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Bee Diversity and Abundance During Peach Bloom in South Carolina, United States

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ABSTRACT

Peach (*Prunus persica* [L.] Batsch) is an important speciality fruit crop in the United States. Peach is self-compatible, but bee pollination enhances fruit sets and diverse populations improve pollination efficiency. However, the bee diversity and abundance in peach orchards in South Carolina are unknown. To understand this, we sampled bees during peach tree bloom at two locations in South Carolina—the Clemson University Musser Fruit Research Center (MFRC) and a peach farm in Ridge Spring, South Carolina. Overall, a total of 651 bees were collected from peach orchards, of which *Bombus* (37%) and *Apis* (32%) were the most dominant genera, followed by *Eucera* (14%), *Andrena* (8%) and *Habropoda* (5%). Diversity indices indicate higher species richness and diversity at the Ridge Spring farm than at MFRC. Dominant species at the MFRC were *Apis mellifera* (36.77%), *Bombus bimaculatus* (29.1%), *B. griseocolis* (12%) and *Eucera hamata* (8%). In contrast, the Ridge Spring farm was dominated by *A. mellifera* (24.17%), *Habropoda laboriosa* (12%), *Andrena barbara* (12%), *E. atriventris* (11.72%) and *B. bimaculatus* (11.35%). In comparing the effectiveness of sampling methods, blue vane traps (BVTs) captured more bees than aerial sweep netting. Furthermore, BVTs predominantly captured larger-sized bees, while smaller-sized bees were more frequently collected using sweep netting. Throughout peach bloom, differences in bee abundance were observed over time as well. Our study sheds light on the bee diversity and abundance in South Carolina peach orchards, revealing variations between locations. This knowledge of bee diversity and abundance will provide baseline information on bee communities in peach orchards and will help develop suitable pollinator conservation programs.

1 | Introduction

Insect pollinators play a vital role in ecosystem function, providing pollination services to more than 85% of flowering plants (Dar et al. 2016; Ollerton 2017). Bees (Apoidea: Anthophila) are known as predominant pollinators, constituting about 92% of the pollination services, followed by dipterans and lepidopterans (Ollerton, Winfree, and Tarrant 2011; Rader et al. 2020). The honey bee (*Apis mellifera*) is considered a principal species for crop pollination and is often introduced to fruit crops during bloom to enhance pollination; however, the presence of wild pollinating insects like bumblebees (*Bombus* spp.) and solitary bees improves insect-mediated crop pollination (Eeraerts, Smagghe, and Meeus 2020; Garibaldi et al. 2013). Understanding pollinator abundance, that is, the number of individuals of a given species, and pollinator diversity, that is, the number of species in a given collection, is critical in maintaining an optimal balance between managed honeybees and wild bee populations. It also helps in developing informed management schemes and policies for bee conservation (Aizen and Feinsinger 1994; Winfree et al. 2009).

Landscape structure and surrounding factors such as floral diversity, honeybee hives and habitat type (closed and open) could

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influence observed bee communities in fruit orchards. Local plant diversity across semi-natural habitats supports wild bee communities in apple orchards by providing floral and nesting resources (Kammerer et al. 2016; Bartholomée et al. 2020), whereas proximity to woodlands drives pollinator visitation in apple orchard ecosystems (Joshi et al. 2016). Honeybees provide primary pollination services in commercial fields and simplified landscapes (Gibbs et al. 2016; Isaacs and Kirk 2010), whereas wild bees supply the majority of crop pollination requirements in more complex ecosystems and natural habitats (Isaacs and Kirk 2010; Mallinger and Gratton 2015; Winfree et al. 2008). However, the use of managed honeybees should also be considered while assessing wild bee communities. The interactions between managed bees and wild bees can be classified as (1) competition for floral and nesting resources, (2) indirect effects via changes in plant communities and (3) transmission of pathogens, which also varies with landscapes and production systems (Mallinger, Gaines-Day, and Gratton 2017). Angelella, McCullough, and O'Rourke (2021) found that honeybee hives decreased wild bee abundance and richness in fruit farms regardless of wildflower strips, whereas Clair et al. (2022) claim that agroecosystem diversity shapes wild bee communities independent of managed honeybees. However, the functional importance of bee diversity constituting managed honeybees and wild bees should be investigated specific to production systems because co-existing managed and wild bees in optimal abundance and diversity could provide synergistic benefits. For example, bumblebee abundance improves the pollination behavior of honeybees in sweet cherry orchards due to functional complementarity and different foraging behaviors, resulting in increased visitation rate and probability of row changes to enhance crop pollination (Eeraerts, Smagghe, and Meeus 2020). Similarly, honeybees and bumblebees increase almond yield in pollinator-dependent (Brittain et al. 2013) and pollinator-independent varieties (Sáez et al. 2020). Despite their pivotal role in enhancing crop pollination, our understanding of bee abundance and diversity, as well as our efforts to protect them, are restricted in limited production systems.

Honeybees pollinate over 130 fruits and vegetables, including apples, peaches, cherries, apricots, almonds, okra, potatoes, onions and others (USDA 2020). The plant reproduction mode, that is, self-compatible or self-incompatible, determines the benefits of bee-mediated pollination. Self-incompatible crops such as sweet cherry (*Prunus avium*), apricot (*P. armeniaca*) and apple (*Malus domestica*) are indeed dependent on bee-mediated pollination for successful reproduction (Gibbs et al. 2017; Joshi et al. 2015), but self-compatible crops such as sour cherry (*P. cerasus*), peach (*P. persica*) and plum (*P. domestica*) are also benefited by bee pollination (Abrol, Sharma, and Monobrullah 2005; Dar et al. 2016). Bee pollinators are essential for different cropping systems, whether self-compatible or -incompatible, in enhancing pollination efficiency, improving crop yields and ensuring global food security.

Peach (*Prunus persica* [L.] Batsch) is an important stone fruit commodity cultivated worldwide, with production concentration in China, followed by the European Union, Turkey, the United States, Chile and Russia. In the United States, California is the leading producer, whereas South Carolina and Georgia rank second and third, respectively, producing peaches primarily for fresh market consumption (USDA-NASS 2022). Peach production is mainly driven by fruit size, quality and shape so crop load needs to be optimized for fruit marketability. The optimal fruit set for peach is 15%–20% of bloom (Westwood 1993). Although peach is a self-compatible crop, bees have been found to increase fruit set and crop yield (Benedek and Nyeki 1996; Weinbaum, Polito, and Kester 1986; Zhang et al. 2015). Comparing bee visits in an open-pollinated system and by hand pollination revealed significantly higher fruit set when bees were present compared to a system without bee visits, clearly indicating the role of pollinators in enhancing peach fruit production (Abrol, Sharma, and Monobrullah 2005; Chaudhary 2008). However, the variation in pollination efficiency among different bee taxa could also affect fruit set and quality (Dong et al. 2011). For example, in controlled conditions, peach flowers pollinated by bumblebee *Bombus hypocrita* had larger fruit diameter and earlier fruit ripening than those pollinated by honeybee *Apis mellifera* (Dong et al. 2011). It is important to note that these results may not fully represent the dynamics of bee communities in open-field conditions, so caution should be exercised when extrapolating these results to southeastern peach orchards. While crop load optimization is a critical aspect of peach production, ensuring balanced fruit set for optimal yield and quality, this study was specifically designed to explore the unknown diversity and abundance of bee communities in peach orchards with their implications for pollination.

