

CHARACTERIZING SOLITARY BEE COMMUNITIES IN THE SOUTHERN
APPALACHIANS AND ENVIRONMENTAL FACTORS PREDICTING HABITAT USE

A Thesis by
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Abstract

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Pollinators, particularly bees, provide essential services for both agricultural and ecosystems worldwide, but data has accumulated documenting population declines, range shifts, and range contractions for many species. Most bee species are understudied, particularly species that are considered ‘solitary,’ those lacking a queen, colony, or division of labor. Instead, solitary bees are individual females that create a nest, lay eggs, and provision offspring all on their own. Understanding the abundance and distribution of bees has become a topic of interest as government programs have encouraged surveying for them. In 2019, I co-coordinated a Citizen Science inventory of pollinating insects on the Blue Ridge Parkway, a 470-mile stretch of road that connects Shenandoah National Park, Virginia, to the great Smokey Mountain National Park, North Carolina. Site adopters collected specimens using passive traps (‘bee bowls’) and active netting. Specimens were retrieved biweekly from April-October, 2019. We characterized the abundance, diversity, distribution, and phenology of solitary bee species among our samples. We then used occupancy models to explore variables that may explain habitat usage among the most abundant solitary bees.

Among over 8000 total inventory specimens, we collected 5262 solitary bees, comprising five families, 29 genera, and 137 species from 59 sites. Diversity hot spots were observed along the length of the Parkway. Netting was an ineffective capture method for solitary bees, overall. White and fluorescent blue passive traps caught more bees than expected across all families except *Colletidae*, in which captures were biased toward traps painted fluorescent yellow. Phenology plots revealed distinct windows of activity across the survey period for different species. A species accumulation curve revealed that we have captured most available diversity, but a few rare species are likely undetected.

Occupancy models for six species of solitary bees: *Eucera hamata*, *Andrena nivalis*, *Andrena perplexa*, *Agapostemon virescens*, *Agapostemon sericeus*, and *Osmia taurus*. Precipitation and bee preferred plant taxa had large impacts on detection and occupancy of species with elevation not being a factor in my models. This is the first-time occupancy models have been used to study solitary bees on the Blue Ridge Parkway and in the Southern Appalachians. Findings here provide a basis for comparison in the future.

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Foreword

This work was completed in collaboration with the National Park Service and United States Geological Survey to gain a better understanding of solitary bees in the southern Appalachians in terms of abundance, distribution, and foraging habitat. The format and references follow that of the journal *Ecology*. This thesis includes two chapters that are each a stand-alone report.

Chapter 1: Solitary Bees of the Blue Ridge Parkway

Introduction

Bees (Hymenoptera: Superfamily Apoidea, Clade Anthophila) are a keystone taxon of insects that are integral to the pollination of agricultural landscapes and wild ecosystems (Buchmann and Nabhan, 1997; Klein et al., 2006; Brown & Paxton., 2009). In the US alone, pollination is valued at \$195 - \$387 billion (1997 to 2016, adjusted for 2020 inflation; Porto et al 2020). Globally, 70% of crops directly benefit from pollination services provided by bees (Ricketts et al., 2008). The stability of bee populations could become priceless as the world population continues to grow and the need for agricultural food products becomes even more integral. As natural ecosystems throughout the world continue to be eroded and simplified due to anthropogenic forces altering landscapes, ecosystem services arising from bee species diversity may also increase in value, as it has been shown that biodiversity in general is able to stabilize landscapes (Cardinale et al., 2012; Tilman, Reich, & Isbell., 2012).

While being imperative to the pollination of wild plants and crops, bees, among other clades of insects, are declining worldwide. The decline of wild and managed bee biodiversity has sparked international attention on their importance to the ecosystems that they service. The major drivers of biodiversity loss are thought to be a combination of land use change and agricultural intensification (Kremen & Merenlender, 2018, Raven & Wagner, 2021). Bees have formed mutualistic relationships with flowers over the course of evolution and each depend on one another for life history stages. Replacing a diverse community of floral partners with monoculture fields may not impact species who are foraging generalists, but oligolectic species cannot tolerate instant alterations to landscapes (Goulson et al., 2005; Scheper et al., 2014).

Among governing bodies and the general public there has been great interest in protecting the European Honey bee (*Apis mellifera*) due to agriculture's reliance on this single managed species (Winfree, 2010). Scientifically, the European honey bee is the most understood bee, and maybe insect, in the world. From 2006 to 2007, there were concerns over honey bee populations due to overwintering colony collapse disorder (CCD) (Cox-Foster et al., 2007; Van

Englesdorp et al., 2009). But intensive research revealed that interactive effects among climate change, pathogens i.e. *Varroa* mites, and a decline in bee health (Hristov et al., 2020) were responsible. Despite honeybees experiencing declines of up to 30% throughout winter months due to CCD in some countries (Gray et al., 2020), globally, honey bee populations have actually increased since 1967; In Asia (426%), Africa (130%), South America (86%), and Oceania (39%) (Hristov et al., 2020; Potts et al., 2010).

In North America, data has accumulated about the status of some wild native species, primarily bumble bees (*Bombus* sp.), Habitat loss, climate change, pathogens and loss of genetic diversity have facilitated *Bombus* species declines in North America. For example, four of nine species surveyed had declined over 90% in the first widespread study (Cameron et al., 2011). In 2015, the Rusty-Patched Bumble Bee (*Bombus affinis*) was listed as critically endangered by the International Union for Conservation of Nature (ICUN) and in 2017 became the first bee in the United States to be placed on the USFWS endangered species list (Hatfield et al., 2014). There have since been 171 bee (*Hymenoptera*) species that have been listed on the ICUN red list for declining populations.

While progress has been made toward assessing the status of pollinator species in these highly familiar taxonomic groups, species in the *Bombus* and *Apis* genera are not necessarily representative of the totality of native bees in North America or globally. In fact, honey bees and bumble bees represent less than 10 percent of world-wide bee species (Danforth et al 2019). Honeybees and bumble bees exhibit eusocial life histories, meaning that they have evolved social organization and a division of labor (Cameron, 1989). While not exclusive to the *Apis* and *Bombus* generally (Ross and Keller, 1995), the vast majority of global bees are solitary (Danforth et al 2019). Solitary bees exhibit no hierarchical organization, e.g., queen or other castes, and lack a hive structure. Instead, they operate as individual bees who forage and provision their eggs independently. Over 70% of the 4,500 bee species in North America are solitary, but information on most species and populations is lacking, and their life histories are less well-understood and studied (Michener, 2000; Lehman & Camp, 2021).

Yet, solitary bee species may be critical providers of ecosystem services. Multiple reports indicate that wild solitary bees are better pollinators than managed bees (Javorek, 2002; Winfree et al., 2010; Eeraerts et al., 2019). The primary benefit of using managed social bees to pollinate

is that most foragers return back to the hive at sunset each day facilitating pollination in a targeted locale and making the hive movable. It is more challenging to encourage solitary bees to stay in an area due to lack of management techniques (Bohart, 1972; Torchio, 1991; Winfree, 2010).

One exception to the eusocial species-dominated datasets is *Osmia*, a genus of concern that is also managed for commercial pollination. *Osmia* are managed primarily for pollination of fruit trees with both native and introduced species being used (Vicens and Bosch, 2000). A fifteen-year survey from 2003-2017 tracked the abundance of the introduced *O. cornifrons*, the invasive *O. taurus*, and six native *Osmia* species. All six native species experienced continual annual decline, likely from competition with the introduced species. Both non-native species became established in the ecosystem and were observed to increase in abundance (Lecroy et al., 2020).

Data for global declines and range contractions of native bee species world-wide continues to accumulate (Potts et al., 2010; Wood et al., 2020; Zattara and Aizen 2021), but alarmingly most native bees remain understudied and unassessed. Efforts to expand inventories and monitoring and mitigate declines have increased across government, private, and non-profit sectors. At the federal level, the United States has prioritized pollinators and their habitat since enacting the Food, Conservation, and Energy Act ('Farm Bill') of 2008 (Winfree, 2010). In 2015, President Obama's Pollinator Health Strategy (Senapathi et al., 2016) created the Pollinator Task Force, which tasked National Park Service (NPS) to lead the research and public outreach of this movement, including the organization of 'BioBlitz' events in over 200 national parks, to help uncover species diversity with the help of schools and citizen scientists. Without such thorough species records, it is challenging to organize effective conservation and management strategies. Species inventories also create a link between the past and future, facilitating the observation and quantification of changes that occur over time in species composition, species ranges and in some cases, species abundances.

The goals of my study were to quantify the abundance, diversity, and distribution of solitary bee species found on the Blue Ridge Parkway (BRP) by analyzing specimens from a citizen science inventory of pollinating insects that I co-coordinated in 2019. I expected to

observe more than 100 species of solitary bees among five families along the Parkway, and that some of these would be novel species records for the area.

Methods and Study System

Study location

Samples for this study were collected by Appalachian State University students and citizen scientists from roadside habitats along the Blue Ridge Parkway (BRP) of North Carolina and Virginia, from April to October 2019. The BRP is a 469 mile transect of road that connects the Great Smoky National Park to Shenandoah National Park, starting in Afton, Virginia and ending in Cherokee, North Carolina. It includes the highest peak on the East Coast, located on Mount Mitchell, reaching 6,684 feet and has a lowest point of 640 feet located on the James River in Roanoke, Virginia. The roadway traverses multiple elevations and habitats. Prior intensive surveying of pollinating insects had not been conducted along this transect of road, though preliminary data from some smaller studies existed. For example, Rayfield (2015), inventoried bumble bees in three national parks at alternate mileposts along a 900 km megatransect in 2015. Though each site was inventoried only once at midsummer for each site, Rayfield's results of high diversity in the BRP, motivated interest in surveying for all bee species.

Study system

The focal taxa for my study was the group of pollinating insects collectively known as "solitary bees." This excludes social bees such as *Apis mellifera* and all *Bombus* species. Solitary bees differ in their life history as there is no hive or queen. Female bees will create burrows in the ground or use cavities in trees as egg chambers where they will lay anywhere from four to eight eggs that will overwinter and then emerge the following spring (Palladini & Maron, 2014). These solitary bees comprise five families: Adrenidae, Apidae, Colletidae, Halictidae, and Megachilidae.

Family *Adrenidae* is a diverse family of ground nesting bees with over 3,000 representatives from arid regions in North America to the Holarctic (Danforth, Minckley, & Neff,

2019). Within Andrenidae, the largest genus is *Andrena* with over 1,500 species. While being completely solitary, species in this genus will form communal nesting sites, e.g. using a shared opening to a nest but creating their own egg chambers independently (Antoine & Forrest, 2021). Andrenidae has many oligolectic species that only forage on flowers from Asteraceae, Apiaceae, Brassicaceae, Ericaceae, Fabaceae, and Rosaceae (Larkin et al. 2006; Danforth, Minckley, & Neff, 2019)

Apidae is the largest family of bees with over 6000 species worldwide (Bossert et al. 2018). It is also the oldest family, with the oldest fossil dating to the late cretaceous period, 95-115 million years ago (Danforth, Minckley, & Neff, 2019). This family includes two of the most studied insect groups with the honey bee (*Apis mellifera*) and the bumble bees (*Bombus*), with the remaining species being a vast array of solitary bees with differing life histories.

Halictidae has over 4,500 species, and three subfamilies- *Nomiinae*, *Nomioidinae*, and *Halictinae*. 80% of *Halictidae* species can be found in *Halictinae* (Danforth, Minckley, & Neff, 2019) and comprise a variety of colorful species from varying shades of metallic greens and blues to brilliant yellows. Most solitary bees have a univoltine life-cycle but there are species in this family that can produce multiple generations per season. (Danforth, Minckley, & Neff, 2019).

Megachilidae is the third largest family and can be found on all continents other than Antarctica (Danforth, Minckley, & Neff, 2019), in environments ranging from tropical forests to deserts. This family has two of the only commercially managed solitary bees; *Megachile rotundata* and *Osmia lignaria*. The more heavily managed of the two, *M. rotundata*, has tripled alfalfa seed production in North America since its introduction in the 1940s (Pitts-Singer & Cane, 2011). It is also an excellent pollinator of canola oil (Robinson et al., 2023). The other, *O. lignaria*, is a native pollinator and used extensively for apple, cherry, and almond production (Boyle et al., 2020).

Colletidae is the smallest family with only 2,600 species worldwide. It is most densely concentrated in Australia and South America, with just a small percentage in North America. All species will secrete a waterproof serum called cellophane around their nests, which gives them their common name, cellophane bees.

Species Inventory Methods

In order to assess the abundance, diversity and distribution of bees in the Southern Appalachians, I co-coordinated a Citizen Science pollinator inventory of the BRP in 2019, with other members of the Geib Lab at Appalachian State University and Paul Super of the National Park Service. A Citizen Science model for the study was utilized due to the need for a large troop of site adopters, because such projects have previously been demonstrated as highly effective for large-scale information gathering, and to achieve the aim of encouraging public involvement in the biodiversity of their National Parks (Bonney et. al, 2015). Citizen Science volunteers were recruited via the NPS listserv and were assigned to sites (mileposts) near their home location. Undergraduate student volunteers were recruited via their Appalachian State University email. All site adopters were provided materials kits and were trained either in person or remotely via publicly posted YouTube videos created by the Geib Lab.

Site selection and establishment

Sixty inventory sites were established along the entire length of the parkway. Fifteen of the sites were existing or newly planted Wildflower Display Areas created by the Blue Ridge Parkway. Sampling methods were tested during a pilot inventory of these fifteen BRP sites in 2018. Forty-four randomly selected sites were added for the full inventory in 2019 and spanned the full length of the BRP megatransect, 496 miles. Mowing regimes different among the site types; wildflower display areas were designated as mowed once per year in the fall, whereas grassy bays and other random sites were designated for mowing approximately every two weeks. In practice, the mowing of all BRP sites by maintenance crews was unpredictable. In addition, one established site was unknowingly abandoned by the volunteer, and that site produced no samples, reducing the total effective sites for this study to $N = 59$.

In March-April 2019, site adopters were instructed to select a location within their assigned mileposts for placing passive traps that they would revisit throughout the duration of the survey. The ideal trap placement was in an area of significant vegetation, such as a grassy bay, that was a good distance from the roadway to minimize anthropogenic disturbance. At each site, volunteers established three sets of three bee-bowl traps made from 12 oz. Solo™ cups that were set 5m apart (15m total). Each set of three passive traps included one white cup (unpainted)

and one each that was painted fluorescent yellow and fluorescent blue (Guerra Paint and Pigment Corp.). Cups were mounted on a PVC stand and filled with a 50% solution of propylene glycol plus a drop of Dawn dish detergent to break the surface tension (Droege et al., 2010). Site adopters were instructed to record site coordinates and note site type observations, grassy bays, wildflower display areas WDAs, overlooks, etc. Volunteers were instructed to trim away grass/brush from the immediate area of the passive traps to facilitate pollinator visual recruitment.

Sample retrieval and storage

Volunteers visited sites biweekly for sample retrieval and site maintenance from April until October 2019. Volunteers filtered out the contents of each cup through a brine shrimp fish net to collect specimens. Specimens were placed in 80% denatured ethanol in Whirl-Paks® with labels including the following information: site, date, observers, and cup color. Volunteers then replaced the cups and refilled with propylene glycol trap solution. Dirty, damaged, or lost traps were replaced as needed. Volunteers would note the weather conditions, flowers they saw, etc. on an observation sheet for each site.

In addition to retrieving samples from the passive traps, volunteers were encouraged to actively collect foraging bees using an insect net during each visit. For active net surveys, volunteers were instructed to collect any bees present within a ten-minute timeframe at each site. Active net surveys were optional and in practice, few volunteers completed them. Collected samples were either mailed to the Geib Lab at Appalachian State University laboratory or deposited at ranger stations along the BRP for regular retrieval. Once inside the laboratory, specimens were stored in the laboratory refrigerator at approximately 4.5 degrees C.

Sample processing and identification

Samples were processed by washing, drying, and pinning for later identification. To begin processing, samples were strained out of whirl packs with a small sieve to remove ethanol preservative. Filtered samples were then placed in an Erlenmeyer flask with 20 mL of water and 5 ml of Dawn Dish Detergent™. Samples were swirled for 30 seconds, and then rinsed. After rinsing the samples were placed in mesh bags and dried in a 1.50 cu. ft. Panda Electric Compact

Portable Laundry Dryer on medium heat for 20 minutes. Dried specimens were then pinned with a given individual number. Pinned specimen boxes were delivered to Sam Droege at the USGS Native Bee Inventory Monitoring Laboratory for resolution to species.

Analyses

Abundance, distribution, and biodiversity

I quantified the abundance of solitary bee families, genera and species found along the BRP and compared records from this inventory to past BRP records (*unpublished data provided by Paul Super*) to assess novel observations.

To assess the distributions of solitary bees, I quantified samples captured per milepost for each family and for all solitary bees combined. I compared capture rates at sites between states (NC and VA) using a two-tailed T-Test, assuming unequal variances.

I calculated species diversity per site, per state (NC and VA), and for the whole BRP using two metrics: Shannon's Diversity Index and Simpson's Diversity Index. Shannon's Diversity Index (Shannon, 1948) was investigated using the Vegan package (Oksanen, F.J et al., 2017) inside of RStudio (Version 1.4.1717). The formula used is:

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

Where the sum of the entire community (p) made up of species (i) is multiplied by the natural log of the entire community (p) of species (i). Higher numbers indicate greater diversity. A more conservative approach was also used with Simpson's Diversity Score (Simpson, 1949). The formula is as follows:

$$D = \frac{N(N-1)}{\sum n(n-1)}$$

Where N is the number of individuals in a total population and n is the individuals of a single species. These calculations were also conducted in RStudio using *vegan* (Oksanen, F.J et al., 2017). Diversity values per site from both indices were then transferred to ArcGIS Pro (Version 2.7.0) where they were visualized as heat maps.

Phenology

To assess peak times of activity for solitary bee species, I plotted the phenology of abundance of individuals over time for species that had at least 100 recorded captures total; overall, fourteen species fit the criteria. Plots were then compared visually.

Effectiveness of collection methods

To analyze , I used the *Vegan* package in R Software (version X) run through with RStudio to create a species accumulation plot with total species caught on the Y-axis and survey sites on the X-axis. I estimated unobserved species three ways, using a Chao index, a jackknife indicator, and data bootstrapping.

To assess the relative effectiveness of the color of passive traps for solitary bees, I first excluded records of specimens caught in nets (1% of all specimens) and any record that lacked information about trap color, leaving $N = 5163$ records for analysis. I used a Chi-Square Goodness of Fit Test to determine whether the proportion of total captures was randomly distributed among the cup colors (fluorescent blue, white, and fluorescent yellow). I also used a one-way Analysis of Variance (ANOVA) to assess differences in mean proportion captured per site in each color, with site as the unit of analysis. Pairwise comparisons were then conducted with a post-hoc Tukey test. I conducted similar analyses for captures within each family.

Results

Abundance, distribution, and biodiversity

The 2019 pollinator inventory of the Blue Ridge Parkway resulted in 8178 bee specimens, of which 5262 were solitary bees. The 5262 solitary bees comprised five families, 29 genera, and 137 species from 59 sites (Table 1, 2 and 3, respectively). The most abundant family

was Halictidae with 1715 representatives (Table 1), while the most abundant genus was *Andrena* with 1106 representatives (Table 2). Sixty-one of the species observed were novel records for the BRP (Table 3).

We caught 2231 bees at 26 sites and 3030 bees at 34 sites in Virginia and North Carolina respectively, with a mean of 87.8 (78.9) solitary bees captured per site. The mean capture rate per site did not differ between the states ($t_{57.9} = -0.165, p = 0.87$). Within Virginia, bees were distributed heavily at four sites, mileposts 38, 136, 189, and 263 as each of them caught over 200 bees- close to a fourth of total Virginia bees (Fig. 2A). North Carolina's most abundant site, milepost 272, was only able to catch 136 species (Fig. 2A).

The average measure of the Shannon Diversity Index was 2.48 with the minimum being 1.03, found at milepost 449. The highest measure of diversity was 3.12, found at milepost 289. The heat map of Shannon's Diversity Index shows that many of the sites house a diverse community of bees with the only exception being right on the border between North Carolina and Virginia (Fig. 3). Simpson's Diversity Index was also used as it is a more conservative measure. Simpson's diversity index average was 0.85. The lowest diversity value was 0.58, found at milepost 32. The maximum value was 0.95, found at milepost 289. Simpson's Diversity Index shows a similar picture when compared to Shannon's. The heat map illustrates the amount of diversity while even using Simpson's index (Fig. 4).

Phenology

Peak times of activity varied across the species compared (Fig. 5). May and June were the peak times of activity for eight of the species (*Agapostemon virescens*, *Lasioglossum coriaceum*, *Lasioglossum cressonii*, *Andrena perplexa*, *Andrena miserabilis*, *Andrena crataegi*, *Andrena nivalis*, and *Eucera hamata*). Five of the species were found in small amounts across the course of the survey (*Agapostemon sericeus*, *Halictus confusus*, *Augochlorella aurata*, *Halictus rubicundus*, *Lasioglossum quebecense*) while one species was found earlier in season, peaking in April (*Osmia taurus*). *Agapostemon sericeus* was found throughout the course of the survey but was the only species that peaked as late as September.

Effectiveness of captures

A random species accumulation plot was used to measure how effectively we found species along the Blue Ridge Parkway (Fig.6). Because the line of the chart is still increasing, it means we did not find all possible species. The Chao index predicts that we missed about twelve species, while a jackknife indicator predicts we missed six species, and bootstrapping the data predicts we missed close to four species. The first instance of sampling done on the Blue Ridge Parkway was conducted in 2008 and 67 species were found. The 2019 survey found an additional 61 novel species that were not found in 2008. Passive traps caught a vast majority of all solitary bees.

Among all capture methods, blue cups caught the highest percentage of bees, comprising 40% of captures, followed by white with 39% of captures, and then yellow with 20% (Fig. 7A). As netting was only engaged regularly at 15 sites, its contribution to total samples was minimal (1% of all captures). Captures were not randomly distributed among passive trap cup colors overall ($X^2_{2, 5163} = 390.3, p < 0.0001$) or within families (Andrenidae $X^2_{2, 1087} = 37.9, p < 0.0001$; Apidae $X^2_{2, 1662} = 458.5, p < 0.0001$; Colletidae $X^2_{2, 33} = 11.4, p = 0.003$; Halictidae $X^2_{2, 1683} = 154.4, p < 0.0001$; Megachilidae $X^2_{2, 687} = 71.6, p < 0.0001$). White and fluorescent blue cups accounted for 70-90% of captures for all families of bees except Colletidae (Fig. 7B). Overall, yellow cups contributed a significantly lower mean proportion of captures per site than blue and white (Table 4, Fig. 8A).

Nearly all species records were represented among samples from blue and white cups. However, among the more rarely observed individuals, the fluorescent yellow cups were necessary for detection. For example, although we found only 33 Colletidae during the entire collection event, 60% were caught in yellow cups (Fig. 7B). In addition, six species represented by only one or two specimens from the duration of sampling were found only in yellow cups (*Andrena cornelli*, *Andrena forbesii*, *Hylaeus sparsus*, *Lasioglossum heterognathum*, *Lasioglossum lustrans*, *Sphecodes pimpinellae*). Of these, all except *Andrena forbesii* were novel species for the BRP (Table 3). Though netting was restricted to only 15 of our 60 sites and contributed only 1% of samples, netting was responsible for one unique species record, *Paranthidium jugatorium* (Table 3).

Discussion

Native solitary bees provide key ecosystem services to natural and agricultural systems and may play a more important role than the non-native honey bee (Winfree et al., 2007). Much is known about honey bees and their population shifts in past years as well as their vulnerability to numerous pesticides, parasites, and landscape modifications but the same cannot be said for the four thousand native bees in North America (Kremen & Ricketts, 2000; Potts et al., 2010; Goulson et al., 2015). The goals of this study were to assess the abundance, distribution, and biodiversity, of solitary bee species found on the Blue Ridge Parkway. Bee abundance was captured through passive pan traps with diversity being analyzed through Shannon's and Simpson's Diversity Index. Distribution was investigated through catch records at each site. To help with further studies, I also investigated the phenology of selected solitary bee species to understand their peak times of activity throughout the collection period. I then assessed the effectiveness of pan trap collections.

