Research Topics

Opportunities and challenges for wild bee conservation

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Opportunities and challenges for wild bee conservation

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Editorial: Opportunities and challenges for wild bee conservation

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Editorial on the Research Topic
Opportunities and challenges for wild bee conservation

It is a tragic irony that the advancements in agriculture, technology, and industrialization that have afforded us the opportunity to study the diversity and ecology of wild bees are also driving the destruction of the habitats crucial to sustaining these species. The excitement of discovering previously unknown species or ecological interactions is tempered by an urgent need for research focused on developing effective conservation and restoration strategies. Without such efforts, many bee species and the vital services they provide could be lost from managed landscapes. Although human activities are driving a biodiversity crisis of historic proportions (Cowie et al., 2022), we are thankfully not helpless in this moment. The same spirit of innovation and discovery that fueled our dramatic successes in shaping landscapes and ecosystems around the world offers our best hope for achieving a sustainable and biodiverse future. The articles assembled in this Research Topic on "*Opportunities and Challenges for Wild Bee Conservation*" represent important steps in that direction.

Of key importance to wild bee conservation in mixed-use landscapes is the protection of semi-natural habitats. For example, Heuel et al. found higher bee richness and increased seed set near natural grasslands than near perennial wildflower strips in Germany. Other papers in this Research Topic underscore the value of forests to bee diversity. For example, Edelkind-Vealey et al. report on the diversity of bees associated with urban forest fragments in the southeastern United States and compare community composition between the forest edge and interior. Similarly, Ulyshen et al. characterize the diverse native bee community associated with fire-maintained pine savanna. Two papers highlight the unique bee fauna associated with forest canopies. Dorey et al. document eight new *Hylaeus* species from Fiji, all from the rainforest canopy. Similarly, Cunningham-Minnick et al. demonstrate that the canopies of North American temperate deciduous forests, historically dismissed as suboptimal pollinator habitats, support distinct assemblages of bees compared to those captured nearer to the forest floor.

Despite the immense importance of protecting and properly managing semi-natural habitats, such efforts alone may be insufficient to conserve bees in many degraded landscapes. As noted by Tetlie and Harmon-Threatt, neonicotinoids, which persist in ecosystems long after their application, represent a potential long-term threat to bees. Kueneman et al. similarly stress the negative impacts of land-use changes on solitary ground-nesting bees, which are often overlooked in conservation efforts. Efforts to restore habitats, as discussed by Payne et al., are key to addressing habitat loss and fragmentation. These efforts must include both floral and nesting resources to support diverse bee communities. Similarly, Kline and Joshi argue that urban and agricultural landscapes, often seen as threats to biodiversity, may offer untapped potential for pollinator conservation if managed with bee-friendly strategies.

Improved monitoring techniques are essential to properly assess bee populations and understand how they respond to different habitat conditions. Studies like those by Mathis et al. and MacLeod et al. underscore the importance of non-lethal sampling methods, such as visual distance surveys, which provide more accurate data without introducing biases. Citizen science initiatives, like those described by Kueneman et al. and MacLeod et al., can also play an important role in increasing data availability and filling gaps in our understanding of bee distributions. Finally, Rousseau et al. report on how deficiencies in data quality and quantity are impeding efforts to assess population trends and prioritize conservation actions.

It is clear from these articles that much about wild bees remains to be discovered and that the survival of these species is increasingly threatened by anthropogenic changes. Effective conservation strategies will require the protection and restoration of habitats, the improvement of monitoring techniques, and the sustained dedication of landowners, policy makers, and the general public.

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Harnessing community science to conserve and study ground-nesting bee aggregations

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Protecting diverse solitary ground-nesting bees remains a pivotal conservation concern. Ground-nesting bees are negatively impacted by anthropogenic land use change that often removes suitable nesting habitat from the landscape. Despite their enormous ecological and agricultural contributions to pollination, solitary, ground-nesting bees are often neglected, partly due to the significant obstacle of discovering exactly where these bees establish their nests. To address this limitation, we have developed a 'community science' project to map aggregations of ground-nesting bees globally. In certain locations, their abundances reach astounding levels, sometimes in the millions, but are scarcely known. Utilizing the iNaturalist platform, which permits geo-referencing of site observations and bee identification, we are providing public education and seeking public engagement to document bee aggregations in order to understand the nesting requirements of diverse species and open new opportunities for their conservation. Conservation priorities may then unequivocally be directed to areas of high species richness, nest densities, and nesting sites of rare bees. Such community-led efforts are vital for successful long-term management of native bees and the biotic and abiotic landscape data from nest-site localities can allow modeling to predict nest-site suitability and to readily test such predictions on the ground. Here, we summarize the progress, current limitations, and opportunities of using a global mapping project (GNBee) to direct conservation efforts and research toward solitary ground-nesting bees.

KEYWORDS

ground-nesting bees, solitary bees, nesting aggregation, community science, citizen science (CS), iNaturalist, species occurrence data, conservation

Introduction

Pollination services provided by bees are essential for sustaining the genetic variability in 85% of flowering plants and vital for securing yields of pollinator-dependent crops (Ollerton, 2017; Zattara and Aizen, 2021; Katumo et al., 2022). For 125 million years, bees have coevolved with and facilitated the vast radiation of flowering plants (300,000 angiosperm species), thus establishing terrestrial food webs (Vannette, 2020). To meet the extraordinary demand of pollinating diverse angiosperms, there are approximately 20,000 bee species, which differ greatly in morphology, life history, nesting habits, and the flower species with which they interact (Danforth et al., 2019). Despite the diversity of bee species, significant conservation concerns exist, and loss of bee diversity can negatively impact terrestrial ecosystems by reducing the genetic diversity of plants, which can lead to reduced ecosystem resilience (Potts et al., 2010).

Bees, like many organisms, face threats from human activities, primarily landscape changes, habitat loss, pesticide use, and invasive parasites (Willis Chan et al., 2019; Willis Chan and Raine, 2021; Zattara and Aizen, 2021). Studies, including those related to climate change, have consistently reported declines in bee populations, with shorter-term assessments at local, regional, or country levels (Biesmeijer et al., 2006; Goulson et al., 2008; Bartomeus et al., 2013; Ollerton, 2017; Powney et al., 2019; Simanonok et al., 2021; Janousek et al., 2023). Longer and broader assessments, biased toward the Northern Hemisphere, also confirm the decline in bee abundance and diversity (Sánchez-Bayo and Wyckhuys, 2019; Thomas et al., 2019). Zattara and Aizen (2021) conducted a global-scale study revealing a steady decline in the number of bee species observed since the 1990s, with 25% fewer species reported between 2006 and 2015 compared to before the 1990s. This collective evidence underscores the urgent need for swift actions to prevent further declines in bee populations.