To improve our understanding of peach pollinator communities in the southeastern United States, we surveyed peach orchards during bloom in South Carolina and compared bee communities collected using two different sampling methods. Sampling methods could be active (sweep net and aspirator) or passive (pan traps, vane traps and malaise traps) which are used either individually or in combination based on study system and research aim. For example, sweep net (SWN) is inexpensive and advantageous when matching bees with floral hosts. However, SWN can be employed for limited duration and catch rates could vary with environmental conditions (wind, temperature and time of day). On the other hand, passive sampling such as blue vane traps (BVTs) is effective in targeting different activity periods of species and avoiding collector bias (Kimoto et al. 2012; Hall 2018; Prendergast et al. 2020). Other methods such as pan/bowl traps and malaise traps can also result in high bycatch with the potential to deplete populations of some species (Prendergast et al. 2020). However, the selection of specific sampling method is also affected by the type of cropping systems, landscape architecture and environmental factors. For example, BVTs were consistent and effective, sampling six times as many wild bee individuals as yellow vane traps in both open and wooded habitats within an agricultural landscape, supporting the use of BVTs in ecological census and population monitoring studies (Hall 2018). Although BVTs are effective for sampling wild bees in fruit (apple) orchards than other pan traps (Joshi et al. 2015; Acharya et al. 2022), a combination of sweep netting and BVTs has been recommended to use to complement each other by collecting distinct species and to reduce species caught in BVTs over time (Gibbs et al. 2017). Based on available literature and effectiveness of employing active and passive sampling methods in orchard systems, we selected sweep netting and blue vane traps for our study. Our specific objectives were (i) to document bee abundance and diversity of South Carolina peach orchards and (ii) to compare the effectiveness of sampling methods and establish a relationship

between bee species and sampling methods. Understanding bee diversity and abundance will help maintain an optimal balance between managed honeybees and wild bees to ensure effective pollination and improved crop yield. Since bees are also valued as bioindicators of the environmental quality of agricultural areas and other ecosystems (Kevan 1999; Ruschioni et al. 2013), and their populations are declining due to various abiotic and biotic stressors such as pesticide use, bee parasites and diseases and loss of diverse floral resources (Oldroyd 2007; Pettis et al. 2013; VanEngelsdorp et al. 2007), our work will also provide baseline information on bee communities found during peach bloom in South Carolina. This baseline information can be used to measure changes in bee community structure and abundance due to orchard management practices such as reduced-risk IPM programs and habitat management (Joshi et al. 2015). This information could also be useful for farmers, researchers and policymakers to develop suitable pollinator conservation programs (Aizen and Feinsinger 1994; González-Varo et al. 2013; Joshi et al. 2015; Potts et al. 2010; Winfree et al. 2009).

2 | Material and Methods

2.1 | Sampling Sites

This study was carried out at two different peach farms: (1) The Clemson University Musser Fruit Research Center (MFRC) in Seneca, South Carolina (34.60465, −82.87768) and (2) a commercial peach farm in Ridge Spring, South Carolina (33.82508, −81.69734; Figure 1). These two locations represent major peach production areas in South Carolina—the 'upstate' (MFRC) and the 'ridge' (Ridge Spring farm). These locations were approximately 145 km from each other and none of them were stocked with honeybee colonies for pollination. We sampled four orchard blocks of *P. persica* at each location to assess the bee abundance and diversity in South Carolina peaches. The MFRC is bordered on three sides by a lake with an intervening strip of forest. The MFRC focuses on research programs predominantly on peaches and nectarines but also study other fruit crops including plums, apricots, apples, strawberries, blueberries, blackberries, figs and grapes. The Ridge Spring farm is a leading commercial peach grower on the East Coast growing 6000 acres of peaches and some vegetables including bell pepper, eggplant and broccoli. At the Ridge Spring farm, four peach cultivars (one per block): Summer Gold, Red Top, Zee Lady and Country Sweet, were sampled. At MFRC, four blocks constituting multiple cultivars were sampled. Although different cultivars may affect bee populations due to flower morphology, nectar and pollen production, our sampling window spanned the entire peach bloom period covering early, mid and late flowering of each cultivar. Bee samples from the four blocks were pooled to represent the bee population at each location.

2.2 | Bee Collection

In spring of 2021 and 2022, bee sampling was conducted during peach bloom starting early March through the first week of April. Each year, five field trips were made to each location to cover the early, full and late peach flowering period until petal fall. We used aerial sweep netting as an active sampling method and blue vane traps (BVTs) as a passive method to capture diverse populations of bee species (Gibbs et al. 2017; Prendergast et al. 2020). At each sampling site, six BVTs in spring 2021 and four BVTs in spring 2022 were deployed in each block at the bud-break stage (i.e., approximately 1 week before peach flowers fully open) in a triangle pattern to cover different parts of each orchard block. BVTs were positioned in row middles (between the trees) at 1.5 m high using wooden stakes. On each trip, we visually inspected the BVTs for trapped bees and transferred them to 50-mL centrifuge tubes. BVTs were cleaned with ethanol wipes and placed back on the wooden stake. No detergent or soap water was used to fill traps for bee collection in consideration of our follow-up experiments focused on pollen removed from collected bees. In aerial netting, during each trip, we allocated 30 min per block to conduct 60 sweeps across the tree canopy between 10:00 AM and 3:00 PM. This method allowed us to collect bees visiting peach flowers and traversing around the trees. All of the collected bees were transferred to 50-mL centrifuge tubes and were placed on ice until brought to the lab and stored at 4°C.

2.3 | Bee Identification

For morphological identification, we followed a similar procedure as described in Tayal, Wilson, and Cieniewicz (2023). Since a subset of bees were identified to only genus level in Tayal, Wilson, and Cieniewicz (2023) to explore a relationship between virus-positive pollen and bee genera, this study focuses on identifying all collected bees ($N = 651$) to species level (regardless of virus testing) to characterise bee diversity in peach orchards. Briefly, each specimen was visualized at a variable magnification (3.5×–90×) dependent on the characteristics used for ID under a simul-focal stereo zoom microscope (AmScope SM-3T Series Trinocular LED Stereo Microscope, United Scope LLC, Irvine, CA, USA) with a 144-LED ring light, and identification was performed using an online source DiscoverLife (discoverlife.org, Ascher and Pickering 2016). However, for the group *Andrena*, Mike Arduser's keys (Arduser 2015) were used to narrow down to subgeneric level before proceeding to employ the DiscoverLife Keys. Also, we carefully verified each specimen's identification by cross-referencing the original species descriptions listed in DiscoverLife (Gibbs et al. 2017; Tayal, Wilson, and Cieniewicz 2023).