Abundance

Of the six families of bees that exist within North America, we were able to capture specimens from five; the only family left out was *Mellitidae*, which is not present on the East Coast. *Halictidae* was the most abundant family caught, closely followed by *Apidae*. Both species are highly abundant throughout the world as they are the two largest bee families (Danforth, 2019). Both families were heavily weighted by two genera within each of them. Of the 1,443 Halictidae bees caught, 482 were *Agapostemon* and 660 were *Lasioglossum*. It has been reported that bee bowls are biased towards *Halictidae* bees as this passive sampling method attracts smaller bodied bees (Gonzalez et al., 2016). Within Apidae, abundance was carried by *Nomada* (597) and *Peponapis* (511). *Nomada* could be so prevalent in the Southern Appalachians because it is a parasitic genus and is solely attracted to *Andrena* (Tengö and Bergström, 1977; Danforth, 2019). *Andrena* was the most abundant genus which gives *Nomada* plenty of opportunity to be successful in the landscape. *Peponapis* was dominated by one species, *Peponapis pruinosa*, which is very attracted to blue passive traps reported by Joshi et al (2015). The most abundant site was Milepost 263 with 421 captures. Of that, there were 209

recorded captures of the species *Peponapis pruinosa* and 83 captures of the parasitic bee, *Nomada maculata*.

Distribution

We were able to capture more solitary bees in Virginia than in North Carolina. Virginia had four sites with over 200 captures while North Carolina's most abundant site had 136 captures (MP 272). Virginia sites were lower in elevation which could allow for more diversity in flowers and overall, a better climate for bees (Peters et al., 2016). It is difficult for small solitary bees to raise and maintain proper body temperature for foraging at high elevations when compared to their larger relatives. Solitary bees can forage more efficiently at low elevation because of the higher ambient temperature when compared to high elevations (Stone, 1994; Danforth, 2019).

Biodiversity

The Southern Appalachian Mountains are a biodiversity hotspot for numerous taxa like plants, lichens, and salamanders (Milanovich et al., 2010; Allen & Lendemer, 2016; Woodbridge & Dovciak, 2022). Within the matrix of the Southern Appalachians, the Blue Ridge Parkway connects two national parks, the Great Smoky Mountains National Park and Shenandoah National Park. This connection acts as a corridor that facilitates plant and animal movement. While being a biodiversity hotspot and ecologically significant to migrations, little has been studied when it comes to bee abundance and diversity. The Blue Ridge Pollinator Project is one of the first efforts to delve into this topic, elucidating a trove of species. Regardless of what metric was used, North Carolina was more diverse than Virginia. With more variable landscapes in North Carolina due to elevation gains and losses, it could provide more niche opportunities to a greater array of solitary bees.

Phenology

Examining the phenologies of the most abundant solitary bee species revealed that the most productive times of capture were during the early months of our surveys, primarily between May and June (Fig. 7). However, there were multiple species present throughout each of the early, middle and late thirds of the sampling period. Never-the-less, the composition of the

communities experienced significant turnover across time, because nearly all species occupied the landscape for only a narrow window, peaking high during one month and then practically disappearing from the landscape. The reason for the narrow phenology of many solitary bees is likely explained by their life history. Unlike social bees, which have a constant supply of workers throughout the season, solitary bees are univoltine, producing one brood of offspring per year. For example, *Osmia* species use pre-existing cavities in wood as egg chambers. They will go to the back of the chamber where they will lay an egg, place a provision of pollen and nectar for the hatchling, and then seal it off. Mothers then create a mud partition and begin the process again (Palladini & Maron, 2014). One cavity could hold anywhere from three to eight eggs. These eggs will overwinter and emerge in the spring (Palladini & Maron, 2014). Similar life history can be used to describe other solitary bees such as *Peponapis pruinosa* (Mathewson, 1968) and *Agapostemon virescens* (Abrams & Eickwort, 1981). Without a constant flow of workers, solitary bees are limited to species of plants they can utilize for nest provisions. Over the course of evolution, solitary bees have likely partitioned the available floral resources, timing their emergence based on environmental cues that align with specific genera or species of flowers

Effectiveness of captures

A vast majority of the common species available for capture were caught. Estimators based on the species accumulation plot (Fig. 7) predicted that we missed twelve species at most. Because the plot was starting to level off, it shows that additional surveying would be slow to produce additional species. With that, it has been noted that very seldomly, do insect surveys reach a true asymptote when a species accumulation plot is used (Gotelli & Cowell, 2001). Nevertheless, it could be possible that additional surveys could turn up rare species that were not caught in 2019.

Bee bowls made up 99% of total solitary captures with netting being minimal (Fig. 3). Bee bowls have been reported to be biased in what they catch as some bee species are not drawn to them (Roulston, Smith, & Brewster, 2007 ; Wilson et al., 2008; Grundel et al., 2011, Gonzalez et al., 2017). Wilson et al (2008) reported that about a third of species caught showed strong bias in the method of capture while Grundel et al (2011) reported that half of the species captured could be caught with either net or cup with the other half favoring just one collection method.

During our survey, netting was optional for Citizen Scientists and only occurred at the fifteen sites managed by Appalachian State Students. Bumblebees (*Bombus*) and carpenter bees (*Xylocopa*) consisted most of the specimens caught in nets, likely due to their large size and audible wing noise, which allows surveyors to hone in on their position. Solitary bees are much smaller and more inconspicuous in a landscape making them hard to locate. They come in a variety of colors, with few having the recognizable black and yellow pattern that bees are associated with.

Bees can see blue, blue-green, ultraviolet, and yellow to orange wavelengths (Joshi et al., 2015). For our study we used common colors; blue, white, and yellow cups (Droege et al., 2010). Blue had the most captures of bees, followed by white, and then yellow. Between families blue and white were close in terms of catches except for *Apidae*. Blue cups caught 823 bees while white cups caught only 411. The main contributor to this was from *Peponapis pruinosa*; 471 of these bees were caught in blue cups, 35 in white, and 5 in yellow. Joshi et al (2015) conducted passive surveying of bees and found that *Peponapis pruinosa* was caught in blue vane traps at a much higher rate than in white and yellow vane traps. They analyzed the light reflectance of the blue, yellow, and white cups and found that white and yellow had much higher and broader reflectance patterns when compared to blue. The high reflectance from the two colors was thought to be too bright for bees to see clearly. With that, most bees don't use the brightness of an object to locate it, but rather color contrasting to find objects (Kevan, 1996). They use the contrast of green from forest floors in combination with target location to find objects of interest. The blue cup could be creating a color contrast that is familiar to bees while also being more visible compared to white and yellow colors.

Conclusion

Widespread declines observed in bee species worldwide (e.g. Aizen et al. 2021) have motivated increased efforts to document and monitor populations. The status of many species' populations remains unknown, and there are still many gaps in our understanding of their life histories and ecology, particularly at low to medium elevations (Kammerer et al., 2020). With that, even less is known about solitary bees – bees that don't create hives like bumblebees

(*Bombus*) and the non-native European Honey bee (*Apis mellifera*). Solitary bees make up a vast majority of bee species found throughout the world but receive a fraction of support and research. The findings from this Citizen Science inventory in the Southern Appalachians should provide an excellent baseline for future comparisons, a particularly important endeavor in this region that has been less touched by climatic changes than other areas, such as the Intermountain West in the US. There, warmer and drier climatic patterns across decades have resulted in loss of floral food resources and pollinator species range shifts (Geib et al., 2015, Miller-Struttman et al., 2015) and range contractions (Cameron et al., 2011). These alarming patterns could only be observed because of the existence of historical specimens and records. Without such data, population changes cannot be revealed (Meiners, Griswold, & Carril, 2019). We expect that our specimens and records will provide the historical context against which future changes in solitary bee population patterns may be revealed.

Tables and Figures

Table 1. Total solitary bees per family observed in 60 sites along the Blue Ridge Parkway in 2019.

Family	Count
Andrenidae	1111
Apidae	1693
Colletidae	33
Halictidae	1715
Megachilidae	710

Table 2. Total solitary bees per genus observed in 60 sites along the Blue Ridge Parkway in 2019.

Family	Genus	Count
Andrenidae	<i>Andrena</i>	1106
Andrenidae	<i>Calliopsis</i>	5
Apidae	<i>Anthophora</i>	15
Apidae	<i>Ceratina</i>	149
Apidae	<i>Eucera</i>	170
Apidae	<i>Habropoda</i>	11
Apidae	<i>Melissodes</i>	125
Apidae	<i>Melitoma</i>	11
Apidae	<i>Nomada</i>	625
Apidae	<i>Peponapis*</i>	513
Apidae	<i>Ptilothrix*</i>	29
Apidae	<i>Svastra*</i>	5
Apidae	<i>Triepeolus</i>	2
Apidae	<i>Xylocopa</i>	38
Colletidae	<i>Colletes</i>	21
Colletidae	<i>Hylaeus</i>	12
Halictidae	<i>Agapostemon</i>	481
Halictidae	<i>Augochlora</i>	38
Halictidae	<i>Augochlorella</i>	145
Halictidae	<i>Augochloropsis</i>	12
Halictidae	<i>Halictus</i>	227
Halictidae	<i>Lasioglossum</i>	766
Halictidae	<i>Sphecodes</i>	46
Megachilidae	<i>Anthidium*</i>	5
Megachilidae	<i>Coelioxys</i>	18
Megachilidae	<i>Hoplitis</i>	13
Megachilidae	<i>Megachile</i>	256
Megachilidae	<i>Osmia</i>	417
Megachilidae	<i>Paranthidium*</i>	1

* Indicates newly observed genera for the BRP

Table 3. Abundance of each solitary bee species observed in 60 sites along the Blue Ridge Parkway national roadway in 2019.

Family	Genus	species	Count
Andrenidae	<i>Andrena</i>	<i>barbara</i> *	2
	<i>Andrena</i>	<i>carlini</i>	54
	<i>Andrena</i>	<i>confederata</i> *	1
	<i>Andrena</i>	<i>cornelli</i> *	1
	<i>Andrena</i>	<i>crataegi</i>	60
	<i>Andrena</i>	<i>erigeniae</i>	14
	<i>Andrena</i>	<i>forbesii</i>	1
	<i>Andrena</i>	<i>illini</i> *	2
	<i>Andrena</i>	<i>imitatrix/morrisonella</i>	12
	<i>Andrena</i>	<i>macra</i> *	4
	<i>Andrena</i>	<i>miserabilis</i>	81
	<i>Andrena</i>	<i>nasonii</i>	47
	<i>Andrena</i>	<i>nivalis</i>	146
	<i>Andrena</i>	<i>nuda</i> *	1
	<i>Andrena</i>	<i>perplexa</i>	269
	<i>Andrena</i>	<i>pruni</i> *	9
	<i>Andrena</i>	<i>rugosa</i> *	2
	<i>Andrena</i>	<i>vicina</i>	74
	<i>Andrena</i>	<i>violae</i>	20
	<i>Andrena</i>	<i>wilkella</i> *	21
	<i>Andrena</i>	<i>sp.</i>	283
	<i>Calliopsis</i>	<i>andreniformis</i>	5
Apidae	<i>Anthophora</i>	<i>abrupta</i> *	6
	<i>Anthophora</i>	<i>terminalis</i>	5
	<i>Anthophora</i>	<i>sp.</i>	4
	<i>Ceratina</i>	<i>calcarata</i>	92
	<i>Ceratina</i>	<i>dupla</i>	8
	<i>Ceratina</i>	<i>mikmaqi</i> *	43
	<i>Ceratina</i>	<i>strenua</i>	3
	<i>Ceratina</i>	<i>sp.</i>	3
	<i>Eucera</i>	<i>atriventris</i> *	21
	<i>Eucera</i>	<i>dubitata</i> *	1
	<i>Eucera</i>	<i>hamata</i>	112
	<i>Eucera</i>	<i>rosae</i> *	31
	<i>Eucera</i>	<i>sp.</i>	5

Table 3. Abundance of each solitary bee species observed in 60 sites along the Blue Ridge Parkway national roadway in 2019 (cont.)

Family	Genus	species	Count
Apidae, continued			
	<i>Habropoda</i>	<i>laboriosa</i>	11
	<i>Melissodes</i>	<i>bimaculatus*</i>	41
	<i>Melissodes</i>	<i>communis*</i>	1
	<i>Melissodes</i>	<i>comptoides*</i>	1
	<i>Melissodes</i>	<i>denticulata</i>	1
	<i>Melissodes</i>	<i>denticulatus</i>	19
	<i>Melissodes</i>	<i>desponsus</i>	28
	<i>Melissodes</i>	<i>sp.</i>	34
	<i>Melitoma</i>	<i>taurea</i>	11
	<i>Nomada</i>	<i>articulata*</i>	14
	<i>Nomada</i>	<i>bidentate group</i>	76
	<i>Nomada</i>	<i>cressonii</i>	35
	<i>Nomada</i>	<i>denticulata</i>	1
	<i>Nomada</i>	<i>depressa*</i>	16
	<i>Nomada</i>	<i>illinoensis/sayi*</i>	11
	<i>Nomada</i>	<i>imbricata</i>	123
	<i>Nomada</i>	<i>lehighensis*</i>	6
	<i>Nomada</i>	<i>luteoloides</i>	40
	<i>Nomada</i>	<i>maculata</i>	219
	<i>Nomada</i>	<i>pygmaea*</i>	30
	<i>Nomada</i>	<i>sulphurata*</i>	5
	<i>Nomada</i>	<i>xanthura*</i>	1
	<i>Nomada</i>	<i>sp.</i>	48
	<i>Peponapis</i>	<i>pruinosa*</i>	513
	<i>Ptilothrix</i>	<i>bombiformis*</i>	29
	<i>Svastra</i>	<i>obliqua*</i>	3
		<i>sp.</i>	2
	<i>Triepeolus</i>	<i>sp.</i>	2
	<i>Xylocopa</i>	<i>virginica</i>	38
Colletidae			
	<i>Colletes</i>	<i>sp.</i>	21
	<i>Hylaeus</i>	<i>modestus</i>	3
	<i>Hylaeus</i>	<i>sparsus*</i>	1
	<i>Hylaeus</i>	<i>sp.</i>	8

Table 3. Abundance of each solitary bee species observed in 60 sites along the Blue Ridge Parkway national roadway in 2019 (cont.)

Family	Genus	species	Count
Halictidae			
	<i>Agapostemon</i>	<i>sericeus</i>	154
	<i>Agapostemon</i>	<i>texanus</i>	2
	<i>Agapostemon</i>	<i>virescens</i>	325
	<i>Augochlora</i>	<i>pura</i>	38
	<i>Augochlorella</i>	<i>aurata</i>	145
	<i>Augochlorella</i>	<i>persimulata*</i>	2
	<i>Augochloropsis</i>	<i>metallica</i>	12
	<i>Halictus</i>	<i>confusus</i>	66
	<i>Halictus</i>	<i>ligatus</i>	22
	<i>Halictus</i>	<i>ligatus/poeyi</i>	45
	<i>Halictus</i>	<i>parallelus</i>	25
	<i>Halictus</i>	<i>rubicundus</i>	67
	<i>Halictus</i>	<i>sp.</i>	2
	<i>Lasioglossum</i>	<i>abanci</i>	2
	<i>Lasioglossum</i>	<i>admirandum</i>	15
	<i>Lasioglossum</i>	<i>bruneri</i>	7
	<i>Lasioglossum</i>	<i>callidum</i>	3
	<i>Lasioglossum</i>	<i>cattellae*</i>	1
	<i>Lasioglossum</i>	<i>coeruleum</i>	13
	<i>Lasioglossum</i>	<i>coriaceum</i>	250
	<i>Lasioglossum</i>	<i>cressonii</i>	85
	<i>Lasioglossum</i>	<i>fuscipenne*</i>	11
	<i>Lasioglossum</i>	<i>heterognathum*</i>	1
	<i>Lasioglossum</i>	<i>hitchensi</i>	6
	<i>Lasioglossum</i>	<i>illinoense</i>	4
	<i>Lasioglossum</i>	<i>imitatum</i>	10
	<i>Lasioglossum</i>	<i>leucocomum*</i>	35
	<i>Lasioglossum</i>	<i>leucozonium</i>	23
	<i>Lasioglossum</i>	<i>lineatulum*</i>	5
	<i>Lasioglossum</i>	<i>lustrans*</i>	1
	<i>Lasioglossum</i>	<i>nigroviride*</i>	1
	<i>Lasioglossum</i>	<i>obscurum</i>	1
	<i>Lasioglossum</i>	<i>oceanicum*</i>	7
	<i>Lasioglossum</i>	<i>pectorale*</i>	6
	<i>Lasioglossum</i>	<i>pilosum</i>	23
	<i>Lasioglossum</i>	<i>quebecense</i>	84
	<i>Lasioglossum</i>	<i>subviridatum</i>	2
	<i>Lasioglossum</i>	<i>trigeminum</i>	14
	<i>Lasioglossum</i>	<i>truncatum</i>	2
	<i>Lasioglossum</i>	<i>versans</i>	24
	<i>Lasioglossum</i>	<i>versatum</i>	12
	<i>Lasioglossum</i>	<i>zonulum*</i>	1
	<i>Lasioglossum</i>	<i>sp.</i>	117

Table 3. Abundance of each solitary bee species observed in 60 sites along the Blue Ridge Parkway national roadway in 2019 (cont.)

Family	Genus	species	Count
Halictidae, continued			
	<i>Sphecodes</i>	<i>aroniae</i> *	8
	<i>Sphecodes</i>	<i>atlantis/cressonii</i> *	7
	<i>Sphecodes</i>	<i>heraclei</i> *	2
	<i>Sphecodes</i>	<i>levis</i>	3
	<i>Sphecodes</i>	<i>pimpinellae</i> *	2
	<i>Sphecodes</i>	<i>ranunculi</i> *	1
	<i>Sphecodes</i>	<i>townesi</i>	11
	<i>Sphecodes</i>	<i>sp.</i>	12
Megachilidae			
	<i>Anthidium</i>	<i>manicatum</i> *	5
	<i>Coelioxys</i>	<i>octodentata</i> *	1
	<i>Coelioxys</i>	<i>sayi</i>	7
	<i>Coelioxys</i>	<i>sp.</i>	10
	<i>Hoplitis</i>	<i>pilosifrons</i>	2
	<i>Hoplitis</i>	<i>producta</i>	2
	<i>Hoplitis</i>	<i>spoliata</i> *	9
	<i>Megachile</i>	<i>brevis</i>	2
	<i>Megachile</i>	<i>gemula</i>	46
	<i>Megachile</i>	<i>latimanus</i> *	6
	<i>Megachile</i>	<i>mendica</i>	86
	<i>Megachile</i>	<i>petulans</i> *	1
	<i>Megachile</i>	<i>pugnata</i> *	14
	<i>Megachile</i>	<i>relativa</i>	24
	<i>Megachile</i>	<i>rotundata</i> *	1
	<i>Megachile</i>	<i>sculpturalis</i> *	6
	<i>Megachile</i>	<i>xylocopoides</i> *	2
	<i>Megachile</i>	<i>sp.</i>	68
	<i>Osmia</i>	<i>atriventris</i> *	7
	<i>Osmia</i>	<i>bucephala</i>	40
	<i>Osmia</i>	<i>collinsiae</i>	8
	<i>Osmia</i>	<i>cornifrons</i>	46
	<i>Osmia</i>	<i>distincta</i>	2
	<i>Osmia</i>	<i>felti</i> *	3
	<i>Osmia</i>	<i>georgica</i>	127
	<i>Osmia</i>	<i>inspergens</i> *	1
	<i>Osmia</i>	<i>pumila</i>	6
	<i>Osmia</i>	<i>subfasciata</i> *	2
	<i>Osmia</i>	<i>taurus</i>	133
	<i>Osmia</i>	<i>texana</i> *	27
	<i>Osmia</i>	<i>sp.</i>	15
	<i>Paranthidium</i>	<i>jugatorium</i> *	1

* Indicates new species record for the BRP

Table 4. ANOVA comparing mean capture rates per site among three colors of passive traps.

<i>Sources</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P value</i>
Between Groups	10376.58	2.00	5188.29	6.35	0.002
Within Groups	142121.80	174.00	816.79		

<i>group 1</i>	<i>group 2</i>	<i>mean</i>	<i>std err</i>	<i>q-stat</i>	<i>lower</i>	<i>upper</i>	<i>p-value</i>
Blue	White	4.86	3.72	1.31	-7.57	17.30	0.626
Blue	Yellow	18.12	3.72	4.87	5.68	30.56	0.002
White	Yellow	13.25	3.72	3.56	0.82	25.69	0.034



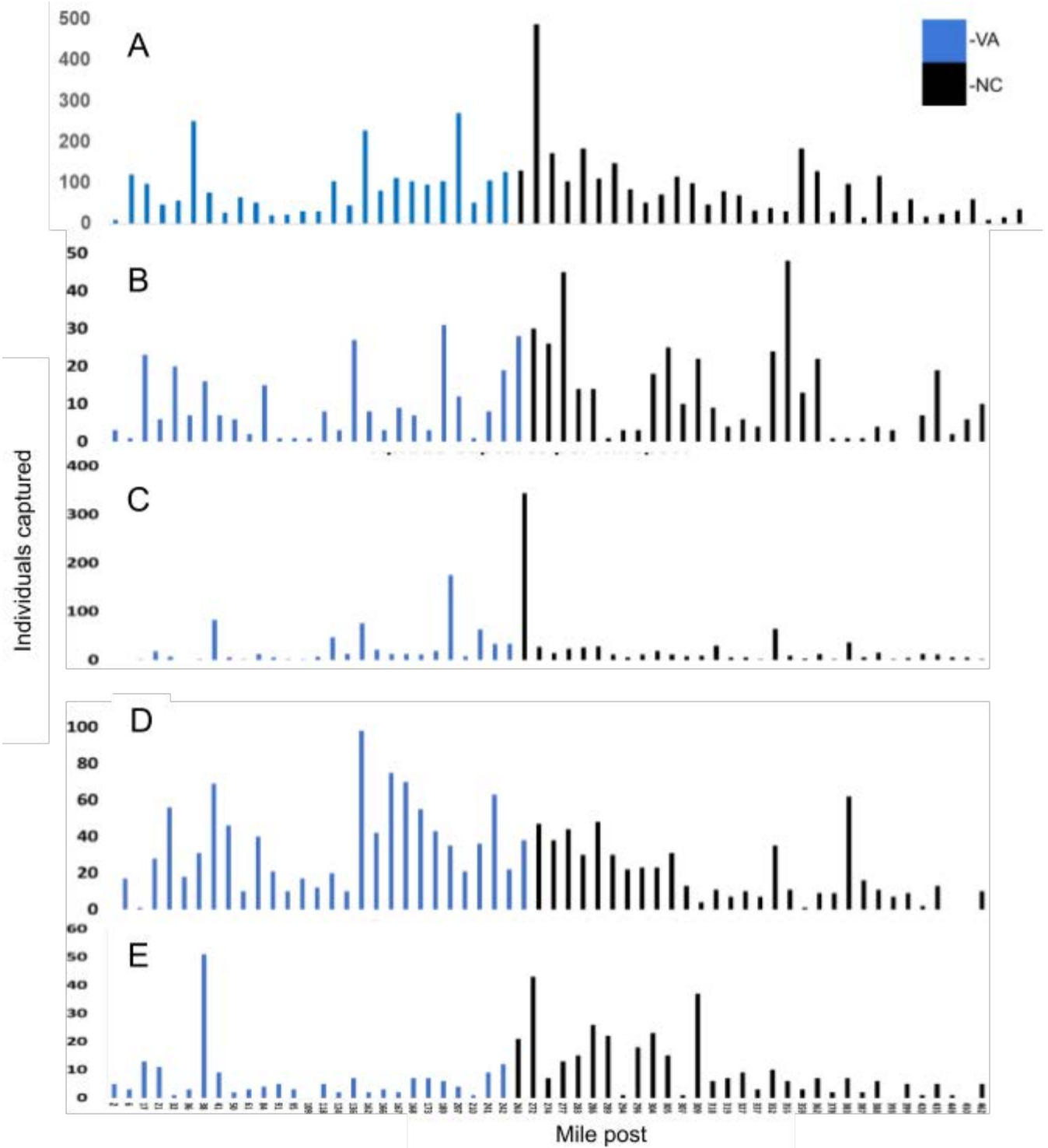


Figure 2. Captures of solitary bees per milepost from passive traps along the Blue Ridge Parkway of Virginia and North Carolina in 2019, including A) all families pooled, B) Andrenidae, C) Apidae, D) Halictidae, and E) Megachilidae.