Bees and their environmental struggles are currently experiencing increased attention in the media, and this is resonating with the public. However, this attention is largely centered around honey bees. The honey bee has been lauded as a conservation concern to the public, perhaps at the behest of commercial interests, and as a result, we are seeing an increase in backyard or rooftop honey bee husbandry. Unfortunately, honey bees, while great for inspiring public interest in insects, have overshadowed critical messaging about bee diversity and biologically sound conservation efforts. Managed honey bees, while beneficial in many agriculture settings, have been shown to outcompete native species (Iwasaki and Hogendoorn, 2022; Page and Williams, 2023) and can spread parasites and pathogens (Stout and Morales, 2009; Prendergast et al., 2022). Indeed, the honey bee is to bee diversity as the chicken is to bird diversity, and as a result, society is fixating on the wrong bees.

Subsection 1: Changing our societal perspective to value diverse ground-nesting bees

When people think of bees in the temperate zone, rather than only imagining a honey bee or bumble bee they should also envision solitary bees. Approximately 75% of described bee species are solitary, meaning each female constructs her own nest, provisions her own brood cells and lays her own eggs (i.e., there is no reproductive division of labor or cooperative brood care). If we combine brood parasitic bees, the solitary bees and their brood parasites account for ~90% of all bee species (Danforth et al., 2019).

Most of your average bee's life occurs during development, from egg to larva to pupa, and these stages are often punctuated by diapause (a period of suspended development, either as adults or last instar larvae). Solitary bee flight activity, which may last only a few weeks in many species, begins with their emergence as newly formed adults. Males typically emerge first and mate with females that store sperm in their spermathecae (Danforth et al., 2019). Males then perish, and females are left to choose a nesting site and begin the process of provisioning for the next generation. While each individual species has a relatively short period of adult flight activity, the diversity of species in one area allows for continual emergence and activity that corresponds with the pollination needs of native flowering species in the region. Solitary female bees generally construct and provision brood cells one at a time. They are 'single mothers hard at work', and their work is typically out of sight and underground.

The solitary, below-ground-nesting strategy is believed to be ancestral in bees and is shared with their crabronid wasp ancestors (Debevec et al., 2012; Sann et al., 2018). Ground-nesting is observed in every bee family and all places where bees occur (Danforth et al., 2019). It is estimated that approximately 75% of all bee species are ground-nesting (Antoine and Forrest, 2020; Harmon-Threatt, 2020). A typical bee takes one (or sometimes more) year(s) to develop and receives no additional parental care after the egg is laid. Successful development can only be achieved when bees nest in soils suitable to their biology with preferred environmental conditions (Harmon-Threatt, 2020), and the nesting substrates chosen by females appear to be specific to each species (Cane, 1991; Antoine and Forrest, 2020).

Antoine and Forrest (2020) provide a comprehensive review of ground-nesting bee site preferences in their published paper. They summarize research on abiotic factors, including soil compaction, moisture, temperature, surface features, and slope, that influence suitable nesting habitats. Their review also covers biotic factors that may influence nesting, such as the abundance of natural enemies, the density of conspecifics, and the availability and quality of floral resources. It is therefore not necessary to re-synthesize these attributes here, however it is paramount to convey that there are still substantial gaps in our understanding of ground-nesting bee biology. In a survey of the literature on the approximately 3,000 bee species in America north of Mexico, Harmon-Threatt (2020) examined the literature on 527 randomly selected species and found that only 20% of those species had any information on nesting biology. Indeed, most of our knowledge regarding nesting biology (nest architecture, immature stages of bees, parasites etc.), come from field observations typically done at a single locality, making it difficult to confidently identify general characteristics of each species (Antoine and Forrest, 2020). Several studies of multiple nesting sites and bee species have begun to uncover and compare the nesting depths (Cane and Neff, 2011) and soil parameters of that characterize each species (Tsiolis et al., 2022; Ulyshen et al., 2023). However, these efforts are only scratching the surface of what is possible and what needs to be done. Therefore, we recognize substantial opportunities to improve our understanding of nesting behavior which can be used to improve bee conservation.

Subsection 2: Conservation and efforts to manage and enhance ground-nesting bees

Bee conservation efforts for diverse wild bees principally focus on enhancing floral resources. As a result, ways to promote food resource availability are relatively well developed and include organized efforts, such as planting pollinator gardens, planting wildflower strips in public spaces, planting in unused agricultural lands or edge habitat, and community campaigns like No Mow May (Potts et al., 2003; Sheffield et al., 2008; Mader et al., 2011; Kirk and Howes, 2012; Rosa García and Miñarro, 2014; M'Gonigle et al., 2017). More recently, conservation efforts have expanded to include methods for enhancing nesting resources of above-ground cavity nesters, such as leaf-cutter bees and mason bees (MacIvor and Packer, 2015; Fortel et al., 2016). While the aforementioned strategies have had some positive and some mixed outcomes, they do not address the core limitations for most bee species (Gathmann and Tscharntke, 2002; Potts et al., 2005; Michener, 2007; Williams et al., 2011; Dicks, 2013). Rather, the vast majority of bee species are ground-nesting and limited by available nesting habitat, and with several notable exceptions discussed below and outlined in Table 1, few studies have tried to enhance nesting resources for ground-nesting bee species.

Particularly relevant to conservation of solitary ground-nesting bees, for most species, there is pronounced natal philopatry (i.e., females tend to nest in the same site as their mother), a condition unique, yet preset across diverse groups of animals (Byer and Reid, 2022). Nesting sites for many ground-nesting bee species can remain active for decades (Danforth et al., 2019) and we do not yet know the upper bounds of fidelity to a nesting location for ground-nesting bee species. This is a major component of ground-nesting bee biology that can build community engagement and facilitate research and conservation efforts. Clearly, nesting sites and nesting resources are not ubiquitous across the landscape and are not uniform in their ability to support bee communities (Potts et al., 2003; Grundel et al., 2010). Therefore, increased focus on the soil requirements and resources for ground-nesting species can improve conservation efforts.