We employed DNA barcoding of the mitochondrial cytochrome oxidase I (COI) gene on a subset of bee samples ($N = 20$) to validate our morphological identification. Based on the morphological identification, we selected one specimen of major species from each location (e.g., for *Apis mellifera*, we used one specimen from MFRC and one specimen from the Ridge Spring farm, with other minor species taken from either location) for COI barcoding. For bee DNA extraction, the middle leg was removed and flash frozen in liquid nitrogen. Bee legs were homogenised using sterile grinding beads (BBs) and mixer mill at 30 Hz for 3 min. As per the E.Z.N.A. Insect DNA Kit instructions (Omega, Bio-Tek, Norcross, GA, USA), 350 μL CTL buffer and 25 μL proteinase K solution was added to each sample, followed by brief vortexing. Samples were incubated for 30 min at 37°C for tissue solubilization and followed the protocol as instructed by the manufacturer. DNA concentration and quality were assessed using the Nanodrop and stored at −80°C for downstream applications.

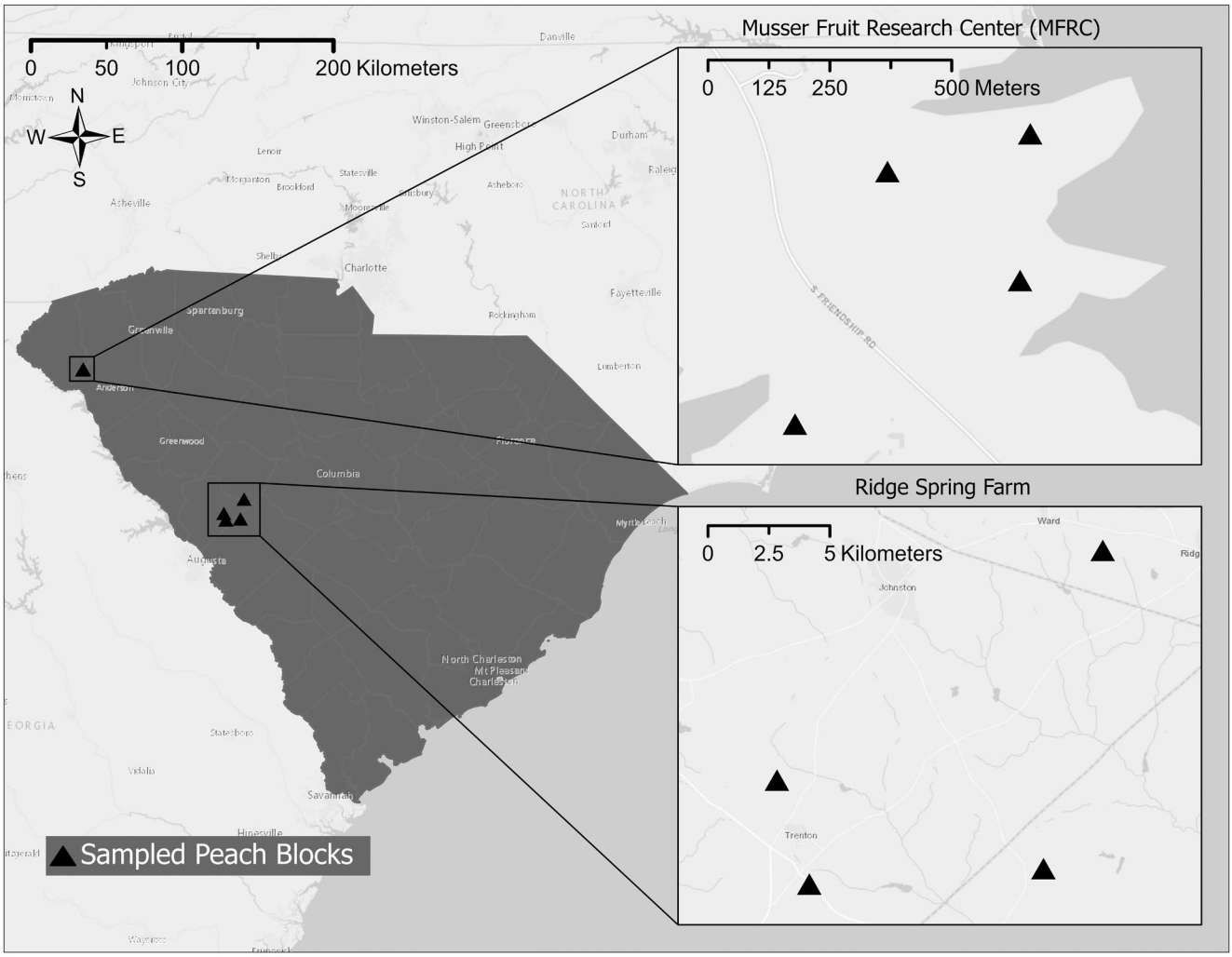


FIGURE 1 | This map illustrates the locations of peach orchards: Clemson University Musser Fruit Research Center (MFRC) and Ridge Spring farm used for bee sampling. Each triangle (▲) represents the peach block within the sampling orchard where bees were collected.

PCRs were set up to amplify the ~710 bp mitochondrial cytochrome oxidase I (COI) region using primers 'HCO2198' and 'LCO1490' (Folmer et al. 1994). PCRs were set up using the Promega Go Taq DNA Polymerase (Thermo Fisher Scientific, MA, USA) with the following cycling conditions: Initial denaturation at 95°C for 2 min, denaturation at 95°C for 30 s, annealing at 52°C for 30 s, extension at 72°C for 1 min for 35 cycles, final extension at 72°C for 10 min and a hold step at 4°C. PCR products were resolved on a 1.5% agarose gel and bidirectionally Sanger sequenced using the PCR primers (Eurofins Genomics LLC.). Sequencing reads were assembled, manually edited and the primer sequences were trimmed off in SeqMan Pro (DNASTAR Inc.). The consensus sequence was saved as a .fas file format and sequences were mapped to a reference database using NCBI BLAST. Voucher specimens for all species are maintained at the Clemson University Arthropod Collection Museum, Clemson, SC.

