flooding Event

By

Archie Sauls, Bachelor of Science

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The Bees of Two Sites in the Big Thicket National Preserve, Texas, with a Consideration of the Effects of a Rare Flooding Event

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ABSTRACT

Native bees are an important part of terrestrial ecosystems due to their coevolution with flowering plants. This study catalogued the bee fauna of two sandyland sites in the Big Thicket National Preserve and assessed whether a community was impacted by a historic hurricane-induced flooding event. It was hypothesized that a change in diversity metrics would be evident following the flood. Datasets were analyzed for differences in species richness, abundance, evenness, and Shannon’s diversity. Similarities between datasets were also assessed using the multivariate tests analysis of similarity (ANOSIM) and similarity of percentages (SIMPER). At two sites over two years of sampling 100 species were documented. Though some species declined dramatically following the storm, it was concluded that the overall bee community did not suffer a substantial decline. Differences detected between datasets constructed from samples taken before and after the flood were mostly attributed to ground nesting bees.

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INTRODUCTION

Pollination and Bees

The relationship between flowering plants and bees is one that cannot be overstated. The idea that some plants actively worked to recruit bees for reproduction wasn't conceptualized until the early 1800s, when German naturalist Christian Sprengel noticed that plants that produced more nectar attracted more insects (Abrol, 2012). Although his findings weren't taken seriously in his time, his work would influence early naturalists, such as Charles Darwin, and help lay the foundations for what we now understand about pollinators. Today we know there are over 200,000 species of plants that require pollination by animals, and insects make up the clear majority of these, with bees often considered to be the most significant (Abrol, 2012; Van der Kooi et al., 2016; Ollerton, 2021).

Bees, along with their near relatives the sphecoid wasps, are classified in the hymenopteran superfamily Apoidea. There are over 3500 species of bees found in the United States (Ascher and Pickering, 2020*)*. Most of these species (over 80%) are solitary, many are colonial, and fewer are eusocial (Michener, 2007). Bees can be distinguished from their hymenopteran relatives by their abundance of highly branched hairs (a useful adaptation for securing pollen grains). They can also be distinguished by their behavior: bees have evolved complete herbivory. Whereas many other pollinators display a similar reliance on the products of flowers, bees are especially productive pollinators due to their behavior. Most hymenopterans use captured or paralyzed arthropods to fulfill their young's protein needs; however, most bees rely solely on the nectar, pollen and oils produced by their flowers (Michener, 2007). It is this feature that makes bees such effective pollinators for many different species of flowering plants. Most pollinating insects only have to feed themselves, but most female bees must visit flowers frequently to maintain their supply of food for their young. Most bees are generalist pollinators and visit several different species of flowers, whereas some are specialists which focus on a particular group of flowers, or even single species (Michener, 2007).

Bees play a key role in the environment by ensuring that the next generation of plants can reproduce. However, some bee species are currently in decline due to several factors. Habitat loss, use of commercial pesticides, and habitat fragmentation have all contributed to the decline of bee populations across the United States (Cameron et al., 2011; Renauld et al., 2016). One study in Illinois found a 45% reduction in bee-plant interactions caused by the local extinction of dozens of species of bees since the 1800's (Burkle et al., 2013).

Gulf Coastal Plain, Big Thicket Concept, and the Big Thicket National Preserve

The Gulf Coastal Plain covers a large swath of the southeastern United States. It is bordered by the Great Plains to the northwest, the Appalachian Mountains to the north, the Atlantic Coastal Plain to the northeast, and the Gulf of Mexico to the south. The Gulf Coastal Plain spans the coastal states from Florida to Texas and borders the Mississippi river as far north as Illinois. The region contains diverse habitats, with pine-dominated habitats being the most common. This area has received a fair amount of work in terms of bee surveys and studies (Cane, 1997; Bartholomew, 2004; Bartholomew and Prowell, 2005; Bartholomew and Prowell, 2006; Bartholomew et al., 2006; Colla et al., 2012; Breland, 2015; Sudan, 2016; Van Gorder, 2016; Simmons, 2017; Owens et al., 2018; Ulyshen et al., 2020).

The portion of the Gulf Coastal Plain that extends into eastern Texas is colloquially known as the Big Thicket. The boundaries and biological definition of the Big Thicket has been the subject of much debate (Parks and Cory, 1936; McLeod, 1971; Gunter, 2015). Regardless, it is clear that the vegetation of the Big Thicket can be described as a continuation of the southeastern mixed forest (Bragg, 2002) and represents its southeastern margin. Early settlers to the Big Thicket traversed various habitats, such as rolling sand hills covered in pine forests that are endemic to much of the southeastern United States. During this period of human settlement, large areas of forest were converted into farmland and harvested for timber (Bragg, 2002). The deforestation fragmented the Big Thicket, leaving relatively small portions of the original habitats scattered across eastern Texas.

The Big Thicket National Preserve is located in southeast Texas. Founded in 1974, it was the first national preserve in the U.S. It currently covers over 40,000 hectares and is divided into fifteen disparate units in various counties of southeastern Texas. Botanically, it has been characterized as a whole several times (McLeod, 1971; Marks and Harcombe, 1981; Watson, 2006). In more recent years several units within the preserve have been extensively surveyed (MacRoberts et al., 2002; Brown et al., 2005, 2006a, 2006b). Various units within the preserve are now well-known to contain interesting habitats, such as dry sandy uplands (referred to herein as sandylands), pitcher plant bogs, and pine savannahs (Watson, 2006). The presence of many different habitats is due to variable ecological factors such as elevation, drainage, soil type and precipitation (Watson, 2006). For example, sandy soils and well-developed drainage patterns lead to xeric habitats including dry savannahs and sandylands. On the other hand, impenetrable clay soils on low, flat areas often produce wet savannahs and bogs (Watson, 2006).

Published studies of terrestrial arthropods in the Big Thicket National Preserve have been few. Recently, several of the units within the preserve have been surveyed for ants (Hill, 2015). In 2010–2012, a few collections of bees were made under the auspices of the National Park Service in the Hickory Creek Savannah Unit (National Park Service, 2010). Roughly 200 specimens representing roughly 20 species of bees from were found (National Park Service, www.nps.gov/bith). In 2017, researchers from Stephen F. Austin State University (SFASU) and Sam Houston State University (SHSU) began a survey of bees in the Turkey Creek Unit that was interrupted by flooding associated with Hurricane Harvey (Bennett, personal communication).

Bee Surveys in the Southeastern United States

Our understanding of the bee fauna of the eastern United States is a result of the work from pioneers such as Michener (1947, 1979), Mitchell (1960, 1962) and many others. Michener (1979) concluded that bee abundance and species richness is lower in the eastern United States than in the western deserts and prairies but higher than the sub-tropic south.

Since these early works, many additional studies on bees have been done in the southeastern United States. In Louisiana, studies emphasizing threatened habitats (Bartholomew, 2004; Bartholomew and Prowell, 2006; Van Gorder, 2016) were conducted and a statewide checklist has recently been produced (Owens et al., 2018). Other significant studies on bees from other states in the South include the following: Georgia (Hanula and Horn, 2011; Breland, 2015; Hanula et al., 2015), Florida (Cane, 1997; Deyrup et al., 2002; Hall and Ascher, 2010; Hall and Ascher, 2014), Mississippi (Sudan, 2016), Alabama (Lozier, 2020), Arkansas (Tripodi and Szalanski, 2015). In Texas, surveys focusing on specific taxa and areas have been conducted. Warriner (2012) examined several university collections for bumblebees. Another study examining bumblebees mapped the distribution of the most common species through the state’s ecoregions (Beckham and Atkinson, 2017). A recent study undertaken by Ballare (2019) documented bee species and examined how land-use impacted bee diversity metrics. East Texas has received relatively little attention when compared to northeastern and north-central regions.

Hurricane Harvey

As in most natural disasters, hurricanes can severely affect the flora and fauna of the area, and though not a common occurrence, several notable storms have impacted the Big Thicket. In 2005, Hurricane Rita struck the southern U.S. and caused extensive tree damage in the Big Thicket National Preserve (Harcombe et al., 2009). More recently, Hurricane Harvey struck south and east Texas and was estimated by the National Oceanic and Atmospheric Administration to be the most significant tropical cyclone rainfall event in United States history. Coastal Texas received over sixty inches of rainfall in a few days, with the values becoming smaller further east from Galveston (Blake and Zalinsky, 2017). The rain caused severe flooding across the southeastern portion of Texas.

Flooding Impacts on Bees and Other Insects

Many if not most terrestrial invertebrate populations are susceptible to flooding. Some of the challenges they may endure include being swept away during high waters, soil compaction, buildup of toxic substances, and water contamination due to runoff (Plum, 2005). A pressing issue faced by terrestrial invertebrates during flooding is the loss of oxygen, and insects have developed several ways to avoid and survive inundation. In a review of flooding's effects on invertebrate communities in grasslands, Plum (2005) categorizes some of the different escape tactics used by flooded invertebrates. Relatively large and mobile invertebrates can attempt to escape to a nearby non-flooded area and wait for the waters to subside (horizontal movement). Others can avoid high waters by climbing and clinging to any debris or vegetation that takes them above the new water line (vertical movement). Some invertebrates are unable to escape the flood waters through movement and may be restricted from doing so by their small size or subterranean lifestyles. Beetles and termites for example were found to greatly reduce their foraging when confronted with several weeks of inundation (Ulyshen, 2014).

Flooding can be equally impactful on bees. While most adult bees are presumably mobile enough to escape any rising waters in the area, immature life stages (larvae and pupae) are immobile and must rely on other methods and protections to survive high waters. The nest is an important means of protection. Bees build nests primarily to rear their young. The nest needs to protect the immature larvae from the environment and potential predators while also preserving larval provisions. The majority of solitary bees (and therefore the majority of all bees) nest in the ground. The nest consists of a main tunnel descending into the ground, from which several smaller tunnels usually branch out. At the end of these branch tunnels is the cell, where the larvae and food provisions are stored. More attention is given to this area than the main tunnels. The walls are usually smoother than the rest of the nest and are sometimes lined with various materials. In most cases these materials form a hydrophobic barrier to the outside which can protect the inner larvae and provisions from excess water (Michener, 2007; Danforth et al., 2019).

The effectiveness with which a nest protects young bees from flooding likely varies from group to group. Most ground nesting bee species have protection from rain and presumably temporary flooding. For example, the nests of *Halictus ligatus* have been shown to be unaffected by moderate moisture levels (Sardiñas et al., 2016) and Pietsch et al. (2016) described a nest of a bee with 80% soil saturation. At least some species seems to be highly resistant to the effects of extreme flooding and fully inundated soils. Norden et al. (2003) found that pre-pupae of *Perdita floridensis* were able to survive in cells for up to six months underwater, and Cane (1997) reported on a species of *Hesperapis* that could survive a category three hurricane’s flooding effects in coastal habitats.

Some studies suggest that certain bee communities can benefit from regular flooding. A 2018 study by Neumüller et al. found that bee communities inhabiting regularly flooded meadows maintained a higher species diversity than meadows that were less prone to floods. Another study recorded a higher frequency of soil nesting bees in areas that experienced low to mild-intensity floods compared to areas that experienced high-intensity floods (Aranda and Aoki, 2018).

There are also reports of negative effects on bees caused by flooding. Fellendorf et al. (2004) observed a population of *Andrena vaga* in Germany on a section of the Rhine River that occasionally flooded its banks. They found a significant decrease (over 50% in some areas) in the population of bees living on a floodplain immediately after record high flooding. This is despite the fact that lab testing of this bee species' brood cells found them to be nearly waterproof.

Objectives

The main objective of this study was to compare the diversity of bees (richness, abundance, evenness, Shannon's diversity) before and after a flooding event caused by Hurricane Harvey at a site in the Big Thicket National Preserve. It was hypothesized that many species, particularly those that rely on the ground for nesting, suffered a decline as a result of the storm. Hypotheses were formulated as follows:

- Hypothesis 1 (null): No significant differences exist in diversity measures between samples taken before and after the flooding event.
- Hypothesis 1 (alternate): Significant differences exist in diversity measures between samples taken before and after the flooding event. Ground nesting bee species were hypothesized to be impacted more than above-ground nesting bee species.
- Hypothesis 2 (null): No significant differences exist in diversity measures between samples taken from a flooded site and an unflooded site of similar habitat.

- Hypothesis 2 (alternate): Significant differences exist in diversity measures between samples taken from a flooded site and an unflooded site of similar habitat.

A second objective of this study was to characterize the bee fauna of two sandyland habitats in the Big Thicket National Preserve and provide a checklist of species.

MATERIALS AND METHODS

Study Sites

Two sites in the Big Thicket National Preserve were chosen for study. These sites represent good examples of xeric sandyland habitats formed by creek deposits. Open, sunny conditions at ground level results in a prevalence of flowering herbs and sun-loving insects such as bees.

The site referred to herein as the "*flooded site*" is located in the southern part of the Turkey Creek Unit, 5.4 km northeast of the intersection of FM 420 and Highway 69 in Hardin County (Figs 1, 2). It is approximately 73 acres with an average elevation of roughly 23 meters above sea level, and is approximately 600 meters northeast of the confluence of Village and Turkey Creeks. The site was estimated to be no higher than five meters above the nearest creek bank. It is traversed by the Sandhill Loop Trail (30.4739°; -94.3377°). The flooded site represents a good example of "sandyland" habitat in the sense of Watson (2006). The soil of this area consists largely of sandy soil up to 0.2 meters in depth in most areas (Web Soil Survey). This soil is over 95% sand and occurs on slopes ranging from one to five percent. The site contains a distinct and diverse community of plants, in contrast to nearby areas with largely closed canopies. The plant community is classified as an upland pine forest, with *Pinus palustris, Pinus taeda, Quercus incana,* and *Quercus margaretta* making up the dominant woody plants (Brown et al., 2005). The understory consists of shrubs and sparse grasses adapted to well-draining, sandy and acidic soils. There are several lines of evidence that flooding occurred at this site. A large flash flood inundated parts of a nearby town of Silsbee in Hardin County (but not areas in Tyler County to the north) following the hurricane (NOAA National Centers for Environmental Information). In addition, a stream gauge located ~15 kilometers downstream of the study site adjacent to Village Creek recorded a near all-time record daily mean stream height of 27.56 feet. The record height for a nearby location, roughly 1.6 miles south of the above stream gauge, was 34 feet, and occurred in 1915 (USGS National Water Information System). Additional observed evidence comprised the following: nearly all survey traps set in early 2017 at the site were displaced, in some cases by 100–200 meters; the construction of the traps (see below) were arguably easily moved by water, but not wind; one trap was found wedged between two small trees roughly one meter above the ground; and additional woody debris comprising large branches were located on the lower limbs of trees and high in shrubs throughout the area.

The site referred to herein as the "*unflooded*" site, another xeric sandyland, is located in the northern part of the Turkey Creek Unit, in Tyler County (Figs 1, 3). It is just south of County Road FM 1943 and is adjacent to Turkey Creek Trail (30.6141°; -94.3472°). It is approximately 36 acres with an average elevation of roughly 42 meters above sea-level, and is approximately 800 meters west of Turkey Creek. The site's soil is mostly sandy and consists of a mixture of Turkey sand, Kirbyville-Niwana complex, and Otanya very fine sandy loam (Web Soil Survey). All three sand types have a surface layer of sand greater than 0.2 meters. The plant community consists of an upland pine forest with *P. palustris* dominating the overstory and *Q. incana* dominating the midstory. Compared to the flooded site, *Q. incana* grew in much thicker stands and the pine overstory was sparser. Evidence of flooding was not observed at this site.

Sampling Methods

A variety of sampling methods were used including Malaise traps, pan traps, vane traps, and aerial netting. Malaise traps are large tent-shaped constructions made of a mesh. There is a central wall, a mesh “roof”, and a funnel that accumulates insects into a chamber at the top. The trap works by taking advantage of an insect’s instinct to crawl or fly upwards after hitting a barrier. Flying insects that strike the central wall of the trap are funneled upward into the chamber of preservative, in this case 80% ethanol. These traps were convenient for this study because they collected many insects, were easily serviced, and required little maintenance after initial setup. They ran continuously during the sampling period and were serviced roughly every two weeks.

Pan traps are small (ca. 3” wide), colored cups (blue, yellow, white) filled with soapy water. Insects are attracted to the colors of the pans and are trapped by the water. Pans of different colors were alternated along transects or set in clusters. Pans were placed ca. 5–10 meters apart in areas relatively free of shade and unobstructed by underbrush. They were set for one roughly 24-hour period about every two weeks to correspond with Malaise trap collection times.

Vane traps are larger than pan traps and work in a similar manner. They consist of colored funnels and panels above to attract insects. A roughly 1-liter chamber below the panels contained the non-toxic preservative agent propylene glycol. These traps ran continuously and were serviced roughly every two weeks on the same schedule as the Malaise traps.

Hand collecting with an aerial net was often conducted for at least 30 minutes at each site during many but not all site visits. This involved sweeping and targeted capture.

Flooded Site Sampling

Sampling from early February to late August in 2017 at the flooded site is herein referred to as the “*pre-flooded*” dataset. One Malaise trap was established near the center of the site. Two ca. 150 meter transects were established for pan traps. The pans were separated by ca. 5–10 meters and transects were separated by ca. 200 meters. Nine pan traps were placed on the ground, nine were elevated 0.3 meters on PVC pipes, nine were elevated one meter on PVC pipes, and nine were elevated roughly two meters by attaching them to nearby *Q. incana* limbs. Supplementary pan traps were occasionally set along trails in the area. Four vane traps (two blue, two yellow) were placed ca. 250 meters apart from each other and far from the other traps.