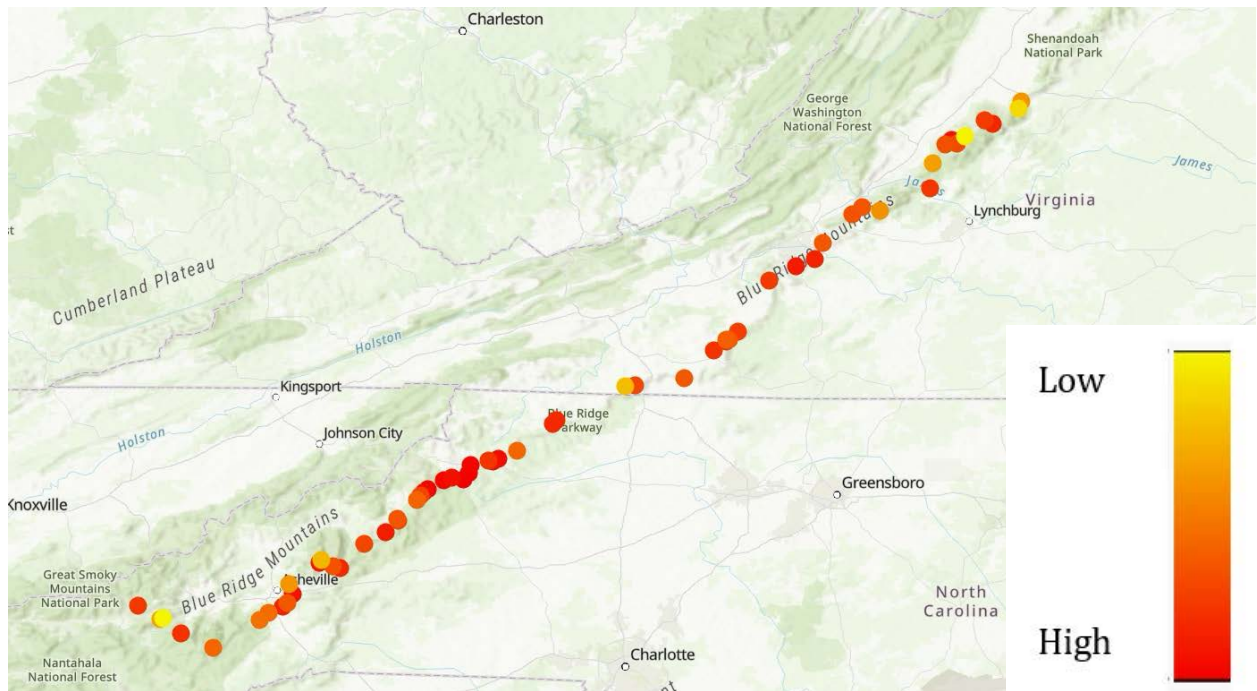


Figure 3. Heatmap displaying diversity of solitary bees captured along the Blue Ridge Parkway in 2019, based on Shannon-Weiner diversity index.

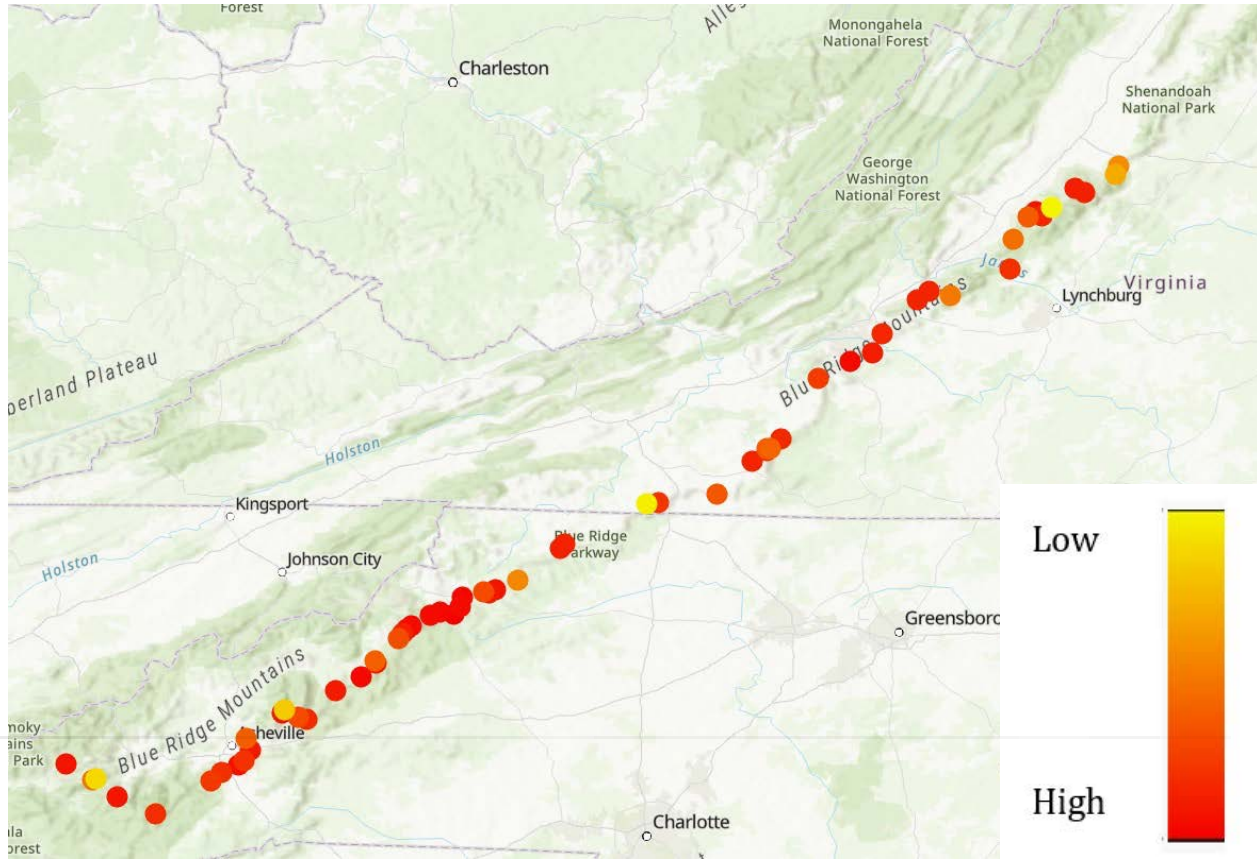


Figure 4. Heatmap displaying diversity of solitary bees captured along the Blue Ridge Parkway in 2019, based on Simpson diversity index.

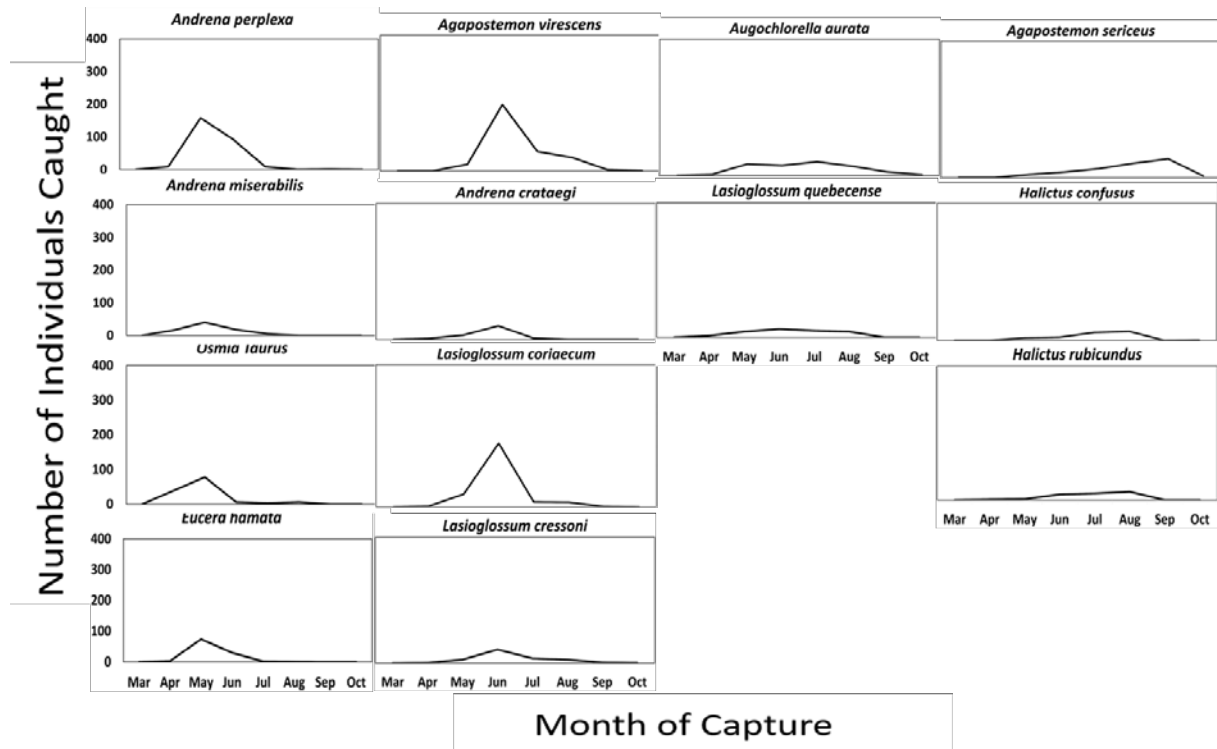


Figure 5. Seasonal phenology of abundant solitary bee species captured along the Blue Ridge Parkway (April-October 2019). Plots were created only for species represented by >100 captured specimens. A) “Early” species peaking in May, B) Species that peak in June, C) species present at low levels without a true peak, and D) “late” species peaking in August or after.

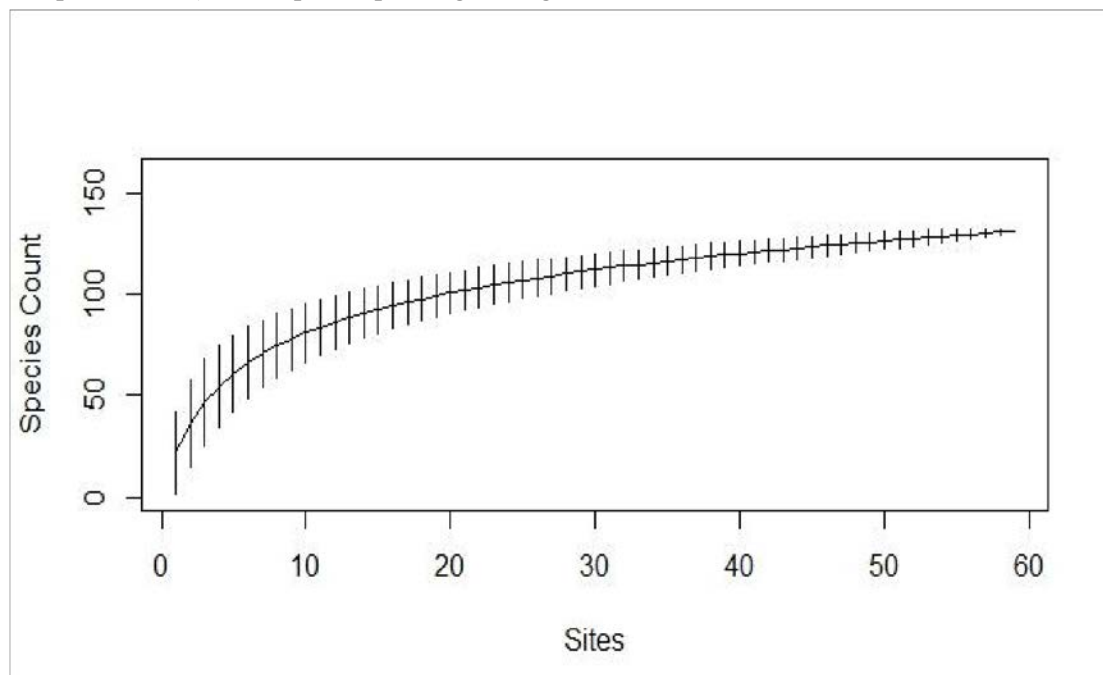


Figure 6. Species accumulation curve, showing the solitary species detected with each added site of the Blue Ridge Parkway inventory, Spring -October 2019.

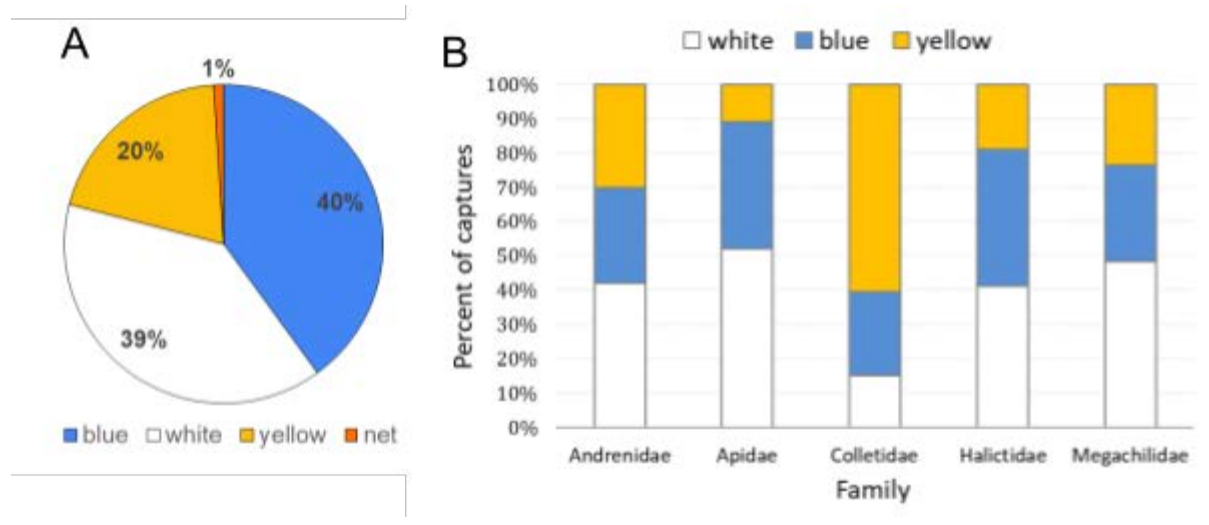


Figure 7. Efficacy of capture methods for solitary bee families. (A) Proportion of total captures among sweep netting and three colors of passive traps used for specimen collection along the Blue Ridge Parkway in April-October 2019. B) Proportion of specimens captured per solitary bee family among the different colors of passive traps.

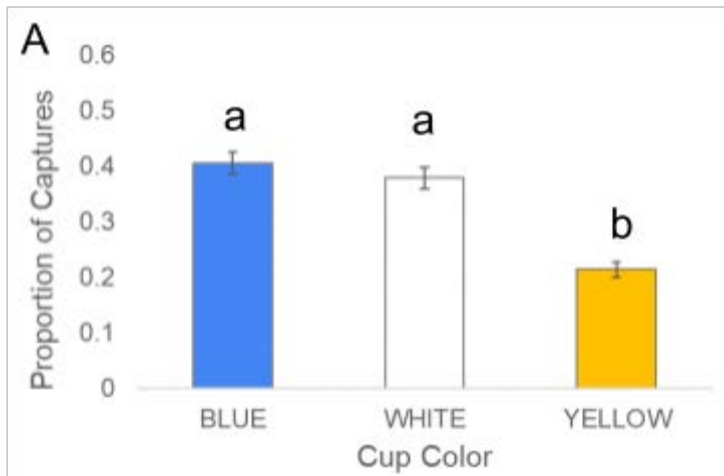


Figure 8. Proposition of total specimen captures of bees among different colors of passive traps. Post hoc pairwise comparisons were conducted using the Tukey HSD test. Error bars represent standard error. Letters above the bars indicate significant differences at $p < 0.05$.

References

- Abrams, Judith, and George C. Eickwort. 1981. "Nest Switching and Guarding by the Communal Sweat Bee *Agapostemon virescens* (Hymenoptera, Halictidae)." *Insectes Sociaux* 28 (2): 105–16. doi:10.1007/bf02223699.
- Allen, Jessica L., and James C. Lendemer. 2016. "Climate Change Impacts on Endemic, High-Elevation Lichens in a Biodiversity Hotspot." *Biodiversity and Conservation* 25 (3): 555–68. doi:10.1007/s10531-016-1071-4.
- Antoine, Cécile M., and Jessica R.K. Forrest. 2020. "Nesting Habitat of Ground-nesting Bees: A Review." *Ecological Entomology* 46 (2): 143–59. doi:10.1111/een.12986.
- Bohart, G. E. 1972. "Management of Wild Bees for the Pollination of Crops." *Annual Review of Entomology* 17 (1): 287–312. doi:10.1146/annurev.en.17.010172.001443.
- Bonney, Rick, Tina B. Phillips, Heidi L. Ballard, and Jody W. Enck. 2015. "Can Citizen Science Enhance Public Understanding of Science?" *Public Understanding of Science* 25 (1): 2–16. doi:10.1177/0963662515607406.
- Bossert, Silas, Elizabeth A. Murray, Eduardo A.B. Almeida, Seán G. Brady, Bonnie B. Blaimer, and Bryan N. Danforth. 2019. "Combining Transcriptomes and Ultraconserved Elements to Illuminate the Phylogeny of Apidae." *Molecular Phylogenetics and Evolution* 130: 121–31. doi:10.1016/j.ympev.2018.10.012.
- Boyle, Natalie K., Derek R. Artz, Ola Lundin, Kimiora Ward, Devon Picklum, Gordon I. Wardell, Neal M. Williams, and Theresa L. Pitts-Singer. 2020. "Wildflower Plantings Promote Blue Orchard Bee, *Osmia lignaria* (Hymenoptera: Megachilidae), Reproduction in California Almond Orchards." *Ecology and Evolution* 10 (7): 3189–99. doi:10.1002/ece3.5952.
- Brown, Mark J.F., and Robert J. Paxton. 2009. "The Conservation of Bees: A Global Perspective." *Apidologie* 40 (3): 410–16. doi:10.1051/apido/2009019.
- Buchmann, Stephen L., and Gary Paul Nabhan. 1997. *The Forgotten Pollinators*. Washington, D.C.: Island Press/Shearwater Books.

- Cameron, Sydney A. 1989. “Temporal Patterns of Division of Labor among Workers in the Primitively Eusocial Bumble Bee, *Bombus Griseocollis* (Hymenoptera: Apidae).” *Ethology* 80 (1–4): 137–51. doi:10.1111/j.1439-0310.1989.tb00735.x.
- Cameron, Sydney A., Jeffrey D. Lozier, James P. Strange, Jonathan B. Koch, Nils Cordes, Leellen F. Solter, and Terry L. Griswold. 2011. “Patterns of Widespread Decline in North American Bumble Bees.” *Proceedings of the National Academy of Sciences* 108 (2): 662–67. doi:10.1073/pnas.1014743108.
- Cardinale, Bradley J., J. Emmett Duffy, Andrew Gonzalez, David U. Hooper, Charles Perrings, Patrick Venail, Anita Narwani, et al. 2012. “Erratum: Corrigendum: Biodiversity Loss and Its Impact on Humanity.” *Nature* 489 (7415): 326–326. doi:10.1038/nature11373.
- Cox-Foster, Diana L., Sean Conlan, Edward C. Holmes, Gustavo Palacios, Jay D. Evans, Nancy A. Moran, Phenix-Lan Quan, et al. 2007. “A Metagenomic Survey of Microbes in Honey Bee Colony Collapse Disorder.” *Science* 318 (5848): 283–87. doi:10.1126/science.1146498.
- Danforth, Bryan N., Robert L. Minckley, John L. Neff, and Frances Fawcett. 2019. *The Solitary Bees: Biology, Evolution, Conservation*. Princeton, NJ: Princeton University Press.
- Eeraerts, Maxime, Ruben Vanderhaegen, Guy Smagghe, and Ivan Meeus. 2019. “Pollination Efficiency and Foraging Behaviour of Honey Bees and Non-apis Bees to Sweet Cherry.” *Agricultural and Forest Entomology* 22 (1): 75–82. doi:10.1111/afe.12363.
- Gonzalez, Victor H., Kristen E. Park, Ibrahim Çakmak, John M. Hranitz, and John F. Barthell. 2016. “Pan Traps and Bee Body Size in Unmanaged Urban Habitats.” *Journal of Hymenoptera Research* 51: 241–47. doi:10.3897/jhr.51.9353.
- Gotelli, Nicholas J., and Robert K. Colwell. 2001. “Quantifying Biodiversity: Procedures and Pitfalls in the Measurement and Comparison of Species Richness.” *Ecology Letters* 4 (4): 379–91. doi:10.1046/j.1461-0248.2001.00230.x.
- Goulson, D., M.E. Hanley, B. Darvill, J.S. Ellis, and M.E. Knight. 2005. “Causes of Rarity in Bumblebees.” *Biological Conservation* 122 (1): 1–8. doi:10.1016/j.biocon.2004.06.017.
- Goulson, Dave, Elizabeth Nicholls, Cristina Botías, and Ellen L. Rotheray. 2015. “Bee Declines Driven by Combined Stress from Parasites, Pesticides, and Lack of Flowers.” *Science* 347 (6229). doi:10.1126/science.1255957.
- Gray, Alison, Noureddine Adjlane, Alireza Arab, Alexis Ballis, Valters Brusbardis, Jean-Daniel

- Charrière, Robert Chlebo, et al. 2020. “Honey Bee Colony Winter Loss Rates for 35 Countries Participating in the Coloss Survey for Winter 2018–2019, and the Effects of a New Queen on the Risk of Colony Winter Loss.” *Journal of Apicultural Research* 59 (5): 744–51. doi:10.1080/00218839.2020.1797272.
- Grundel, Ralph, Krystalynn J. Frohnapple, Robert P. Jean, and Noel B. Pavlovic. 2011. “Effectiveness of Bowl Trapping and Netting for Inventory of a Bee Community.” *Environmental Entomology* 40 (2): 374–80. doi:10.1603/en09278.
- Hristov, Peter, Rositsa Shumkova, Nadezhda Palova, and Boyko Neov. 2020. “Factors Associated with Honey Bee Colony Losses: A Mini-Review.” *Veterinary Sciences* 7 (4): 166. doi:10.3390/vetsci7040166.
- Javorek, S. K., K. E. Mackenzie, and S. P. Vander Kloet. 2002. “Comparative Pollination Effectiveness among Bees (Hymenoptera: Apoidea) on Lowbush Blueberry (Ericaceae: *Vaccinium Angustifolium*).” *Annals of the Entomological Society of America* 95 (3): 345–51. doi:10.1603/0013-8746(2002)095[0345:cpeabh]2.0.co;2.
- Joshi, Neelendra K., Timothy Leslie, Edwin G. Rajotte, Melanie A. Kammerer, Mark Otieno, and David J. Biddinger. 2015. “Comparative Trapping Efficiency to Characterize Bee Abundance, Diversity, and Community Composition in Apple Orchards.” *Annals of the Entomological Society of America* 108 (5): 785–99. doi:10.1093/aesa/sav057.
- Kevan, Peter, Martin Giurfa, and Lars Chittka. 1996. “Why Are There so Many and so Few White Flowers?” *Trends in Plant Science* 1 (8): 252. doi:10.1016/1360-1385(96)20008-1.
- Klein, Alexandra-Maria, Bernard E Vaissière, James H Cane, Ingolf Steffan-Dewenter, Saul A Cunningham, Claire Kremen, and Teja Tscharntke. 2006. “Importance of Pollinators in Changing Landscapes for World Crops.” *Proceedings of the Royal Society B: Biological Sciences* 274 (1608): 303–13. doi:10.1098/rspb.2006.3721.
- Kremen, C., and A. M. Merenlender. 2018. “Landscapes That Work for Biodiversity and People.” *Science* 362 (6412). doi:10.1126/science.aau6020.
- Kremen, Claire, and Taylor Ricketts. 2000. “Global Perspectives on Pollination Disruptions.” *Conservation Biology* 14 (5): 1226–28. doi:10.1046/j.1523-1739.2000.00013.x.
- Larkin, Leah L., John L. Neff, and Beryl B. Simpson. 2006. “Phylogeny of the *Callandrena* Subgenus of *Andrena* (Hymenoptera: Andrenidae) Based on Mitochondrial and Nuclear