2.4 | Data Analysis

Since most of the data were insect counts, we separated the total number of bees into different taxonomic groups, that is, genus and species level for each location. Diversity indices: (i) Shannon–Weiner index ($H' = -\sum Pi \ln Pi$) and (ii) Simpson's index ($D = 1/\sum Pi^2$)—where Pi is the relative number of each species (ni/N), ni is the number of species found in total number of species (N) and ln is the natural log—were calculated (O'Brien and Arathi 2019). The Shannon diversity index values between both farms were compared using the Hutcheson t-test (Hutcheson 1970). The effect of the sampling method (i.e., BVTs vs. aerial netting) was compared using the nonparametric Kruskal–Wallis test. We also performed a chi-square test to determine the relationship between the sampling method and bee genera. All analyses were carried out using Microsoft Excel and JMP (Statistical Analysis Software (SAS) Institute, Cary, NC, USA).

3 | Results

3.1 | Bee Diversity Indices

We estimated two diversity indices, the Shannon–Weiner index and Simpson–diversity index, for MFRC and Ridge Spring farm to assess bee diversity. A significant difference in species diversity as computed by Shannon–Weiner diversity index estimate between two farms (MFRC: 1.75, Ridge Spring farm: 2.18, $t = 5.8$,

$p < 0.0001$) was observed (Figure 2A). Similarly, Simpson diversity index estimates were higher for the Ridge Spring farm ($D = 0.87$) compared to the MFRC ($D = 0.75$), indicating a more diverse population at the Ridge Spring farm than MFRC (Figure 2B).

3.2 | Bee Species Composition at Peach Farms

In total, we collected 651 bees belonging to 11 different bee genera and 24 species in our 2-year survey during peach bloom (Table 1). Overall, *Bombus* spp. and *Apis* represented 67% of the bees in our collection, followed by *Eucera* spp. (14%), *Andrena* spp. (8%), *Habropoda* spp. (6%) and *Xylocopa* spp. (3%) (Figure 3). A few specimens of other genera including *Colletes*, *Megachile* and *Halictus*, were also found in peach orchards. At the MFRC, we found a total of 378 individual bees belonging to seven different genera and 15 species. *Apis mellifera* (37%) and *Bombus bimaculatus* (29%) were the dominant species at MFRC representing 66% of the collection followed by *B. griseocolis* (12%) and *Eucera hamata* (8%). Other species included *Xylocopa virginica*, *B. impatiens*, *B. pennsylvanicus* and *B. auricoms*. A few specimens of *E. atriventris* and *Habropoda laboriosa* were also found at MFRC (Table 1).

At the Ridge Spring farm, we collected a total of 273 bees belonging to 11 different genera from 20 species. Similar to MFRC, *Apis mellifera* (24.17%) was the most abundant species collected at the Ridge Spring farm; however, the abundance of *Habropoda laboriosa* (12.2%), *E. atriventris* (11.9%), *B. bimaculatus* (11.5%), *Andrena barbara* (11.1%) and *E. hamata* (9.3%) was comparable. Other species included *B. impatiens* (7%), *B. griseocolis* (4.1%) and *Andrena perplexa* (1.5%). The MFRC and Ridge Spring farm exhibited four and nine unique bee species, respectively, and shared a common presence of 11 bee species (Figure 4). Representative pictures of major bee species can be found in Figures S1 and S2.

3.3 | Distribution of Bee Communities Over the Peach Bloom Period

We further assessed the distribution of major bee genera spanning early bloom, full bloom and late bloom periods at each location. At MFRC, *Apis* was dominant in early to full bloom, whereas the abundance of *Bombus* was higher in the late bloom period, consistent in 2021 and 2022 (Figure 5A). At the Ridge Spring farm, the distribution of five dominant genera, *Apis*, *Bombus*, *Eucera*, *Habropoda* and *Andrena*, was assessed. In contrast to the MFRC, there was an absence of a dominant genus pattern at Ridge Spring farm with all genera prevalent throughout the bloom period. Notably, *Habropoda*, *Andrena* and *Apis* were dominant in the early- to full-bloom stages, with a subsequent increase in the abundance of *Apis* and Eucera at full bloom (Figure 5B). Similar to MFRC, the prevalence of *Bombus* surged by the first week of April (late bloom), which was observed in both 2021 and 2022 (Figure 5B).

3.4 | Validation in Morphological Identification With DNA Barcoding

Our COI sequencing analysis shows that 18 of 20 specimens confirmed morphological identification with query cover > 97% and per cent identity > 90% except for *B. impatiens* (88.78%; Table 2). However, *Eucera atriventris* sampled from MFRC and the Ridge Spring farm mapped to the *E. acerba* accession in GenBank with query cover of 100% and per cent identity of > 97%. No records of *E. atriventris* COI sequences were found in NCBI database; thus, we decided to use the morphological identification and now have deposited a reference sequence for *E. atriventris*.

3.5 | Comparison of Collection Methods

We compared the bee abundance between two collection methods, that is, BVTs and the aerial sweep netting. Although we did not find any significant difference in the total number of bees collected between BVTs and aerial netting ($H = 1.96$, $p = 0.1087$), more bees were captured in BVTs compared to aerial netting (Figure 6A). Further establishing the relationship between sampling method and bee diversity, chi-square analysis showed a significant association between major bee genera (*Apis*, *Bombus*, *Habropoda*, *Andrena*, *Eucera and Xylocopa*) and sampling methods. *Bombus* and *Eucera* were predominantly captured using BVTs, whereas aerial netting was more effective for trapping *Apis* spp. (Figure 6B). In BVTs, *Bombus* represented 49.1% of the collected bees followed by *Eucera* (18.5%), *Apis* (16%), *Andrena* (9.7%) and *Habropoda* (5.1%). Sweep netting captured more than

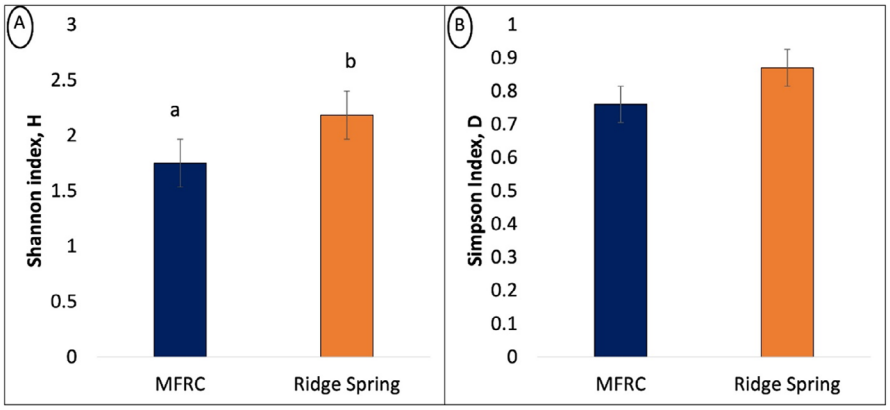


FIGURE 2 | Comparison of diversity indices: (A) Shannon–Weiner index and (B) Simpson index values for the bee species during peach bloom at Musser Fruit Research Center (MFRC) and the Ridge Spring farm in South Carolina. Different letters indicate significant differences (Hutcheson *t*-test, $p < 0.05$). [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 | List of different bee species and their abundance found at Musser Fruit Research Center (MFRC) and the Ridge Spring farm in South Carolina.