To date, only a handful of studies have actively tried to promote the richness and abundance of ground-nesting bee species by constructing man-made or environmentally altered nesting habitat (Table 1). The most successful example of this work pertains to the sole species of managed ground-nesting bees, *Nomia melanderi* (Cane, 2008). Despite *N. melanderi's* peculiar affinity to bare, smooth, damp, salty alkaline soils, this gregarious, generalist bee has become the best studied species of ground-nesting bee in the world (Cane, 2023). Its success as a managed pollinator in the US is largely driven by its ability to propagate within man-made bee beds constructed in the vicinity of alfalfa fields. Since it can tolerate colder temperatures, it emerges when many other bees remain inactive to pollinate alfalfa alongside another managed stem nesting bee, *Megachile rotundata* (Pitts-Singer and Cane, 2011). Together they produce seed valued at $22 billion annually. The pairing of ground-nesting bee biology with agricultural objectives can offer substantial opportunities and benefits in agricultural systems and similar outcomes may be possible for other agricultural crops and non-crop plant species. Thus, there is a natural alliance between farmers and native ground-nesting bees that should be nurtured.

Subsection 3: Citizen science applied to the discovery of ground-nesting bees

Large-scale environmental science often requires a 'community science' approach (also called 'citizen science' or 'participatory science'). In this research methodology, non-professionals contribute their time, energy or expertise to a research aim. Community science makes the activity of discovery and observation available to all, not just a privileged few, and is an effective method of upscaling research projects and adoption of innovations both temporally and spatially (Pocock and Evans, 2014). As a result, research that involves community science is becoming increasingly common and includes projects on climate change, invasive species, conservation biology, ecological restoration, and monitoring of all sorts (Silvertown, 2009; Dance, 2022). For example, the Christmas Bird Count, run by the National Audubon Society, has taken place every year since 1900, generating one of the most impressive biological datasets that we have (63 million observations). Indeed, in many countries, community scientists are the bedrock of biological recording and monitoring.

Community science has previously been applied to projects on bees; for example, identifying the diversity of bees found on flowers across an urban gradient in France (Deguines et al., 2016), and assessing the numbers of squash bees found on farmland in Michigan, USA (Appenfeller et al., 2020). In an encouraging study, Maher et al. (2019) used a community science approach to locate and investigate the nesting requirements of four species of gregarious ground-nesters (394 nesting sites across the UK and Ireland): *Andrena cineraria* and *A. fulva* (Andrenidae), *Halictus rubicundus* (Halictidae) and *Colletes hederae* (Colletidae). Even with the limited foraging ranges of most bees, locating nesting sites is a substantial challenge in studying and/or conserving ground-nesting bees (O'Connor et al., 2012; Antoine and Forrest, 2020). It is therefore significant that a community science project successfully overcame this obstacle, and Maher et al.'s (2019) study also suggests this approach could be used to discover nesting site locations at larger scales. However, to do so, a more robust and sustained effort must be employed.

Project GNBee (GNBee.org) champions a community science approach to research, conservation of ground-nesting bees. This project aims to connect amateur observers (nest site discoverers) to experts in real time, working together to identify and validate new ground-nesting bee records. To date, Project GNBee contains over 2,500 observations of over 240 bee species. Contributions have been made by over 1300 people worldwide, and real-time records can be

TABLE 1 Studies that actively manage ground-nesting bees (excluding *Nomia melanderi*).

Location	Approch	Outcome	Reference
Baden-Württemberg, Germany	Removed vegetation, creating patches of bare ground. Soil nesting bee diversity and richness was recorded.	Increased biodiversity of ground-nesting bees.	Wesserling and Tscharntke (1995)
Surrey, England	Removed vegetation, creating patches of bare ground. Soil nesting bee diversity and richness was recorded.	Increased biodiversity of ground-nesting bees.	Edwards (1996)
West Sussex, England	Removed vegetation, creating patches of bare ground. Soil nesting bee diversity and richness was recorded.	Increased biodiversity of ground-nesting bees.	Edwards (1998)
Oregon, USA	Created experimental plots for endangered legume (Kincaid's lupine).	Documented nesting of *Lasioglossum anhypops.*	Severns (2004)
Oxford, Englend	Constructed 3 x 5 m slightly slopping bays, with a rear vertical face of 30 cm, to attract ground-nesting bees.	All bays were colonized in the first year and 80 solitary bees and wasps were recorded after 3 years.	Gregory and Wright (2005)
Logan, Utah, USA	Made soil plots with and without a pebble layer on top.	Found that flat stream pebbles promoted aggregations of the bee *Halictus rubicundus*.	Cane (2015)
Grand Lyon, France	Constructed 1 m soil squares with varying sand content in an urban setting. Removed plant growth within soil squares.	Documented 16 species of bees nesting in their plots. Soil texture had little influence on bee richness.	Fortel et al. (2006)
Göttingen, Germany	Removed vegetation in grasslands and examined nesting activity rates. Examined effect of adjacent floral resources.	Recoreded that the number of bee nests in areas with removed cover was 14 times higher. Documented a positive corralation between nesting activity and proximity to floral resrouces.	Gardein et al. (2022)
20 regions in Germany	Constructed nesting hills to attract ground-nesting bees.	Increased biodiversity of groud nesting bees. Bees preferred south facing sites with high soil temperatures. Substrate composition played a minor role in community assembly.	Neumüller et al. (2022)
Kent, England	Prepared plots of bare soil within an orchard with the aim of attracting ground-nesting bees.	Found that soil stoniness and increased soil temperature facilitated ground-nesting bees, and that increased vegetation cover and hydraulic conductivity inhibited ground-nesting bees in their study plots. While not significant across the study, soil compaction had a large influence on the length of time for nesting recruitment in the plots.	Tsioli et al. (2022)
Kent, England	Treated areas within apple orchards with herbicide to increase bare ground.	Fourteen species of ground-nesting solitary/eusocial bees were identified over three years and most nests occurred in areas free of vegetation, including areas treated with herbicide.	Fountain et al. (2023)

found at iNaturalist (https://www.inaturalist.org/projects/ground-nesting-bees-3e6882c0-a112-4ddb-b043-1da25638ce96). All observations are geolocated and thus provide the basis for studies of nesting biology, behavior, and ecology of ground-nesting bee species at local, regional and national scales (Figure 1). Furthermore, sampling and gathering observational data at nesting sites can help develop species distribution models to predict where additional nest sites are located and also prioritize conservation efforts at local and regional scales.