This sampling scheme was repeated at the flooded site in 2019 with minor adjustments. This dataset is referred to herein as "*post-flooded*." Sampling took place from early February to late October. Yellow vane traps and pan traps elevated one and two meters were discontinued due to poor results.

Unflooded Site Sampling

Sampling at the unflooded site in 2017 was minor and not systematic. A single, continuously operating blue vane trap was established in the site and was serviced every two weeks. This was supplemented with occasional hand collecting and pan trapping.

Sampling of the unflooded site in 2019 was increased relative to 2017 to match the sampling effort for the flooded site. Pan trap transects were replaced by pan trap clusters. Sets of three pan traps (one of each color) were placed in a cluster with each trap separated by ca. five meters. Clusters were separated by ca. 50 meters. This alteration was necessary due to the higher nature of undergrowth and the inability to establish a clear transect. Specimen collection and servicing of the traps took place on the same days as for the flooded site.

Specimen Processing

Samples were cleaned, sorted, and preserved in 80% ethanol at SFASU before being delivered to SHSU for further processing, where Dr. John Pascarella (Department of Biological

Sciences) carried out pinning, labeling and identification of specimens. Literature used to identify species included Mitchell (1960, 1962), Gibbs et al. (2013), and online keys from the Discover Life Bee Species Guide (Ascher and Pickering, 2020). Most specimens, with the main exception of most male *Lasioglossum* species, were identified to species; a few were given morphospecies identities. Specimens are archived in the entomology collections at SFASU and SHSU.

Analysis

In order to make statistical comparisons across years and sites, collection data needed to be standardized. Some samples had to be removed that did not have equivalent collections in the alternate collection period. For example, due to interference from Hurricane Harvey in 2017, sampling after late August did not occur in 2017. As such, the last five trapping intervals were removed from 2019 to balance the sampling efforts across years. Limited instances of trap failure was another source of differences between years. Specimens that were captured using non-standard methods (e.g., hand collecting) were excluded from analyses that compared years. Other than two specimens assigned to morphospecies, all specimens not identified to species were excluded from the following diversity analyses. *Lasioglossum* males were also excluded due to the high number of unidentified specimens. The remaining specimens comprise what is herein referred to as the "*standard*" and *"standardized"* dataset. One species, *Megachile petulans*, was further excluded from analyses where nesting substrate was the focus due to uncertainty of its nesting habits.

As opposed to the standardized dataset, some analyses and graphics were produced using all specimens. The remaining specimens comprise what is herein referred to as the "*total"* dataset. Herein various datasets can be referred to as the pre-flooded standard, pre-flooded total, post-flooded standard, post-flooded total, unflooded standard, and unflooded total datasets.

Some analyses required data to be pooled by combining all specimens from one site for the entire standardized sampling period in a year. In other cases, analyses required replication within a year. This replication was done by dividing the yearly sampling period into "*rounds*" or roughly two-week periods that corresponded to the runtimes of Malaise and vane traps. The standard datasets were made up of 13 rounds between late February and late August. Specimens from all traps operating within a round were pooled for some analyses.

Species richness estimators with 95% confidence intervals were generated in R version 4.03 using the function "ChoaSpecies" in the SpadeR package (version 0.1.1). These estimators are used to predict the actual number of species that occur at a site using incidence or abundance data. These values were produced for different sites and years using both total and standard datasets. Species accumulation curves for both total and standard datasets were generated in order to visualize new species detection over time. This was done in R using the function "specaccum" in the Vegan package (version 2.5-7). Both collector's curves (simple curves that plot species accumulation chronologically) and rarefaction curves (smooth curves generated using random resampling of data) were created (Gotelli and Colwell, 2001).

Shannon's diversity index values and Pielou's evenness index values were calculated for different sites and years using both total and standard datasets. Shannon's diversity index values (H') were calculated using the following formula.

$$H' = -\sum p_i ln p_i$$

In this formula (p_i), the relative abundance of individuals of species (i), is multiplied by the natural log of (p_i). Pielou's evenness values (E') were calculated by dividing H' values by the natural log of the total number of species (S).

$$E' = H'/\ln(S)$$

Hutcheson's t-tests were performed between pairs of Shannon's diversity index values generated from standard datasets using the statistics software PAST (Paleontological Statistics; Hammer et al., 2001) version 4.05. Hutcheson's modified t-test uses Shannon's index values and their associated variances to generate a test statistic (Hutcheson, 1970). The Hutcheson's test statistic is calculated as follows.

$$t = \frac{H'_1 - H'_2}{\sqrt{Variance\ H'_1 + Variance\ H'_2}}$$

Group variances are approximated using the following formula.

$$Var\ H' = \frac{\sum p_i\ (lnp_i)^2 - [\sum(p_i lnp_i)]^2}{N} + \frac{S-1}{2N^2}$$

The degrees of freedom for the test were calculated using the following formula.

$$df = \frac{(Var\ H'_1 + Var\ H'_2)^2}{\frac{(Var\ H'_1)^2}{N_1} + \frac{(Var\ H'_2)^2}{N_2}}$$

Various univariate tests were performed to compare species richness, abundance, and species diversity of three datasets (pre-flooded, post-flooded, and unflooded). Select datasets were tested for normality using the Shapiro-Wilk's test with the "shapiro.test" function in R. If normality was not rejected, a one-way analysis of variance was done. If a significant ANOVA result was found, Tukey's pairwise comparisons were made in order to determine which groups differed. The non-parametric Kruskal-Wallis test and Dunn's pairwise tests were performed when normality for a dataset was rejected.

In order to further look for differences among the three datasets an analysis of similarity (ANOSIM) was used. ANOSIM is a non-parametric, multivariate, distance-based test which compares the similarity between and within specified groups. An abundance matrix was created with species as columns and sampling rounds as rows. Matrices were created for all bees, ground nesting bees, and above-ground nesting bees from the standard dataset. The abundance values in these matrices were then converted into Bray-Curtis dissimilarity indices using PAST according to the following formula.

$$d_{jk} = 1 - \frac{\sum_i |x_{ji} - x_{ki}|}{\sum_i (x_{ji} + x_{ki})}$$

Where (*j*) and (*k*) correspond to different groups, (*i*) corresponds to an individual species and *x* corresponds to the abundance of species (*i*) in groups (*j*) or (*k*). The numerator is determined by taking the sum of each species' absolute differences in abundance between both sites. The denominator is the total number of specimens at both sites.

ANOSIM, using the dissimilarity index values, generates a test statistic (R), a measure of dissimilarity between the compared groups. An R value of 1 indicates complete dissimilarity between groups, a value of 0 indicates a lack of dissimilarity between groups, and negative values indicate that there is more dissimilarity within groups than between groups. Similarity percentages (SIMPER) analyses were done in conjunction with ANOSIM in order to determine which species were contributing most to dissimilarity between datasets.

RESULTS

General Results Based on Total Data

In total, 5723 specimens representing 100 species were collected at both sites across both years (Table 1). These species occurred among 34 genera in 5 families: Andrenidae (3 genera, 12 species), Apidae (14 genera, 28 species), Colletidae (2 genera, 7 species), Halictidae (8 genera, 30 species) and Megachilidae (7 genera, 23 species). *Lasioglossum* (Halictidae) was the most species-rich genus (19 species). *Melissodes communis* was the most collected species; 1548 specimens were captured over both years. Majorities of species and specimens were ground nesting bees (73.0% [73 species] and 93.4% [5345 specimens], respectively), smaller percentages were above-ground nesting (26.0% [26 species] and 6.6% [376 specimens], respectively), and a single species (*Megachile petulans*) had uncertain nesting habits (1.0% and 0.03% [2 specimens] respectively). Most of the species and specimens were free-living as opposed to kleptoparasitic (86.0% and 97.01%, respectively). Two species, *Epeolus lectoides* and *Osmia atriventris* are newly recorded for the state of Texas.

Flooded site

Sampling of the flooded site in 2017 (pre-flooded, total dataset) resulted in 62 species and 1950 specimens. Species richness estimates predicted between 111 (1st order jackknife) and 127 (2nd order jackknife) species occur at the flooded site (Table 3). Shannon's diversity and Pielou's evenness index values for the pre-flooded dataset were 2.71 and 0.66.

Sampling of the flooded site in 2019 (post-flooded, total dataset) resulted in 61 species and 1776 specimens. Species richness estimates predicted between 68 (ACE) and 84 (2nd order jackknife) species. Shannon's diversity and Pielou's evenness index values of the post-flooded dataset dropped to 2.51 and 0.61, respectively.

Sampling over both years at the flooded site resulted in 84 species and 3726 specimens. Species richness estimates predicted between 111 (1st order jackknife) and 127 (ACE and 2nd order jackknife) species. Shannon's diversity and Pielou's evenness index values were 2.73 and 0.62, respectively. Collector's accumulation curves for the flooded site are presented in Figs 4–5.

Unflooded site

The limited sampling done in 2017 at the unflooded site resulted in 254 specimens and 26 species. Sampling in 2019 at this site (unflooded, total dataset) resulted in 66 species and 1743 specimens. Richness estimates predicted between 92 (1st order jackknife) and 120 (Chao1) occurring species (Table 3). Shannon's diversity and Pielou's evenness index values from the unflooded dataset were 2.43 and 0.58. A collector's curve generated for the unflooded site in is shown in Figure 6.

Comparisons Based on Standardized Data

Based on the standardized datasets, 85 species and 3594 specimens were documented from both sites: 69 species from the flooded site (51 species from the pre-flooded group, 52 species from the post-flooded groups), and 58 species from the unflooded site (Table 2). Richness estimates for the pre-flooded group ranged from 58 to 67 species (Chao1 and 2nd order jackknife, respectively), 65 to 74 species for the post-flooded group (Chao1 and 2nd order jackknife, respectively), and 83 to 110 species in the unflooded site (1st order jackknife and Chao1, respectively; Table 3). Collector's curves and sample-based rarefaction curves are shown in figures 7–11. Of the 69 species collected at the flooded site in both years, from 2017 to 2019, 36 species decreased in abundance, 31 species increased in abundance, and two species had the same abundance in both years.

Mean species richness values calculated as an average of the 13 sampling rounds were 15.1 for the pre-flooded, 11.7 for the post-flooded, and 13.4 for the unflooded datasets (Fig. 12). Normality was nearly rejected for the post-flooded dataset for species richness (W = 0.86, p = 0.051). Median richness values were 14 for the pre-flooded, 13 for the post-flooded, and 12 for the unflooded datasets (Fig. 12). A Kruskal-Wallis test showed a near-significant difference in median richness values among the datasets (H [2] = 4.77, p = 0.09). Dunn's post-hoc pairwise tests revealed a significant difference between the pre-flooded and post-flooded datasets (Z = 2.12, p = 0.03), no significant difference between the pre-flooded and unflooded datasets (Z = 1.57, p = 0.11), and no significant difference between the post-flooded and unflooded datasets (Z = 0.55, p = 0.58).

The mean abundances calculated as an average of the sampling rounds for the pre-flooded, post-flooded, and unflooded datasets were 88.2, 103, and 85.3, respectively (Fig. 13). Normality was rejected for the post-flooded (W = 0.81, p = 0.01) and unflooded (W = 0.79, p = 0.01) abundance datasets. Median abundances were 74 for the pre-flooded, 47 for the post-flooded, and 70 for the unflooded datasets (Fig. 13). These differences were not significant (H [2] = 1.02, p = 0.6).

Pielou's evenness, based data pooled for the entire sampling period, was 0.66 for the pre-flooded dataset, 0.54 for the post-flooded dataset, and 0.63 for the unflooded datasets (Table 2).

Shannon's diversity index values were calculated on data pooled for the entire sampling period. These values were 2.61, 2.15, and 2.57 for the pre-flooded, post-flooded, and unflooded datasets, respectively (Table 2). Hutcheson's t-tests found significant differences detected between the pre-flooded vs. post-flooded (t [2483] = 7.56, p = 6E-14) and post-flooded vs. unflooded dataset comparisons (t [2438.5] = -6.71, p = 2.4E-11; Table 5). Pre-flooded vs. unflooded diversity values were not significantly different.

Ground nesting bees

Based on the standardized datasets, 59 ground nesting bee species and 3300 specimens were documented from both sites over both years: 52 species from the flooded site (39 species from the pre-flooded group, 40 species from the post-flooded groups), and 42 species from the unflooded site (Table 2). Of the 52 species collected at the flooded site in both years, from 2017 to 2019, 27 species decreased in abundance, 23 species increased in abundance, and two species had the same abundance in both years.

The mean species richness values of the collecting rounds for ground nesting bees were 12.4 for the pre-flooded, 8.6 for the post-flooded, and 10.1 for the unflooded datasets (Fig. 12). Normality for these datasets were not rejected by Shapiro-Wilke's tests. Analysis of variance showed a significant difference between datasets (F [2, 36] = 6.47, p = 0.004). A Tukey's pairwise test showed a significant difference between the pre-flooded and post-flooded datasets (Q = 5.05, p = 0.003), a near significant difference between the pre-flooded and unflooded datasets (Q = 3.09, p = 0.059), and no significant difference between the post-flooded and unflooded site (Q = 1.96, p = 0.36). The median richness values among rounds were 12 in the pre-flooded, 9 in the post-flooded, and 10 in the unflooded datasets (Fig. 12).

The mean abundance values among rounds for ground nesting bees were 83 for the pre-flooded, 96 for the post-flooded, and 75 for the unflooded datasets (Fig. 13). Normality was rejected for the post-flooded dataset (W = 0.79, p = 0.005) and the unflooded dataset (W = 0.78, p = 0.003). The median abundances among rounds were 70 in the pre-flooded, 38 in the post-flooded, and 49 in the unflooded datasets (Fig. 13). No significant differences in abundance of rounds were detected (H [2] = 1.25, p = 0.5).

Pielou's evenness, based on standardized data pooled for the entire sampling period, was 0.66 for the pre-flooded dataset, 0.52 for the post-flooded dataset, and 0.61 for the unflooded datasets (Table 2).

Shannon's diversity index values for each group were 2.43, 1.91, and 2.27 for the pre-flooded, post-flooded, and unflooded datasets, respectively (Table 2). Hutcheson's t-tests on pairwise comparisons for the three values revealed significant differences in diversity between all comparisons (Table 6).

Above-ground nesting bees

Based on the standardized datasets, 25 above-ground nesting bee species and 292 specimens were documented from both sites over both years: 16 species from the flooded site (12 species from the pre-flooded group, 11 species from the post-flooded groups), and 15 species from the unflooded site. Of the 16 species collected at the flooded site in both years, from 2017 to 2019, eight species decreased in abundance, seven species increased in abundance, and one species had the same abundance in both years.

Mean species richness values among rounds were 2.62 for the pre-flooded dataset, 2.69 for the post-flooded dataset, and 3.23 for the unflooded dataset (Fig. 12). Normality was rejected for the pre-flooded dataset (W = 0.85, p = 0.03). The median richness of rounds values were two for the pre-flooded, three for the post-flooded, and three for the unflooded datasets (Fig. 12). No significant differences in median richness of rounds for above-ground nesting bees were detected.

The mean abundances among rounds were 5.4 for the pre-flooded, 6.9 for the post-flooded, and 10.2 for the unflooded datasets (Fig. 13). Normality was rejected for the unflooded dataset (W = 0.80, p = 0.01). The median abundances were five for the pre-flooded, seven for the post-flooded, and six for the unflooded datasets (Fig. 13). A Kruskal-Wallis test found no differences in the median abundances of rounds of the above-ground nesting bees of the three groups.

Pielou's evenness, based on standardized data pooled for the entire sampling period, was 0.65 for the pre-flooded dataset, 0.73 for the post-flooded dataset, and 0.63 for the unflooded datasets (Table 2).

Hutcheson's t-tests were used to compare pairwise values of the species diversity indices for the three datasets (1.61 pre-flooded, 1.74 post-flooded, and 1.72 unflooded datasets; Table 2). No significant differences were detected between any of the above-ground species diversity index comparisons (Table 7).

Analysis of Similarity (ANOSIM) and Similarity Percentages Analysis (SIMPER)

ANOSIM and SIMPER provided additional methods to search for differences between groups using a multivariate approach. When run on the dataset for all bees using standardized data, a small amount of dissimilarity between groups was detected at a near significant level (R = 0.07, p = 0.056). Pairwise comparisons between groups suggest that a small amount of dissimilarity may exist between the pre-flooded and post-flooded datasets (R = 0.09, p = 0.067). The dissimilarity between the pre-flooded and unflooded datasets was higher (R = 0.16, p = 0.013). No significant difference between the post-flooded and unflooded datasets was detected (R = -0.008, p = 0.472; Table 8).

When the ground nesting bees standardized dataset was analyzed with ANOSIM a similar amount of dissimilarity was found to that of all bees (R = 0.06, p = 0.064). Pairwise comparisons of the pre-flooded and post-flooded datasets also showed similar values to that found for all bees

(R = 0.086, p = 0.076). A small, yet significant difference was detected between the pre-flooded and unflooded datasets (R = 0.151, p = 0.014), and no significant difference was detected between the post-flooded and unflooded datasets (R = - 0.016, p = 0.522; Table 9).

When the above-ground nesting bees standardized dataset was analyzed, ANOSIM found no significant differences between the datasets (R = 0.051, p = 0.074). Pairwise comparisons showed no significant difference between the pre-flooded and post-flooded datasets (R = -0.002, p = 0.445), a small yet significant amount of dissimilarity between the pre-flooded and unflooded datasets (R = 0.105, p = 0.038), and a smaller amount of dissimilarity between the post-flooded and unflooded datasets (R = 0.057, p = 0.101; Table 10).