Bee species	MFRC	Ridge Spring	Total no. of bees
Apis mellifera	139	66	205
Bombus bimaculatus	110	31	141
Bombus griseocolis	45	11	56
Eucera hamata	30	25	55
Andrena barbara	4	33	37
Habropoda laboriosa	3	33	36
Eucera atriventris	3	32	35
Bombus impatiens	10	19	29
Xylocopa virginica	15	3	18
Agapostemon viriscens	4	2	6
Bombus auricomus	6	0	6
Bombus pennsylvanicus	6	0	6
Andrena perplexa	0	4	4
Colletes thoracicus	0	3	3
Andrena commoda	1	1	2
Andrena dunningi	0	2	2
Andrena miserabilis	0	2	2
Megachile xylocopoides	0	2	2
Andrena crategi	1	0	1
Andrena fenningeri	1	0	1
Andrena thoracicus	0	1	1
Halictus ligatus	0	1	1
Xylocopa micans	0	1	1
Augochlorella aurata	0	1	1

3/4 of *Apis* spp. followed by *Bombus* (9.8%), *Habropoda* (6.4%) and *Xylocopa* (6.4%; Figure 6B).

4 | Discussion

Our study documenting the abundance and diversity of bee populations provides baseline information on bee communities found in peach orchards in South Carolina. In our 2-year survey, 651 individual bees were captured during peach bloom, comprising 24 bee species belonging to 11 bee genera. Honeybees (*Apis* spp.) and bumblebees (*Bombus* spp.) were the most dominant bees in our collection. Although the bee species composition was different between orchards in terms of abundance and richness (Figure 2, Table 1), *Apis mellifera* was the most abundant species, followed by *B. bimaculatus*, *B. griseocolis*, *E. hamata*, *Habropoda laboriosa* and *E. atriventris*. The Ridge Spring farm had a significantly higher bee diversity than MFRC (Figure 2); however, the latter had higher bee abundance. The observed differences in pollinator diversity and abundance at both orchards could be attributed to several factors, including landscape complexity, production system, management practices and climate differences (Eeraerts et al. 2017; Eeraerts, Smagghe, and Meeus 2019; Földesi et al. 2016; Olsson et al. 2015; Petersen and Nault 2014).

In South Carolina, orchards are surrounded by heterogeneous landscapes, including natural habitats, fallow fields and diverse crop systems, providing floral and nesting resources for sustaining bee populations (Kennedy et al. 2013). Since more diverse plant species enhance pollinator diversity (Blaauw and Isaacs 2014; Nicholls and Altieri 2013; Williams et al. 2015), the isolated location of the MFRC, surrounded by a lake, may restrict the bees' access to alternative floral resources, resulting in lower bee diversity at the MFRC than at the Ridge Spring farm (Figure 2A,B). The observed higher abundance of dominant species at the MFRC than at the Ridge Spring farm (Table 1) could be attributed to different cultivation and management practices such as pesticide exposure and honeybee colonies. The MFRC is a research farm where different fruit crops and peach cultivars are planted for various purposes, including rootstock seed production, variety evaluations and numerous other horticulture, entomology and pathology experiments (Rodriguez-Bonilla et al. 2023), whereas the Ridge Spring farm is a commercial peach farm producing thousands of tonnes of peaches annually. Since research and commercial orchards use different cultural practices, the specific effects of different management practices on bee populations should be further investigated. Other factors affecting bee populations include proximity to natural habitats and the presence of managed honeybee hives (Joshi et al. 2015; Mallinger and Gratton 2015; Angelella, McCullough, and O'Rourke 2021). Although neutral and negative interactions have been reported between honeybees and wild bees in different production systems (Garibaldi et al. 2013; Mallinger et al. 2017; Angelella, McCullough, and O'Rourke 2021; Clair et al. 2022), our study sites did not have honeybee colonies brought into the orchards, so their impacts on observed wild bee communities cannot be assessed. Peach is self-compatible, so although bee pollination increases fruit set (Benedek and Nyeki 1996; Weinbaum, Polito, and Kester 1986; Zhang et al. 2015), most peach producers do not bring in honeybee hives to their orchards. Optimal fruit set varies by crop and is estimated at 15%–20% of bloom for peach (Westwood 1993; Chen, Okie, and Beckman 2016). While enhanced pollination typically increases fruit set, it may result in higher cost of thinning for the grower. Overloaded trees can lead to smaller- and lower-quality fruits (Westwood 1993), so extensive thinning is required to maintain marketable fruit quality and orchard productivity. Therefore, balancing pollination efficiency with crop load management is essential for achieving optimal fruit production.

Bee abundance and diversity could also vary across regions and countries due to differences in climate, land use and management practices (Kennedy et al. 2013). The warmer and drier climate can influence phenology of both plants and pollinators which could potentially lead to mismatches in pollination timing (Forrest 2015; Shi et al. 2021). Previous studies conducted on pollinator diversity in peach orchards in Jammu and Kashmir,

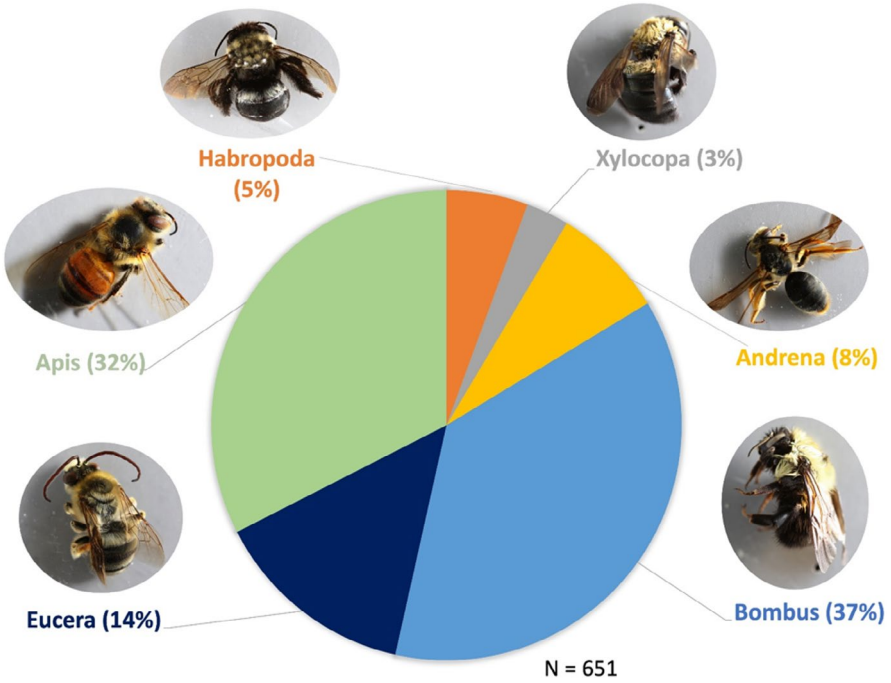


FIGURE 3 | The relative proportion of major bee genera collected during peach bloom in South Carolina; data pooled from the years 2021 and 2022. [Colour figure can be viewed at wileyonlinelibrary.com]