- DNA Data: Polyphyly and Convergent Evolution.” *Molecular Phylogenetics and Evolution* 38 (2): 330–43. doi:10.1016/j.ympev.2005.10.003.
- LeCroy, Kathryn A., Grace Savoy-Burke, David E. Carr, Deborah A. Delaney, and T'ai H. Roulston. 2020. “Decline of Six Native Mason Bee Species Following the Arrival of an Exotic Congener.” *Scientific Reports* 10 (1). doi:10.1038/s41598-020-75566-9.
- Lehmann, David M., and Allison A. Camp. 2021. “A Systematic Scoping Review of the Methodological Approaches and Effects of Pesticide Exposure on Solitary Bees.” *PLOS ONE* 16 (5). doi:10.1371/journal.pone.0251197.
- Lim, Kayun, Seunghyun Lee, Michael Orr, and Seunghwan Lee. 2022. “Harrison’s Rule Corroborated for the Body Size of Cleptoparasitic Cuckoo Bees (Hymenoptera: Apidae: Nomadinae) and Their Hosts.” *Scientific Reports* 12 (1). doi:10.1038/s41598-022-14938-9.
- Mathewson, John. 1968. “Nest Construction and Life History of the Eastern Cucurbit Bee, *Peponapis Pruinosa* (Hymenoptera: Apoidea).” *Journal of the Kansas Entomological Society* 41 (2): 255–61. doi:http://www.jstor.org/stable/25083703.
- Meiners, Joan M., Terry L. Griswold, and Olivia Messinger Carril. 2019. “Decades of Native Bee Biodiversity Surveys at Pinnacles National Park Highlight the Importance of Monitoring Natural Areas over Time.” *PLOS ONE* 14 (1). doi:10.1371/journal.pone.0207566.
- Michener, Charles Duncan. 2007. *The Bees of the World*. Baltimore, MD: The Johns Hopkins University Press.
- Milanovich, Joseph R., William E. Peterman, Nathan P. Nibbelink, and John C. Maerz. 2010. “Projected Loss of a Salamander Diversity Hotspot as a Consequence of Projected Global Climate Change.” *PLoS ONE* 5 (8). doi:10.1371/journal.pone.0012189.
- Palladini, Jennifer D., and John L. Maron. 2014. “Reproduction and Survival of a Solitary Bee along Native and Exotic Floral Resource Gradients.” *Oecologia* 176 (3): 789–98. doi:10.1007/s00442-014-3028-1.
- Peters, Marcell K., Andreas Hemp, Tim Appelhans, Christina Behler, Alice Classen, Florian

- Detsch, Andreas Ensslin, et al. 2016. “Predictors of Elevational Biodiversity Gradients Change from Single Taxa to the Multi-Taxa Community Level.” *Nature Communications* 7 (1). doi:10.1038/ncomms13736.
- Pitts-Singer, Theresa L., and James H. Cane. 2011. “The Alfalfa Leafcutting Bee, *Megachile rotundata*: The World’s Most Intensively Managed Solitary Bee.” *Annual Review of Entomology* 56 (1): 221–37. doi:10.1146/annurev-ento-120709-144836.
- Porto, Rafaella Guimarães, Rita Fernandes de Almeida, Oswaldo Cruz-Neto, Marcelo Tabarelli, Blandina Felipe Viana, Carlos A. Peres, and Ariadna Valentina Lopes. 2020. “Pollination Ecosystem Services: A Comprehensive Review of Economic Values, Research Funding and Policy Actions.” *Food Security* 12 (6): 1425–42. doi:10.1007/s12571-020-01043-w.
- Potts, Simon G, Stuart P Roberts, Robin Dean, Gay Marris, Mike A Brown, Richard Jones, Peter Neumann, and Josef Settele. 2010. “Declines of Managed Honey Bees and Beekeepers in Europe.” *Journal of Apicultural Research* 49 (1): 15–22. doi:10.3896/ibra.1.49.1.02.
- Potts, Simon G., Jacobus C. Biesmeijer, Claire Kremen, Peter Neumann, Oliver Schweiger, and William E. Kunin. 2010. “Global Pollinator Declines: Trends, Impacts and Drivers.” *Trends in Ecology & Evolution* 25 (6): 345–53. doi:10.1016/j.tree.2010.01.007.
- Raven, Peter H., and David L. Wagner. 2021. “Agricultural Intensification and Climate Change Are Rapidly Decreasing Insect Biodiversity.” *Proceedings of the National Academy of Sciences* 118 (2). doi:10.1073/pnas.2002548117.
- Ricketts, Taylor H., James Regetz, Ingolf Steffan-Dewenter, Saul A. Cunningham, Claire Kremen, Anne Bogdanski, Barbara Gemmill-Herren, et al. 2008. “Landscape Effects on Crop Pollination Services: Are There General Patterns?” *Ecology Letters* 11 (5): 499–515. doi:10.1111/j.1461-0248.2008.01157.x.
- Robinson, Samuel V.J., Ralph V. Cartar, Stephen F. Pernal, Riley Waytes, and Shelley E. Hoover. 2023. “Bee Visitation, Pollination Service, and Crop Yield in Commodity and Hybrid Seed Canola.” *Agriculture, Ecosystems & Environment* 347: 108396. doi:10.1016/j.agee.2023.108396.
- Ross, Kenneth G., and Laurent Keller. 1995. “Ecology and Evolution of Social Organization: Insights from Fire Ants and Other Highly Eusocial Insects.” *Annual Review of Ecology and Systematics* 26 (1): 631–56. doi:10.1146/annurev.es.26.110195.003215.

- Roulston, T'ai H., Stephen A. Smith, and Amanda L. Brewster. 2007. "A Comparison of Pan Trap and Intensive Net Sampling Techniques for Documenting a Bee (Hymenoptera: Apiformes) Fauna." *Journal of the Kansas Entomological Society* 80 (2): 179–81. doi:10.2317/0022-8567(2007)80[179:acopta]2.0.co;2.
- Scheper, Jeroen, Menno Reemer, Ruud van Kats, Wim A. Ozinga, Giel T. van der Linden, Joop H. Schaminée, Henk Siepel, and David Kleijn. 2014. "Museum Specimens Reveal Loss of Pollen Host Plants as Key Factor Driving Wild Bee Decline in the Netherlands." *Proceedings of the National Academy of Sciences* 111 (49): 17552–57. doi:10.1073/pnas.1412973111.
- Senapathi, Deepa, Mark A. Goddard, William E. Kunin, and Katherine C. Baldock. 2016. "Landscape Impacts on Pollinator Communities in Temperate Systems: Evidence and Knowledge Gaps." *Functional Ecology* 31 (1): 26–37. doi:10.1111/1365-2435.12809.
- Shannon, C E. 1948. "A Mathematical Theory of Communication." *The Bell System Technical Journal*, 3, 27.
- Simpson, E H. 1949. "Measurement of Diversity." *Nature* 163: 688. doi:https://doi.org/10.1038/163688a0.
- Stone, G. N. 1994. "Patterns of Evolution of Warm-up Rates and Body Temperatures in Flight in Solitary Bees of the Genus *Anthophora*." *Functional Ecology* 8 (3): 324. doi:10.2307/2389825.
- Tengö, Jan, and Gunnar Bergström. 1977. "Cleptoparasitism and Odor Mimetism in Bees: Do *Nomada* Males Imitate the Odor of *Andrena* Females?" *Science* 196 (4294): 1117–19. doi:10.1126/science.196.4294.1117.
- Tilman, David, Peter B. Reich, and Forest Isbell. 2012. "Biodiversity Impacts Ecosystem Productivity as Much as Resources, Disturbance, or Herbivory." *Proceedings of the National Academy of Sciences* 109 (26): 10394–97. doi:10.1073/pnas.1208240109.
- Torchio, P.F. 1991. "Bees as Crop Pollinators and the Role of Solitary Species in Changing Environments." *Acta Horticulturae*, no. 288: 49–61. doi:10.17660/actahortic.1991.288.3.
- Van der Sluijs, Jeroen P. 2020. "Insect Decline, an Emerging Global Environmental Risk." *Current Opinion in Environmental Sustainability* 46: 39–42. doi:10.1016/j.cosust.2020.08.012.

- Van Engelsdorp, Dennis, Jay D. Evans, Claude Saegerman, Chris Mullin, Eric Haubruge, Bach Kim Nguyen, Maryann Frazier, et al. 2009. “Colony Collapse Disorder: A Descriptive Study.” *PLoS ONE* 4 (8). doi:10.1371/journal.pone.0006481.
- Vicens, Narcís, and Jordi Bosch. 2000. “Weather-Dependent Pollinator Activity in an Apple Orchard, with Special Reference to *Osmia Cornuta* and *Apis Mellifera* (Hymenoptera: Megachilidae and Apidae).” *Environmental Entomology* 29 (3): 413–20. doi:10.1603/0046-225x-29.3.413.
- Wilson, Joseph S., Terry Griswold, and Olivia J. Messinger. 2008. “Sampling Bee Communities (Hymenoptera: Apiformes) in a Desert Landscape: Are Pan Traps Sufficient?” *Journal of the Kansas Entomological Society* 81 (3): 288–300. doi:10.2317/jkes-802.06.1.
- Winfree, Rachael, Neal M. Williams, Jonathan Dushoff, and Claire Kremen. 2007. “Native Bees Provide Insurance against Ongoing Honey Bee Losses.” *Ecology Letters* 10 (11): 1105–13. doi:10.1111/j.1461-0248.2007.01110.x.
- Winfree, Rachael. 2010. “The Conservation and Restoration of Wild Bees.” *Annals of the New York Academy of Sciences* 1195 (1): 169–97. doi:10.1111/j.1749-6632.2010.05449.x.
- Wood, T. J., D. Michez, R. J. Paxton, M. Drossart, P. Neumann, M. Gérard, M. Vanderplanck, et al. 2020. “Managed Honey Bees as a Radar for Wild Bee Decline?” *Apidologie* 51 (6): 1100–1116. doi:10.1007/s13592-020-00788-9.
- Woodbridge, Margaret, and Martin Dovciak. 2022. “Logging Legacies in a Plant Biodiversity Hotspot: Altered Distribution and Abundance Patterns of the Shrub Layer in the Southern Appalachians.” *Forest Ecology and Management* 516: 120245. doi:10.1016/j.foreco.2022.120245.
- Zattara, Eduardo E., and Marcelo A. Aizen. 2021. “Worldwide Occurrence Records Suggest a Global Decline in Bee Species Richness.” *One Earth* 4 (1): 114–23. doi:10.1016/j.oneear.2020.12.005.

Chapter 2: Modeling Detection and Occupancy of Solitary Bees in the Southern Appalachians

Climate change is altering species distributions worldwide, leading to a “universal redistribution of life on Earth” (Pecl et al., 2017). In North America and the US, flora and fauna alike are expected to shift northward in latitude and upward in elevation (Lawton et al., 2013), and empirical evidence for species movements is accumulating (Hill and Field, 2021). Anticipating how individual species’ distributions may shift in response to climate change requires, at minimum, an accurate assessment of their biogeographies and an understanding of the environmental factors driving their occupancies of patches across a landscape.

Mapping current species distributions may seem like a simple initial step; yet, this information is unavailable for many taxa, particularly invertebrates (Cardoso et al, 2011). Despite making up over 90% of all animals on earth, most invertebrate species remain undescribed, and few have accurately quantified ranges (Cardoso et al, 2011). Considering even a seemingly ubiquitous group of invertebrates, such as bees (clade Anthophila), illustrates the challenges involved and the human power needed for such an endeavor; there may be hundreds of species present in any one location, with minute morphological characteristics that separate them. This requires intensive sampling, specimen curation, and careful microscopy skills to resolve specimen identities. Habitat data must also be collected concurrently with sampling if we are interested in explaining and predicting the species observed.

An additional concern when assessing the spatial distribution of species is that even when humans invest significant effort in locating individuals, they may still miss them when they are actually there. There are many characteristics and behaviors that increase the likelihood of species escaping detection, such as the ability to fly, having diminutive size, or being inconspicuous in a landscape. Compensatory methods have been developed to mitigate this issue of ‘false absences’, such as repeated surveys at each site. These patterns of detections and absences allow researchers to estimate a species’ detection probability, which can help with resolving false and true absences (Mackenzie et al., 2002). This distinction is one of importance for land managers and government agencies as they set aside land for protected species. Too

many false absences can underestimate a species true range of occupancy across a landscape and skew habitat suitability models, resulting in setting aside inadequate space or suboptimal types of spaces (Hirzel and La Lay, 2008).

Occupancy models (Mackenzie et al., 2002) were developed to estimate a species' presence in a way that compensates for imperfect detection. This makes an occupancy model an effective tool to study hard-to-find organisms or species with large ranges that preclude adequate intensive searches due to time or money constraints (MacIvor and Packer, 2016). Occupancy models take into account the detection (p) probabilities and predicts the probability of occupancy (Ψ) across a landscape (Cole et al., 2019).

Here I aim to develop Occupancy models for a group of pollinating insects, collectively known as “solitary bees,” that is, members of order Hymenoptera, superfamily Apoidea, clade Anthophila that lack a group living life history and have no hierarchical caste structure. The base knowledge of solitary bee ecology and habitat requirements is much lower, especially at low and medium elevations, when compared to their social relatives (Kammerer et al., 2020).

Solitary bees present particular challenges for modeling species ranges because they are very difficult to find and identify in the field compared to bumble bees (*Bombus* spp.) and honeybees (*Apis mellifera*). Bumble bees are relatively large, produce audible cues (buzzing), and are heavy enough to physically make inflorescences droop during pollination, all of which allow surveyors to home in on their position. Bumble bees are also able to be resolved to the species level in the field based on tergite patterns and one or two additional characteristics. Other common species like the European Honey Bee are large enough and have a distinctive pattern on their abdomen that make field identification possible. In contrast solitary bees are often small and dark in color and produce quieter wing sounds, making them more difficult to locate and distinguish from other flower visiting taxa such as flies or wasps. High powered microscopes are needed to detect minute features located all around the body of a solitary bee to correctly resolve its species identity. Solitary bees also comprise five families and hundreds of species in any given habitat, making pinpointing one species time consuming and difficult.

I aimed to contribute toward the knowledge deficit about solitary bee life history by developing occupancy models for eleven species based on presence/absence data generated from a Citizen Science inventory along the Blue Ridge Parkway, a federal roadway running through

the Southern Appalachian Mountains. Models such as these would help elucidate the foraging habitat needs of solitary bee species and identify environmental variables that could be used to predict their presence in other unassessed areas. My specific objective was to measure detection and occupancy across different time scales for each species. I explored whether these environmental variables would predict species occupancy over the entire time scale of the survey or whether dividing the season into smaller blocks would result in detecting a shift in variables that best predict where to find species and where they choose to occupy. I hypothesized that biologically relevant variables such as minimum and maximum temperature, precipitation, bee preferred floral taxa, and elevation were impacting the space use of bee species and their distribution across the Blue Ridge Parkway and would be implicated as important predictors in the occupancy models.

Methods

Study Site and System

This study utilized presence/absence data for solitary bee species in the Southern Appalachians of North Carolina and Virginia. Though social taxa such as honeybees (*Apis* species) and bumble bees (*Bombus* species) dominate both the public consciousness about bees and the scientific literature (Matias et al., 2017), solitary bees far outnumber their social counterparts, making up over 14,000 species globally (3500 in the US) in five families: Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae (Lehman and Camp, 2021). Solitary bees are distinguished from their social counterparts by their lack of a familial nest group. Species in some genera will form communal nesting sites, aggregating egg laying sites or using a shared opening to a nest. However, each solitary female creates an independent egg chamber (Antoine & Forrest, 2021) and lacks assistance for collecting food, raising offspring and/or carrying out other maintenance tasks.

Life history strategies among solitary bees are extremely diverse. Most solitary bees have a univoltine life-cycle but there are species that can produce multiple generations per season. *Augochlora pura* (Halictidae), a common North American east coast bee, will hatch variable numbers of generations every year (Danforth, Minckley, & Neff, 2019). Species in the genera

Agapostemon (Danforth, Minckley, & Neff, 2019) and *Lasioglossum* (Danforth, Minckley, & Neff, 2019) can also exhibit this multi-generation annual life cycle.

Solitary bees tend to have narrower preferences for food sources than social species. The family Andrenidae, for example, has many oligolectic species that only forage on flowers from Asteraceae, Apiaceae, Brassicaceae, Ericaceae, Fabaceae, and Rosaceae (Danforth, Minckley, & Neff, 2019). The largest percentage of brood parasites are found within Apidae, spread throughout three subfamilies (Apinae, Nomadinae, and Xylocopinae) and comprising twenty percent of all species in this group (Danforth, 2019; Lim et al., 2022). There are many more typical ground nesting bees like the long-horned bees (subfamily Eucerini), digger bees (Anthophora), and small carpenter bees (Ceratina).

The family Megachilidae has extreme niche variability within its member species and can be found on all continents other than Antarctica (Danforth, Minckley, & Neff, 2019). They can occupy environments ranging from tropical forests to deserts and use a diverse array of nesting substrate. They will nest in stones, tree branches, in pre-existing cavities in the ground, stems, galls, snail shells, and arboreal termite mounds. Megachilids will use about anything to then fill their nests. Nothing is off limit as they will use mud, flower petals, leaves, plant resin, soil, gravel, plant trichomes, and even plastic shopping bags in urban environments (MacIvor and Moore, 2013; Danforth, Minckley, & Neff, 2019).

The Colletidae are most densely concentrated in Australia and South America. Phylogenetic studies show that Colletid bee populations would commonly disperse between South America and Australia via Antarctica before it froze over (Almeida et al. 2011). This family is almost purely solitary, with five species being kleptoparasites. All species secrete a waterproof serum called cellophane around their nests.

Inventory methods

Presence and absence records for solitary bees in the Southern Appalachians were generated from repeated sampling of passive propylene glycol traps (“bee bowls”) at 60 sites along the Blue Ridge Parkway national roadway from April until October of 2019. The sites spanned 456 miles, starting in Cherokee, North Carolina and ending at Waynesboro, Virginia.

Sample collections from fifteen sites central to Boone, NC were managed by Appalachian State University students, while collections from the remaining 45 sites were managed by citizen scientist volunteers. Of the 60 total sites, 15 sites were established or newly established wildflower display areas (WDA) meaning that they were mowed only once in the fall. This allowed the natural flora found at the WDA sites to continue to grow throughout the season and produce inflorescences. The remaining 45 sites were randomly selected and were mowed once approximately every two weeks by mowers contracted by the National Park Service (NPS). The survey sites varied in abiotic and biotic factors such as elevation, latitude, habitat type, quantity of vegetation and abundance of bee-preferred flora species.

Inventory methods were based on protocols developed by Droege et al (2010). At each site there were three triplets of bowls five meters apart in a transect spanning a total of 15 meters. A triplet consisted of one white unpainted Solo® cup, and one each of yellow and blue painted cups coated in silica flat paint mixed with fluorescent pigment (Guerra Paint and Pigment Corp, BLV00012, FLB00003 and FLY00003). Inside all cups was a 50% solution of propylene glycol and water with a small amount of Dawn® dish detergent. The dish soap diminished the water tension which prohibited insects from walking on the surface. The propylene glycol kept insects trapped at the bottom of the cup due to it having a higher density than water and allowed storage of insects in the bowl traps through storms. Vegetation surrounding the cups was trimmed to ground level to ensure visibility and access by the insects. Sites were visited biweekly for sample retrieval, site maintenance, and to conduct active net surveys when weather permitted.

Euthanized bees from each collection event were stored with an identifying paper label in unique Whirlpaks® filled with 80% denatured ethanol and were then stored at room temperature at Appalachian State University until further processing. Bees were washed, dried, pinned, and labeled prior to delivery to the USGS Native Bee Inventory and Monitoring Lab (BIML) for identification to species.

Occupancy Models

To contribute to knowledge deficits of solitary bee ecology in the Southern Appalachians, I used presence/absence data from the 2019 Parkway inventory to explore foraging habitat requirements of solitary bees (their “foraging niche”). Occupancy models were chosen over other

modeling frameworks such as species distribution modeling (SDM) or niche modeling because occupancy models account for imperfect detection. Many species distribution models assume a constant detection probability throughout sites (Jha, Nameer, Jayadevan, 2022). Occupancy models use both presence and absence data in relation to covariates to develop probabilities of detection and occurrence of hard-to-find species. SDMs do outperform occupancy models of species that are highly detectable; however, when both modeling techniques are used for species with low detectability, occupancy models produce more accurate measures of a species distribution because they account for false absences (Comte and Grenouillet, 2013).

I expected low detectability for each individual solitary bee species and thus felt that occupancy models would provide the most effective way to investigate where bees are foraging and why they are choosing those areas. In implementing the occupancy models, I assumed that all sites were closed to changes in occupancy, detection of a species at a site was independent of detecting species at other sites, there were no false detections, probability of detection was constant across sites if the species is present, and probability of occupancy was constant across sites (Mackenzie et al., 2002).

Out of the 131 species of solitary bee caught, I initially chose eleven species, comprising five families and seven genera to model. These species were chosen because they were represented by at least 90 individuals that originated from at least one third ($N = 20$) of the total sites. However, occupancy models did not converge for five species, leaving six species for which I was able to develop final models: *Eucera hamata*, *Andrena nivalis*, *Andrena perplexa*, *Agapostemon virescens*, *Agapostemon sericeus*, and *Osmia taurus*.

One reason for lack of model convergence in some species was likely aggregation/lack of dispersion of the 20 sites where the species were observed. Occupancy models are data hungry due to the complexity of estimating detection and occupancy over multiple survey sessions (Perkins-Taylor & Frey, 2020; Jha, Nameer, Jayadevan, 2022). Thus, models will only operate effectively if a species is represented by enough samples that are from distributed sites. Occupancy data is also binomial so if all my target species came from one site, my models would not run. Setting the criteria for all species included in occupancy modeling at 20 sites meant that the species were observed at least one third of total sites, increasing the chances for dispersion.

I modeled each of the six species across the entire time span of the survey (12 collection events) to try and obtain a general overview of drivers of foraging for each species. I then assessed whether predictors varied across the season, by dividing the sampling sessions into three time blocks. Early season corresponded to the first four sampling sessions (4/25 - 6/19), middle season was the middle four sampling sessions (6/20 - 8/14), and the late season was the last four sampling sessions (8/15 - 10/9).

I chose seven biologically relevant variables known to be important to bees or their floral partners to include in models for detection and occupancy; diversity of bee preferred plant taxa at each site, 2019 minimum and maximum temperature during the survey, elevation of sites, and 2019 survey precipitation. Bees that responded to precipitation were then also modeled with 2018 winter precipitation and 2018 annual precipitation. Data on bee-preferred plant taxa were from a 2001 inventory of the BRP (Walker, 2002). The remaining variables were from PRISM and collected at a 4 km resolution (PRISM Climate Group, 2019).