Pairwise SIMPER analyses using pre-flooded, post-flooded, and unflooded standardized datasets for all bees showed that three species accounted for over 50% of the dissimilarity between the pre-flooded and post-flooded datasets (*Melissodes communis* [31.47%], *Perdita obscurata* [11.24%], *Lasioglossum apopkense* [7.58%], *Augochlorella karankawa* [6.98%], *and Lasioglossum vierecki* [5.16%]; Table 11). Five species contributed to the majority (over 50%) of the dissimilarity values between the pre-flooded and unflooded datasets (*M. communis* [26.97%], *L. apopkense* [7.77%], *A. karankawa* [7.27%], *Lasioglossum tegulare* [6.32%], *and L. vierecki* [4.91%]; Table 12). Four species contributed to over 50% of dissimilarity between the post-flooded and unflooded datasets (*M. communis* [30.31%], *P. obscurata* [10.58%], *L. apopkense* [8.10%], and *L. tegulare* [6.45%]; Table 13).

DISCUSSION

This study comprised the first comprehensive survey of bees in the Big Thicket region of southeastern Texas and produced a checklist of bees for two sites in the Big Thicket National Preserve. It focused on sandyland habitats, which were suspected to have high species richness for bees. Moreover, it attempted to determine whether a bee community was affected by a rare flooding events caused by Hurricane Harvey in the summer of 2017. Comparisons of sites were made with the null hypothesis that pre-flooded and post-flooded datasets would have no significant differences in diversity measures. Alternatively, pre-flooded and post-flooded datasets were hypothesized to have differences in diversity measures. In particular, different groups of bees based on nesting habits were predicted to show different degrees of change over time. The second null hypothesis stated that post-flooded and unflooded datasets would have no significant differences in diversity measures, as opposed to the alternative, which hypothesized change over time.

In total, 100 species were captured at two sites over two years. Eighty-four species were collected at the flooded site over two years (62 in 2017, 61 in 2019). Species richness estimators predicted that 111–127 species may occur at the flooded site. Sixty-nine species were collected at the unflooded site over two years (26 in 2017, 66 in 2019). Richness estimators predicted that 94–121 species may occur at this unflooded site. The number of species found in this study are comparable to other surveys of bees that have been conducted in south (Bartholomew, 2004; Hall and Ascher, 2010; Van Gorder, 2016; Lozier, 2020). Accumulation curves suggested that the methods employed in this study constituted enough sampling effort to capture a majority of the species occurring at each site.

Comparisons of Pre-Flooded and Post-Flooded Datasets

The pre-flooded and post-flooded standardized datasets were very similar based on a number of metrics used in this study. This is consistent with the null hypothesis, which was supported by several lines of evidence. Both datasets had a similar overall species richness (51 in 2017, 52 in 2019) and abundance (1146 in 2017, 1339 in 2019). This held true for ground nesting bees (39 species in 2017, 40 in 2019; 1076 individuals in 2017, 1248 in 2019) and above-ground nesting bees (12 species in 2017, 11 in 2019; 70 individuals in 2017, 90 in 2019; Table 2). Most species found at the flooded site in 2017 were still present in 2019 (34 of 51 species at the flooded site). Over both years, the number of species that decreased in abundance was relatively similar to the number of species that increased or stayed the same in abundance. This is true for all bees, ground nesting bees, and above-ground nesting bees. Analyses of abundances for all bees, ground nesting bees, and above-ground nesting bees, as determined by the median values of the collecting rounds, showed no significant differences between the datasets.

There was also evidence that supported the alternative hypothesis that differences in the bee fauna would be detected between the pre-flooded and post-flooded datasets, particularly with regard to ground nesting bees. In contrast to overall species richness for all bees, median species richness values of the collecting rounds dropped a small, yet statistically significant amount from 14 to 13 (Fig. 12). This drop was also detected in the mean species richness of collecting rounds for the dataset comprised of ground nesting bees (12.4 in 2017, 8.6 in 2019; Fig. 16); a corresponding drop in median values for above-ground nesting bees was not observed. In addition, datasets comprised of all bees contained a dissimilar number of unique species (11 in

2017, 5 in 2019; Table 4). There was also a statistically significant decrease in Shannon's diversity for all bees (2.61 in 2017, 2.15 in 2019), ground nesting bees (2.43 in 2017, 1.91 in 2019), but not above-ground nesting bees. These changes were mirrored by decreases in overall evenness for both all bees (0.66 in 2017, 0.54 in 2019) and ground nesting bees (0.66 in 2017, 0.52 in 2019). No statistical tests on above-ground nesting bees supported the alternative hypothesis. However, evenness values for this group increased from 0.65 in 2017 to 0.73 in 2019 (Table 2). When comparing ANOSIM results for above-ground nesting bees the metrics suggest no differences between pre-flooded and post-flooded groups. However, though small, and narrowly outside of significance, the R value in ANOSIM comparing ground nesting bees of these groups reveals weak evidence for a difference in community composition (R = 0.086, p = 0.076; Table 9). Furthermore, SIMPER analysis revealed that several species substantially contributed to the levels of dissimilarity revealed by ANOSIM. These species tended to be those that occurred in high numbers, and the direction of change was not consistent. For example, *Melissodes communis* was detected 372 times in 2017 and 623 times in 2019 based on standardized data. *Perdita obscurata* also increased substantially from 52 to 234, as did the nest parasite *Sphecodes brachycephalus*, which increased from 36 to 63. Species that decreased in 2019 included *Lasioglossum apopkense* (114 to 60), *Augochlorella karankawa* (103 to 1), and *Lasioglossum vierecki* (99 to 40). Notably, all of these species inhabit the ground in the larval and pupal stages. The above-ground nesting species that contributed the most to the dissimilarity between the pre-flooded and post-flooded datasets was *Apis mellifera*, which ranked 11th on the list of species and decreased in abundance from 30 to 25 (Table 11). These ANOSIM and SIMPER results should be viewed with caution, given that distance-based analyses in community ecology have been shown to underperform in some cases when datasets contain taxa with high variances, as is the case here (Warton et al., 2012).

Considering all the evidence, the degree to which the flood impacted the bee fauna of the flooded site appears to be rather minor, at least in a general sense. A large-scale change at the community level was not detected. Overall species richness remained nearly unchanged (51 in 2017 vs 52). On the other hand, certain univariate metrics revealed differences (e.g., richness by round, Shannon's diversity values) that were pronounced in ground nesting bees but not in above-ground nesting bees, as hypothesized. Additionally, ANOSIM and SIMPER suggested that the small amount of dissimilarity between datasets can be attributed almost entirely to ground nesting bees.

Though an obvious inundation of the flooded site took place, the intensity and duration of the flood are not known. It could be that the flood was short in duration, allowing the well-draining, sandy soil of the site to mitigate any potential negative effects. It's possible that detection of species in 2019 was due to high survivorship of the flooding event, migration from nearby areas, or a mixture of both. Regardless, this community of pollinators displayed a notable resilience towards this historic flooding event.

As summarized by Danforth et al., 2019, responses of bees to flooding have only been examined in a few instances (Visscher et al., 1994; Cane, 1997; Fellendorf et al., 2004; Neumüller et al., 2018). Neumüller et al. (2018) concluded that flooding had a low, long-term impact on bee assemblages in regularly flooded meadows and suggested that most bee species have sufficient dispersal abilities to reestablish their populations following disturbance caused by flooding. Some species in this study, however, suffered sharp declines in abundance following the flood (*Augochlorella karankawa* and several *Lasioglossum* species). Similarly, Fellendorf et al.

(2004) observed a marked decline in abundance of *Andrena vaga* following a flood, and suspected asphyxiation caused substantial larval death. The species that declined in this study may have suffered a similar fate. Aranda and Aoki (2018), found that different groups of hymenopterans are more prone to inhabit areas with specific flooding intensities and that those that utilize soil respond significantly to certain kinds of regular flooding events. The results of this study lend further support to the idea that certain groups of hymenopterans are more susceptible than others to flooding.

Comparisons Involving the Unflooded Dataset and Future Research

The unflooded site was included to provide an additional comparison for the flooded site datasets. The site provided an additional 13 species overall. Relative to the pre-flooded dataset, few differences in univariate statistics were found. Weak support for the alternative hypothesis of differences between these groups came from minor, yet significant, differences in Shannon's diversity indices and the median species richness values of the rounds. Further support for the alternative hypothesis came from the ANOSIM comparisons of unflooded and pre-flooded datasets which revealed low dissimilarity across all bees ($R = 0.16$, $p = 0.013$), ground nesting bees ($R = 0.15$, $p = 0.014$), and above-ground nesting bees ($R = 0.11$, $p = 0.038$; Table 8–10).

Comparing the unflooded and post-flooded datasets, Shannon's species diversity values were significantly different for all bees (2.57 vs. 2.15, respectively), ground nesting bees (2.27 vs. 1.91, respectively), but not above-ground nesting bees (1.72 vs. 1.74, respectively; Tables 5–7). Other univariate metrics showed no differences. Furthermore, the ANOSIM tests showed no variation in community composition for all bee groups (Tables 8–10). This is surprising due to the potential for change due to both distance and flooding. This further contrasts with the ANOSIM results comparing unflooded and pre-flooded datasets (above) which found significant differences across all groups of bees. Taken together, these findings suggest that temporal differences were more important in contributing to variation between groups than distance and flooding combined.

Future surveys should involve more units throughout the Big Thicket National Preserve that represent more habitats than this study emphasized. These areas are known to have an abundance of ecologically interesting habitats, and many units within the preserve have been poorly sampled for insects. Combined with the fact that this region will undoubtedly continue to experience powerful storms, many opportunities may present themselves to further our understanding of the effects of major disturbances on the biota of the Big Thicket.

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FIGURES

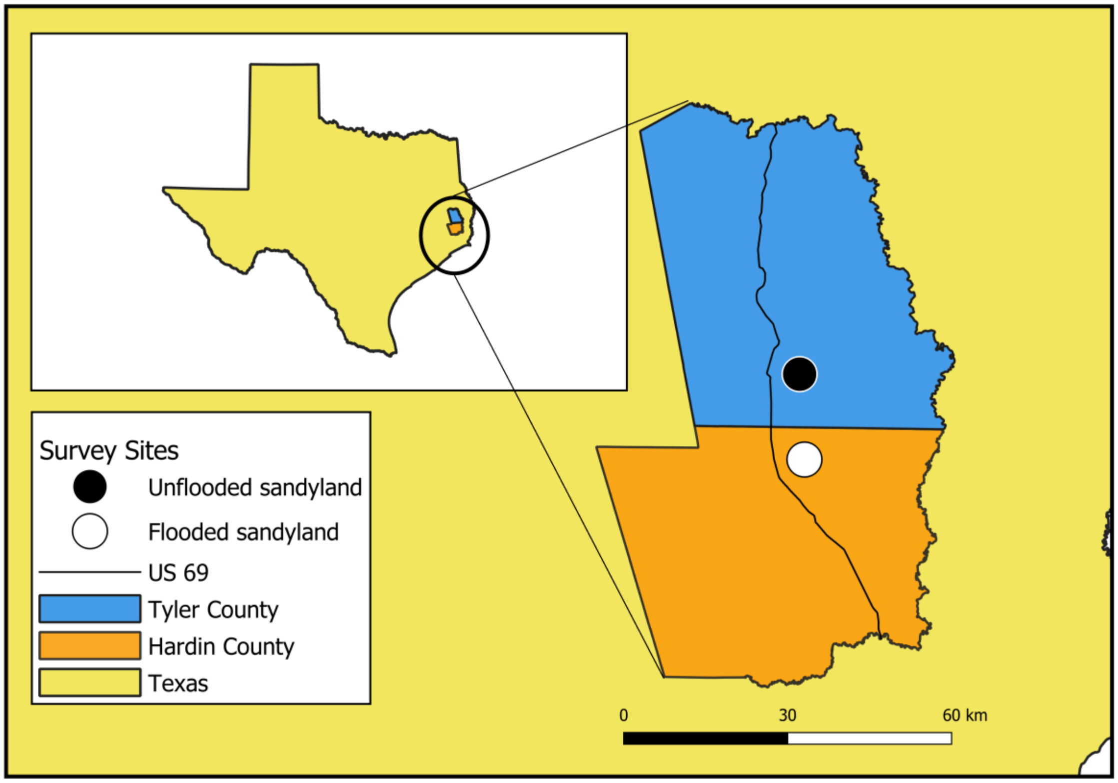

Figure 1. Site map showing the locations of two study sites in Hardin and Tyler Counties, Texas.

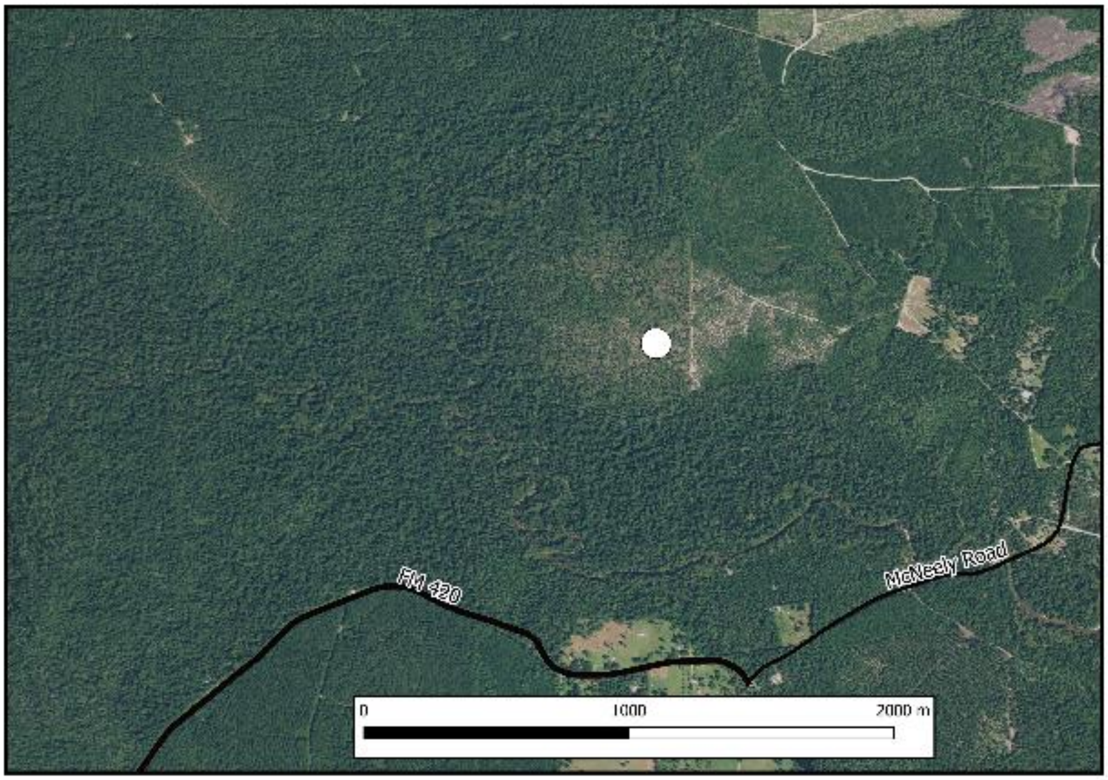

Figure 2. Flooded sandyland in Hardin County, Texas near FM 420.

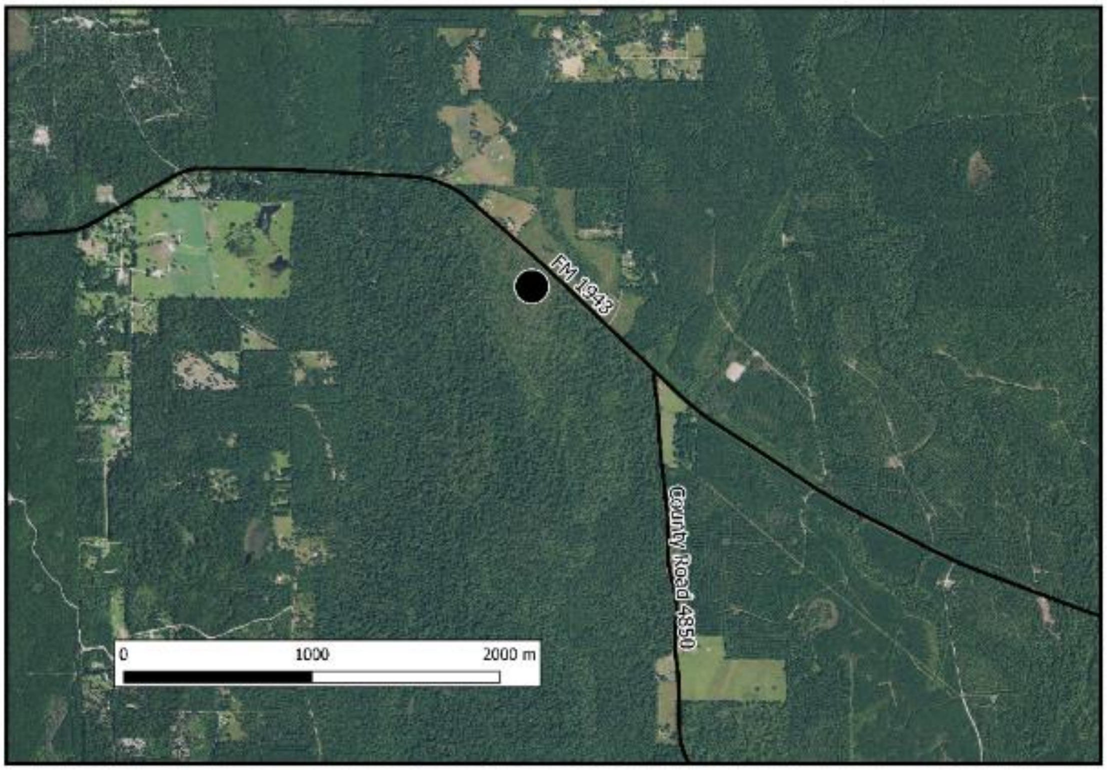

Figure 3. Unflooded sandyland in Tyler County, Texas adjacent to FM 1943.