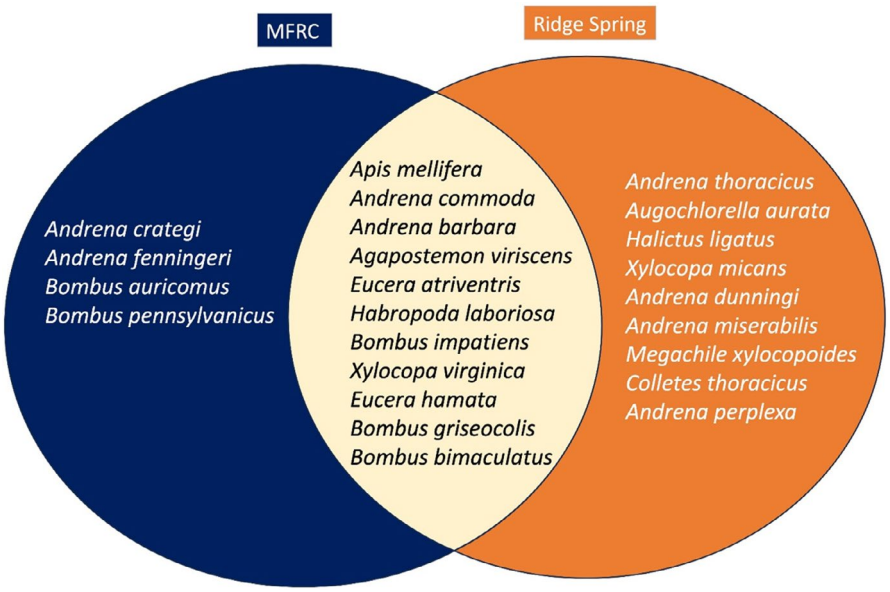


FIGURE 4 | Venn diagram illustrating bee species found only at MFRC (in blue), the Ridge Spring farm (in orange) and the common species found at both locations (in yellow). [Colour figure can be viewed at wileyonlinelibrary.com]

India, found *Apis* spp., *Lassioglossum marganaum*, *Xylocopa* spp. and *Andrena* spp. were the dominant taxa (Abrol, Sharma, and Monobrullah 2005; Dar et al. 2016). In our study, *Apis mellifera*, *Bombus* spp. and *Eucera* spp. were the most dominant species found in South Carolina peach orchards, signifying the importance of geographical conditions like climate, flora, fauna and topography affecting bee communities (Hoiss et al. 2012; Murray, Kuhlmann, and Potts 2009; Pyke et al. 2016). Our results showing a high abundance of bumblebees during peach bloom are consistent with the findings of Eeraerts et al. (2017), who also found the dominance of bumblebees in wild bee population groups in wild cherry orchards during bloom in Belgium.

In general, higher bee abundance is expected to influence pollination services through increased floral visitation rates (Herrera 1989; Mallinger and Gratton 2015); however, a diverse bee population enhances pollination efficiency because of different foraging behavior, emergence and activity periods, pollen load and pollen deposition rates, varying significantly among different bee species (Delaplane and Mayer 2000; Kendall and

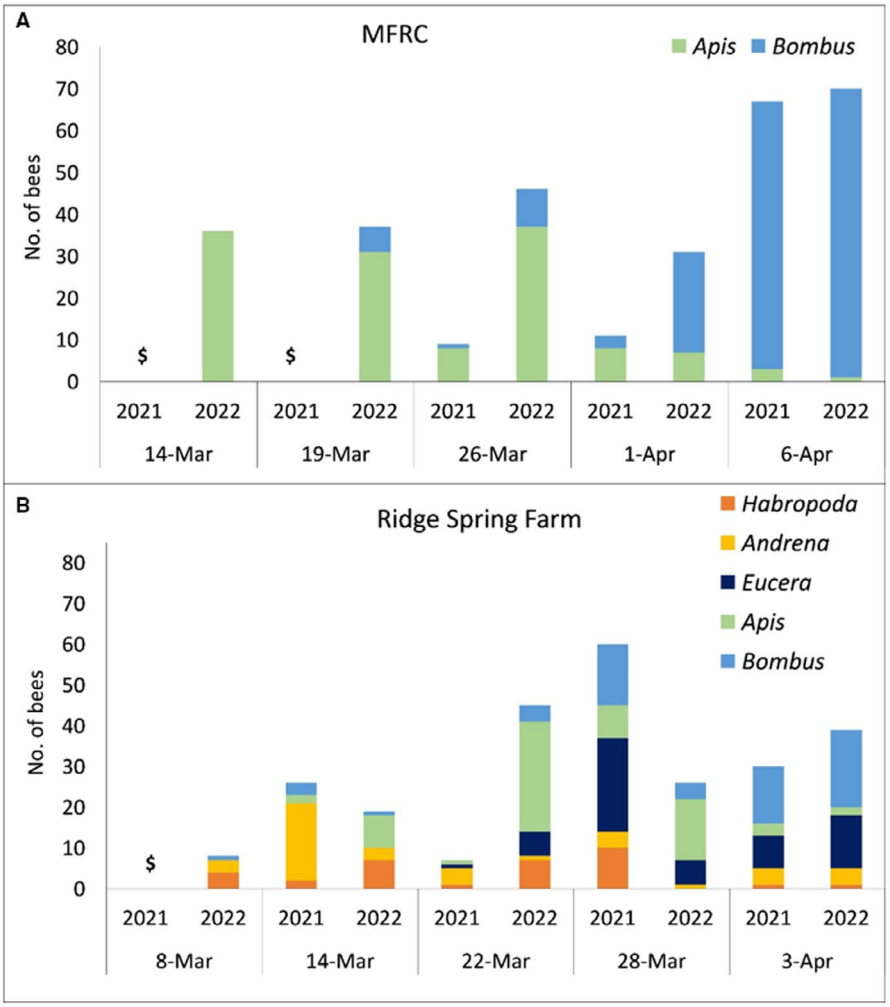


FIGURE 5 | Assessment of dominant bee communities during peach bloom at (A) MFRC and at the (B) Ridge Spring farm. The symbol $ represents a sampling trip in which we were unable to collect bees due to unfavourable weather conditions and hence was excluded from this comparisons. [Colour figure can be viewed at wileyonlinelibrary.com]