Model Selection and Analysis

I developed occupancy models for presence and absence of solitary bee species using the “unmarked” package in R software (Version 1.4.1717) (Fiske and Chandler, 2011), run through Rstudio Integrated Development Environment (IDE). Unmarked allows users to fit hierarchical models of taxa abundance to estimate the proportion of sites occupied (Ψ) and the detection probability per site (p). Parameters controlling detection and occupancy processes can be used as covariates. All variables were modeled first as detection to see if any had influence on the ability to find the species and because detection is tied into occupancy through the equation:

$$\begin{aligned}
 y_i | z_i &\sim \text{Bernoulli}(p * z_i) \\
 z_i &\sim \text{Bernoulli}(\psi) \\
 \text{logit}(p) &= \alpha_0 + \alpha_1 * \text{covariate}_1 \\
 \text{logit}(\psi) &= \beta_0 + \beta_1 * \text{covariate}_1
 \end{aligned}$$

Y is the data at site i , z is the true occupancy state at site i , ψ is occupancy probability, α are the parameters to estimate for the detection probability (p), and β are the parameters to estimate for the occupancy probability (ψ). Z_i is the true occupancy state drawn from a Bernoulli distribution

(Fiske and Chandler, 2011). I compared models using AIC values. Within the modeling frame, the AIC with the lowest value is usually the most parsimonious model (Burnham and Anderson, 1998; Mackenzie et al., 2002). The final model selected for detection of each species had the lowest AIC value and had a difference > 2.0 from the null model that contained no variables (Burnham and Anderson, 1998). Occupancy variables were chosen in the same manner but with the detection variable included. A full occupancy model was chosen with the same parameters used as the detection model.

Competing occupancy models (AIC > 2.0 of null) of the same species were averaged using the R package ‘AICcmodavg’ (Mazerolle, 2023). Averaging models creates more accurate standard errors by incorporating all competing models in relation to model weight (Burnham and Anderson, 1998; Symonds and Moussali, 2011).

Visualization

Once models were chosen by comparison of AIC values, I visualized them in two ways; I created marginal effect plots using the ggplot package in R and developed predictive maps using ArcGIS Pro. Marginal effect plots show the relationship between detection and occupancy of a species in relation to the variable that is being tested. I included upper and lower errors in my plots to show the relative accuracy of the models. Predictive maps allowed me to clearly show which sites had high and lower probabilities of detection and occupancy of the selected species.

Results

Eucera hamata

This species was caught enough to create a model for the full survey and the early season. The modeled variables for Detection (p) and occupancy (Ψ) probabilities did not shift when examining both sets of models $P(\text{Bee preferred plant taxa})$ and $\Psi(\text{2019 survey precipitation})$ had the lowest AIC in their respective model list (Table 1). When looking at all 12 detection histories, detection probability was 0.09 ± 0.02 . When just looking at the early season, detection probability jumped to 0.27 ± 0.07 . For both modeling setups, the chance of detection decreased in areas with greater bee preferred floral taxa. The sites with the highest chance of detection across the full survey and early season averaged 11 bee preferred flower species (Fig. 1C and Fig. 2C).

Occupancy across all 12 surveys was 0.62 ± 0.16 (Table 1). The sites in the top 25th percentile had on average 77.03 inches of precipitation over the course of the season while the sites with the lowest predicted occupancy had 54.02 inches of precipitation (Fig. 1D). Occupancy probability during the early season was 0.56 ± 0.14 (Table 1). Precipitation had a positive relationship with *E. hamata* occupancy and there is a higher rate of occupancy in North Carolina than Virginia for both models (Fig. 1F and Fig. 2F). Monitored sites in the upper 25th percentile of predicted occupancy averaged 77.24 inches of rain during sampling while sites in the lower 25th percentile only averaged 50.74 inches of rain during the early season (Fig. 2D). Because *E. hamata* peaked in May and then was all but gone by July, so my attempts to model middle and late season did not run due to a lack of captures across the 59 sites.

Andrena nivalis

Across the full survey, the best fitting model was $p(\text{maximum temperature})$ and $\Psi(\text{null})$. The full season detection was 0.08 ± 0.02 . Because the occupancy variable was null, it was not modeled. Instead, I focused on the early season. The best performing variable predicting detection remained as maximum temperature but the highest performing occupancy variable became maximum temperature. Detection probability had a slightly positive relationship with maximum temperature during early season captures (Fig. 2A). Detection probability rose to 0.21 ± 0.08 (Table 2). Interestingly, the sites with the highest probability of detection ($p = 0.25$) were near Asheville, NC- one of the most populated areas on the entire Blue Ridge Parkway (Fig. 2E). As the maximum temperature of sites increased, occupancy probability decreased (Fig 2B). *A. nivalis* occupancy probability of the landscape across the early season was 0.67 ± 0.16 . Sites in the 25th percentile of predicted occupancy had an average maximum temperature of 75.72°F while sites in the bottom 25th percentile had an average maximum temperature of 85.40°F . Models show that *A. nivalis* can potentially occupy a large area on the Blue Ridge Parkway, with high chances of Ψ across North Carolina and Virginia (Fig. 2F).

Andrena perplexa

The most parsimonious model of *A. perplexa* for the full survey season was not a complete occupancy model. The top model was $p(\text{Bee preferred plant taxa})$, $\Psi(\text{null})$ with an

AIC value of 394.98 and an AICwt of 0.25 (Table 3). Detection probability of *A. perplexa* was 0.10 ± 0.02 . Because the top occupancy variable was null, naive occupancy was used instead of traditional occupancy. The amount of sites they were present at was divided by total sites for a naive occupancy probability of 0.59. The second top model, p(Bee preferred plant taxa) Ψ (Bee preferred plant taxa) has a slightly higher AIC value of 395.10 and an AIC wt of 0.24. With the AIC value and weight being so close, the second model could be worth investigating more. I was able to model the early season but not the middle or the late season. The top model for the early season was p(Bee preferred plant taxa) Ψ (Bee preferred plant taxa) with detection probability being 0.34 ± 0.06 and occupancy of 0.69 ± 0.14 . Bee preferred plant taxa had a negative relationship with detection while it had a positive relationship with occupancy. Sites that had on average 11 bee preferred plant taxa present had higher rates of detection while sites with greater than 165 bee preferred plant taxa had higher rates of occupancy (Fig. 4C and Fig. 4D). There were high rates of error occupancy for this species though. Detection was high across the full length of the parkway while occupancy peaked in parts of Virginia and the southern sites around Asheville (Fig. 4E and Fig. 4F).

Agapostemon virescens

When analyzing *A. virescens*, it was the only species that had shifts in its detection variable and occupancy variable from one season to the next. When modeling all the full survey, the best model was Ψ (winter rainfall), p(2018 precipitation). Detection was 0.18 ± 0.03 with a predicted occupancy of 0.62 of the area with a SE of 0.12 (Table 4). This model predicts that much of the Blue Ridge Parkway could be occupied by *A. virescens* with the exception of the most southern sites based on rain from the previous year (Fig 5F). This was the only species where winter precipitation had any impact on foraging behavior. The best performing sites had on average 29.7 inches of precipitation during winter months (Fig. 5D). Early season foraging variables then shifts to Ψ (tmin), p(2019 rain). Detection probability was 0.25 ± 0.06 and displayed a negative relationship with increasing rainfall at sites (Table 4). Occupancy probability was 0.71 ± 0.12 and showed a negative trend with minimum temperatures 9(Fig. 6B). Sites that had minimum temperatures of 42.07°F were in the upper 25th percentile for predicted occupancy while the lower 25th had minimum temperatures of 47.0°F (Fig. 6D). The model

predicted that detection of the species is higher in Virginia than in North Carolina whereas occupancy was higher in North Carolina than Virginia (Fig. 6E and Fig. 6F). In the middle season, the occupancy variable stayed consistent with the early season model while the detection variable shifted back to p(2018 annual rain) (Table 4). Detection was high with an average of 0.33 ± 0.07 but occupancy was lower with an average of 0.46 ± 0.12 . The minimum temperature rose half of a degree to 42.5°F for the best predicted sites of occupancy while the worst performing sites stayed consistent, averaging 47.0°F (Fig 7C). Detection was again more likely in Virginia while occupancy was higher in North Carolina (Fig 7E and 7F).

Agapostemon sericeus

A. sericeus was caught throughout the middle season with some caught at the beginning of the late season. Because of their phenology, only the middle season was able to be modeled. The covariates that created the most parsimonious model was 2019 precipitation for both the detection and occupancy probabilities. Detection was 0.26 ± 0.09 (Table 5). The sites with the highest detection probability were sites that averaged 53.9 inches of rain (Fig. 8C). Occupancy for the middle season was 0.61 ± 0.21 . *A. sericeus* was occupying landscapes that received on average 50.1 inches of rain (Fig. 8D). While this bee did have the latest phenology out of the species modeled, there were still not enough occurrences for a late season model to be created. *A. sericeus* had a higher predicted occupancy in Virginia than North Carolina because of the amount of precipitation that Virginia received (Fig. 8F).

Osmia taurus

O. taurus had enough occurrences and was observed at enough sites for it to be modeled across all detection events and the early season. The covariates that created the best model for both occasions was $\Psi(\text{rain})$, p(Bee Preferred Plant Taxa). This species had low detection success, 0.07 ± 0.02 and 0.23 ± 0.06 , for all 12 survey events and early season, respectively (Table 6). For both models, the sites with the highest chance of detection all had 0 bee preferred floral species present while the sites with the lowest chance of detection had 308 (Fig. 9C and 10C). Occupancy was fairly consistent when comparing the full survey history to the early season. Occupancy dropped slightly from 0.80 ± 0.19 to an occupancy of 0.75 ± 0.17 (Table 6). There

was also a slight drop in the amount of precipitation that the best performing sites received from the full survey and the early season. The full season's highest predicted occupancy received an average of 76.9 inches of rain while early season received an average of 73.8 inches of rain (Fig. 9D and Fig. 10D). There was a greater amount of precipitation in North Carolina than Virginia which led to a higher chance of occupancy at sites in North Carolina (Fig 10F).

Discussion

Global climate change is reorganizing regional biota across the planet. Among pollinating insect species, particularly bumble bees, range shifts and range contractions have been observed (Colla et al., 2012; Kerr et al., 2015). Where climate effects have been stark, such as Europe and the Intermountain Western US, lowland species have moved upward in elevation (Miller-Struttman et al., 2015; Marshall et al., 2020) changing the composition of communities. Documenting change in real time and predicting those of the future requires prior knowledge of past and current species biogeography, and ideally the environmental factors that have determined their occupancy across a patchy landscape.

Unlike their social relatives, bumble bees and honeybees, solitary bees have not garnered the same intensity of assessment of their ranges and status, yet face the same problems with anthropogenic land use and a changing climate. Solitary bees are often small, quick, and have a narrow phenology which can make them difficult to find and study (Maher, Monco, & Ings, 2019). With those difficulties, there still remains many uncertainties of the distribution and drivers of solitary bees at medium and low elevations (Kammerer et al., 2020).

I aimed to resolve this deficit by using occupancy models to try and understand solitary bees in the Appalachian Mountains. Climate change effects in this region have yet to reach the stark intensity of other regions, though data is already accumulating to support increases in temperature and precipitation or precipitation intensity. Historical data for solitary bees in the Southern Appalachians are lacking, so assessment of species distributions, ranges and the environmental factors driving the patterns could not come soon enough.

I modeled precipitation, temperature, elevation, and abundance of bee preferred flower taxa present because I hypothesized that they were driving our ability to detect certain species

and driving the foraging habitat for bees. I looked at this hypothesis broadly across our survey time (April to October, 2019) and then more seasonally where I broke up the full survey in early, mid, and late season.

Finding from my detection and occupancy models highlighted precipitation as a recurrent theme. I used three measures of precipitation; annual precipitation the year before the survey, winter precipitation the year before the survey, and total precipitation during the survey. Out of the ten models made, precipitation was an important covariate in either detection or occupancy eight times. The general reaction of insects when exposed to areas of substantial rainfall is to simply vacate the area. While the mechanism to how insects are able to sense incoming storms is still unknown it is thought it has to do with the drop in barometric pressure (Lawson & Rands, 2019; Pellegrino et al. 2013). Environmental noise created by rain makes navigating landscapes difficult for bees because sensory intake and perception can be altered by droplets; additionally, rainfall can obscure a pollinator's olfactory system by removing important scent emissions from flowers (Starr and Mason, 1966; Lawson and Rands, 2019).

Of the species modeled, two showed to have a higher chance of occupancy as rainfall increased; *Osmia taurus* and *Ecuera hamata*. While it is not common in the bee world, genera such as *Bombus*, *Andrena*, *Anthophora*, and *Osmia* have representatives that can forage through rain (Free 1960, Boyle-Makowski and Philogène 1985, Boyle-Makowski 1987, Barta 1994, Vicens and Bosch, 2000). Vicens and Bosch (2000) showed that in Maine, *Osmia* species were able to forage in wind and rain during spring. My full survey model and the early season model of *O. taurus* collaborated on those findings. Sites that had the highest chance of occupancy were sites that exceed 80 inches of rain for the season. For both models, as 2019 precipitation increased, so did the occupancy of *O. taurus*. This species is a cavity dwelling bee so it would not have to worry as much as ground dwelling bees in rainy environments. Other surveys like ; McKinney & Park (2012) show the opposite for another species in the same genus, *O. cornifrons*. That project showed that *O. cornifrons* did not forage or provision their cells on days with precipitation.

All models that included precipitation as its detection variable indicated that as precipitation increased, detection decreased meaning we were not able to find these bees at rainy sites. Both species that exhibited this relationship are from the genus *Agapostemon* with the

species being *sericeus and virescens*. This genus consists of medium sized bees, measuring anywhere from 0.3 to 0.6 inches and are ground dwelling bees who lay eggs in burrows. While a handful of bees are able to pollinate in rain, *Agapostemon* does not (Viscens and Bosh, 2000). The foraging range for bees of *Agapostemon's* size is low compared to other bees, making where they live may also be where they forage. While larger bees in alpine settings are able to move between mountaintops and fight strong winds, small and medium sized bees may have a maximum foraging range of only 150-600m and are more sensitive to environmental conditions (Gathmann and Tschanrtke, 2002). Ground dwelling bees who live in high precipitation areas could either have difficulty finding suitable nesting areas or face the threat of their burrows being destroyed (Drummond et al., 2017). Other studies have found similar results; Kammerer et al (2020) found that in spring, areas that received less precipitation had higher bee abundance and diversity. Drummond et al (2017) concluded from their 29 year study that precipitation reduces that amount of optimal foraging days for bees.

An unexpected result of this study was the negative relationship between detection probability and amount of bee preferred floral taxa present at mileposts. The sites that had the most bee-preferred flowers (n= 300) had the lowest probability of detection for three out of the six species analyzed (*Osmia taurus, Andrena perplexa, and Eucera hamata*). Going into the analysis, it was thought that detection and occupancy probabilities would be higher at sites with great abundance of bee preferred floral taxa because of the importance flowers are to the life cycle of bees. Flowers are essential not only to the adult bees who are actively foraging but also to the next generation of bees because adults will provision egg cells with a pollen ball for new hatchlings. The pollen ball provides essential nutrients in the form of lipids and proteins as well as important gut bacteria from the mother to give the juvenile the best chance of survival when it emerges (López-Urbe, Ricigliano, and Simone-Finstrom, 2020).

There have been surveys using passive traps that report small batches of bees caught in dense flower communities (Cane et al., 2000; Mayer, 2005) but Westerberg et al (2021) seems to be the first paper to study the impact of varying densities of flower communities on passive trap effectiveness. Overall they reported a negative relationship between flower density and passive pan traps effectiveness but also stated that results were influenced by insect taxa, timing of sampling, flower colors and the spatial scale but do not provide definitive mechanisms.

A driver of this phenomenon is pollinator limitation. This is when a patch of flowers is so highly compact, the chance of an insect interaction is decreased due to competition from surrounding flowers (Sih & Baltus, 1987; Pettersson & Sjödin, 2000; Steven et al., 2003) and could explain why detection was much higher at sites with very few bee preferred floral taxa present. A cup would have much less of a chance of capturing a bee when the density of flowers was high. Over a third of all sites had at least 100 different species of flowers present which could severely limit capture rate. The color of cups could also produce negative detection relationships. Pan trapping cups were painted fluorescently in three colors; yellow, blue, and white which are common for pan trapping (Campbell & Hanula, 2007; Toler et al., 2005; Droege et al., 2010). While those colors could be good general colors for captures, there could still be survey bias as some genera may look for specific colors that are not represented in the study.

In my models, only one covariate could be used on detection and occupancy. This drawback can go hand-in-hand with low capture rates of species because these models need high capture rates for more complex models. Sometimes the simplest explanation can be the best explanation but solitary bees are complex organisms and likely wouldn't choose a spot to forage based on one variable. For even the most abundant solitary bees, capture rates were too low to model multiple covariates. A lack of solid historical data in this region meant the areas of high detection and occupancy for species was unknown at the time of the 2019 survey.

With one variable, these models can serve as a good general explanation as to where solitary bees could be in the Southern Appalachians and why they are there. My models show that solitary bees are foraging in varying habitats and could be built on. Future researchers would now know general drivers of foraging habitat and where we were able to catch the highest abundance of bees in the Southern Appalachians. Certain species could be found more readily and more robust models could then be developed. Different areas for passive trapping could be surveyed since we know that we would have better capture rates at areas with little to no flowers present. More specific sites in terms of amount of seasonal precipitation could be chosen to achieve higher capture rates.

Future efforts that would greatly inform our predictions for the solitary bees of the Southern Appalachians would be to model the most important environmental variables for the bees, such as precipitation, and how each of those factors is predicted to change across the

landscape. If the shifting climate of the region creates a warmer dryer climate, this may increase detectability and occupancy to point. However, more data and more complex multivariate models would also aid these predictions. In any case, I have developed baseline models that future researchers can build onto.

Tables

Table 1: Model selection for *Eucera hamata* based on AIC and AIC wt. Predictions were made on highlighted models

Species	Season	Model Selection						
		Model	K	AIC	Δ AIC	AIC wt.	Ψ (SE)	p(SE)
<i>Eucera hamata</i>	12 detections	Ψ (rain), p(plant)	4	306.59	0.00	0.32	0.62(0.13)	0.09(0.02)
		Ψ (.), p(plant)	3	307.88	1.30	0.17	-	-
		Ψ (tmin), p(plant)	4	308.55	1.96	0.12	-	-
		Ψ (Elevation), p(plant)	4	308.60	2.01	0.12	-	-
		Ψ (tmax), p(plant)	4	308.63	2.05	0.11	-	-
		Ψ (plant), p(plant)	4	309.36	2.78	0.08	-	-
		Ψ (.), p(.)	2	311.38	4.80	0.03	-	-
		Ψ (.), p(tmin)	3	311.66	5.07	0.03	-	-
		Ψ (.), p(rain)	3	312.78	6.20	0.01	-	-
		Ψ (.), p(tmax)	3	313.33	6.74	0.01	-	-
		Ψ (.), p(Elevation)	3	313.59	7.01	0.01	-	-
		Ψ (rain), p(plant)	4	197.26	0.00	0.24	0.59(0.14)	0.26(0.07)
	Ψ (.), p(plant)	3	197.45	0.19	0.22	-	-	
	Ψ (tmin), p(plant)	4	198.47	1.21	0.13	-	-	
	Ψ (Elevation), p(plant)	4	198.52	1.26	0.13	-	-	
	Ψ (tmax), p(plant)	4	198.57	1.31	0.12	-	-	
	Ψ (plant), p(plant)	4	199.07	1.81	0.10	-	-	
	Ψ (.), p(.)	2	201.88	4.62	0.02	-	-	
	Ψ (.), p(tmin)	3	201.89	4.63	0.02	-	-	
	Ψ (.), p(rain)	3	203.29	6.03	0.01	-	-	
	Ψ (.), p(Elevation)	3	203.99	6.73	0.01	-	-	
	Ψ (.), p(tmax)	3	204.05	6.79	0.01	-	-	
	Ψ (.), p(.)	2	31.35	0.00	0.27	0.05(0.04)	0.26(0.21)	
	Ψ (.), p(tmax)	3	31.75	0.40	0.22	-	-	
	Ψ (.), p(plant)	3	32.43	1.08	0.16	-	-	
	Ψ (.), p(tmin)	3	32.70	1.35	0.14	-	-	
	Ψ (.), p(Elevation)	3	32.99	1.64	0.12	-	-	
	Ψ (.), p(rain)	3	33.25	1.90	0.10	-	-	
	Ψ (.), p(plant)	3	16.68	0.00	0.30	0.02^a	0.004(0.009)	
	Ψ (.), p(.)	2	17.14	0.46	0.24	-	-	
	Ψ (.), p(rain)	3	17.58	0.90	0.19	-	-	
	Ψ (.), p(tmin)	3	18.73	2.06	0.11	-	-	
	Ψ (.), p(tmax)	3	19.28	2.60	0.08	-	-	
Ψ (.), p(elevation)	3	19.35	2.67	0.08	-	-		

Table 2: Model selection for *Andrena nivalis* based on AIC and AIC wt. Predictions were made on highlighted models

Species	Season	Model Selection						
		Model	K	AIC	Δ AIC	AIC wt.	Ψ (SE)	p(SE)
<i>Andrena nivalis</i>	12 detections	$\Psi(\cdot), p(\text{tmax})$	3	325.89	0.00	0.35	0.77(0.22)	0.08(0.02)
		$\Psi(\text{tmax}), p(\text{tmax})$	4	327.49	1.60	0.16	-	-
		$\Psi(\text{plant}), p(\text{tmax})$	4	327.68	1.79	0.14	-	-
		$\Psi(\text{tmin}), p(\text{tmax})$	4	328.06	2.17	0.12	-	-
		$\Psi(\text{rain}), p(\text{tmax})$	4	328.16	2.27	0.11	-	-
		$\Psi(\text{Elevation}), p(\text{tmax})$	4	328.17	2.28	0.11	-	-
		$\Psi(\cdot), p(\text{Elevation})$	3	333.66	7.77	0.01	-	-
		$\Psi(\cdot), p(\text{plant})$	3	333.67	7.78	0.01	-	-
		$\Psi(\cdot), p(\text{tmin})$	3	336.86	10.97	0.00	-	-
		$\Psi(\cdot), p(\cdot)$	2	339.31	13.42	0.00	-	-
		$\Psi(\cdot), p(\text{rain})$	3	339.90	14.01	0.00	-	-
		$\Psi(\text{tmax}), p(\text{tmax})$	4	186.65	0.00	0.33	0.67(0.14)	0.21(0.08)
		$\Psi(\cdot), p(\text{tmax})$	3	188.57	1.92	0.13	-	-
		$\Psi(\cdot), p(\text{plant})$	3	188.65	2.00	0.12	-	-
	$\Psi(\text{elevation}), p(\text{tmax})$	4	189.07	2.42	0.10	-	-	
	$\Psi(\text{plant}), p(\text{tmax})$	4	189.25	2.60	0.09	-	-	
	$\Psi(\text{tmin}), p(\text{tmax})$	4	189.78	3.13	0.07	-	-	
	$\Psi(\cdot), p(\cdot)$	2	190.18	3.53	0.06	-	-	
	$\Psi(\text{rain}), p(\text{tmax})$	4	190.29	3.64	0.05	-	-	
	$\Psi(\cdot), p(\text{tmin})$	3	192.00	5.35	0.02	-	-	
	$\Psi(\cdot), p(\text{elevation})$	3	192.18	5.53	0.02	-	-	
	$\Psi(\cdot), p(\text{rain})$	3	192.39	5.74	0.02	-	-	
	Middle	$\Psi(\text{tmax}), p(\text{tmax})$	4	74.57	0.00	0.48	0.27(0.09)	0.11(0.09)
		$\Psi(\text{plant}), p(\text{tmax})$	4	76.37	1.80	0.20	-	-
		$\Psi(\cdot), p(\text{tmax})$	3	76.80	2.23	0.16	-	-
		$\Psi(\text{elevation}), p(\text{tmax})$	4	78.70	4.22	0.06	-	-
		$\Psi(\text{rain}), p(\text{tmax})$	4	79.11	4.54	0.05	-	-
		$\Psi(\text{tmin}), p(\text{tmax})$	4	79.11	4.54	0.05	-	-
		$\Psi(\cdot), p(\text{elevation})$	3	84.44	9.87	0.00	-	-
		$\Psi(\cdot), p(\text{rain})$	3	93.00	18.43	0.00	-	-
		$\Psi(\cdot), p(\text{plant})$	3	94.29	19.72	0.00	-	-
		$\Psi(\cdot), p(\cdot)$	2	94.45	19.88	0.00	-	-
		$\Psi(\cdot), p(\text{tmin})$	3	94.68	20.11	0.00	-	-
		$\Psi(\cdot), p(\text{tmax})$	3	12.57	0.00	0.64	0.02^a	0.004(0.004)
		$\Psi(\cdot), p(\text{plant})$	3	15.62	3.05	0.14	-	-
		$\Psi(\cdot), p(\text{tmin})$	3	16.69	4.12	0.08	-	-
	$\Psi(\cdot), p(\cdot)$	2	17.14	4.57	0.07	-	-	
	Late ^c	$\Psi(\cdot), p(\text{rain})$	3	18.32	5.75	0.04	-	-
		$\Psi(\cdot), p(\text{elevation})$	3	18.34	5.78	0.04	-	-