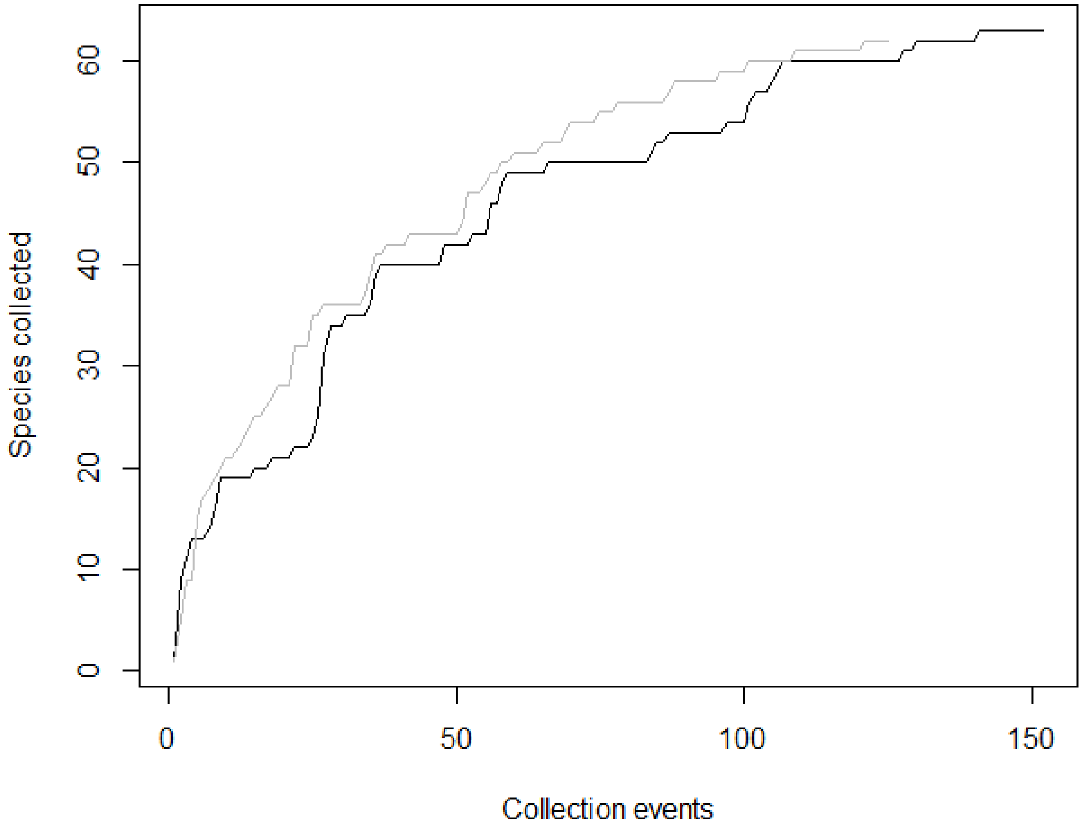

Figure 4. Bee species accumulation curves (collector's curves) for pre-flooded (black curve; up to 62 species) and post-flooded (gray curve; up to 61 species) total datasets.

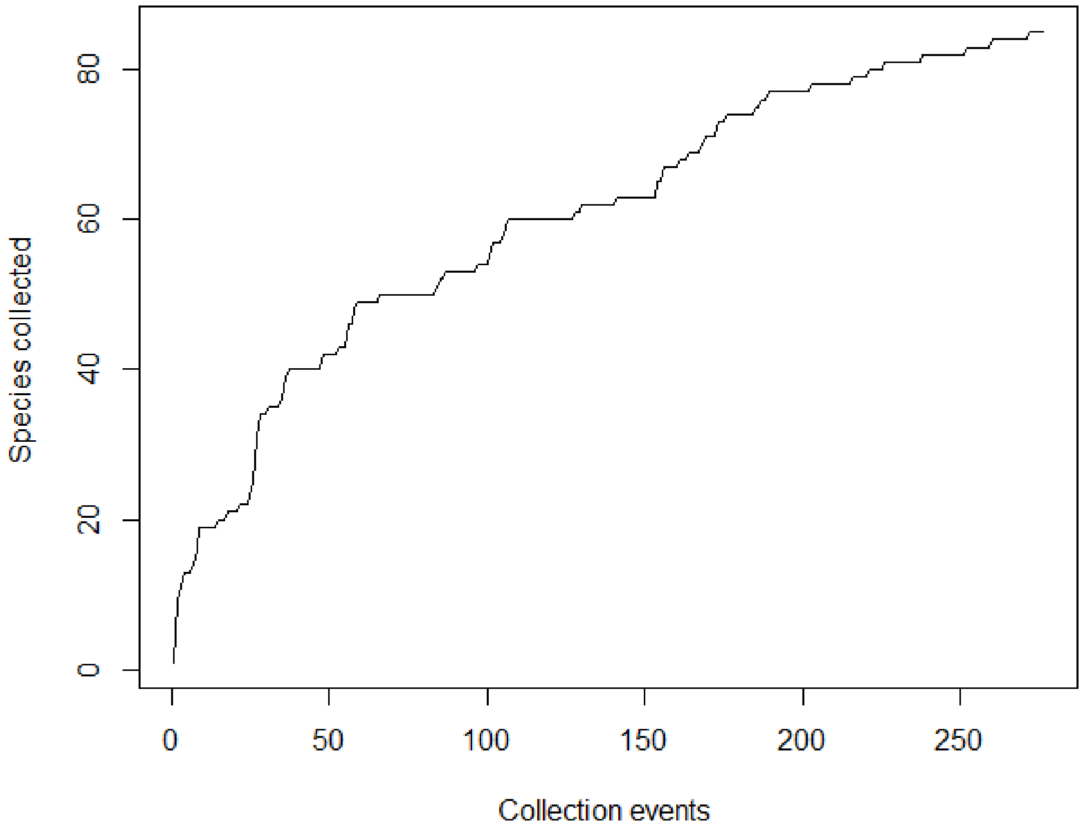

Figure 5. Bee species accumulation curve (collector's curve) for both years at the flooded site combined using total datasets (up to 84 species).

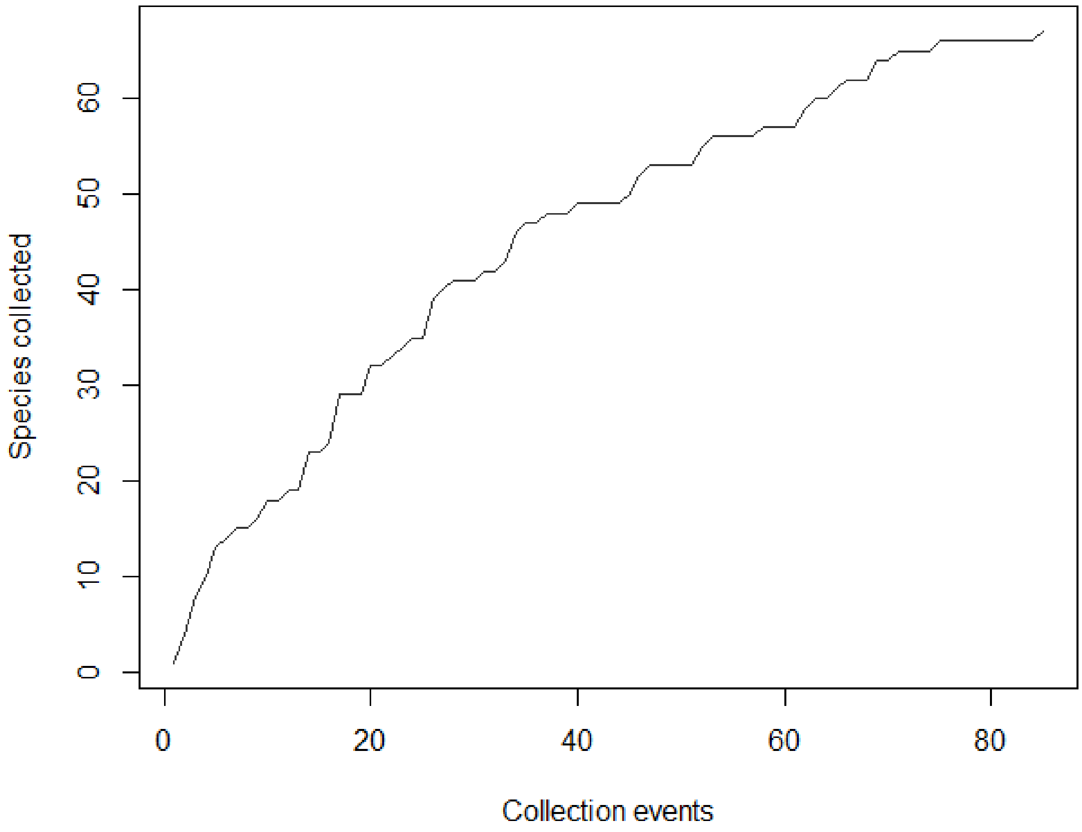

Figure 6. Bee species accumulation curve (collector's curve) for the unflooded total dataset (2019 samples only; up to 66 species).

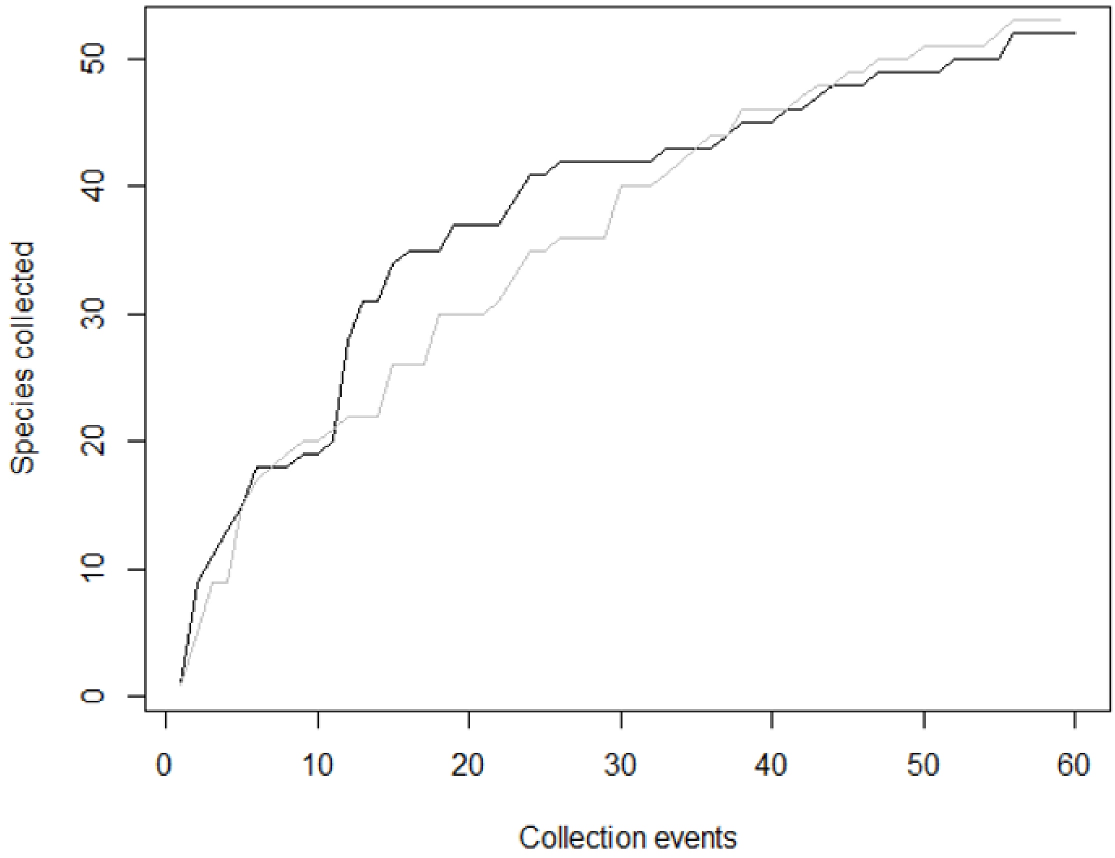

Figure 7. Bee species accumulation curves (collector's curves) for pre-flooded (black curve; up to 51 species) and post-flooded (gray curve; up to 52 species) standardized datasets.

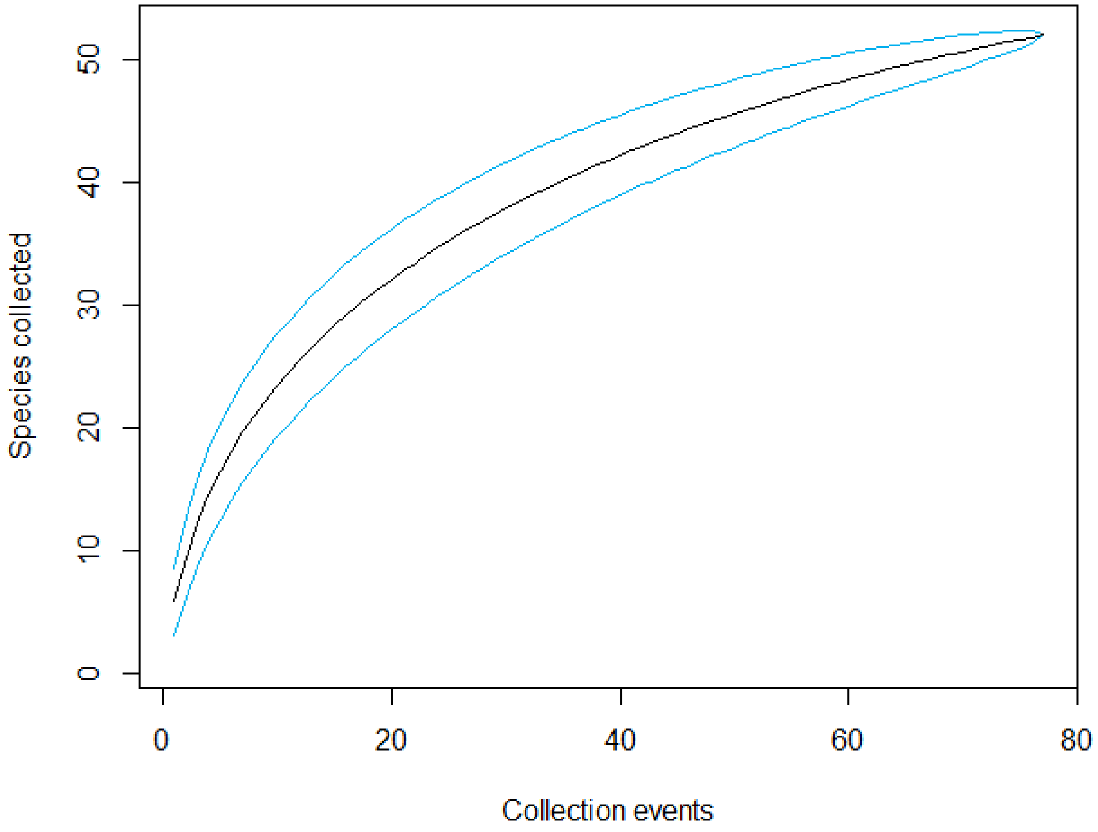

Figure 8. Sample-based bee species accumulation rarefaction curve for the pre-flooded standardized dataset (up to 51 species). Upper and lower lines represent a 95% confidence interval.

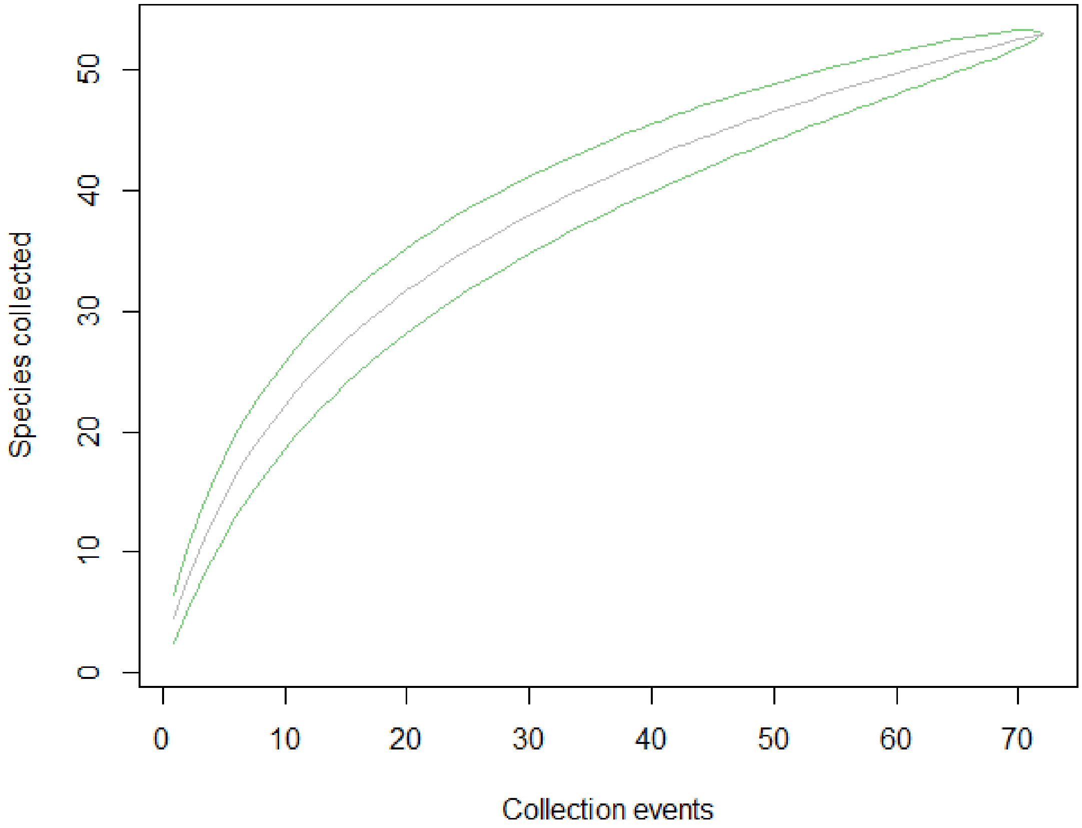

Figure 9. Sample-based bee species accumulation rarefaction curve for the post-flooded standardized dataset (up to 52 species). Upper and lower lines represent a 95% confidence interval.