Discussion

The development of a robust global database that identifies ground-nesting bee sites has significant implications for understanding native bee ecology and offers new opportunities for native bee conservation. However, we must acknowledge several limitations. First, there is significant observation bias toward common bee species that make large and conspicuous aggregations. While such large aggregations are an intended focal target of Project GNBee, due to their sizable ecological contribution, many species nest at low densities with a few nests scattered over a large geographic area. Still others species nest under leaf litter or in dense vegetation. In these less visible cases, our community-driven approach to uncovering their nesting locations is far more difficult. Therefore, the detectability, which drives the species composition of our observations, will be biased. Second, the quality of our data is limited by the collective knowledge of our community. Thus, we seek experts and experienced amateurs to visit these sites and provide additional observations. Repeated observations from known sites, as well as observations in the literature, not currently available in Project GNBee, will help generate a consensus and

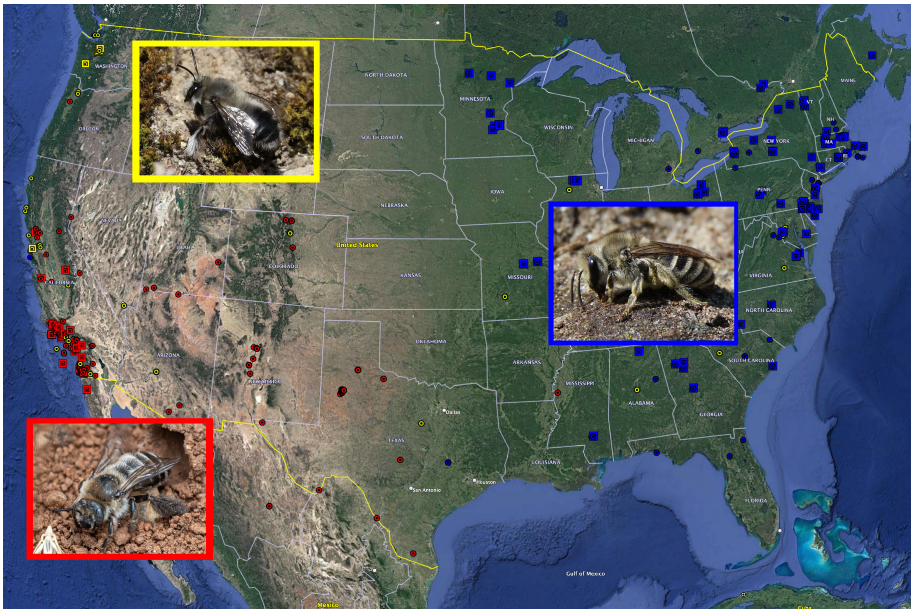

FIGURE 1
Potential to study bees at distinct scales and taxonomic levels: yellow = local and *Anthophora*, red = regional and *Diadasia*, and blue = national and *Colletes*. Yellow squares are records of *Anthophora pacifica*, red squares are records of *Diadasia bituberculata*, and blue squares are records of *Colletes inaequalis*.

improve the quality of the data by adding new sites and tracking bee seasonality and population dynamics through time.

Despite certain limitations and biases, Project GNBee can help fill current gaps in knowledge. The GNBee database has already incorporated rare bee nesting sites with high conservation priority, nest aggregations over 80 years in age, and numerous previously unknown high-density sites, several containing hundreds of thousands to well over a million individual solitary bees (Guilian et al., in prep; Hoge et al., in prep). Thus, we now can meaningfully prioritize discrete locations for research and conservation of ground-nesting bees.

Uniquely, aggregations can connect with people. A nesting aggregation is a place where bees live, much like a place in which humans live. One can return to nesting aggregations day after day to observe bees during their flight activity – a feature not possible in most animal community science projects. As such, these locations are part of a basic, local heritage. This can enhance efforts of property owners and land management agencies to prioritize the conservation of their resident bees. Signage (e.g., ‘Wild bee crossing’) that delivers educational information to the public should also be made available at these sites. Such on-site education and outreach could have profound impact on public sentiment and support. When possible, conservation agencies may seek to extend more robust protection to the most biologically significant nest sites, either through land acquisitions or through partnerships that establish guardians of these sites. We hope to make such recommendations in the future.

Beyond the conservation envelope, we are already able to study and compare the requirements of ground-nesting bees from locations in our own backyards to sites around the world. As such, we can move beyond single site descriptions of nesting biology and begin to understand the broader range of biotic and abiotic conditions that are required for a ground-nesting bee aggregation to persist. Furthermore, we can then attribute the degree of success (based on population size) of these local populations to their nesting conditions. This approach may help uncover meaningful predictors of nesting success within a species, across multiple species, and though space and time. While several attributes may be ‘reliably’ sourced using GIS, many attributes can be validated by the ‘community of scientists’ engaged with the project, who can send samples for further analysis. By using both remote sensing and community participation at scale, we plan to refine our models for predicting where individual bee species will be most likely to nest and how successful they are likely to become. Exploiting this framework, we may offer the building blocks needed to promote a more inclusive and robust community of pollinators that include the ground-nesting bees and lead to their successful management.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

JK: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing. CD: Writing – review & editing. BD: Funding acquisition, Supervision, Writing – review & editing.

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Supplementary material

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Bee-diverse habitats positively affect seed set in wild plant species

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Introduction: Interactions between flowering plants and visiting wild bees are crucial for ensuring pollination and subsequent plant reproductive success. However, bee diversity in an area has rarely been recorded in relation to seed set in native plants. In this project, we investigated the effect of local wild bee communities on seed set in four common wild plant species.

Methods: Potted plants of *Centaurea jacea*, *Cichorium intybus*, *Sinapis arvensis*, and *Salvia pratensis* were placed for pollination experiments, in two distinct habitat types that we expected to show distinct bee communities, namely near-natural grassland and perennial wild flower strips, in Germany.

Results: Our results showed that near-natural grassland had a higher bee species richness and an increased seed set compared with flower strips that displayed a higher bee abundance in most study locations. Although we found effects of bee diversity on seed set, we did not detect a significant effect of bee abundance. Furthermore, the seed set in response to wild bee diversity differed across the plant species.

Discussion: We conclude that bee-friendly habitats ensure a high seed set in wild plants, but that the impact varies between different plant species.