Table 3: Table selection *Andrena perplexa* based on AIC and AIC wt. Predictions were made on highlighted models

Sepecies	Season	Model Selection								
		Model	K	AIC	Δ AIC	AIC wt.	Ψ (SE)	p(SE)		
<i>Andrena perplexa</i>	12 dectections	Ψ (.), p(plant)	3	394.98	0.00	0.25	0.59^a	0.10(0.02)		
		Ψ (plant), p(plant)	4	395.10	0.12	0.24	-	-		
		Ψ (tmax), p(plant)	4	396.70	1.72	0.11	-	-		
		Ψ (tmin), p(plant)	4	397.04	2.06	0.09	-	-		
		Ψ (Elevation), p(plant)	4	397.05	2.07	0.09	-	-		
		Ψ (rain), p(plant)	4	397.11	2.13	0.09	-	-		
		Ψ (.), p(tmin)	3	398.39	3.41	0.05	-	-		
		Ψ (.), p(.)	2	398.52	3.54	0.04	-	-		
		Ψ (.), p(tmax)	3	400.18	5.20	0.02	-	-		
		Ψ (.), p(rain)	3	400.54	5.56	0.02	-	-		
		Ψ (.), p(Elevation)	3	400.74	5.76	0.01	-	-		
				Ψ(plant), p(plant)	4	242.34	0.00	0.34	0.73(0.11)	0.33(0.06)
	Early		Ψ (.), p(plant)	3	243.04	0.71	0.24	-	-	
			Ψ (tmax), p(plant)	4	244.73	2.39	0.10	-	-	
			Ψ (tmin), p(plant)	4	244.86	2.52	0.10	-	-	
			Ψ (Elevation), p(plant)	4	245.03	2.69	0.09	-	-	
			Ψ (rain), p(plant)	4	245.05	2.71	0.09	-	-	
			Ψ (.), p(.)	2	248.77	6.43	0.01	-	-	
			Ψ (.), p(tmin)	3	249.49	7.15	0.01	-	-	
			Ψ (.), p(Elevation)	3	250.32	7.98	0.01	-	-	
			Ψ (.), p(tmax)	3	250.94	8.60	0.00	-	-	
			Ψ (.), p(rain)	3	250.98	8.64	0.00	-	-	
		Middle		Ψ (plant), p(elevation)	4	42.94	0.00	0.22	0.63(0.04)	0.03(0.02)
				Ψ (tmax), p(Elevation)	4	42.97	0.03	0.22	-	-
			Ψ (.), p(Elevation)	3	44.17	1.23	0.12	-	-	
			Ψ (.), p(.)	2	44.77	1.83	0.09	-	-	
			Ψ (.), p(rain)	3	45.08	2.14	0.08	-	-	
			Ψ (.) p(tmax)	3	45.58	2.64	0.06	-	-	
			Ψ (.) p(tmin)	3	45.70	2.76	0.06	-	-	
			Ψ (.), p(plant)	3	46.22	3.28	0.04	-	-	
			Ψ (elevation), p(elevation)	4	46.47	3.53	0.04	-	-	
			Ψ (tmin), p(elevation)	4	46.47	3.53	0.04	-	-	
			Ψ (rain), p(elevation)	4	46.47	3.53	0.04	-	-	
	Late ^c			Ψ (.), p(.)	-	-	-	-	-	-
			Ψ (.), p(rain)	-	-	-	-	-	-	
			Ψ (.), p(tmin)	-	-	-	-	-	-	
			Ψ (.), p(tmax)	-	-	-	-	-	-	
			Ψ (.), p(elevation)	-	-	-	-	-	-	
			Ψ (.), p(plant)	-	-	-	-	-	-	

Table 4: Model selection for *Agapostemon virescens* based on AIC and AIC wt. Predictions were made on highlighted models

Species	Season	Model Selection						
		Model	K	AIC	Δ AIC	AIC wt.	Ψ(SE)	p(SE)
<i>Agapostemon virescens</i>	12 detections	Ψ(·), p(rain)	3	484.76	0.00	0.26	0.56^a	0.18(0.03)
		Ψ(Elevation), p(rain)	4	485.03	0.26	0.23	-	-
		Ψ(tmax), p(rain)	4	485.03	0.90	0.16	-	-
		Ψ(rain), p(rain)	4	486.66	1.89	0.10	-	-
		Ψ(tmin), p(rain)	4	486.67	1.91	0.10	-	-
		Ψ(plant), p(rain)	4	487.04	2.28	0.08	-	-
		Ψ(·), p(·)	2	490.08	5.32	0.02	-	-
		Ψ(·), p(plant)	3	490.43	5.66	0.02	-	-
		Ψ(·), p(Elevation)	3	491.94	7.18	0.01	-	-
		Ψ(·), p(tmax)	3	492.17	7.41	0.01	-	-
		Ψ(·), p(tmin)	3	492.27	7.51	0.01	-	-
		Ψ(tmin), p(rain)	4	193.46	0.00	0.69	0.70(0.10)	0.26(0.06)
	Ψ(rain), p(rain)	4	197.04	3.58	0.12	-	-	
	Ψ(Elevation), p(rain)	4	198.79	5.32	0.05	-	-	
	Ψ(·), p(rain)	3	198.79	5.33	0.05	-	-	
	Ψ(tmax), p(rain)	4	199.35	5.89	0.04	-	-	
	Ψ(plant), p(rain)	4	200.70	7.23	0.02	-	-	
	Ψ(·), p(Elevation)	3	200.80	7.34	0.02	-	-	
	Ψ(·), p(·)	2	202.21	8.75	0.01	-	-	
	Ψ(·), p(tmax)	3	203.37	9.91	0.00	-	-	
	Ψ(·), p(tmin)	3	204.30	10.83	0.00	-	-	
	Ψ(·), p(plant)	3	204.43	10.97	0.00	-	-	
	Ψ(tmin), p(rain)	4	184.66	0.00	0.65	0.59(0.13)	0.32(0.06)	
	Ψ(·), p(rain)	3	187.66	3.26	0.13	-	-	
	Ψ(plant), p(rain)	4	189.65	4.99	0.05	-	-	
	Ψ(tmax), p(rain)	4	190.22	5.41	0.04	-	-	
	Ψ(rain), p(rain)	4	190.22	5.55	0.04	-	-	
	Ψ(Elevation), p(rain)	4	190.22	5.56	0.04	-	-	
	Ψ(·), p(plant)	3	192.02	7.36	0.02	-	-	
	Ψ(·), p(·)	2	192.02	7.98	0.01	-	-	
	Ψ(·), p(Elevation)	3	194.31	9.64	0.01	-	-	
	Ψ(·), p(tmax)	3	194.39	9.73	0.01	-	-	
	Ψ(·), p(tmin)	3	194.83	10.17	0.01	-	-	
	Ψ(·), p(plant)	3	75.57	0.00	0.20	0.12^a	0.10(0.07)	
	Ψ(tmax), p(plant)	4	76.22	0.64	0.14	-	-	
	Ψ(tmin), p(plant)	4	76.29	0.71	0.14	-	-	
	Ψ(·), p(·)	2	77.16	1.58	0.09	-	-	
	Ψ(·), p(tmax)	3	77.31	1.73	0.08	-	-	
	Ψ(Elevation), p(plant)	4	77.52	1.94	0.08	-	-	
	Ψ(rain), p(plant)	4	77.53	1.96	0.08	-	-	
	Ψ(plant), p(plant)	4	77.76	2.19	0.07	-	-	
	Ψ(·), p(tmin)	3	78.05	2.48	0.06	-	-	
Ψ(·), p(Elevation)	3	79.04	3.46	0.04	-	-		
Ψ(·), p(rain)	3	79.34	3.77	0.03	-	-		

Table 5: Model selection for *Agapostemon sericeus* based on AIC and AIC wt. Predictions were made on highlighted models

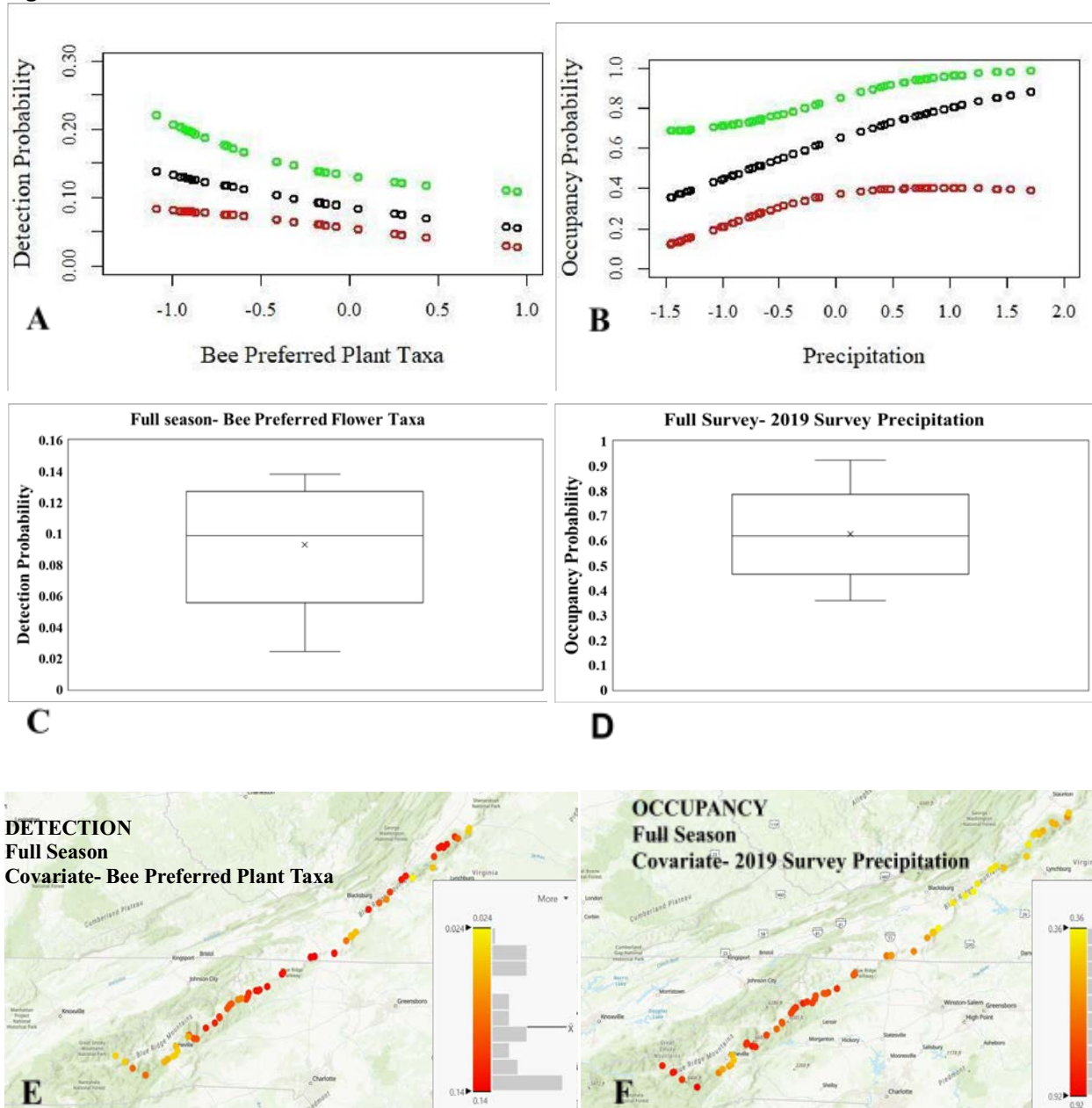
Species	Season	Model Selection							
		Model	K	AIC	Δ AIC	AIC wt.	Ψ (SE)	p(SE)	
<i>Agapostemon sericeus</i>	12 detections ^b	Ψ (plant), p(rain)	4	489.74	0.00	0.74	0.95(0.02)	0.13(0.02)	
		Ψ (rain), p(rain)	4	494.20	4.46	0.08	-	-	
		Ψ (.), p(rain)	3	494.38	4.64	0.07	-	-	
		Ψ (Elevation), p(rain)	4	495.29	5.55	0.05	-	-	
		Ψ (tmin), p(rain)	4	495.75	6.01	0.04	-	-	
		Ψ (tmax), p(rain)	4	496.66	6.93	0.02	-	-	
		Ψ (.), p(Elevation)	3	502.11	12.38	0.00	-	-	
		Ψ (.), p(tmin)	3	503.30	13.57	0.00	-	-	
		Ψ (.), p(tmax)	3	514.97	25.23	0.00	-	-	
		Ψ (.), p(plant)	3	518.32	28.59	0.00	-	-	
		Ψ (.), p(.)	2	520.37	30.63	0.00	-	-	
		Early ^d	Ψ (.), p(elevation)	3	114.49	0.00	0.30	0.24^a	0.06(0.02)
			Ψ (.), p(rain)	3	114.52	0.03	0.29	-	-
	Ψ (.), p(tmin)		3	115.86	1.37	0.15	-	-	
	Ψ (.), p(.)		2	115.92	1.43	0.15	-	-	
	Ψ (.), p(plant)		3	117.64	3.15	0.06	-	-	
	Ψ (.), p(tmax)		3	118.03	3.54	0.05	-	-	
	Middle	Ψ (rain), p(rain)	4	194.27	0.00	0.42	0.50(0.11)	0.30(0.09)	
		Ψ (.), p(rain)	3	195.84	1.57	0.19	-	-	
		Ψ (Elevation), p(rain)	4	196.20	1.93	0.16	-	-	
		Ψ (tmin), p(rain)	4	197.26	2.98	0.09	-	-	
		Ψ (tmax), p(rain)	4	197.80	3.53	0.07	-	-	
		Ψ (plant), p(rain)	4	198.12	3.84	0.06	-	-	
		Ψ (.), p(Elevation)	3	204.48	10.21	0.00	-	-	
		Ψ (.), p(tmin)	3	206.28	12.01	0.00	-	-	
		Ψ (.), p(.)	2	207.98	13.70	0.00	-	-	
		Ψ (.), p(tmax)	3	208.30	14.03	0.00	-	-	
		Ψ (.), p(plant)	3	209.73	15.45	0.00	-	-	
	Late ^d	Ψ (.), p(tmin)	3	170.05	0.00	0.71	0.34^a	0.14(0.03)	
		Ψ (.), p(elevation)	3	173.14	3.10	0.15	-	-	
		Ψ (.), p(rain)	3	173.84	3.79	0.11	-	-	
		Ψ (.), p(tmax)	3	177.57	7.52	0.02	-	-	
		Ψ (.), p(.)	2	179.25	9.20	0.01	-	-	
		Ψ (.), p(plant)	3	179.82	9.78	0.01	-	-	

Table 6: Model selection for *Osmia taurus* based on AIC and AIC wt. Predictions were made on highlighted models

Species	Season	Model Selection						
		Model	K	AIC	Δ AIC	AIC wt.	Ψ (SE)	p(SE)
<i>Osmia taurus</i>	12 detections	Ψ (rain), p(plant)	4	312.02	0.00	0.64	0.76(0.11)	0.07(0.02)
		Ψ (.), p(plant)	3	315.87	3.85	0.09	-	-
		Ψ (Elevation), p(plant)	4	316.00	3.98	0.09	-	-
		Ψ (plant), p(plant)	4	316.96	4.93	0.05	-	-
		Ψ (.), p(rain)	3	317.53	5.51	0.04	-	-
		Ψ (tmax), p(plant)	4	317.90	5.87	0.03	-	-
		Ψ (tmin), p(plant)	4	317.92	5.89	0.03	-	-
		Ψ (.), p(tmin)	3	322.57	10.55	0.00	-	-
		Ψ (.), p(.)	2	322.95	10.93	0.00	-	-
		Ψ (.), p(tmax)	3	323.29	11.27	0.00	-	-
		Ψ (.), p(Elevation)	3	323.46	11.43	0.00	-	-
		Ψ (rain), p(plant)	4	209.59	0.00	0.70	0.74(0.11)	0.23(0.05)
		Ψ (.), p(plant)	3	213.64	4.05	0.09	-	-
		Ψ (.), p(rain)	3	214.93	5.34	0.05	-	-
	Ψ (plant), p(plant)	4	215.26	5.67	0.04	-	-	
	Ψ (tmin), p(plant)	4	215.66	6.07	0.03	-	-	
	Ψ (tmax), p(plant)	4	215.67	6.08	0.03	-	-	
	Ψ (Elevation), p(plant)	4	215.80	6.21	0.03	-	-	
	Ψ (.), p(tmin)	3	219.00	9.41	0.01	-	-	
	Ψ (.), p(.)	2	219.08	9.49	0.01	-	-	
	Ψ (.), p(tmax)	3	220.95	11.36	0.00	-	-	
	Ψ (.), p(Elevation)	3	221.08	11.49	0.00	-	-	
	Middle	Ψ (.), p(plant)	3	16.68	0.00	0.30	0.02^a	0.004(0.008)
		Ψ (.), p(.)	2	17.14	0.46	0.24	-	-
		Ψ (.), p(rain)	3	17.58	0.90	0.19	-	-
		Ψ (.), p(tmin)	3	18.73	2.06	0.11	-	-
		Ψ (.), p(tmax)	3	19.28	2.60	0.08	-	-
		Ψ (.), p(elevation)	3	19.35	2.67	0.08	-	-
	Late ^c	-	-	-	-	-	-	-
		-	-	-	-	-	-	-
		-	-	-	-	-	-	-
		-	-	-	-	-	-	-
-		-	-	-	-	-	-	

Figures

Figure



1. Occupancy and detection of *Eucera hamata* over the full survey, April-October 2019. A) Detection probability B)

Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities.

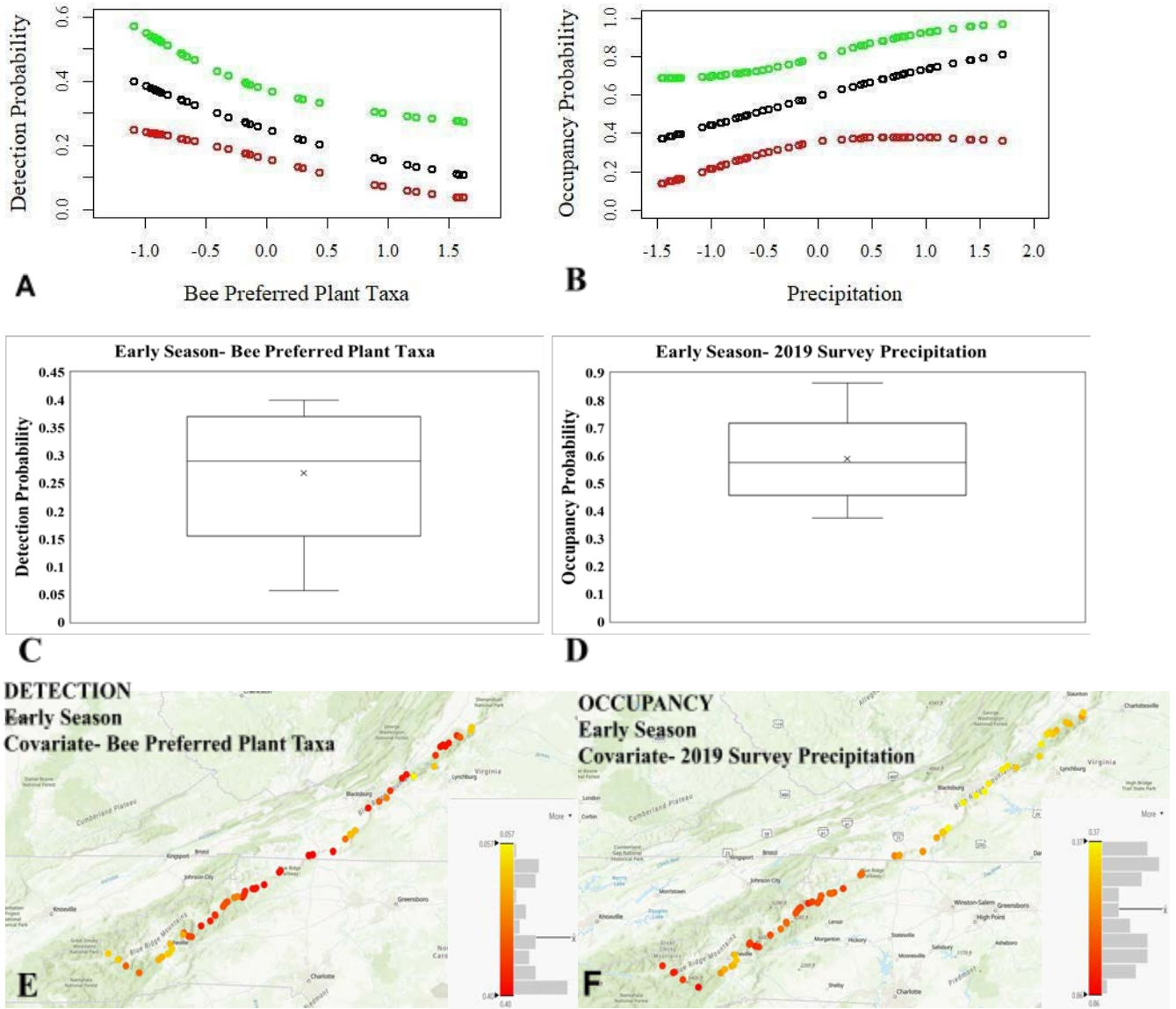


Figure 2. Occupancy and Detection of *Eucera hamata* during early season, April-July, 2019. A) Detection probability B) Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities.