Solomon 1973; Monzón, Bosch, and Retana 2004; Thomson and Goodell 2001; Zhang et al. 2015). For example, the presence of wild bees (e.g., bumblebees) enhanced the movement of honeybees in pollinator-dependent crops such as sunflower (Greenleaf and Kremen 2006), apple (Mallinger and Gratton 2015), sweet cherry (Eeraerts, Smagghe, and Meeus 2020) and almond (Brittain et al. 2013), resulting in improved fertilization and fruit set. In apples, *Osmia cornifrons* shown to be at least 80 times more efficient at pollinating apple than honeybees (Kuhn and Ambrose 1984). Although peach is a self-compatible crop, under controlled conditions, pollination by *B. hypocrita* resulted in increased fruit sizes compared to honeybee pollination (Zhang et al. 2015). A possible explanation could be that bees with larger wings could have better flying ability (Mostajeran, Edriss, and Basiri 2006), so they could visit more flowers in a shorter time. Also, larger bee body size could also be associated with larger pollen-carrying capacity, providing an advantage over smaller bees. For example, large-bodied mining bee (*Andrena* spp.) and bumblebee (*Bombus* spp.) carry and deposit more pollen in apple flowers compared to honeybees (Kendall and Solomon 1973; Thomson and Goodell 2001). However, the implications of greenhouse studies in comparison to open-field conditions should be carefully considered. Since greenhouse environments provide controlled settings that allow for detailed observations, they may not fully replicate the ecological interactions and environmental variability present in natural orchard ecosystems (Fletcher, Johnson, and McFarlane 1990; Evans, Hunger, and Siegerist 1999; Pyke et al. 2016). Consequently, while greenhouse studies contribute valuable knowledge, the findings must be interpreted with caution when applied to open-field settings, where environmental factors such as weather, plant diversity and landscape features play significant roles (Forrest 2015; Kammerer et al. 2016; Pyke et al. 2016; Bartholomée et al. 2020; Shi et al. 2021).

Furthermore, assessing the bee communities over the peach bloom period, we found that *Apis* was dominant in the early- to full-bloom period, whereas the *Eucera* and *Bombus* populations were higher in late bloom (Figure 5). Since a pattern of dominance of different bee taxa during peach bloom stages is observed, future research should focus on determining the functional importance of bee abundance and diversity on pollination efficiency and fruit set in peach orchards. Although peaches are relatively low in nectar production compared to other stone fruits (Nyeki et al. 2001), the abundance of different bee taxa could also be affected by the availability of other food resources (Blaauw and Isaacs 2014; Gilpin et al. 2022; Nyeki et al. 2001).

TABLE 2 | Summary of confirmation of morphological identification of bee specimens with COI barcoding, and their comparison with reference accessions through NCBI BLAST analysis.

Specimen no.	Sampling site	Morphological ID	COI barcoding ID	GenBank accession (from this study)	QC%	% ID	Reference accession
1	MFRC	*Agopostemon viriscens*	*Agopostemon viriscens*	PP512759	100%	100%	MG337211.1
2	Ridge Spring	*Agopostemon viriscens*	*Agopostemon viriscens*	PP512760	100%	99.52%	MG342996.1
3	MFRC	*Andrena barbara*	*Andrena barbara*	PP512761	100%	100%	HM422950.1
4	Ridge Spring	*Andrena barbara*	*Andrena barbara*	PP512762	100%	100%	HM422950.1
5	Ridge Spring	*Andrena miserabillis*	*Andrena miserabillis*	PP512763	100%	90.69%	FJ582038.1
6	MFRC	*Apis mellifera*	*Apis mellifera*	PP512764	100%	100%	KU601503.1
7	Ridge Spring	*Apis mellifera*	*Apis mellifera*	PP512765	100%	100%	KU601504.1
8	Ridge Spring	*Bombus bimaculatus*	*Bombus bimaculatus*	PP512766	100%	98.24%	HM422932.1
9	MFRC	*Bombus griseocolis*	*Bombus griseocolis*	PP512767	100%	93.22%	BK063647.1
10	Ridge Spring	*Bombus impatiens*	*Bombus impatiens*	PP512769	100%	88.78%	GU806805.1
11	MFRC	*Bombus pennsylvanicus*	*Bombus pennsylvanicus*	PP512770	97%	97.62%	MG279447.1
12	Ridge Spring	*Colletes thoracicus*	*Colletes thoracicus*	PP512771	100%	99.23%	DQ872687.1
13	MFRC	*Eucera atriventris*	*Eucera acerba*	PP512772	100%	96.47%	MG251089.1
14	Ridge Spring	*Eucera atriventris*	*Eucera acerba*	PP512773	100%	96.52%	MG251089.1
15	MFRC	*Eucera hamata*	*Eucera hamata*	PP512774	100%	98.44	MG251092.1
16	Ridge Spring	*Eucera hamata*	*Eucera hamata*	PP512775	99%	96.64%	MG251092.1
17	MFRC	*Habropoda laboriosa*	*Habropoda laboriosa*	PP512776	100%	99.85%	HQ929823.1
18	Ridge Spring	*Habropoda laboriosa*	*Habropoda laboriosa*	PP512777	100%	100%	HQ929823.1
19	MFRC	*Xylocopa virginica*	*Xylocopa virginica*	PP512778	100%	100%	HQ929860.1
20	Ridge Spring	*Xylocopa virginica*	*Xylocopa virginica*	PP512779	100%	100%	KR898114.1