KEYWORDS

pollination, near-natural grassland, wild flower strip, plant reproduction, wild bee

1 Introduction

The majority of plant species in Germany have continually decreased in occurrence over the past six decades, with native plant species experiencing severe declines and with the highest relative losses in species that used to be moderately common (Eichenberg et al., 2020; Jansen et al., 2020). In the modern human-influenced landscape, agricultural land use intensity is steadily increasing (Sirami et al., 2019; Schils et al., 2022) concomitant with the increasing usage of fertilizers and pesticides and the overall homogenization of the landscape (Socher et al., 2013; Gossner et al., 2016). Agricultural intensification results in the population decrease of native plant species because of habitat loss (Robinson and

Sutherland, 2002; Meyer et al., 2015). In addition to these direct drivers, pollinator reductions indirectly affect plant decline. About 78% of angiosperms are dependent on insect pollination (Ollerton et al., 2011), and these species show the strongest population declines (Biesmeijer et al., 2006).

Amongst pollinating insects, wild bees are particularly effective in providing pollination services (Garibaldi et al., 2013). The relationship between melittophilic plants and their pollinators is complex, and the interacting partners depend upon each other. When a visiting bee transfers pollen from another conspecific to the flower stigma, fertilization occurs and subsequently seeds develop. In plant species that depend on cross-pollination, bees therefore directly affect the next generation of their host plants (Turnbull et al., 2000). Bees themselves use flowers mainly as food sources and consequently depend upon them for their own reproduction (Zurbuchen and Müller, 2012; van der Meersch et al., 2022). This results in a loop with bees influencing the food resources for upcoming bee generations by shaping the next generations of plants.

Wild bee species differ in their phenology and in their preferences, including the degree of specialization for specific host plants, resulting in seasonal differences in wild bee communities and plant-bee interaction patterns within any one year (Westrich, 2019). Moreover, bee species richness is directly linked to the diversity of available plants (Zurbuchen and Müller, 2012; Kennedy et al., 2013). Semi-natural habitats that are flower-rich and -diverse act as hosts to the highest numbers of wild bee species, particularly rare and threatened species (Neumüller et al., 2020). In addition to local floral resources, the availability of nesting sites (Requier and Leonhardt, 2020) and the surrounding landscape structure are key factors for bee species diversity and abundance (Söderman et al., 2018; Beckmann et al., 2019; Herbertsson et al., 2021; Baden-Böhm et al., 2023). However, wild bees are negatively affected by modern agricultural management (Winfree et al., 2009), as this results in a loss of adequate habitats and restricts floral resource availability. The lack of food resources is one of the major reasons for bee decline (Biesmeijer et al., 2006; Potts et al., 2010; Scheper et al., 2014). Bees require large amounts of pollen to rear their offspring and are thus directly affected by the decrease of available flowering plants and the loss of flower-rich habitats (Müller et al., 2006). This particularly affects oligolectic (flower-specialized) bees that restrict their visits to a small range of plant species (Müller and Kuhlmann, 2008). The absence of specific host plants in a habitat leads to a lack of the corresponding oligolectic bee species, independently of other living conditions (Westrich, 2019). A decreasing number of wild bees results in fewer potential pollinators and lower pollination services to local flora, which in turn results in reduced food resources for bees. With these effects accumulating over several generations, substantial risks build up for both bees and plants.

The establishment of (wild) flower strips has become a popular measure for counteracting the loss of food resources of wild bees and for ensuring their pollination services in agricultural landscapes (Buhk et al., 2018; Albrecht et al., 2020; Hevia et al., 2021). By placing flower strips close to agricultural fields, crop yield increases because of higher pollinator availability (Tschumi et al., 2016; Dainese et al., 2019; Albrecht et al., 2020). However, this effect decreases with increasing distance to an ecological compensation area (Albrecht et al., 2007).

Crop pollination is essential for the provision of food for the increasing human population (Aizen and Harder, 2009). Thus, many studies have been performed in the context of the effect of bees on crop production for the resulting higher demands for human foodstuffs and on conservation measures to promote crop-pollinating bee species (Kremen et al., 2023; Osterman et al., 2023; Scheper et al., 2023). For example, small patches of native vegetation established within crop fields (prairie strips) increase flower resources for wild bees and positively influence the wild bee community (Kordbacheh et al., 2020) giving greater chances for bee-mediated plant pollination (Borchardt et al., 2023). Another example is, that the proximity to pollinator-supporting wild flower strips increases the quality and quantity of highbush blueberry yield (Blaauw and Isaacs, 2014a).

Nevertheless, the pollination service carried out by wild bees is not only important for the production of crops (Klein et al., 2007), but also ensures pollination in natural ecosystems (Steffan-Dewenter and Tscharntke, 1999; Blaauw and Isaacs, 2014b). Melittophilic plants highly depend on bees, and even plant species that do not solely depend on pollinators for reproduction can increase their seed set by up to 80% when pollinators providing cross-pollination are present (Rodger et al., 2021). The number of produced seeds depends on the number of bee visits and frequently on the bee species (Tobajas et al., 2024). Whereas many crops are pollinated by common and widespread bee species, diverse bees including rare and specialized ones are pollinators of many wild plant species (Garibaldi et al., 2013; Woodcock et al., 2019). However, plants species often differ in their pollinator assemblies. Flowers show specializations to restrict visits or, from the plant's perspective, to filter out ineffective pollinators (Stang et al., 2009; Schwarz et al., 2021). Pollinator specialization can increase pollination efficiency through effective pollen transfer and reduced pollen loss (Fenster et al., 2004). This is important as pollen is a limiting factor in plant reproduction (Knight et al., 2005). The reproductive success of a plant is often measured as seed set, which can be used to quantify the efficiency of pollinators. In a meta-analysis on various wild flower species and their interrelationships with bees, seed set has been shown to be positively correlated to bee visits, although their effects differ vastly among plant species (Herbertsson et al., 2021). For example, bee species richness and abundance have a positive effect on the seed set of native grassland species such as *Campanula glomerata*, but not on *Hypochaeris radicata* (Albrecht et al., 2007). *Salvia frutticosa* and other wild species of Mediterranean scrubland had a reduced seed set after fires that negatively influence the solitary bee community and reduce visitation rates (Ne'eman et al., 2000). In addition to the quantity of seeds, their properties, such as weight, size, or seed coat robustness, can determine the dispersal, persistence, and establishment of the next plant generation (Saatkamp et al., 2019). A higher seed weight is linked to a more robust seed coat that provides protection for the embryo and enables it to survive in less favorable places and during unfavorable times (Niklas, 2008). It is also linked to the endospermic tissue, providing nutrients and the storage of energy required especially for the initial growth of the plantlet (Lamont and Groom, 2013). Therefore, dry seed weight is thought to be a good indicator of available resources to the seedling (Saatkamp et al., 2019).