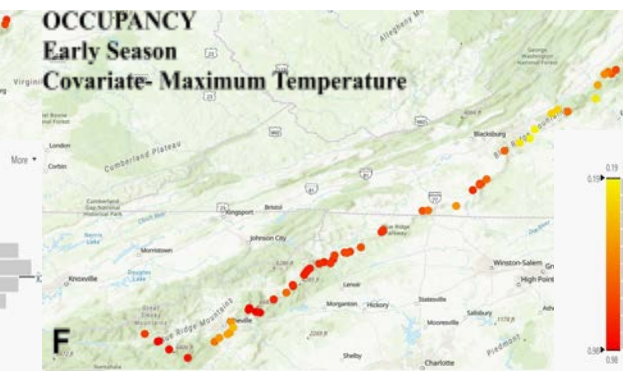
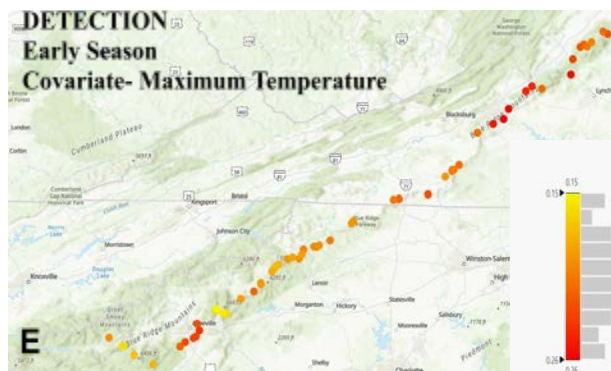
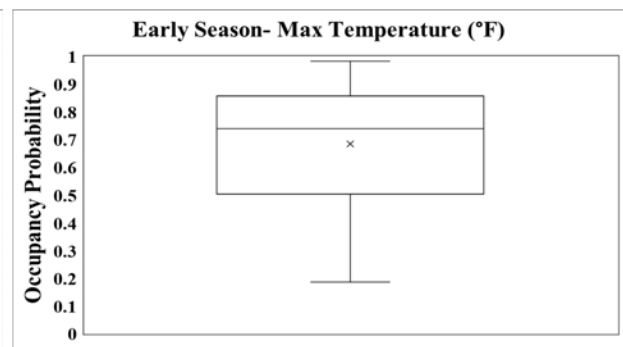
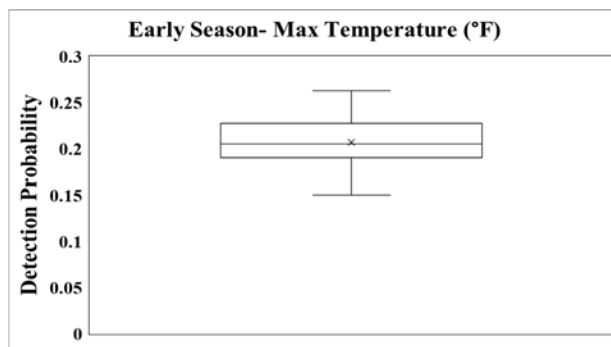
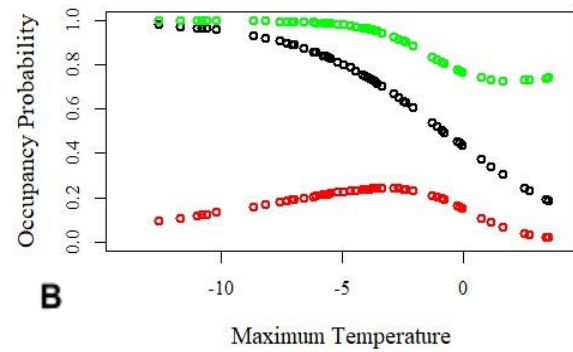
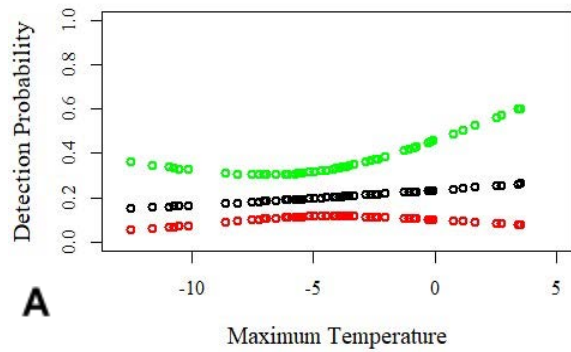


Figure 3. Occupancy and Detection of *Andrena nivalis* during early season, April-July, 2019. A) Detection probability B) Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities.

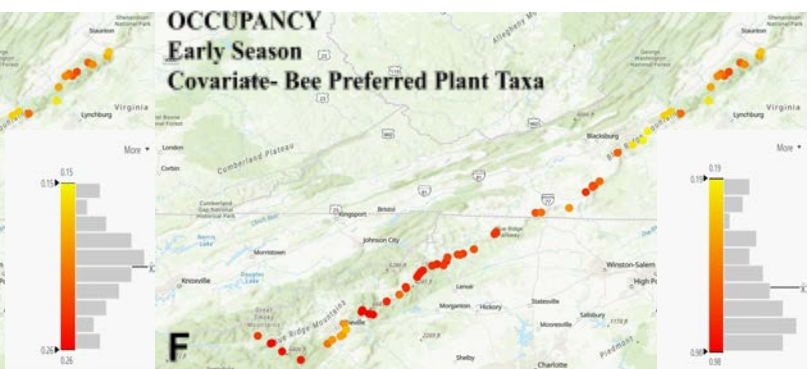
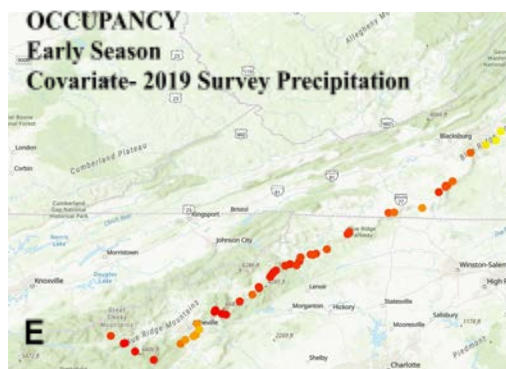
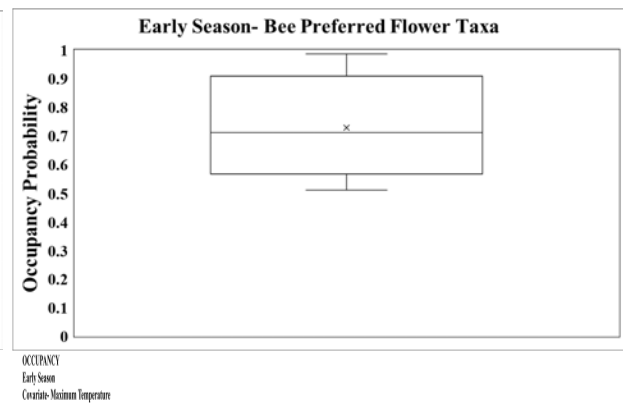
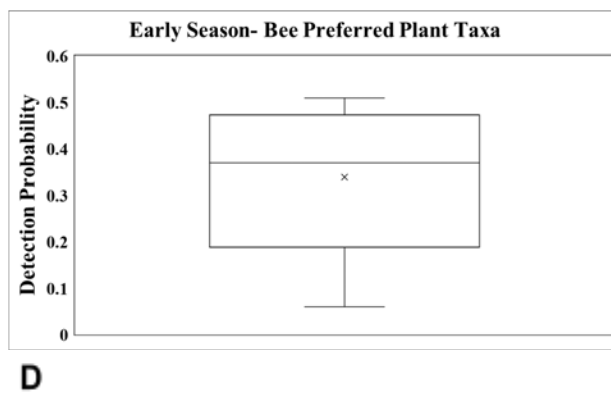
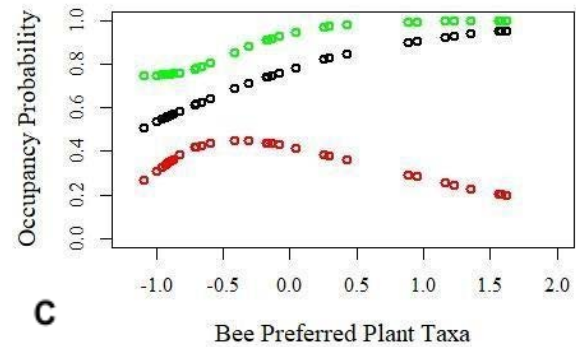
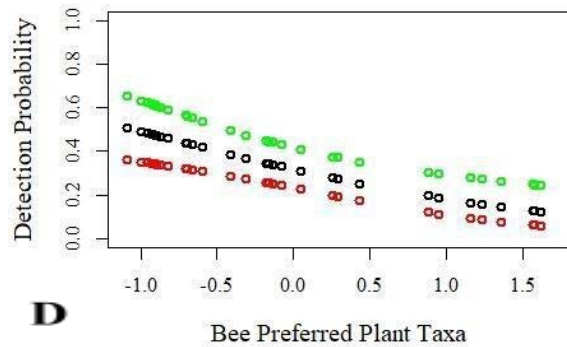


Figure 4. Occupancy and Detection of *Andrena perplexa* during early season, April-July, 2019. A) Detection probability B) Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities

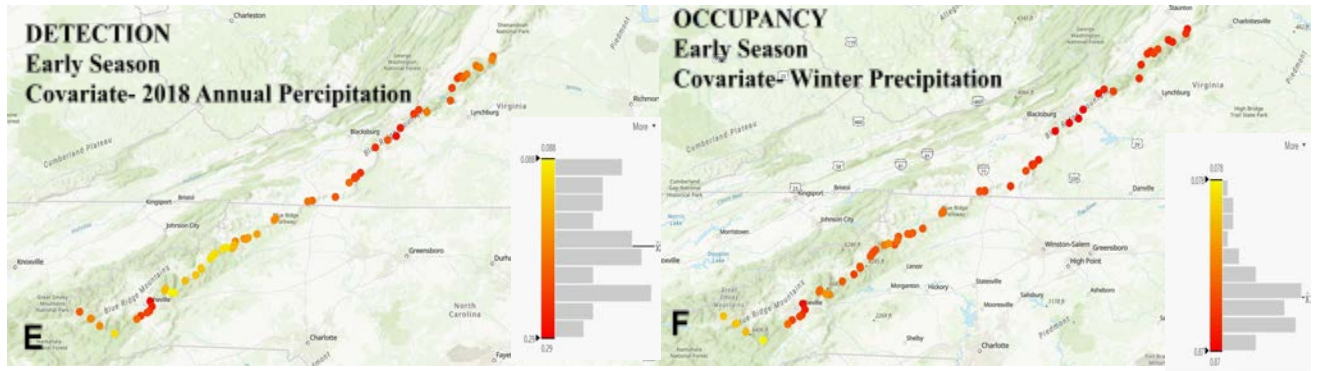
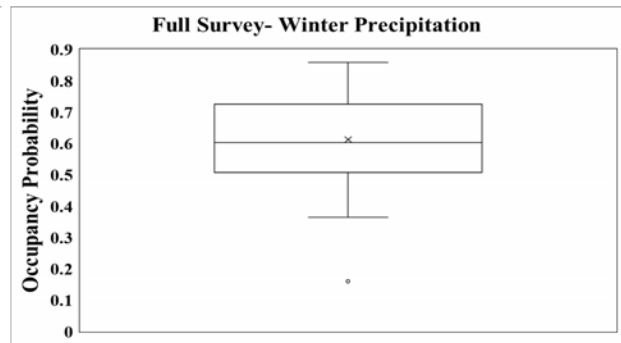
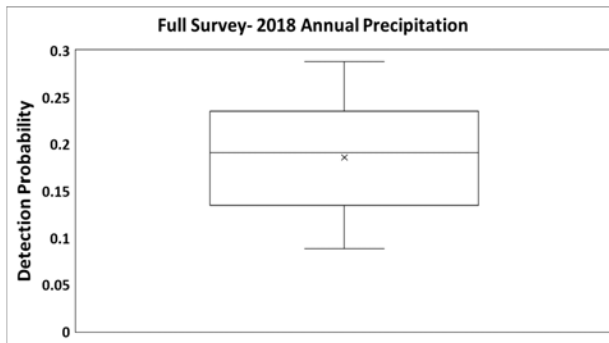
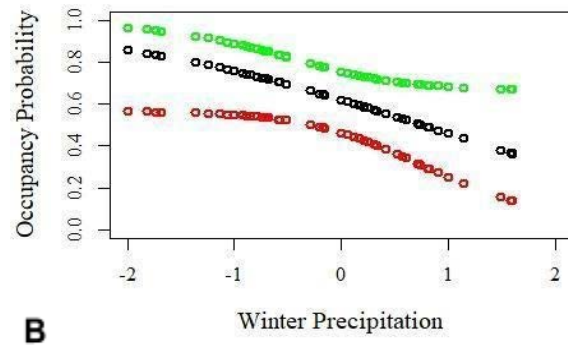
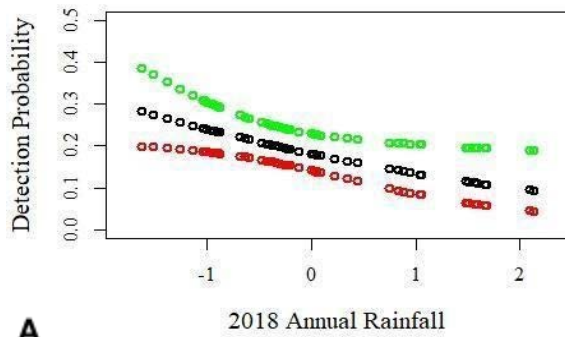
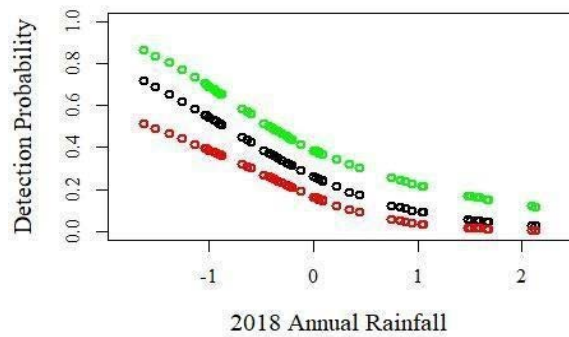
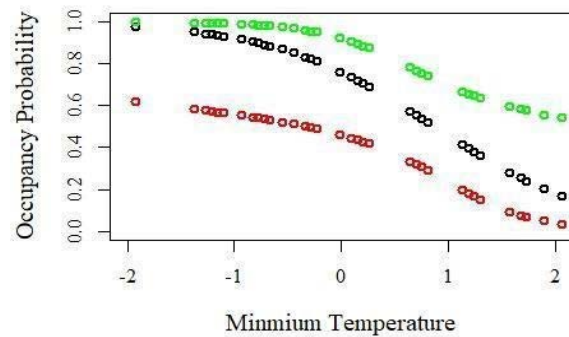


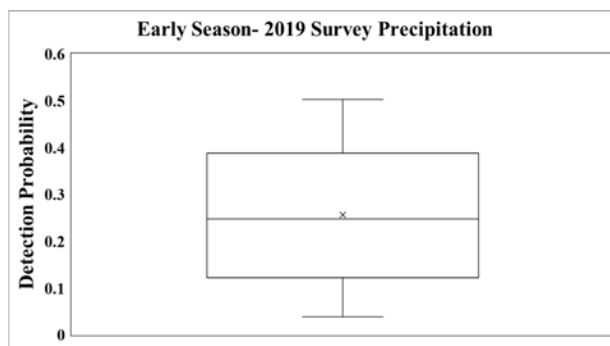
Figure 5. Occupancy and detection of *Agapostemon virescens* over the full survey, April-October 2019. A) Detection probability B) Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities.



D



C



D

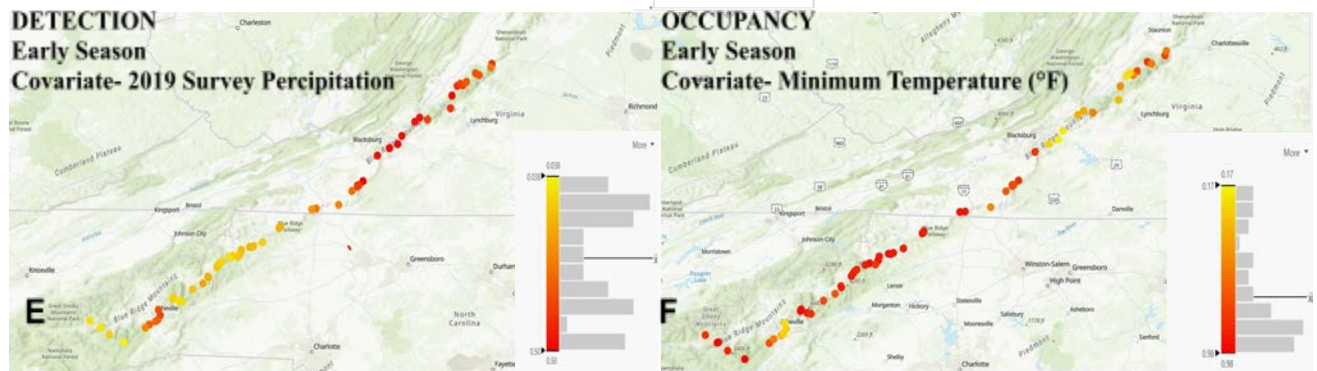
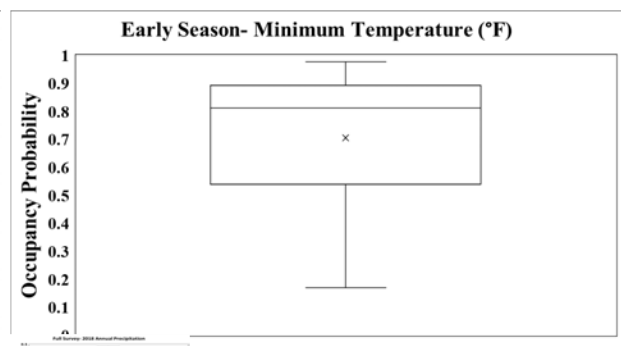


Figure 6. Occupancy and Detection of *Agapostemon virescens* during early season, April-July, 2019. A) Detection probability B) Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities

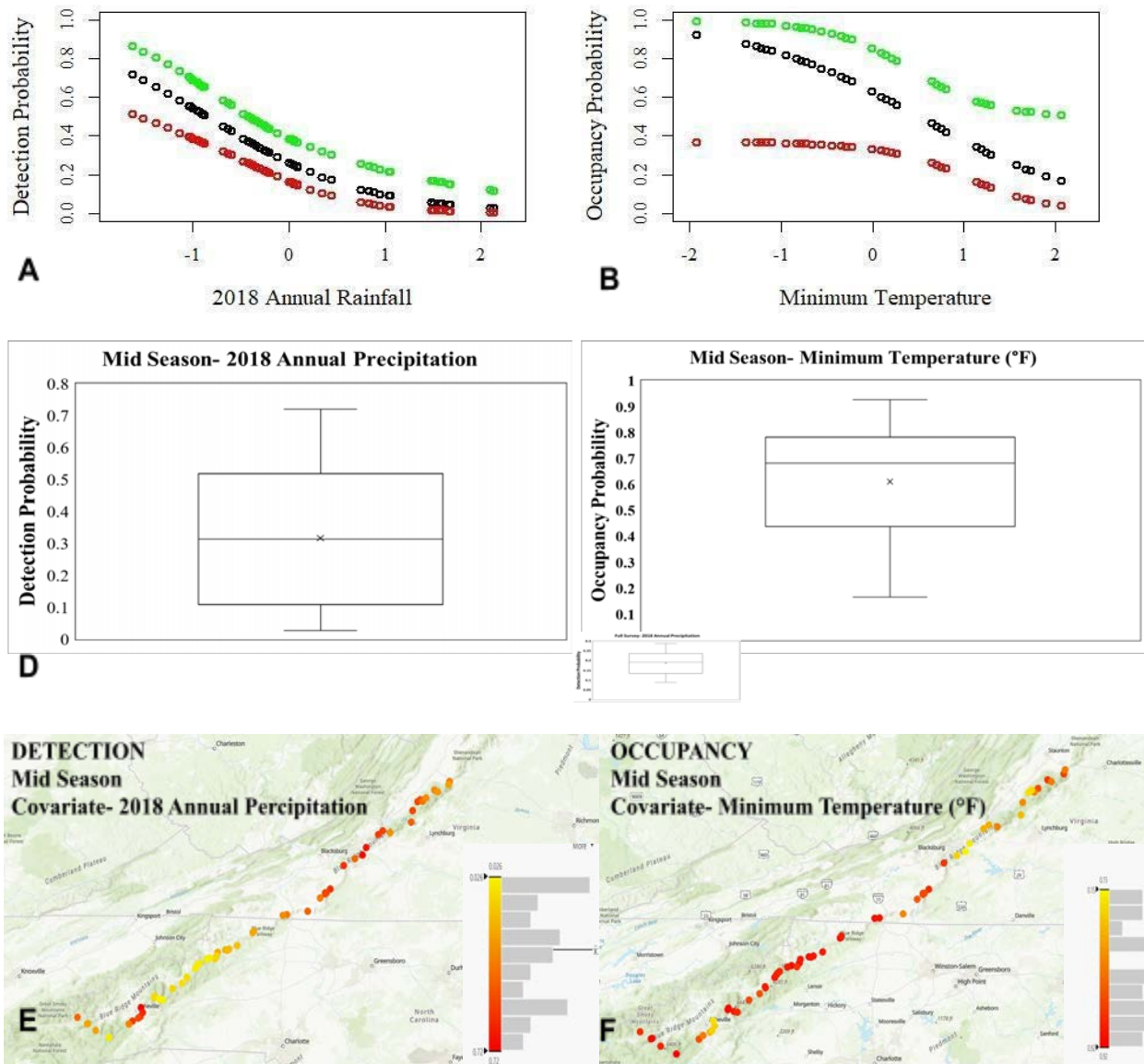
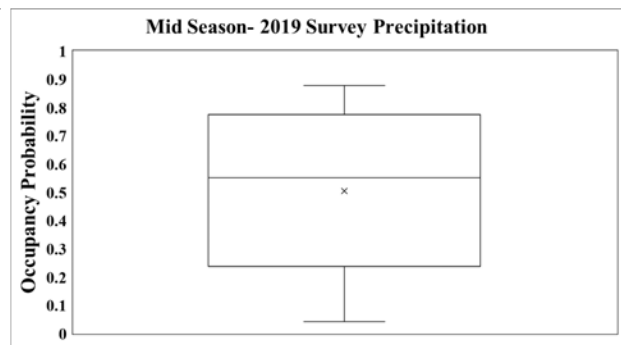
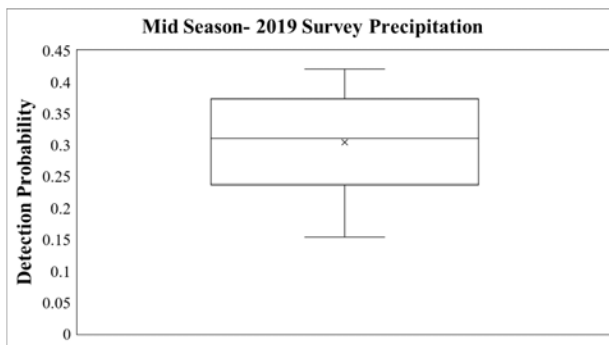
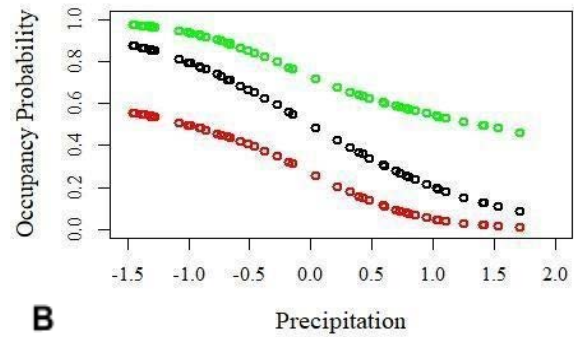
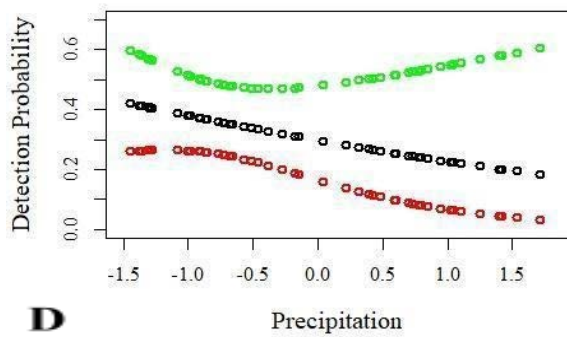


Figure 7. Occupancy and Detection of *Agapostemon virescens* during mid season, July-August, 2019. A) Detection probability B) Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities



OCCUPANCY
Early Season
Covariate-Maximum Temperature

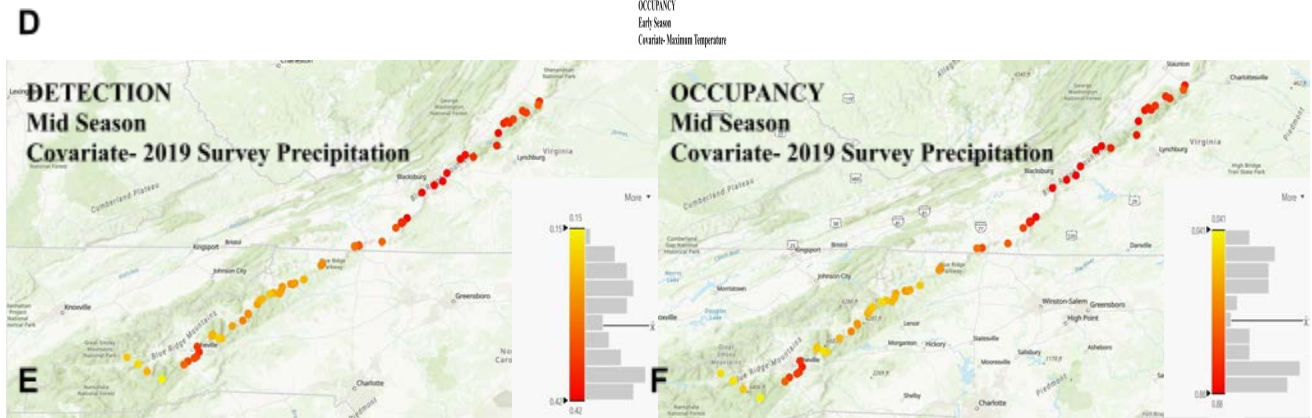
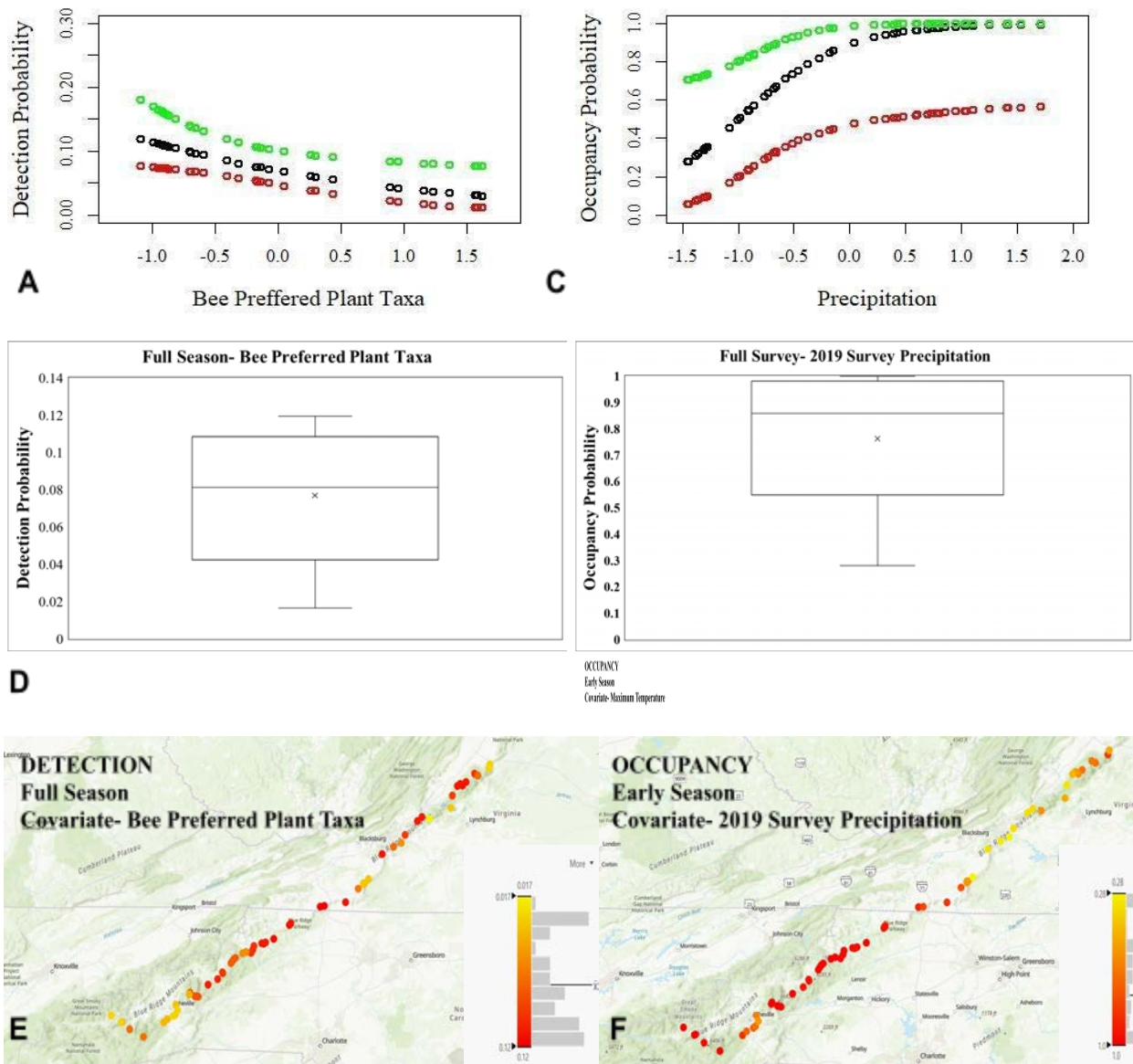
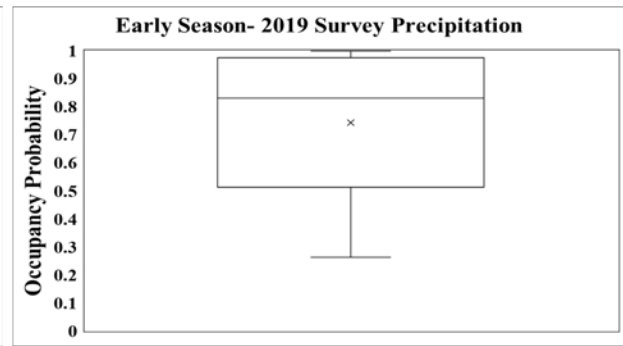
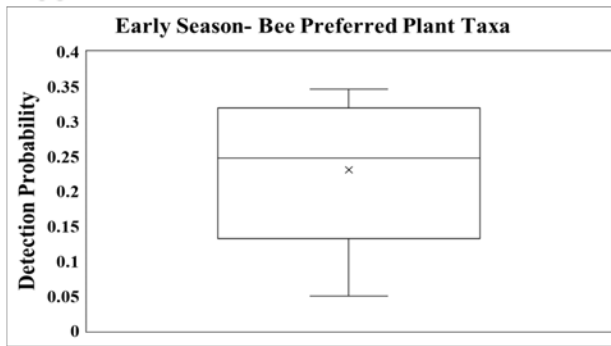
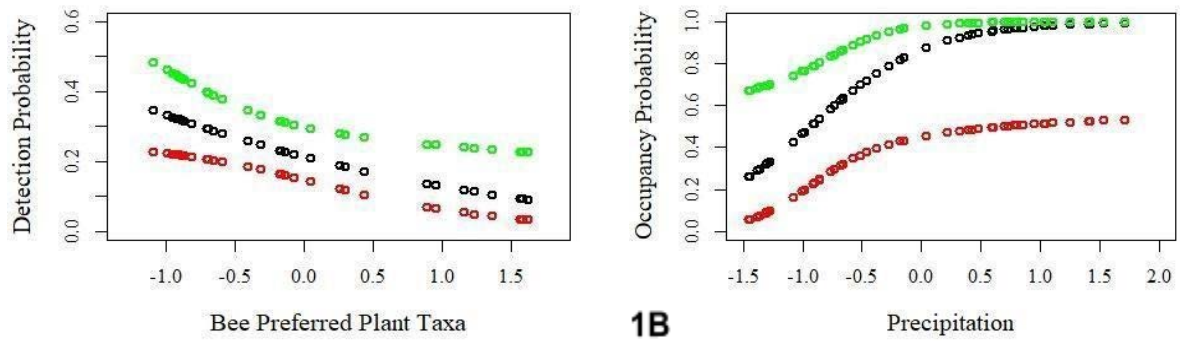


Figure 8. Occupancy and Detection of *Agapostemon sericeus* during mid season, July-August, 2019. A) Detection probability B) Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities *Osmia taurus*



Figures 9. Occupancy and detection of *Osmia taurus* over the full survey, April-October 2019. A) Detection probability B) Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities.



E OCCUPANCY
Early Season
Covariate-Maximum Temperature

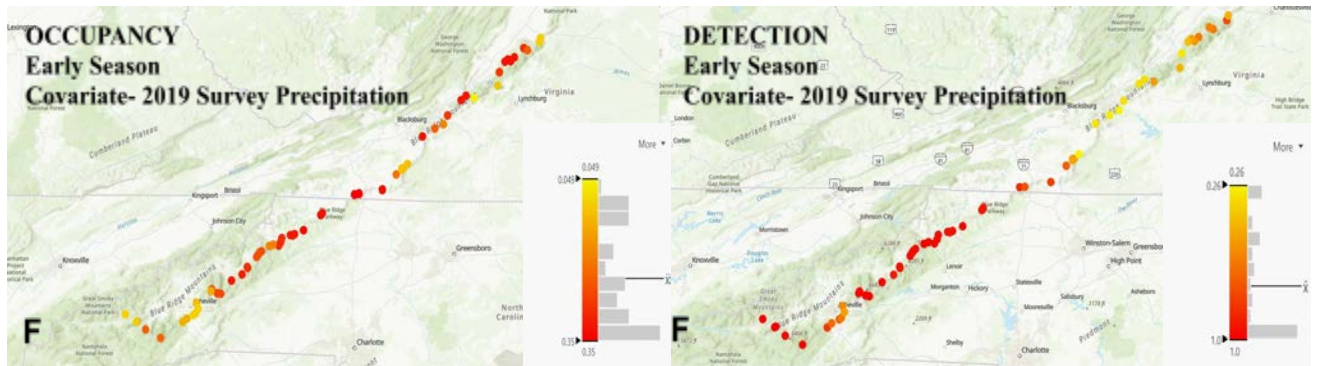


Figure 10. Occupancy and Detection of *Osmia taurus* during early season, April-July, 2019. A) Detection probability B) Occupancy probability C) Boxplot of detection probabilities D) Boxplot of occupancy probabilities E) Site level detection probabilities F) Site level occupancy probabilities

References

- Almeida, Eduardo A., Marcio R. Pie, Seán G. Brady, and Bryan N. Danforth. 2011. “Biogeography and Diversification of Colletid Bees (Hymenoptera: Colletidae): Emerging Patterns from the Southern End of the World.” *Journal of Biogeography* 39 (3): 526–44. doi:10.1111/j.1365-2699.2011.02624.x.
- Boyle, Natalie K., Derek R. Artz, Ola Lundin, Kimiora Ward, Devon Picklum, Gordon I. Wardell, Neal M. Williams, and Theresa L. Pitts-Singer. 2020. “Wildflower Plantings Promote Blue Orchard Bee, *Osmia Lignaria* (Hymenoptera: Megachilidae), Reproduction in California Almond Orchards.” *Ecology and Evolution* 10 (7): 3189–99. doi:10.1002/ece3.5952.
- Burnham, Kenneth P., and David R. Anderson. 1998. “Practical Use of the Information-Theoretic Approach.” *Model Selection and Inference*, 75–117. doi:10.1007/978-1-4757-2917-7_3.
- Campbell, Joshua W., and J. L. Hanula. 2007. “Efficiency of Malaise Traps and Colored Pan Traps for Collecting Flower Visiting Insects from Three Forested Ecosystems.” *Journal of Insect Conservation* 11 (4): 399–408. doi:10.1007/s10841-006-9055-4.
- Cane, James, Robert Minckley, and Linda Kervin. 2000. “Sampling Bees (Hymenoptera: Apiformes) for Pollinator Community Studies: Pitfalls of Pan-Trapping.” *Journal of the Kansas Entomological Society* 73 (4): 225–31. doi:<http://www.jstor.org/stable/25085973>.
- Cardoso, Pedro, Terry L. Erwin, Paulo A.V. Borges, and Tim R. New. 2011. “The Seven Impediments in Invertebrate Conservation and How to Overcome Them.” *Biological Conservation* 144 (11): 2647–55. doi:10.1016/j.biocon.2011.07.024.
- Cole, Jerry S., Rodney B. Siegel, Helen L. Loffland, Morgan W. Tingley, Erin A. Elsey, and Matthew Johnson. 2019. “Explaining the Birds and the Bees: Deriving Habitat Restoration Targets from Multi-species Occupancy Models.” *Ecosphere* 10 (4). doi:10.1002/ecs2.2718.
- Comte, Lise, and Gaël Grenouillet. 2013. “Species Distribution Modelling and Imperfect Detection: Comparing Occupancy versus Consensus Methods.” *Diversity and Distributions* 19 (8): 996–1007. doi:10.1111/ddi.12078.

- De Wan, Amielle A., Patrick J. Sullivan, Arthur J. Lembo, Charles R. Smith, John C. Maerz, James P. Lassoie, and Milo E. Richmond. 2009. "Using Occupancy Models of Forest Breeding Birds to Prioritize Conservation Planning." *Biological Conservation* 142 (5): 982–91. doi:10.1016/j.biocon.2008.12.032.
- Droege, Sam, Vincent J. Tepedino, Gretchen Lebuhn, William Link, Robert L. Minckley, Qian Chen, and Casey Conrad. 2010. "Spatial Patterns of Bee Captures in North American Bowl Trapping Surveys." *Insect Conservation and Diversity* 3 (1): 15–23. doi:10.1111/j.1752-4598.2009.00074.x.
- Drummond, Francis A., Alison C. Dibble, Constance Stubbs, Sara L. Bushmann, John S. Ascher, and Jennifer Ryan. 2017. "A Natural History of Change in Native Bees Associated with Lowbush Blueberry in Maine." *Northeastern Naturalist* 24 (m15): 49–68. doi:10.1656/045.024.m1502.
- Fiske, Ian, and Richard Chandler. 2011. "Unmarked: An r Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance." *Journal of Statistical Software* 43 (10). doi:10.18637/jss.v043.i10.
- Free, J. B. 1960. "The Pollination of Fruit Trees." *Bee World* 41 (6): 141–51. doi:10.1080/0005772x.1960.11096783.
- Gathmann, Achim, and Teja Tscharntke. 2002. "Foraging Ranges of Solitary Bees." *Journal of Animal Ecology* 71 (5): 757–64. doi:10.1046/j.1365-2656.2002.00641.x.
- Hirzel, Alexandre H., and Gwenaëlle Le Lay. 2008. "Habitat Suitability Modelling and Niche Theory." *Journal of Applied Ecology* 45 (5): 1372–81. doi:10.1111/j.1365-2664.2008.01524.x.
- Jha, Ashish, Praveen J, and P.O. Nameer. 2022. "Contrasting Occupancy Models with Presence-Only Models: Does Accounting for Detection Lead to Better Predictions?" *Ecological Modelling* 472: 110105. doi:10.1016/j.ecolmodel.2022.110105.
- Kammerer, Melanie, Sarah C. Goslee, Margaret R. Douglas, John F. Tooker, and Christina M. Grozinger. 2021. "Wild Bees as Winners and Losers: Relative Impacts of Landscape Composition, Quality, and Climate." *Global Change Biology* 27 (6): 1250–65. doi:10.1111/gcb.15485.

- Lawson, David A., and Sean A. Rands. 2019. "The Effects of Rainfall on Plant–Pollinator Interactions." *Arthropod-Plant Interactions* 13 (4): 561–69. doi:10.1007/s11829-019-09686-z.
- Lehmann, David M., and Allison A. Camp. 2021. "A Systematic Scoping Review of the Methodological Approaches and Effects of Pesticide Exposure on Solitary Bees." *PLOS ONE* 16 (5). doi:10.1371/journal.pone.0251197.
- Lim, Kayun, Seunghyun Lee, Michael Orr, and Seunghwan Lee. 2022. "Harrison's Rule Corroborated for the Body Size of Cleptoparasitic Cuckoo Bees (Hymenoptera: Apidae: Nomadinae) and Their Hosts." *Scientific Reports* 12 (1). doi:10.1038/s41598-022-14938-9.
- López-Urbe, Margarita M., Vincent A. Ricigliano, and Michael Simone-Finstrom. 2020. "Defining Pollinator Health: A Holistic Approach Based on Ecological, Genetic, and Physiological Factors." *Annual Review of Animal Biosciences* 8 (1): 269–94. doi:10.1146/annurev-animal-020518-115045.
- MacIvor, J. Scott, and Andrew E. Moore. 2013. "Bees Collect Polyurethane and Polyethylene Plastics as Novel Nest Materials." *Ecosphere* 4 (12): 1–6. doi:10.1890/es13-00308.1.
- MacIvor, J. Scott, and Laurence Packer. 2016. "The Bees among Us: Modelling Occupancy of Solitary Bees." *PLOS ONE* 11 (12). doi:10.1371/journal.pone.0164764.
- MacKenzie, Darryl I., James D. Nichols, Gideon B. Lachman, Sam Droege, J. Andrew Royle, and Catherine A. Langtimm. 2002. "Estimating Site Occupancy Rates When Detection Probabilities Are Less than One." *Ecology* 83 (8): 2248–55. doi:10.1890/0012-9658(2002)083[2248:esorwd]2.0.co;2.
- MacKenzie, Darryl I., James D. Nichols, J. Andrew Royle, Kenneth H. Pollock, Larissa L. Bailey, and James E. Hines. 2018. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. London i pozostałe: Academic Press, an imprint of Elsevier.
- Maher, Stephanie, Fabrizio Manco, and Thomas C. Ings. 2019. "Using Citizen Science to Examine the Nesting Ecology of Ground-nesting Bees." *Ecosphere* 10 (10). doi:10.1002/ecs2.2911.

- Matias, Denise Margaret, Christian Borgemeister, and Henrik von Wehrden. 2017. “Thinking beyond Western Commercial Honeybee Hives: Towards Improved Conservation of Honey Bee Diversity.” *Biodiversity and Conservation* 26 (14): 3499–3504. doi:10.1007/s10531-017-1404-y.
- Mazerolle, Mark. 2023. *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3.2, <https://cran.r-project.org/package=AICcmodavg>.
- McKinney, Matthew I., and Yong-Lak Park. 2012. “Nesting Activity and Behavior of *Osmia Cornifrons* (Hymenoptera: Megachilidae) Elucidated Using Videography.” *Psyche: A Journal of Entomology* 2012: 1–7. doi:10.1155/2012/814097.
- Pellegrino, Ana Cristina, Maria Fernanda Peñaflo, Cristiane Nardi, Wayne Bezner-Kerr, Christopher G. Guglielmo, José Maurício Bento, and Jeremy N. McNeil. 2013. “Weather Forecasting by Insects: Modified Sexual Behaviour in Response to Atmospheric Pressure Changes.” *PLoS ONE* 8 (10). doi:10.1371/journal.pone.0075004.
- Perkins-Taylor, Ian E, and Jennifer K Frey. 2020. “Predicting the Distribution of a Rare Chipmunk (*Neotamias Quadrivittatus Oscuraensis*): Comparing Maxent and Occupancy Models.” *Journal of Mammalogy* 101 (4): 1035–48. doi:10.1093/jmammal/gyaa057.
- Pettersson, Mats W., and Erik Sjödin. 2000. “Effects of Experimental Plant Density Reductions on Plant Choice and Foraging Behaviour of Bees (Hymenoptera:Apoidea).” *Acta Agriculturae Scandinavica, Section B - Soil & Plant Science* 50 (1): 40–46. doi:10.1080/090647100750014402.
- Pitts-Singer, Theresa L., and James H. Cane. 2011. “The Alfalfa Leafcutting Bee, *Megachile Rotundata*: The World’s Most Intensively Managed Solitary Bee.” *Annual Review of Entomology* 56 (1): 221–37. doi:10.1146/annurev-ento-120709-144836.
- PRISM Climate Group, Oregon State University, <https://prism.oregonstate.edu>, data created 4 Feb 2014, accessed 16 Dec 2020.
- Robinson, Samuel V.J., Ralph V. Cartar, Stephen F. Pernal, Riley Waytes, and Shelley E. Hoover. 2023. “Bee Visitation, Pollination Service, and Crop Yield in Commodity and Hybrid Seed Canola.” *Agriculture, Ecosystems & Environment* 347: 108396. doi:10.1016/j.agee.2023.108396.

- Shebl, Mohamed. 2016. "Nesting Biology and Seasonality of Long-Horned Bee *Eucera Nigrilabris* Lepeletier (Hymenoptera, Apidae)." *Sociobiology* 63 (4): 1031. doi:10.13102/sociobiology.v63i4.1181.
- Sih, Andrew, and Marie-Sylvie Baltus. 1987. "Patch Size, Pollinator Behavior, and Pollinator Limitation in Catnip." *Ecology* 68 (6): 1679–90. doi:10.2307/1939860.
- Starr, J. R., and B. J. Mason. 1966. "The Capture of Airborne Particles by Water Drops and Simulated Snow Crystals." *Quarterly Journal of the Royal Meteorological Society* 92 (394): 490–99. doi:10.1002/qj.49709239405.
- Steven, Janet C., Thomas P. Rooney, Owen D. Boyle, and Donald M. Waller. 2003. "Density-Dependent Pollinator Visitation and Self-Incompatibility in Upper Great Lakes Populations of *Trillium Grandiflorum*." *Journal of the Torrey Botanical Society* 130 (1): 23. doi:10.2307/3557522.
- Toler, Trent, Edward Evans, and Vincent Tepedino. 2005. "Pan-Trapping for Bees (Hymenoptera : Apiformes) in Utah's West Desert: The Importance of Color Diversity." *The Pan-Pacific Entomologist*, 4, 81 (3): 103–13.
- Vicens, Narcís, and Jordi Bosch. 2000. "Weather-Dependent Pollinator Activity in an Apple Orchard, with Special Reference to *Osmia Cornuta* and *Apis Mellifera* (Hymenoptera: Megachilidae and Apidae)." *Environmental Entomology* 29 (3): 413–20. doi:10.1603/0046-225x-29.3.413.
- Westerberg, Lars, Hilda-Linn Berglund, Dennis Jonason, and Per Milberg. 2021. "Color Pan Traps Often Catch Less When There Are More Flowers Around." *Ecology and Evolution* 11 (9): 3830–40. doi:10.1002/ece3.7252.
- Zarrillo, Tracy A., John S. Ascher, Jason Gibbs, and Kimberly A. Stoner. 2016. "New and Noteworthy Records of Bees (Hymenoptera: Apoidea: Anthophila) for Connecticut." *Journal of the Kansas Entomological Society* 89 (2): 138–57. doi:10.2317/0022-8567-89.2.138.

Vita

Drew Milavec was born and raised in Charlotte, North Carolina where he attended Butler High School. He had a love of sports and attended Eckerd College in Saint Petersburg, Florida in the fall of 2016. He accepted an offer to play soccer for the school but after one semester, decided to transfer to Appalachian State University where he obtained his B.S in Biology while minoring in Anthropology. While in his undergraduate studies, Drew discovered passion for science and the outdoors while living in Boone, North Carolina. He learned how to fly fish in the plethora of creeks that covered the area, how to rock climb, learned jiu-jitsu, played on the Appalachian State Club Soccer team, held multiple jobs, and studied bees. After helping conduct a bee survey in the Geib Lab from 2018-2019, he started his Master's project in 2020 using data collected the year prior. He quickly learned through his graduate studies that not all bees are studied equally; social bees got lots of attention from researchers but what seemed like a forgotten group, the solitary bees, received a fraction of the research. He decided to learn more about solitary bees and conduct his research project on them. He was accepted to two conferences to present his work on solitary bees but was only able to attend one conference because of COVID. Drew's goal in life is to love the land, be able to fund his passion for fishing and climbing, and to never slow down.