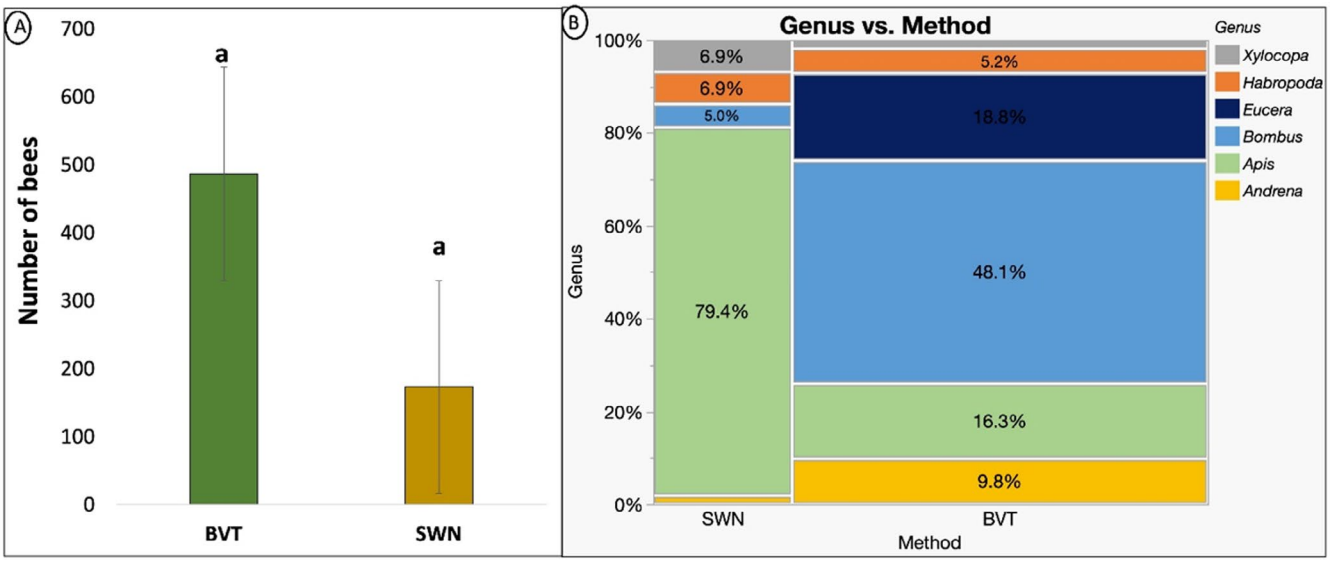


FIGURE 6 | (A) Comparison of bee collection methods: Blue vane traps (BVTs) and sweep netting (SWN). Similar letters indicate nonsignificant differences (Kruskal–Wallis test, $p < 0.05$) and (B) Chi-square analysis of association between collection method and bee genus. [Colour figure can be viewed at wileyonlinelibrary.com]

Future studies on activity patterns of different bees visiting peach flowers and their role in pollination services will enhance our understanding of behavioral ecology of different bee species in peach orchards (Bhalla, Verma, and Dhaliwal 1983; Crane 1972; Free 1993).

Our validation of morphological identification using COI barcoding revealed that, with the exception of *E. atriventris*, all other specimens were identified to their respective species using both methods (Table 2). The observed discrepancy in the COI sequences of *E. atriventris* mapping to the closely related species *E. acerba* is an important consideration of our study. This could be due to the ambiguity caused by DNA barcoding, especially among closely related species with similar genetic markers or due to the absence of sufficient sequences of *E. atriventris* sequences in the NCBI database. Since *E. atriventris* is a 'common' *Eucera* for the eastern United States and *E. acerba* is a western species (Discoverlife.org/Eucera acerba n.d.) and *E. atriventris* can be distinguished from most other Eucera by the long distance from the edge of clypeus to the compound eye (Discoverlife.org/Eucera n.d.), we will uphold our initial morphological identification for these specimens. However, we acknowledge this limitation and suggest further genetic analysis involving additional loci or whole-genome sequencing to fully resolve such taxonomic uncertainties. Interestingly, we observed some evidence of mixed bases in the Sanger-sequencing chromatograms for some specimens of *Agapostemon*, *Andrena*, *Bombus* and *Eucera*, which could be attributed to the existence of potential heteroplasmy in the mitochondrial COI gene. Heteroplasmy is the presence of different mitochondrial haplotypes within an individual and it has been verified in bees such as *Bombus morio* (Ricardo, Francoso, and Arias 2020), Hawaiian *Hylaeus* bees (Magnacca and Brown 2010a, 2010b) and *Halictus smaragdulus* (Sonet et al. 2018). Although heteroplasmy could affect inferences based on COI barcoding in phylogenetic and population genetic studies (Ricardo, Francoso, and Arias 2020), our reason for analyzing COI barcodes was to help confirm morphological identification. Therefore, although the heteroplasmy observation was interesting, it did not affect our results in a meaningful way.

Comparing the effectiveness of different sampling methods, more bees were captured in BVTs than in aerial sweep netting (Figure 6A). Previously, BVTs have been found to be most effective and recommended for estimating pollinator abundance and diversity in other cropping systems, including apples, sour cherries (Gibbs et al. 2017; Joshi et al. 2015), open and wooded habitats (Hall 2018) and biodiversity hotspots (Prendergast et al. 2020). As previously reported in apple and cherry orchards (Gibbs et al. 2017), we also found that the composition of the bee community was significantly different when using BVTs or sweep netting. The majority of the bees trapped in BVTs were large-bodied *Bombus* spp. and *Eucera* spp., in contrast, sweep netting was more effective for honeybees (Figure 6B). The high trapping rate of *Bombus* spp. and *Eucera* spp. could be due to the light reflectance characteristics of BVTs (Joshi et al. 2015), which mimic the preferred host plants of these bees, attracting long-foraging-range bees to the BVTs (Dawkins and Krebs 1979; Gwynne and Rentz 1983). However, southeastern blueberry bee *Habropoda laboriosa* were captured in comparable proportion in BVTs and sweep netting. It is generally considered that bees captured in blue vane traps have been nonpollinating as they are flying in from adjacent areas (Gibbs et al. 2017) but their functional role needs to be determined as long-tongued bees (e.g., *Eucera hamata*) that do not go to shallow flowers like apple or peach. Using a combination of passive (BVTs) and active (sweep netting) sampling methods complement each other and together constitute a good approach to capture diverse bee populations in peach orchards.

In conclusion, the bee communities of peach orchards in South Carolina are dominated by *A. mellifera* and *B. bimaculatus*, followed by *B. griseocolis*, *E. hamata*, *H. laboriosa* and *E. atriventris*. Bee abundance and diversity vary at both peach orchards;

the Ridge Spring farm had higher diversity but lower abundance, whereas the MFRC had lower diversity but high abundance. The BVTs and sweep netting captured different bee species, so using a combination of them is recommended in such studies. Long-term studies to monitor bee populations over multiple seasons and years, as well as effect of cultural practices, such as pesticide application, and habitat management on bee communities should be investigated. Understanding the effects of climate change on bee behavior, phenology and population dynamics would be crucial to inform conservation strategies. Future work should be focused on studying peach–pollinator interaction, explicitly investigating the functional importance of bee abundance and diversity on peach pollination success and crop yield, which would help maintain optimal balance in bee population for improved crop yield and developing suitable pollinator conservation programs.

Author Contributions

Mandeep Tayal: conceptualization, methodology, data curation, investigation, formal analysis, funding acquisition, writing – original draft, writing – review and editing. **Christopher Wilson:** methodology, data curation, writing – review and editing, investigation. **Zoe Marquez de la Plata:** methodology, data curation, writing – review and editing. **Elizabeth Cieniewicz:** conceptualization, methodology, investigation, supervision, funding acquisition, writing – review and editing, validation.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting our findings of this study are available at the Dryad repository at https://doi.org/10.5061/dryad.stqjq2c9m.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.