The surrounding landscape also influences bee-mediated pollination events or seed set (Albrecht et al., 2020; Herbertsson et al., 2021; Ammann et al., 2024). Diverse structures (e.g., open structures for nesting, woody vegetation) and artificial pollinator-promoting structures (e.g., wild flower plantings) in the surrounding landscape have a positive effect on bee diversity (Neumüller et al., 2020; Neumüller et al., 2022), although, as mentioned above, these effects decrease with distance (Albrecht et al., 2007; Ekroos et al., 2015). Notwithstanding, few studies have focused on the impact of the occurring wild bee diversity within a habitat on seed set. Near-natural habitats or areas established as conservation measures for wild bees are thought to promote pollination within a habitat, but pollination success and its dependency on the wild bees of a habitat are only rarely determined for wild plants.

In this study, we have investigated the effect of various habitats and the presence of wild bees on the pollination efficiency of four wild plant species in Germany. Our main goal has been to reveal whether the bee community of a specific habitat is linked to a higher pollination efficiency as measured by seed weight. We have conducted pollination experiments on near-natural grasslands hosting a diverse flora and fauna, and on perennial wild flower strips established as conservation measures for wild bees within the BienABest project (www.bienabest.de) at nine study sites in southern Germany. Potted plants were placed in the field for three days to allow pollination by the bee community of the habitat. The bee abundance and species diversity within each habitat were monitored throughout the season as part of the wild bee monitoring scheme of the BienABest project. The selected plant species, namely *Sinapis arvensis* (Brassicaceae), *Salvia pratensis* (Lamiaceae), *Centaurea jacea* (Asteraceae), and *Chichorium intybus* (Asteraceae) differ in various traits such as phylogeny, blooming phenology, flower color, and flower morphology and are all visited by large numbers of various bee species (Zurbuchen and Müller, 2012; Kuppler et al., 2023). Specifically, we have asked the following questions. (1) Does the wild bee diversity differ between two habitats, namely near-natural grassland and perennial wild flower strips? (2) Does the wild bee diversity of the different habitats affect seed set across different plant species? (3) Do any effects on seed set differ between the tested plant species?

2 Materials and methods

2.1 Study sites

The pollination experiments were performed within agricultural areas at nine different study sites in south-west Germany (see Figure 1A and Supplementary Table S1). The study sites were part of the BienABest project (www.bienabest.de; see Neumüller et al., 2020 and Neumüller et al., 2021 for the BienABest study design and establishment of study plots). The BienABest project aimed to safeguard the ecosystem service of pollination and to enhance wild bee diversity in agricultural landscapes. Flower strips were established as conservation measures at various sites in Germany, accompanied by extensive wild bee monitoring during the years 2018 to 2022.

The study sites extended over 180 km latitudinally and 175 km longitudinally. The landscape of each site was an agricultural matrix

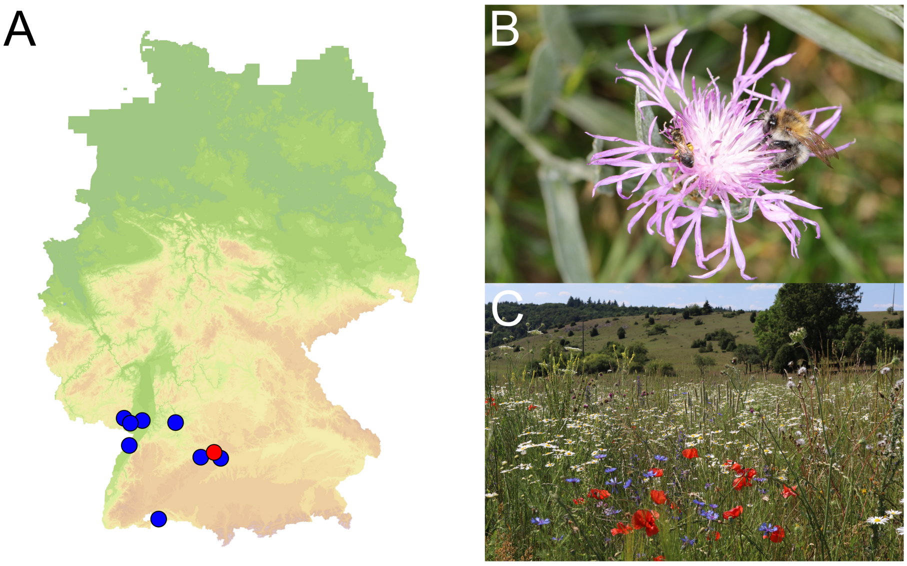

FIGURE 1
(A) Map showing the nine study sites located south-west Germany. Each dot represents a site. Within each site, a total of four plots of 0.3 ha each were investigated. Two plots were located within near-natural grassland areas, and two were identical to the wild flower strips implemented for the BienABest wild bee monitoring. **(B)** *Halictus tumulorum* and *Bombus pascuorum* bees on the study species *Centaurea jacea*. **(C)** Example of a study site on the Swabian Alb (red dot on map 1A): established wild flower planting with *Cichorium intybus* in the foreground, near-natural grassland plots in the background. [Map © GeoBasis-DE / BKG 2018; photos H. Burger].

of arable land and/or intensively-used grassland and incorporated bodies of semi-natural grassland. At each study site, 0.3-ha plots were established on various habitats within a 500-m radius. Two plots each of the two different habitat types were used at each study site, resulting in 36 plots (2 x 2 plots at each of the nine study sites) for the pollination experiments and observed bee data. The pollination experiments were performed on study plots with two different habitat types within each study site: near-natural habitats and perennial wild flower strips (Figure 1C). Near-natural habitat plots were placed in extensively managed grassland such as calcareous grassland, mostly in nature conservation areas. The semi-natural grasslands were characterized by a high diversity of native flowering plants and were rich in diverse structures (e.g., open soil for nesting or woody vegetation). The habitats were managed by occasional grazing by sheep and met the needs of a diverse spectrum of naturally occurring flora and fauna. The wild flower strips were established on tilled arable land in 2017 by using a seed mixture consisting of ca. 50 plant species (autochthonous seeds, provided by Rieger-Hofmann, Blaufelden, Germany). The seed mixture consisted of annual and perennial plant species that are regionally native or cultivated plant species and included the study plant species used in the pollination experiments. Half of each wild flower strip was mown once a year at peak bloom in June as a measure to increase plant diversity and to induce a second bloom, prolonging the blooming season to promote pollinators. When the experiments of this project were performed in the year 2020, the wild flower strips were well established, with mainly perennial plants flowering. On average, 38 plant species (minimum 26, maximum 42 species) from the seed mixtures were established in each flower strip. The flower cover varied between seasons but was well pronounced when pollination experiments were performed.