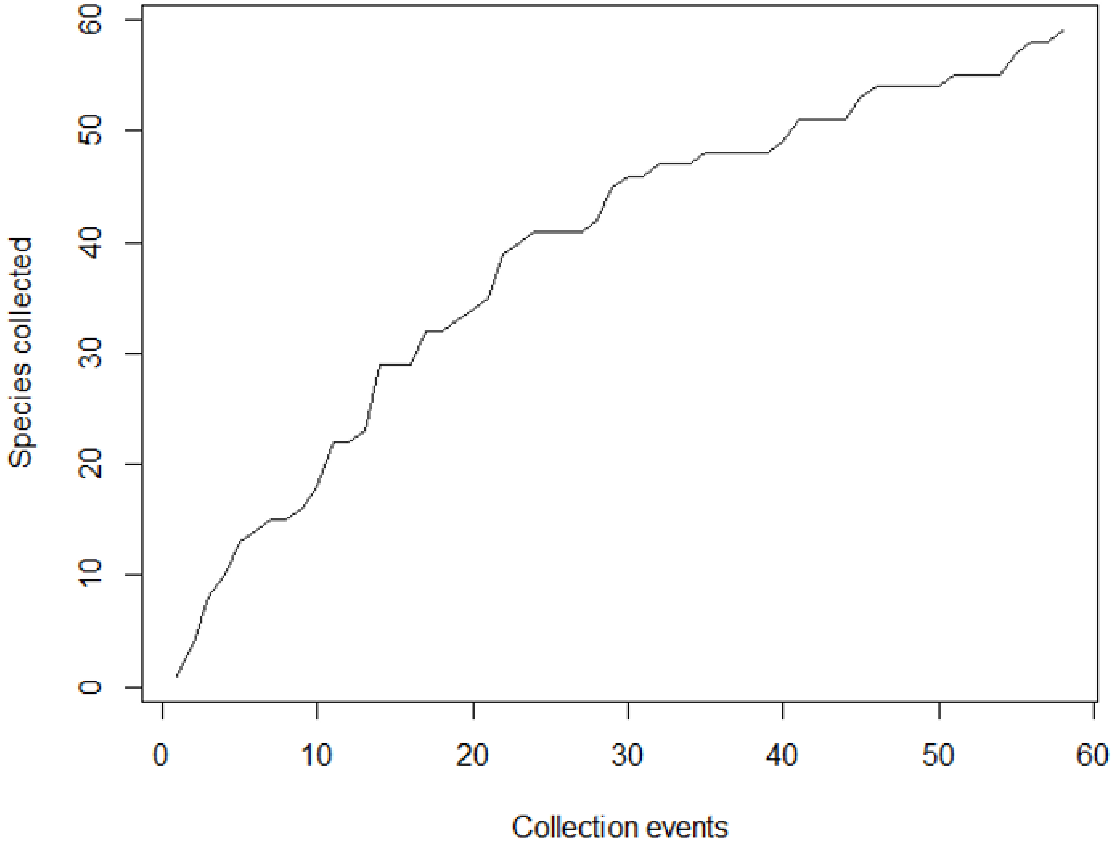

Figure 10. Bee species accumulation curve (collector's curve) for the unflooded standardized dataset (up to 58 species).

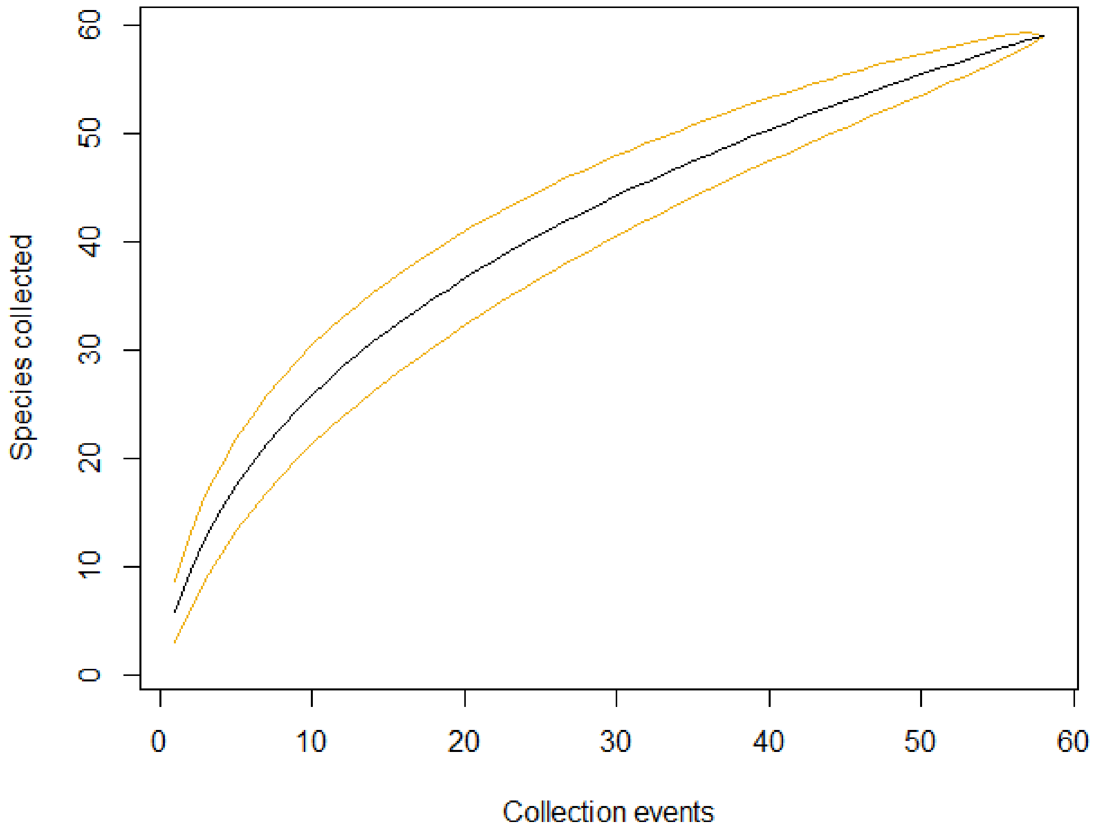

Figure 11. Sample-based bee accumulation rarefaction curve for the unflooded standardized dataset (up to 58 species). Upper and lower lines represent a 95% confidence interval.

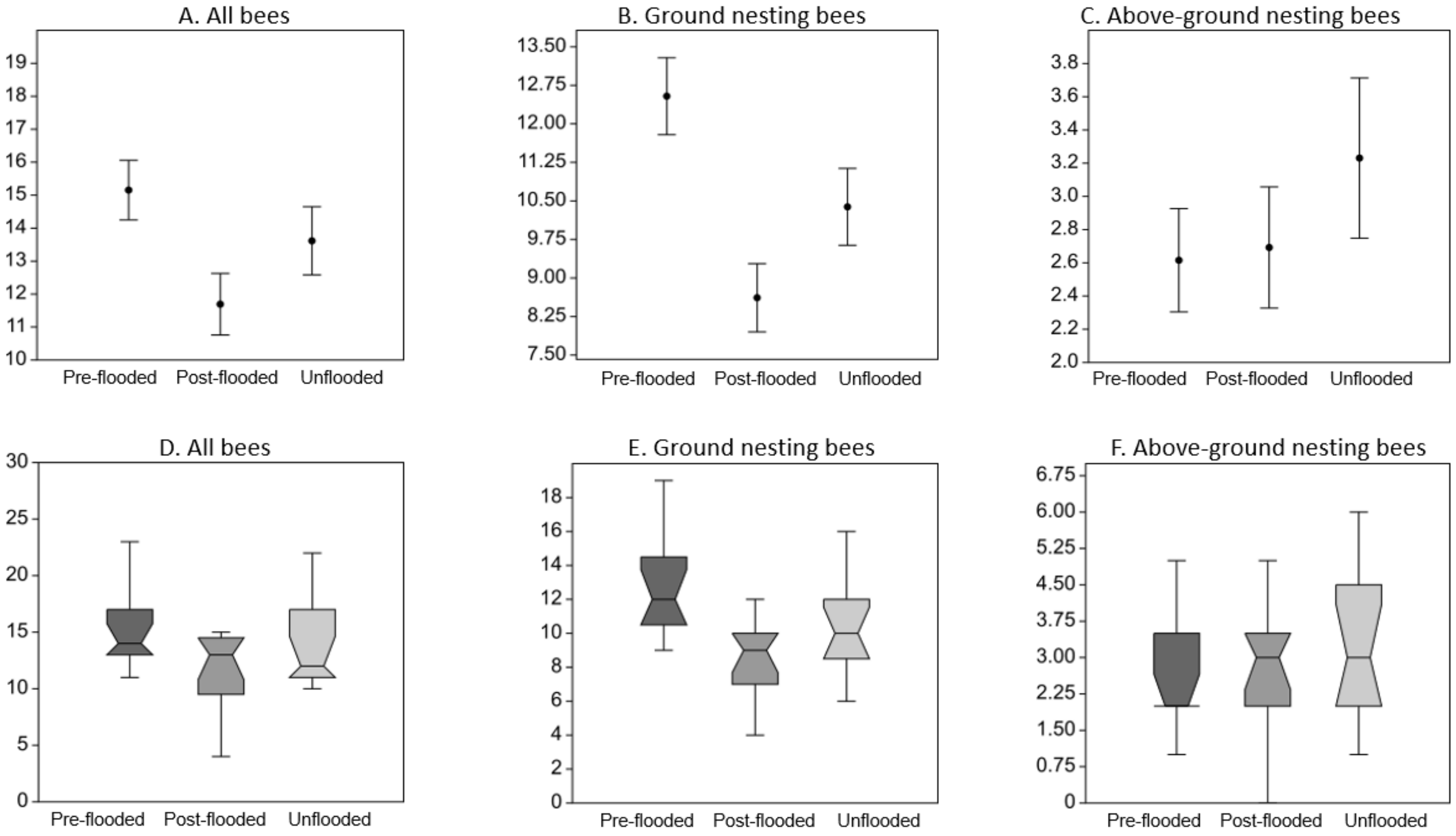

Figure 12. A–C: Mean and whisker plots of bee species richness calculated by collecting round based on standardized datasets. Whiskers represent one standard deviation. D–F: Boxplots of median bee species richness calculated by collecting round based on standardized datasets. Notches indicate 95% confidence intervals; whiskers indicate ranges.

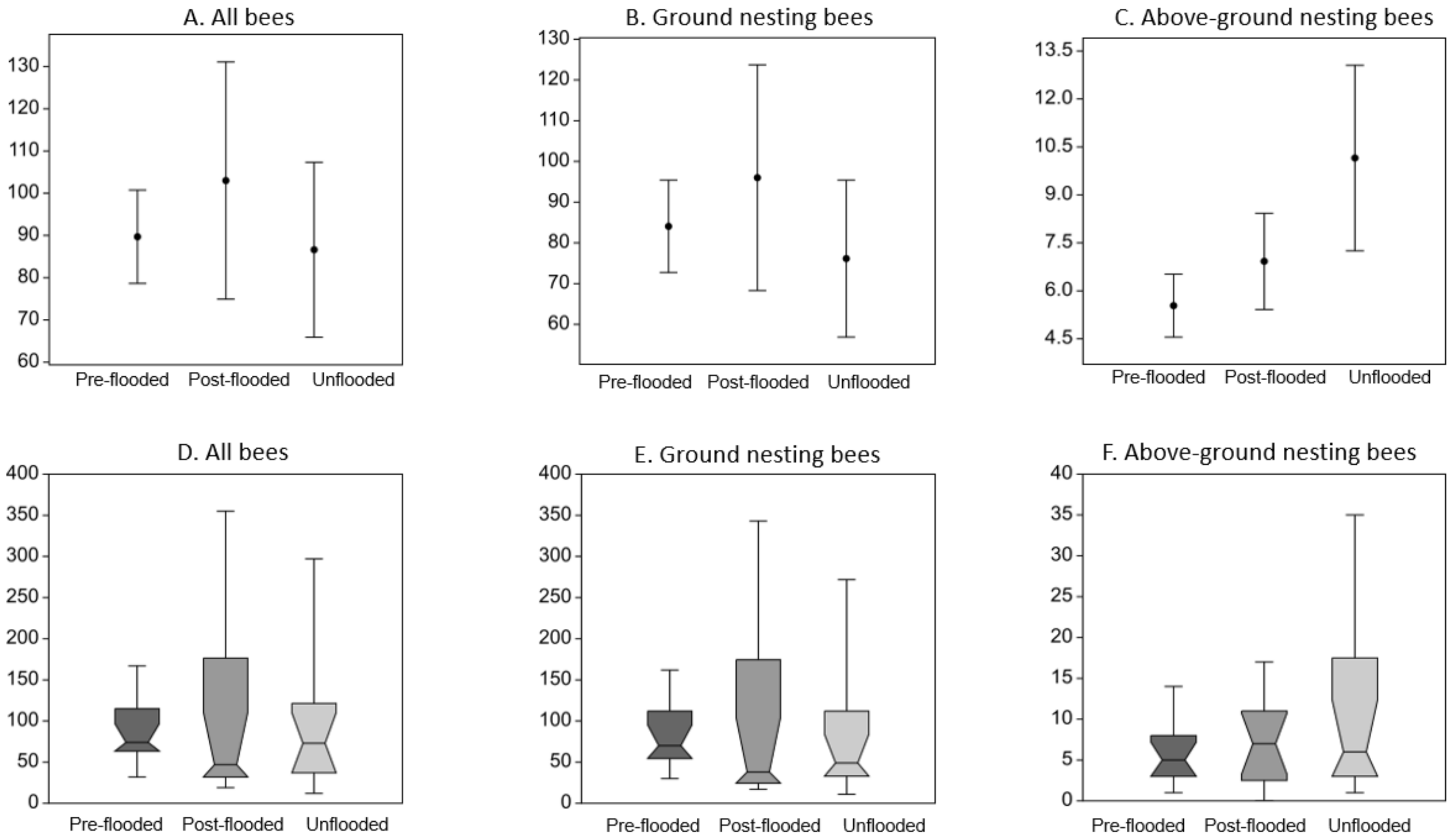

Figure 13. A–C: Mean and whisker plots of bee species abundance calculated by collecting round based on standardized datasets. Whiskers represent one standard deviation. D–F: Boxplots of median bee species abundance calculated by collecting round based on standardized datasets. Notches indicate 95% confidence intervals; whiskers indicate ranges.

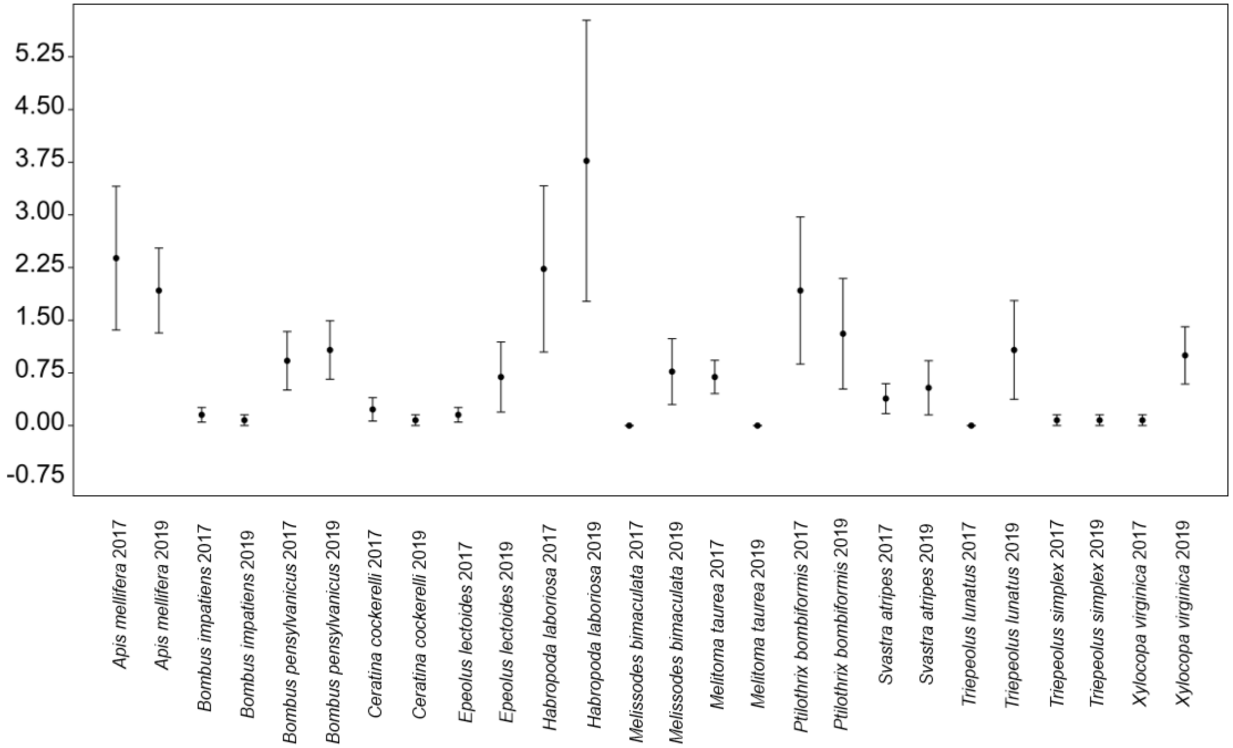

Figure 14. Mean and whisker plots of bee abundances per species in the family Apidae calculated by collecting round for pre-flooded (2017) and post-flooded (2019) standardized datasets. Whiskers represent one standard deviation.