2.2 Plant species

The four different bee-pollinated plant species (Figure 2) were common species occurring at all study sites and were part of the established seed mixture. The species differed in floral cues and phenology (Figure 2) and required cross pollination for seed set (see control plants in pollination experiments). The species were chosen to be frequently visited by a broad spectrum of both generalist and specialist wild bees (Figure 1B; Kuppler et al., 2023).

Sinapis arvensis (L.) (Figure 2D) is an annual Brassicaceae flowering from May onward. For experiments, *S. arvensis* seeds (Rieger-Hofmann GmbH, Blaufelden, Germany) were sown into 16 x 16 cm flowering pots with 2 to 3 individuals per pot.

Salvia pratensis (L.) (Figure 2C) is a perennial Lamiaceae blooming from May to August. It is self-compatible but requires pollinators for pollen transfer (Moughan et al., 2021). Its flowers are specialized for pollination by large bees, e.g., bumblebees, and are rarely visited by insects other than bees (Moughan et al., 2021). This species can produce a maximum of 4 seeds per floret.

Both Asteraceae species, i.e., *Centaurea jacea* (L.) (Figure 2A), and *Cichorium intybus* (L.) (Figure 2B), are perennial and bloom from June/July until the end of season. Bees are the most abundant visitors of *Centaurea jacea* (Hirsch et al., 2003). All perennial species (*S. pratensis, C. jacea, C. intybus)* were cultivated in 16 x 16 cm flower pots with single plants per pot in the plant-rearing area of the Botanical Garden Ulm for at least one year prior to the experiments.

2.3 Pollination experiment

Experiments were performed in the spring and midsummer of 2020. Immediately before starting to bloom, plants were placed in pollinator-excluding cages of fine mesh to ensure that flowers could only be pollinated during the field experiments. When in full bloom, plants were brought into the study sites to be pollinated by the local bee community. Some plants remained in the flight cages as controls for self-pollination; no seed set occurred in the controls. The two different blooming seasons resulted in two different flower pairings. For the spring experiments, 4 pots of *S. pratensis* and 6 pots of *S. arvensis*, and for the summer experiments, 4 individuals of

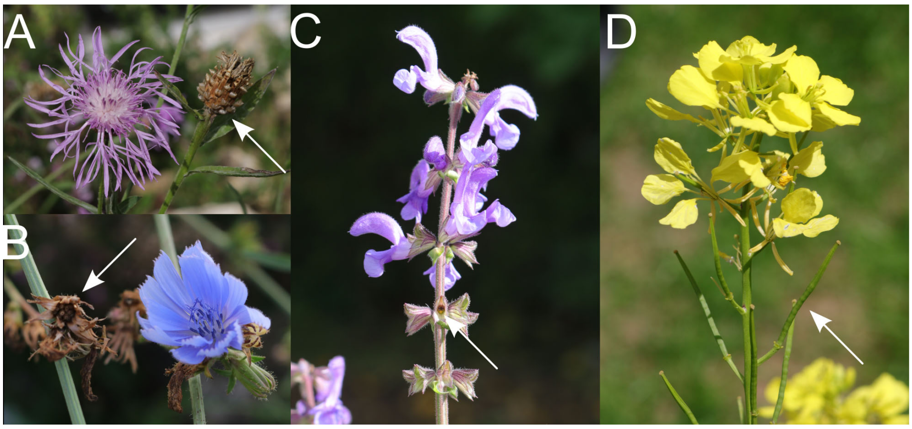

FIGURE 2
Flowers of the four different plant species used in the pollination experiments: *Centaurea jacea* **(A)**, *Chichorium intybus* **(B)**, *Salvia pratensis* **(C)**, and *Sinapis arvensis* **(D)**. White arrows indicate ripening seed structures. [Photos H. Burger].

C. jacea and *C. intybus* were placed in the field per habitat type per study site, respectively. The plants were left on the study plots for 72h when sunny weather was forecast. All plant pots for one plot were placed on two trays (ca. 35 cm x 50 cm x 4 cm) and were located at least 1.5 m from the edges of the plots. The plants were provided with at least 2.5 l water per plant tray to avoid drought stress during the experiments. Subsequently, plants were moved back into the mesh cage where they were checked regularly for seed maturation. Seeds were harvested when flowers or siliques turned dry and were then spread out to dry to avoid the growth of mold. The seed number was then counted and weighed using accurate weighing scales (accuracy of 0.1 mg).

For *S. arvensis*, 10 siliques per plant were chosen, and their intact seeds (round, with a diameter of at least 1 mm) were extracted manually and weighed to obtained an average weight per seed. For plants with fewer siliques, all siliques were measured. All seeds of the respective plant were then counted and weighed, and the average weight of intact seeds was calculated. As *S. pratensis* has a constant number of 4 seeds per flower, only the number of intact seeds of ten flowers were counted, and the relevant seeds were weighed. Again, the total number of flowers per plant was counted, and the seeds were retrieved, sorted, and weighed. For the Asteraceae species, intact seeds were broken off the dried flowers and processed as described above.

2.4 Bee data

Wild bee monitoring data for the season of 2020 were received from the BienABest project (for detailed information on bee monitoring see Neumüller et al., 2020; Neumüller et al., 2022 and Verein Deutscher Ingenieure e.V, 2023). Between April and September 2020, five sampling events took place per plot covering the entire season at intervals of 3 to 4 weeks, starting with the flowering of the *Taraxacum* sect *ruderalis* dandelion. Each sampling event consisted of two 25 min transect walks per plot, one in the morning and one in the afternoon, during which collectors were able to move freely within the plot. Sampling was performed by wild bee experts to guarantee reliable species determination. All observed bee individuals (males and females) were caught with an entomological net, except for those that could be determined at first sight, and were identified to species level in the field. Individuals that could not identified in the field were taken to the laboratory and identified using a binocular microscope and standard literature. Sampling was conducted only during sunny weather (cloud cover maximum 30%), at temperatures higher than 10°C and under low wind conditions.