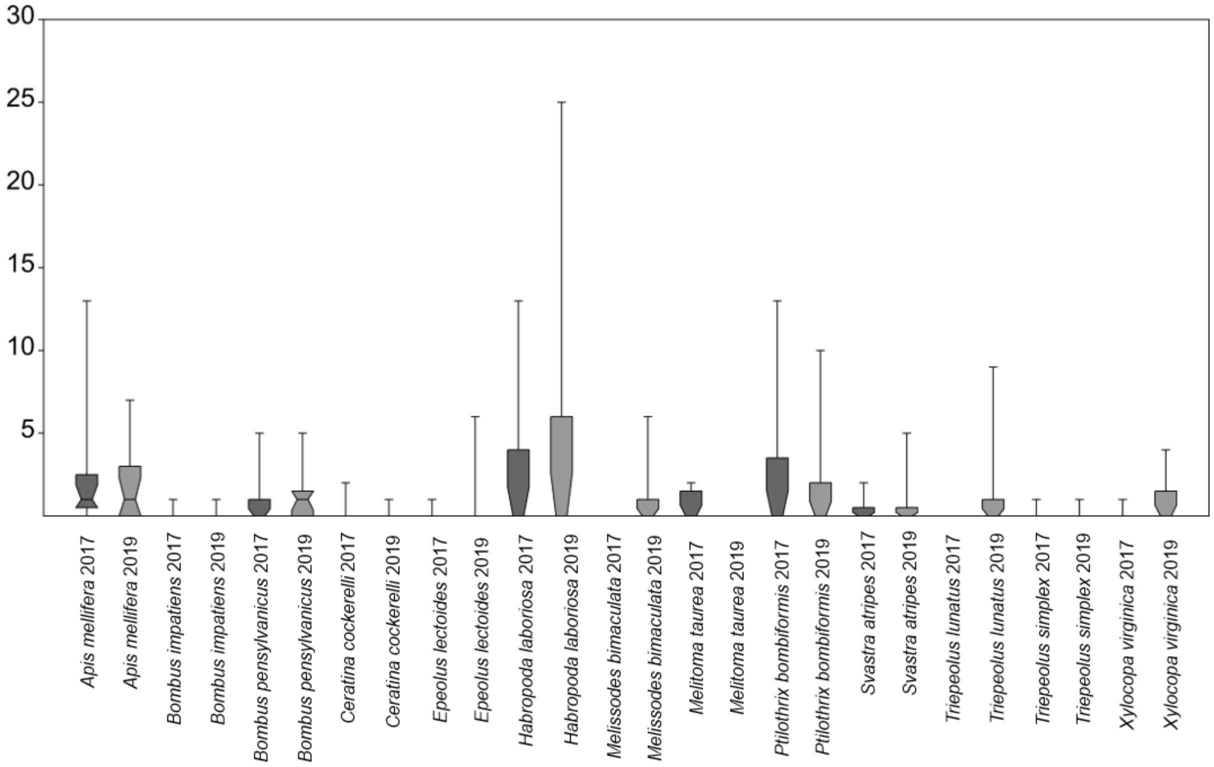

Figure 15. Boxplots of median bee abundances per species in the family Apidae calculated by collecting round for pre-flooded (2017) and post-flooded (2019) standardized datasets. Notches indicate 95% confidence intervals; whiskers indicate ranges.

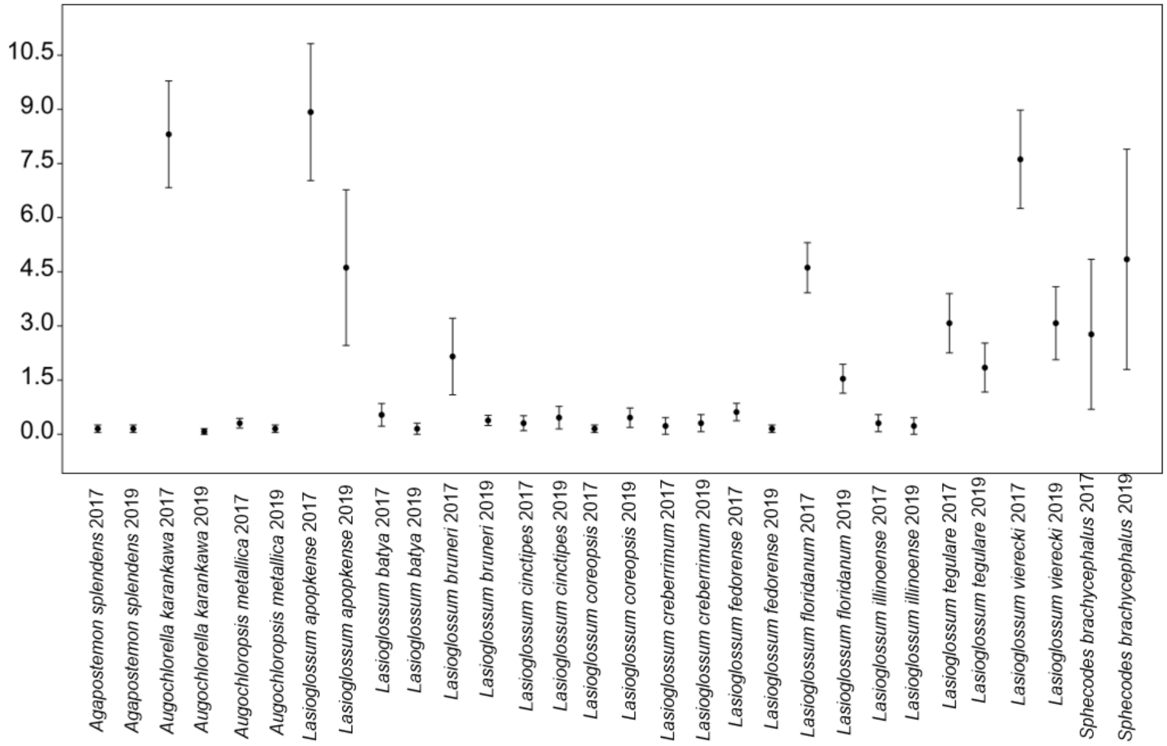

Figure 16. Mean and whisker plots of bee abundances per species in the family Halictidae calculated by collecting round for pre-flooded (2017) and post-flooded (2019) standardized datasets. Whiskers represent one standard deviation.

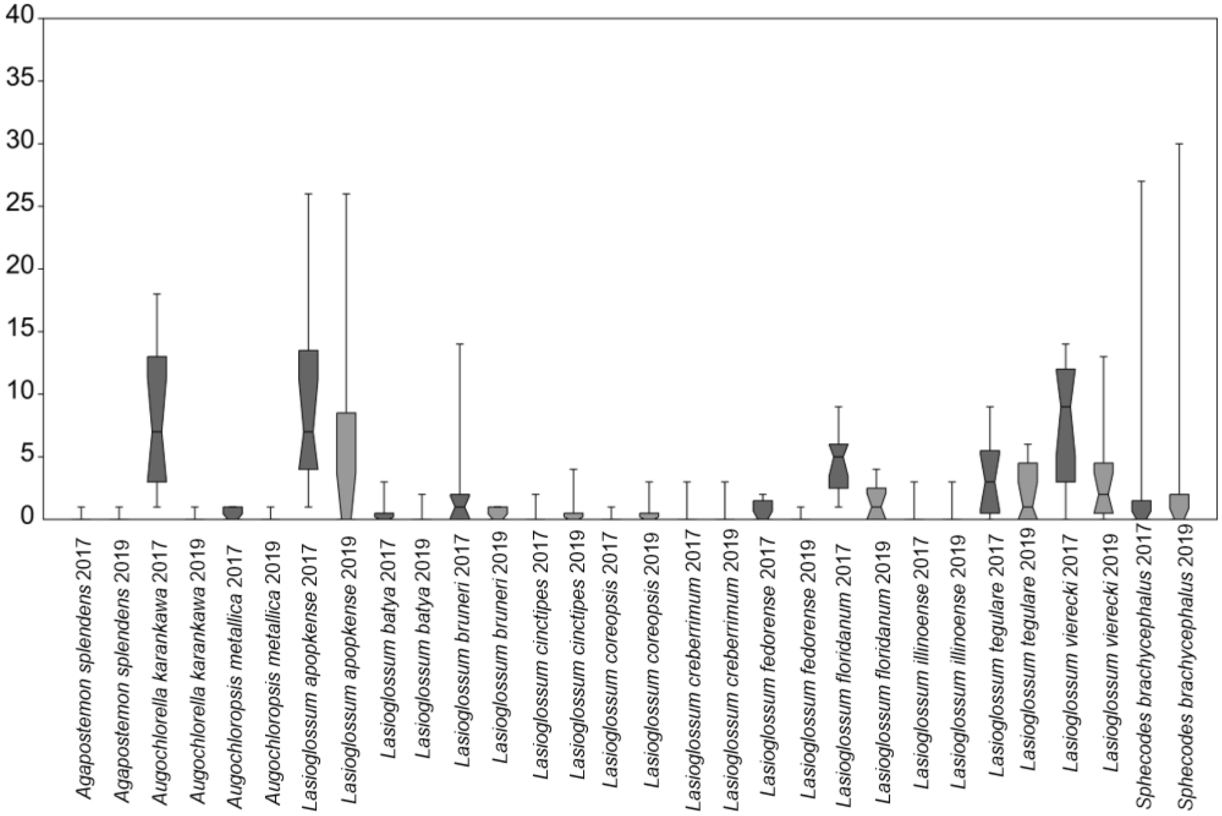

Figure 17. Boxplots of median bee abundances per species in the family Halictidae calculated by collecting round for pre-flooded (2017) and post-flooded (2019) standardized datasets. Notches indicate 95% confidence intervals; whiskers indicate ranges.

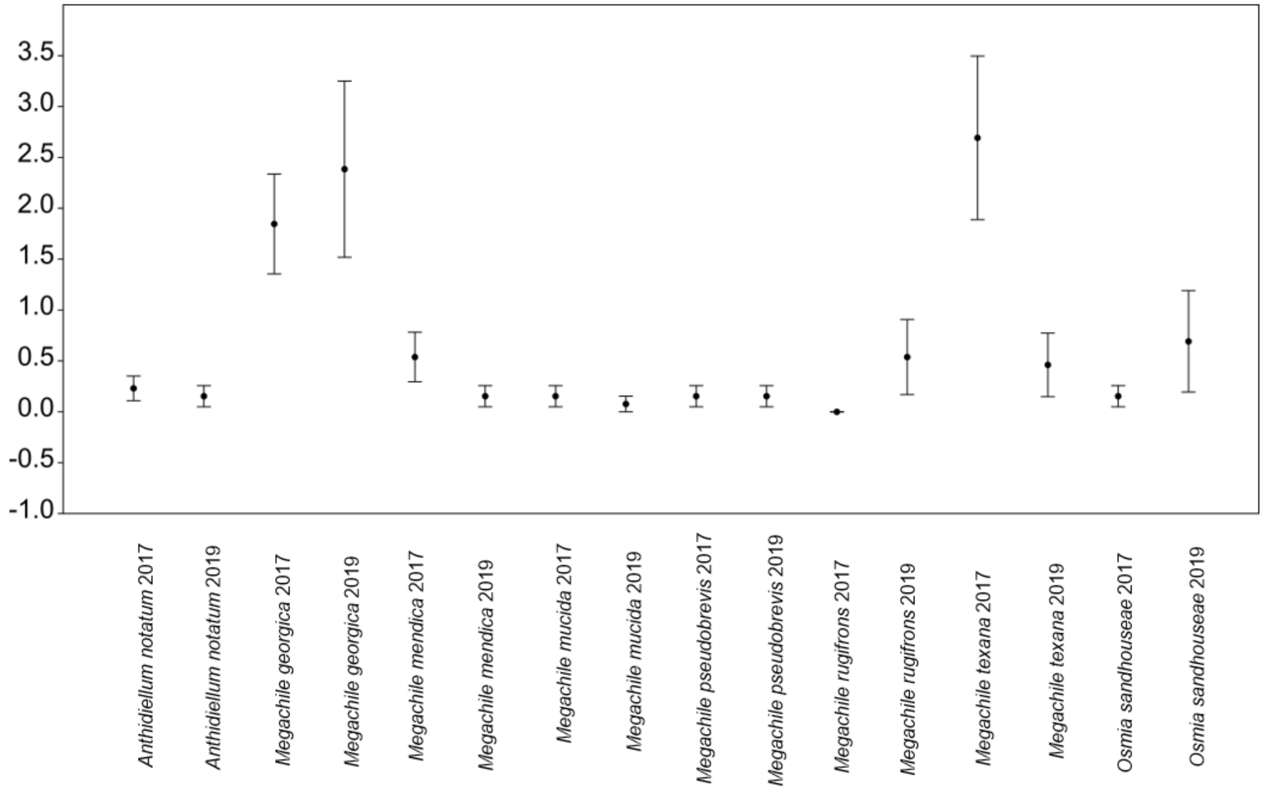

Figure 18. Mean and whisker plots of bee abundances per species in the family Megachilidae calculated by collecting round for pre-flooded (2017) and post-flooded (2019) standardized datasets. Whiskers represent one standard deviation.

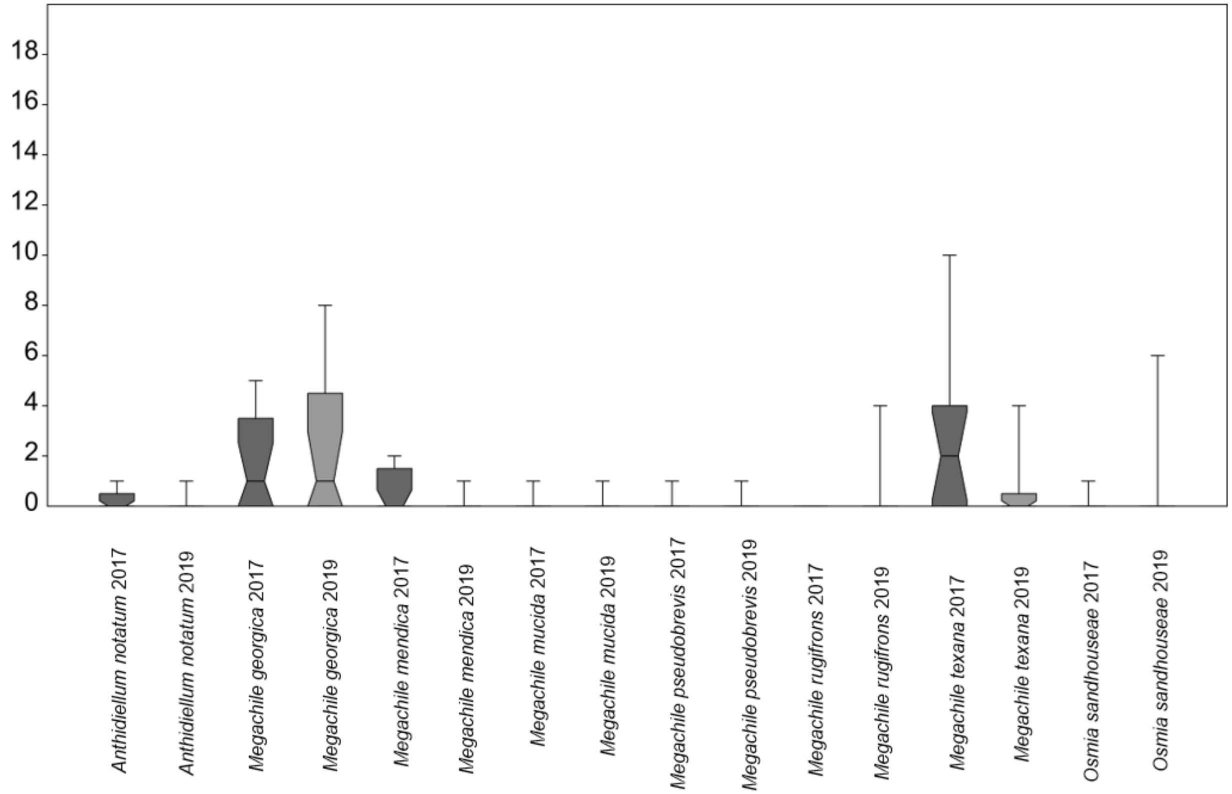

Figure 19. Boxplots of median bee abundances per species in the family Megachilidae calculated by collecting round for pre-flooded (2017) and post-flooded (2019) standardized datasets. Notches indicate 95% confidence intervals; whiskers indicate ranges.

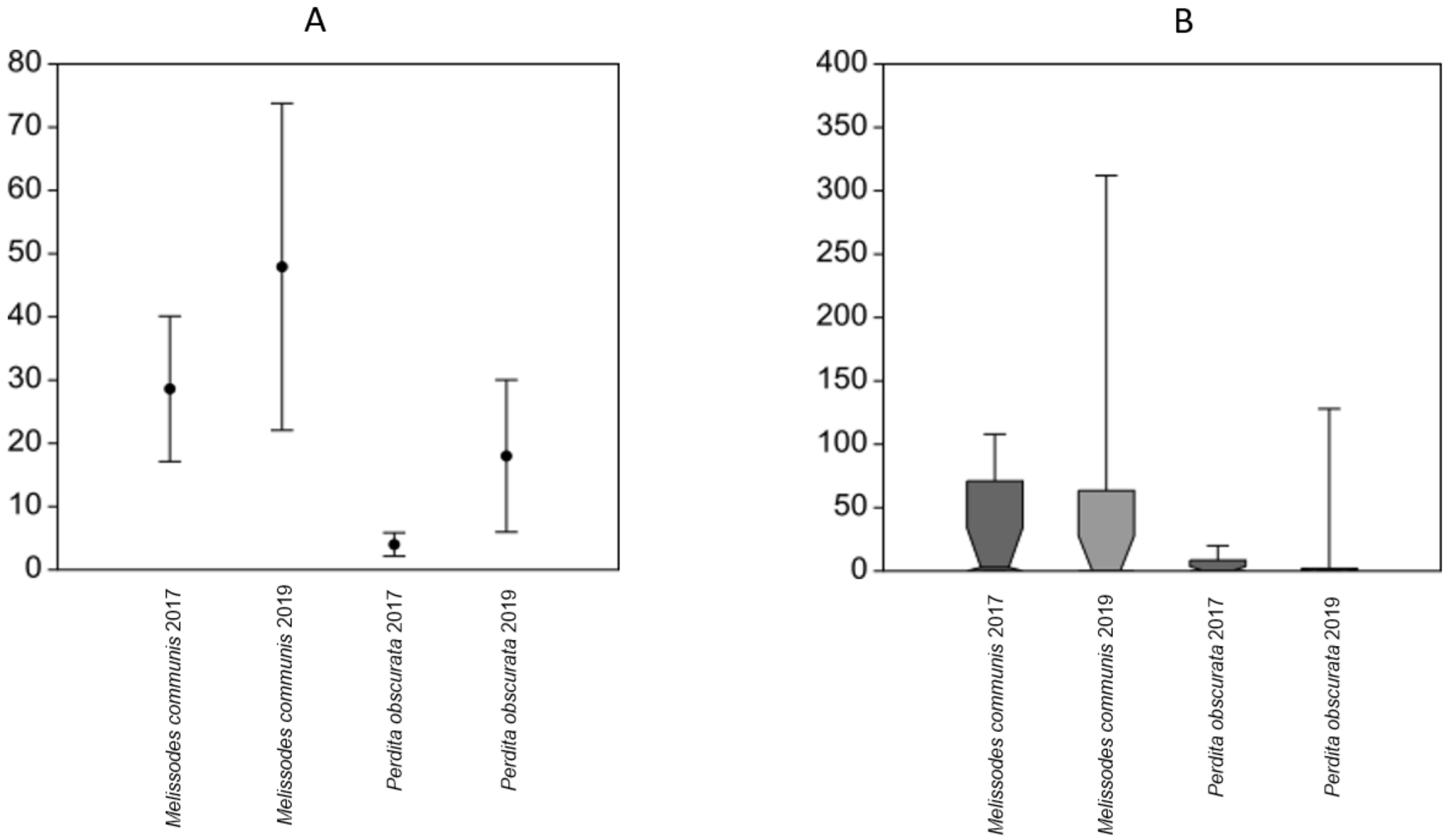

Figure 20. Mean and whisker plots of bee abundances (A) and boxplots of median bee abundances (B) of *Melissodes communis* (Apidae) and *Perdita obscurata* (Andrenidae) calculated by collecting round for pre-flooded (2017) and post-flooded (2019) standardized datasets. Whiskers of mean and whisker plots represent one standard deviation. Notches on boxplots indicate 95% confidence intervals; whiskers indicate ranges.

TABLES

Table 1. Abundances and nesting habits of bees captured in the Big Thicket National Preserve, Texas organized by site and year based on all samples. A = above-ground nesting, G = ground nesting. Specimens identified to genus only are excluded. Nest parasites are indicated by "*".

	Flooded Site		Unflooded Site		
	2017	2019	2017	2019	
Andrenidae	82	311	17	592	Nesting
Andrena dollomellea	0	0	0	1	G
Andrena fulvipennis	0	0	4	2	G
Andrena gardineri	1	0	0	0	G
Andrena imitatrix	1	0	0	0	G
Andrena miserabilis	0	2	0	1	G
Andrena violae	0	1	0	0	G
Calliopsis andreniformis	0	1	0	0	G
Perdita bishoppi	3	53	5	534	G
Perdita cambarella	0	10	0	1	G
Perdita halictoides	0	0	0	1	G
Perdita ignota	3	0	8	8	G
Perdita obscurata	74	244	0	44	G
Apidae	606	823	114	559	Nesting
Anthophora abrupta	1	0	0	5	G
Apis mellifera	39	25	0	66	A
Bombus griseocollis	1	0	0	0	A
Bombus impatiens	3	2	0	2	A
Bombus pensylvanicus	14	25	6	16	A
Ceratina calcarata	0	0	21	11	A
Ceratina cockerelli	8	4	2	3	A
Ceratina shinnersi	0	0	0	1	A
Ceratina strenua	0	3	1	15	A
Epeolus ilicis	0	2	0	0	G*
Epeolus lectoides	2	11	0	4	G*
Habropoda laboriosa	30	49	0	32	G
Holcopasites illinoiensis	1	0	0	0	G*
Melissodes bimaculata	1	10	4	5	G

(continued)

	Flooded Site		Unflooded Site		
	2017	2019	2017	2019	
Apidae	606	823	114	559	Nesting
Melissodes communis	454	634	75	385	G
Melissodes comptoides ?	0	1	0	0	G
Melissodes druriellus	0	0	0	1	G
Melissodes sp. 2	0	1	0	0	G
Melissodes tepaneca	3	0	0	0	G
Melitoma taurea	13	0	2	5	G
Nomada rubicunda	0	1	0	0	G*
Nomada vincta	0	0	0	1	G*
Ptilothrix bombiformis	27	17	1	1	G
Svastra atripes	5	10	2	1	G
Svastra compta	1	0	0	0	G
Triepeolus luantus	0	14	0	1	G*
Triepeolus simplex	1	1	0	0	G*
Xylocopa virginica	2	13	0	4	A
Colletidae	1	5	0	6	Nesting
Colletes inaequalis	0	1	0	2	G
Colletes nudus	0	1	0	0	G
Colletes productus	0	1	0	0	G
Colletes thoracicus	1	1	0	1	G
Hylaeus affinis	0	0	0	1	G
Hylaeus floridanus	0	1	0	1	G
Hylaeus georgicus	0	0	0	1	G
Halictidae	1098	543	121	510	Nesting
Agapostemon splendens	8	2	1	2	G
Agapostemon texanus	2	0	0	0	G
Augochlora pura	0	1	0	0	A
Augochlorella karankawa	208	12	1	0	G
Augochloropsis metallica	5	3	0	8	G
Augochloropsis sumptuosa	0	1	0	1	G
Halictus ligatus	0	0	2	0	G
Lasioglossum apopkense	170	209	4	117	G
Lasioglossum batya	14	3	9	3	G
Lasioglossum birkmanni	0	3	0	2	G
Lasioglossum bruneri	56	13	5	23	G

(continued)

	Flooded Site		Unflooded Site		
	2017	2019	2017	2019	
Halictidae	1098	543	121	510	Nesting
Lasioglossum callidum	0	0	0	1	G
Lasioglossum cinctipes	8	6	0	0	G
Lasioglossum coreopsis	10	12	0	9	G
Lasioglossum creberrimum	4	8	0	5	G
Lasioglossum disparile	2	0	0	0	G
Lasioglossum fedorense	18	16	9	94	G
Lasioglossum floridanum	182	58	15	56	G
Lasioglossum illinoense	6	4	0	1	G
Lasioglossum lustrans	1	0	0	0	G
Lasioglossum pruinosum	4	0	0	0	G
Lasioglossum tarponense	4	2	7	1	G
Lasioglossum tegulare	145	61	19	123	G
Lasioglossum trigeminum	0	0	0	1	G
Lasioglossum vierecki	203	58	46	52	G
Lasioglossum weemsi	1	0	3	1	G
Nomia nortoni	0	0	0	1	G
Sphecodes atlantis	0	1	0	5	G*
Sphecodes brachycephalus	47	70	0	3	G*
Sphecodes sp. 1	0	0	0	1	G*
Megachilidae	112	82	2	52	Nesting
Anthidiellum notatum	3	2	0	1	A
Coelioxys immaculata	2	0	0	0	A*
Coelioxys octodentata	0	0	0	1	A*
Coelioxys sayi	1	0	0	0	A*
Dianthidium curvatum	0	2	0	3	A
Hoplitis truncata	2	0	0	0	A
Megachile deflexa	1	0	0	0	G
Megachile frugalis	1	4	0	0	A
Megachile georgica	29	39	0	24	A
Megachile lippiae	1	0	0	0	A
Megachile melanophaea	1	0	0	0	G
Megachile mendica	10	6	0	4	G
Megachile mucida	2	1	0	3	G
Megachile petulans	0	1	0	1	X
Megachile pseudobrevis	3	2	0	6	A

(continued)

	Flooded Site		Unflooded Site		
	2017	2019	2017	2019	
Megachilidae	112	82	2	52	Nesting
Megachile rugifrons	0	7	0	1	G
Megachile texana	50	6	1	5	G
Megachile xylocopoides	2	0	0	0	A
Osmia atriventris	1	0	0	2	A
Osmia chalybea	1	0	0	0	A
Osmia sandhouseae	2	10	1	0	A
Osmia texana	0	2	0	0	A
Stelis lateralis	0	0	0	1	A*

Table 2. Diversity metrics of bees based on standardized datasets for two sites. The flooded site was sampled in 2017 (referred to in the text as "pre-flooded") and 2019 (referred to in the text as "post-flooded").

	Diversity metrics							
Site, year, subset	Richness	Mean Richness	Median Richness	Abundance	Mean Abundance	Median Abundance	Shannon's diversity index	Pielou's evenness index
Flooded, 2017, all bees	51	15.08	14	1146	88.23	74	2.61	0.66
Flooded, 2019, all bees	52	11.69	13	1339	103	47	2.15	0.54
Flooded, both years, all bees	69	20.62	21	2485	191.15	128	2.73	0.62
Unflooded, 2019, all bees	58	13.39	12	1109	85.31	70	2.57	0.63
All sites, all years, all bees	85	26.08	28	3594	276.46	183	2.62	0.59
Flooded, 2017, ground	39	12.39	12	1076	82.77	70	2.43	0.66
Flooded, 2019, ground	40	8.62	9	1248	96	38	1.91	0.52
Flooded, both years, ground	52	16.46	17	2324	178.77	117	2.27	0.57
Unflooded, 2019, ground	42	10.08	10	976	75.08	49	2.27	0.61
All sites, all years, ground	59	19.69	20	3300	253.85	136	2.37	0.58
Flooded, 2017, above	12	2.62	2	70	5.39	5	1.61	0.65
Flooded, 2019, above	11	2.69	3	90	6.92	7	1.79	0.73
Flooded, both years, above	16	4.08	4	160	12.31	11	1.97	0.65
Unflooded, 2019, above	15	3.23	3	132	10.15	6	1.72	0.63
All sites, all years, above	25	6.23	7	292	22.46	20	1.94	0.60

Table 3. Species richness estimates of bees based on total and standardized datasets. Each estimate's upper and lower 95% confidence intervals are provided.

	Chao1 (Chao, 1984)	ACE (Chao and Lee, 1992)	1st order jackknife	2nd order jackknife
Flooded, 2017, total, all bees	80 (68–117)	83 (71–113)	80 (72–96)	89 (75–118)
Flooded, 2019, total, all bees	75 (65–107)	80 (69–108)	77 (69–92)	84 (71–112)
Flooded, both years, total, all bees	117 (97–170)	127 (104–176)	111 (100–130)	127 (108–160)
Unflooded, 2017, total, all bees	31 (27–51)	30 (27–44)	32 (28–43)	34 (28–56)
Unflooded, 2019, total, all bees	127 (87–239)	103 (82–148)	93 (82–112)	114 (95–146)
Unflooded, both years, total, all bees	121 (87–221)	99 (82–137)	94 (84–112)	113 (95–144)
Flooded, 2017, standard, all bees	58 (53–81)	63 (56–86)	64 (57–78)	67 (57–95)
Flooded, 2019, standard, all bees	65 (55–93)	72 (60–102)	68 (60–83)	74 (62–103)
Flooded, both years, standard, all bees	104 (81–171)	96 (81–132)	91 (81–108)	106 (89–136)
Unflooded, 2019, standard, all bees	110 (76–209)	96 (74–147)	83 (73–101)	101 (84–133)

Table 4. Species captured that were unique to each dataset and their abundances (N). Asterisks indicate that species that were only detected from non-standardized methods.

Flooded site, pre-flooded	N	Flooded site, post-flooded	N	Unflooded site	N
*Agapostemon texanus**	2	*Andrena voilae**	1	*Andrena dollomellea*	1
*Andrena gardineri**	1	*Augochlora pura*	1	*Ceratina shinnersi*	1
*Andrena imitatrix**	1	*Calliopsis andreniformis*	1	*Coelioxys octodentata*	1
Bombus griseocollis	1	*Colletes nudus*	1	*Hylaeus affinis*	1
Coelioxys immaculata	2	*Colletes productus**	1	*Hylaeus georgicus*	1
Coelioxys sayi	1	*Epeolus ilicis*	2	*Lasioglossum callidum*	1
Holcopasites illinoiensis	1	*Melissodes comptoides ?**	1	*Lasioglossum trigeminum*	1
Hoplitis truncata	2	*Melissodes sp 2.**	1	*Melissodes druriellus**	1
Lasioglossum disparile	2	*Nomada rubicunda**	1	*Nomada vincta**	1
*Lasioglossum lustrans**	1	*Osmia texana*	2	*Nomia nortoni*	1
Lasioglossum pruinosum	4			*Perdita halictoides*	1
Megachile deflexa	1			*Sphecodes sp. 1*	1
*Megachile lippiae**	1			*Stelis lateralis*	1
*Megachile melanophaea**	1				
Megachile xylocopoides	2				
Melissodes tapanaea	3				
Osmia chalybea	1				
*Svastra compta**	1				

Table 5. Hutcheson's t-test for significance of differences among Shannon's diversity index values for site/year comparisons using standardized data for all bees.

Site, year	Pre-flooded (2017)	Post-flooded (2019)	Unflooded (2019)
Shannon's values	2.61	2.15	2.57
Flooded, 2017 (pre-flooded)			
Flooded, 2019 (post-flooded)	t(2583) = 7.56 p = 6E-14		
Unflooded, 2019	t(2237.8) = 0.63 p = 0.53	t(2438.5) = -6.71 p = 2.4E-11	

Table 6. Hutcheson's t-test for significance of differences among Shannon's diversity index values for site/year comparisons using standardized data for ground nesting bees.

Site, year	Pre-flooded (2017)	Post-flooded (2019)	Unflooded (2019)
Shannon's values	2.43	1.91	2.27
Flooded, 2017 (pre-flooded)			
Flooded, 2019 (post-flooded)	t(2332.1) = 8.72 p = 5.39E-18		
Unflooded, 2019	t(1999.8) = 2.70 p = 0.007	t(2185.1) = -5.69 p = 1.5E-08	

Table 7. Hutcheson's t-test for significance of differences among Shannon's diversity index values for site/year comparisons using standardized data for above-ground nesting bees.

Site, year	Pre-flooded (2017)	Post-flooded (2019)	Unflooded (2019)
Shannon's values	1.61	1.74	1.72
Flooded, 2017 (pre-flooded)			
Flooded, 2019 (post-flooded)	t(131.77) = -0.76 p = 0.44		
Unflooded, 2019	t(143.94) = -0.62 p = 0.54	t(217.04) = 0.16 p = 0.88	

Table 8. ANOSIM site/year comparison results using bees of all nesting habits and a Bray-Curtis index.

Overall dissimilarity: R = 0.067, p = 0.056			
Site, year	Pre-flooded (2017)	Post-flooded (2019)	Unflooded (2019)
Flooded, 2017 (pre-flooded)			
Flooded, 2019 (post-flooded)	R = 0.086 p = 0.067		
Unflooded, 2019	R = 0.158 p = 0.013	R = -0.007 p = 0.466	

Table 9. ANOSIM site/year comparison results using ground nesting bees and a Bray-Curtis index.

Overall dissimilarity: R =0.06 , p = 0.064			
Site, year	Pre-flooded (2017)	Post-flooded (2019)	Unflooded (2019)
Flooded, 2017 (pre-flooded)			
Flooded, 2019 (post-flooded)	R = 0.086 p = 0.076		
Unflooded, 2019	R = 0.151 p = 0.014	R = -0.016 p = 0.522	

Table 10. ANOSIM site/year comparison results using above-ground nesting bees and a Bray-Curtis index.

Overall dissimilarity: R = 0.051, p = 0.074			
Site, year	Pre-flooded (2017)	Post-flooded (2019)	Unflooded (2019)
Flooded, 2017 (pre-flooded)			
Flooded, 2019 (post-flooded)	R = -0.002 p = 0.445		
Unflooded, 2019	R = 0.105 p = 0.038	R = 0.057 p = 0.101	

Table 11. SIMPER analysis of the pre-flooded and post-flooded datasets using all nesting habits and a Bray-Curtis dissimilarity index.

Taxon	Average dissimilarity	Contributive percent difference	Cumulative percent difference	Mean abundance pre-flooded group	Mean abundance post-flooded group
Melissodes communis	24.49	31.47	31.47	28.6	47.9
Perdita obscurata	8.749	11.24	42.72	4	18
Lasioglossum apopkense	5.9	7.583	50.3	8.77	4.62
Augochlorella karankawa	5.434	6.983	57.28	7.92	0.0769
Lasioglossum vierecki	4.013	5.158	62.44	7.62	3.08
Sphecodes brachycephalus	3.252	4.18	66.62	2.77	4.85
Habropoda laboriosa	2.996	3.85	70.47	2.23	3.77
Lasioglossum floridanum	2.004	2.575	73.05	4.31	1.54
Megachile texana	1.94	2.493	75.54	2.62	0.462
Lasioglossum tegulare	1.91	2.455	77.99	3.08	1.85
Apis mellifera	1.855	2.384	80.38	2.31	1.92
Megachile georgica	1.55	1.992	82.37	1.77	2.38
Ptilothrix bombiformis	1.402	1.802	84.17	1.92	1.31
Lasioglossum bruneri	1.372	1.764	85.94	1.92	0.385
Bombus pensylvanicus	1.123	1.443	87.38	0.923	1.08
Osmia sandhouseae	0.6464	0.8307	88.21	0.154	0.692
Svastra atripes	0.6355	0.8167	89.03	0.385	0.538
Xylocopa virginica	0.6184	0.7948	89.82	0.0769	1
Lasioglossum batya	0.4997	0.6423	90.46	0.538	0.154
Lasioglossum cinctipes	0.4425	0.5687	91.03	0.308	0.462
Megachile mendica	0.4405	0.5661	91.6	0.538	0.154
Melitoma taurea	0.4141	0.5322	92.13	0.692	0
Lasioglossum coreopsis	0.398	0.5115	92.64	0.154	0.462
Lasioglossum fedorense	0.3953	0.508	93.15	0.615	0.154
Triepeolus luantus	0.3535	0.4543	93.6	0	1.08
Melissodes bimaculata	0.3356	0.4312	94.04	0	0.769
Lasioglossum creberrimum	0.3219	0.4138	94.45	0.231	0.308
Lasioglossum illinoense	0.2595	0.3335	94.78	0.308	0.231
Augochloropsis metallica	0.2576	0.331	95.11	0.308	0.154
Perdita bishoppi	0.2534	0.3257	95.44	0.231	0
Epeolus lectoides	0.2524	0.3244	95.76	0.154	0.692
Anthidiellum notatum	0.2294	0.2949	96.06	0.231	0.154
Ceratina cockerelli	0.2235	0.2872	96.35	0.231	0.0769
Agapostemon splendens	0.1713	0.2202	96.57	0.154	0.154
Megachile pseudobrevis	0.1689	0.2171	96.78	0.154	0.154
Bombus impatiens	0.1653	0.2124	97	0.154	0.0769
Melissodes tepaneca	0.1569	0.2017	97.2	0.231	0
Megachile rugifrons	0.1473	0.1893	97.39	0	0.538

(continued)

Taxon	Average dissimilarity	Contributive percent difference	Cumulative percent difference	Mean abundance pre-flooded group	Mean abundance post-flooded group
Andrena miserabilis	0.129	0.1658	97.55	0	0.154
Lasioglossum pruinosum	0.1271	0.1634	97.72	0.154	0
Megachile mucida	0.1194	0.1535	97.87	0.154	0.0769
Hoplitis truncata	0.1124	0.1444	98.01	0.154	0
Lasioglossum tarponense	0.1087	0.1397	98.15	0.154	0
Lasioglossum birkmanni	0.09287	0.1194	98.27	0	0.154
Megachile frugalis	0.08655	0.1112	98.38	0	0.308
Lasioglossum disparile	0.08447	0.1086	98.49	0.0769	0
Augochlora pura	0.07403	0.09514	98.59	0	0.0769
Triepeolus simplex	0.07156	0.09196	98.68	0.0769	0.0769
Coelioxys sayi	0.07095	0.09118	98.77	0.0769	0
Perdita ignota	0.0665	0.08546	98.86	0.0769	0
Sphecodes atlantis	0.0657	0.08443	98.94	0	0.0769
Epeolus ilicis	0.06542	0.08408	99.02	0	0.154
Colletes thoracicus	0.0645	0.0829	99.11	0	0.0769
Augochloropsis sumptuosa	0.0645	0.0829	99.19	0	0.0769
Melissodes comptoides ?	0.06171	0.0793	99.27	0	0.0769
Bombus griseocollis	0.05618	0.0722	99.34	0.0769	0
Osmia chalybea	0.05618	0.0722	99.41	0.0769	0
Andrena imitatrix	0.04953	0.06365	99.48	0.0769	0
Megachile petulans	0.04466	0.0574	99.53	0	0.0769
Dianthidium curvatum	0.04466	0.0574	99.59	0	0.0769
Megachile deflexa	0.04437	0.05702	99.65	0.0769	0
Anthophora abrupta	0.04437	0.05702	99.71	0.0769	0
Coelioxys immaculata	0.04437	0.05702	99.76	0.0769	0
Megachile xylocopoides	0.03307	0.04249	99.81	0.0769	0
Calliopsis andreniformis	0.03271	0.04204	99.85	0	0.0769
Osmia texana	0.03271	0.04204	99.89	0	0.0769
Holcopasites illinoiensis	0.03146	0.04043	99.93	0.0769	0
Colletes nudus	0.02717	0.03492	99.97	0	0.0769
Colletes inaequalis	0.02717	0.03492	100	0	0.0769

Table 12. SIMPER analysis of the pre-flooded and unflooded datasets using all nesting habits and a Bray-Curtis dissimilarity index.

Taxon	Average dissimilarity	Contributive percent difference	Cumulative percent difference	Mean abundance pre-flooded group	Mean abundance unflooded group
Melissodes communis	20.85	26.97	26.97	28.6	29.6
Lasioglossum apopkense	6.004	7.766	34.74	8.77	6.08
Augochlorella karankawa	5.619	7.269	42.01	7.92	0
Lasioglossum tegulare	4.881	6.314	48.32	3.08	8.62
Lasioglossum vierecki	3.794	4.908	53.23	7.62	3.08
Lasioglossum fedorense	3.648	4.718	57.95	0.615	7.15
Perdita obscurata	3.395	4.392	62.34	4	2.92
Apis mellifera	3.346	4.328	66.67	2.31	4.85
Perdita bishoppi	2.542	3.288	69.95	0.231	3.46
Habropoda laboriosa	2.517	3.256	73.21	2.23	2.46
Lasioglossum floridanum	2.459	3.18	76.39	4.31	3.77
Megachile texana	1.978	2.559	78.95	2.62	0.385
Sphecodes brachycephalus	1.792	2.318	81.27	2.77	0.154
Lasioglossum bruneri	1.691	2.187	83.45	1.92	1.38
Megachile georgica	1.415	1.831	85.28	1.77	1.77
Ptilothrix bombiformis	1.05	1.358	86.64	1.92	0.0769
Bombus pensylvanicus	0.9731	1.259	87.9	0.923	0.615
Ceratina strenua	0.5227	0.676	88.58	0	1.15
Melitoma taurea	0.4926	0.6372	89.21	0.692	0.385
Lasioglossum batya	0.4805	0.6216	89.84	0.538	0.154
Ceratina calcarata	0.4364	0.5645	90.4	0	0.846
Lasioglossum coreopsis	0.4346	0.5621	90.96	0.154	0.615
Megachile mendica	0.4058	0.5249	91.49	0.538	0
Augochloropsis metallica	0.4045	0.5232	92.01	0.308	0.538
Svastra atripes	0.3542	0.4581	92.47	0.385	0.0769
Megachile pseudobrevis	0.3359	0.4345	92.9	0.154	0.462
Sphecodes atlantis	0.3031	0.3921	93.3	0	0.385
Anthophora abrupta	0.2678	0.3463	93.64	0.0769	0.385
Melissodes bimaculata	0.2606	0.3371	93.98	0	0.385
Lasioglossum creberrimum	0.2548	0.3295	94.31	0.231	0.308
Lasioglossum illinoense	0.2468	0.3192	94.63	0.308	0.0769
Xylocopa virginica	0.2191	0.2834	94.91	0.0769	0.308
Megachile mucida	0.2187	0.2829	95.19	0.154	0.231
Anthidiellum notatum	0.2061	0.2666	95.46	0.231	0.0769
Ceratina cockerelli	0.2058	0.2661	95.73	0.231	0
Epeolus lectoides	0.2049	0.2651	95.99	0.154	0.308
Agapostemon splendens	0.2029	0.2625	96.25	0.154	0.154
Bombus impatiens	0.1762	0.228	96.48	0.154	0.154
Melissodes tepaneca	0.1604	0.2075	96.69	0.231	0
Lasioglossum cinctipes	0.1591	0.2058	96.9	0.308	0

(continued)

Taxon	Average dissimilarity	Contributive percent difference	Cumulative percent difference	Mean abundance pre-flooded group	Mean abundance unflooded group
Lasioglossum pruinosum	0.1295	0.1676	97.06	0.154	0
Colletes inaequalis	0.1261	0.1632	97.23	0	0.154
Perdita ignota	0.1187	0.1536	97.38	0.0769	0.0769
Hoplitis truncata	0.1149	0.1486	97.53	0.154	0
Lasioglossum tarponense	0.1112	0.1439	97.67	0.154	0
Osmia atriventris	0.1003	0.1297	97.8	0	0.154
Osmia sandhouseae	0.09632	0.1246	97.93	0.154	0
Colletes thoracicus	0.08965	0.116	98.04	0	0.0769
Lasioglossum callidum	0.08965	0.116	98.16	0	0.0769
Andrena miserabilis	0.08965	0.116	98.27	0	0.0769
Lasioglossum disparile	0.08538	0.1104	98.39	0.0769	0
Andrena dollomellea	0.07565	0.09785	98.48	0	0.0769
Hylaeus floridanus	0.07565	0.09785	98.58	0	0.0769
Coelioxys sayi	0.0721	0.09326	98.67	0.0769	0
Dianthidium curvatum	0.06891	0.08913	98.76	0	0.0769
Augochloropsis sumptuosa	0.06632	0.08578	98.85	0	0.0769
Lasioglossum trigeminum	0.06335	0.08195	98.93	0	0.0769
Lasioglossum birkmanni	0.06335	0.08195	99.01	0	0.0769
Lasioglossum weemsi	0.0582	0.07528	99.09	0	0.0769
Bombus griseocollis	0.05745	0.07431	99.16	0.0769	0
Osmia chalybea	0.05745	0.07431	99.24	0.0769	0
Megachile petulans	0.05157	0.06671	99.3	0	0.0769
Andrena imitatrix	0.05077	0.06567	99.37	0.0769	0
Ceratina shinnersi	0.0505	0.06532	99.43	0	0.0769
Megachile deflexa	0.04555	0.05892	99.49	0.0769	0
Coelioxys immaculata	0.04555	0.05892	99.55	0.0769	0
Stelis lateralis	0.03822	0.04944	99.6	0	0.0769
Sphecodes sp. 1	0.03822	0.04944	99.65	0	0.0769
Hylaeus georgicus	0.03822	0.04944	99.7	0	0.0769
Coelioxys octodentata	0.03764	0.04869	99.75	0	0.0769
Hylaeus affinis	0.03452	0.04465	99.79	0	0.0769
Megachile xylocopoides	0.03401	0.04399	99.84	0.0769	0
Holcopasites illinoiensis	0.03236	0.04186	99.88	0.0769	0
Triepeolus simplex	0.03236	0.04186	99.92	0.0769	0
Triepeolus luantus	0.02017	0.02609	99.95	0	0.0769
Perdita halictoides	0.02017	0.02609	99.97	0	0.0769
Nomia nortoni	0.02017	0.02609	100	0	0.0769

Table 13. SIMPER analysis of the post-flooded and unflooded datasets using all nesting habits and a Bray-Curtis dissimilarity index.

Taxon	Average dissimilarity	Contributive percent difference	Cumulative percent difference	Mean abundance post-flooded group	Mean abundance unflooded group
Melissodes communis	24.79	30.31	30.31	47.9	29.6
Perdita obscurata	8.651	10.58	40.89	18	2.92
Lasioglossum apopkense	6.628	8.104	48.99	4.62	6.08
Lasioglossum tegulare	5.271	6.445	55.44	1.85	8.62
Lasioglossum fedorense	3.687	4.508	59.95	0.154	7.15
Habropoda laboriosa	3.522	4.307	64.25	3.77	2.46
Apis mellifera	3.459	4.23	68.48	1.92	4.85
Perdita bishoppi	2.528	3.091	71.57	0	3.46
Lasioglossum floridanum	2.524	3.087	74.66	1.54	3.77
Lasioglossum vierecki	2.196	2.686	77.35	3.08	3.08
Sphecodes brachycephalus	2.103	2.572	79.92	4.85	0.154
Megachile georgica	1.743	2.131	82.05	2.38	1.77
Bombus pensylvanicus	1.191	1.456	83.51	1.08	0.615
Lasioglossum bruneri	0.8188	1.001	84.51	0.385	1.38
Ptilothrix bombiformis	0.7905	0.9666	85.47	1.31	0.0769
Xylocopa virginica	0.7592	0.9283	86.4	1	0.308
Lasioglossum coreopsis	0.6922	0.8464	87.25	0.462	0.615
Osmia sandhouseae	0.6893	0.8428	88.09	0.692	0
Svastra atripes	0.5686	0.6953	88.79	0.538	0.0769
Melissodes bimaculata	0.5491	0.6714	89.46	0.769	0.385
Ceratina strenua	0.5482	0.6704	90.13	0	1.15
Ceratina calcarata	0.465	0.5686	90.7	0	0.846
Augochloropsis metallica	0.4615	0.5643	91.26	0.154	0.538
Triepeolus luantus	0.3892	0.4759	91.74	1.08	0.0769
Megachile pseudobrevis	0.3865	0.4725	92.21	0.154	0.462
Lasioglossum cinctipes	0.3847	0.4705	92.68	0.462	0
Sphecodes atlantis	0.3777	0.4618	93.14	0.0769	0.385
Lasioglossum creberrimum	0.3701	0.4526	93.59	0.308	0.308
Melitoma taurea	0.361	0.4415	94.04	0	0.385
Megachile texana	0.3536	0.4324	94.47	0.462	0.385
Epeolus lectoides	0.3397	0.4154	94.88	0.692	0.308
Anthophora abrupta	0.2512	0.3071	95.19	0	0.385
Andrena miserabilis	0.2479	0.3031	95.49	0.154	0.0769
Agapostemon splendens	0.2372	0.29	95.78	0.154	0.154
Lasioglossum batya	0.2189	0.2677	96.05	0.154	0.154
Megachile mucida	0.201	0.2457	96.3	0.0769	0.231
Colletes thoracicus	0.1725	0.211	96.51	0.0769	0.0769

(continued)

Taxon	Average dissimilarity	Contributive percent difference	Cumulative percent difference	Mean abundance post-flooded group	Mean abundance unflooded group
Colletes inaequalis	0.1657	0.2027	96.71	0.0769	0.154
Bombus impatiens	0.1629	0.1992	96.91	0.0769	0.154
Lasioglossum birkmanni	0.1591	0.1945	97.1	0.154	0.0769
Megachile rugifrons	0.1516	0.1854	97.29	0.538	0
Megachile mendica	0.1511	0.1848	97.48	0.154	0
Augochloropsis sumptuosa	0.1378	0.1685	97.64	0.0769	0.0769
Anthidiellum notatum	0.1333	0.163	97.81	0.154	0.0769
Dianthidium curvatum	0.1205	0.1473	97.95	0.0769	0.0769
Lasioglossum callidum	0.119	0.1456	98.1	0	0.0769
Osmia atriventris	0.1087	0.1329	98.23	0	0.154
Megachile petulans	0.09755	0.1193	98.35	0.0769	0.0769
Andrena dollomellea	0.09225	0.1128	98.46	0	0.0769
Hylaeus floridanus	0.09225	0.1128	98.58	0	0.0769
Augochlora pura	0.09029	0.1104	98.69	0.0769	0
Megachile frugalis	0.0892	0.1091	98.8	0.308	0
Lasioglossum illinoense	0.08671	0.106	98.9	0.231	0.0769
Augochlorella karankawa	0.07718	0.09437	99	0.0769	0
Lasioglossum trigeminum	0.07258	0.08875	99.09	0	0.0769
Perdita ignota	0.07258	0.08875	99.17	0	0.0769
Melissodes comptoides ?	0.07132	0.08721	99.26	0.0769	0
Epeolus ilicis	0.06898	0.08434	99.35	0.154	0
Lasioglossum weemsi	0.06515	0.07966	99.43	0	0.0769
Ceratina shinnersi	0.05479	0.06699	99.49	0	0.0769
Triepeolus simplex	0.04867	0.05951	99.55	0.0769	0
Stelis lateralis	0.03978	0.04864	99.6	0	0.0769
Sphecodes sp. 1	0.03978	0.04864	99.65	0	0.0769
Hylaeus georgicus	0.03978	0.04864	99.7	0	0.0769
Coelioxys octodentata	0.03911	0.04782	99.75	0	0.0769
Hylaeus affinis	0.03555	0.04347	99.79	0	0.0769
Calliopsis andreniformis	0.03449	0.04217	99.83	0.0769	0
Osmia texana	0.03449	0.04217	99.87	0.0769	0
Ceratina cockerelli	0.03449	0.04217	99.92	0.0769	0
Colletes nudus	0.02828	0.03457	99.95	0.0769	0
Perdita halictoides	0.02017	0.02466	99.98	0	0.0769
Nomia nortoni	0.02017	0.02466	100	0	0.0769

VITA

Archie Sauls grew up in Dallas, Texas and as a child was fascinated by any creature that flew in the air or crawled along the soil. He graduated from Duncanville High School in 2013 and began attending Stephen F. Austin State University that fall, declaring a major in Biology. In May of 2017, he graduated and received the degree of Bachelor of Science.

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Style manual: The Pan-Pacific Entomologist

This thesis was typed by Archie Sauls.