This method for the bee survey was undertaken with the aim of recording high numbers of bee species and floral resources for wild bees with standardized monitoring methods according to Verein Deutscher Ingenieure e.V, 2023 and represents a trade-off between the highest standardization and the recording of the complete species inventory in an appropriate period of time. The methodology was additionally verified by Herrera-Mesías et al., 2022.

2.5 Statistical analysis

All analyses were performed using R (version 4.2.2, The R Foundation for Statistical Computing). The nearest weather station for each study site was determined, and the corresponding weather data for each day and site was retrieved from the Deutscher Wetter Dienst (DWD, www.dwd.de; Supplementary Table S1).

2.5.1 Bee data analyses and predictions

Individual-based species accumulation curves were calculated from the BienABest wild bee monitoring data to compare the species richness and the abundance of bees recorded on the two habitat types by using the R package iNEXT (Hsieh et al., 2016). This package was also used to calculate Shannon indices H' for the whole year, taking into consideration the habitat type on each study site. The Shannon index H' gives overall diversity while taking the species richness and the abundance for each species into account. As it combines these two factors of the bee community, it also provides an indication of the relevance of rare species in our analyses.

In order to predict bee abundance and diversity for each date (first entire day of the 72 h pollination experiment), generalized additive models (GAM) were constructed using the 'mgcv' R package (Wood, 2012). Models were based on BienABest wild bee monitoring data and weather data. We included the day and the maximum temperature as smoothing factors and the plot ID, the study site, and the habitat type as variables in the models (see Supplementary Table S2). We then used the *predict()* function in order to predict the species richness and abundance of bees for each of the days and plots of the pollination experiment. These predictions are used as independent variables in the further analyses.

2.5.2 Seed set analyses

Linear mixed models (LMMs) for the seed weight were constructed using the *lm* function in the lme4 package (Bates et al., 2015). We made a total of 399 measurements of seed weight for all plant species. For better compatibility between plant species, a quotient was calculated by dividing the seed weight of individual measurements by the maximum observed value within each species. These values for relative seed weight allowed better comparisons between species.

First, three models for seed set analyses were designed as models with relative seed weight as the dependent variable. One of the three bee variables (species richness, abundance, or Shannon H') were used as an independent variable in the three global models. Furthermore, we included the plant species and habitat type (wild flower strip or near-natural grassland) as variables and the study site as a random effect in all models.

As a result of the significances of the global models, six plant-species-specific generalized linear models (GLMs) were designed for species richness and the Shannon index H' (for each of the 3 tested plant taxa) in which the daily mean temperature of the experimental day was added as a continuous factor, and the study site was added as a random factor to the models. Because of the statistical results of the global models (see pairwise tests for each model in

Supplementary Tables S3 and S4) and considerations of the biology of the plants, *C. intybus* and *C. jacea* were treated as one group ("Asteraceae") in these analyses. Therefore, for Asteraceae models, plant species remained as a random factor.

3 Results

3.1 Bee diversity of habitats

A total of 10,922 bee individuals of 210 bee species were recorded, which could be grouped into 4,572 individuals of 187 bee species on near-natural grassland and 6,350 individuals of 163 bee species on wild flower strips (Figure 3), resulting in a significant difference of species richness between habitat types (non-overlapping confidence intervals). Of these 210 species, ca. 68% (143 species) overlapped, 47 species only occurred on near-natural grassland, and 23 species occurred only on wild flower strips. The average number of individuals per species was higher on wild flower strips (mean ± SD [lowest value, highest value]: 38.9 ± 117.4 [1, 1119] individuals/species, 40 singletons) than on near-natural grassland (24.4 ± 70.6 [1, 561] individuals/species, 39 singletons). Extremely abundant species (more than 100 individuals in total) made up ca. 61% of bee individuals observed on near-natural grassland (10 species, most abundant *Bombus terrestris* bumblebees) and ca. 75% of bee individuals observed on wild flower strips (15 species, most abundant *B. lapidarius* bumblebees). Shannon diversities H' of each habitat type within the individual study sites indicated an overall high diversity with average indices of H' = 2.73 (SD: 0.37; [1.69, 3.33]) for near-natural grassland and H' = 2.79 (SD: 0.41; [1.77, 3.33]) for wild flower strips.

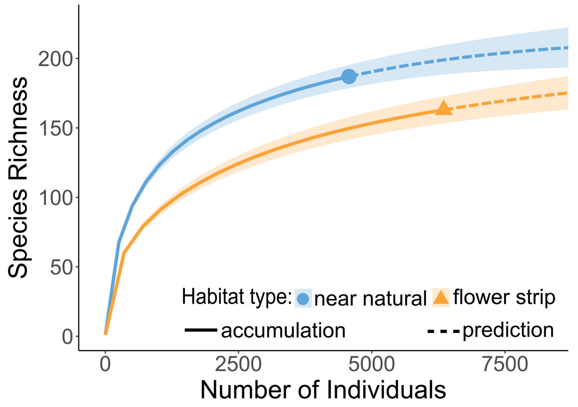

FIGURE 3
Individual-based randomized species accumulation curves comparing wild bee richness and abundance between the two habitat types of near-natural grassland and wild flower strips on the study sites.

3.2 Overall seed set

The global models across all plant species showed that the standardized seed weight was significantly positively correlated with the bee species richness of the experimental day (Figure 4B and Table 1) and with the Shannon index H' of the entire season (Figure 4A and Table 1). Furthermore, both models revealed significant differences between the habitat types, with near-natural habitats outperforming wild flower strips in both cases and differences among the plant species (Table 1).

When testing for the dependency of standardized seed weight on the bee abundance, we found no significant effect, although here again, we determined significant differences between the habitat types, with near-natural habitats outperforming wild flower strips, and among the various plant species (Figure 4C and Table 1).

3.3 Species-specific seed sets

Because of significant differences between plant species in the global models, we performed pairwise comparisons: no significant differences between the two Asteraceae species, *C. intybus* and *C. jacea*, were revealed, but these species showed significant differences from *S. arvensis* and *S. pratensis*, which again did not exhibit significant differences from each other (see Supplementary Tables S3 and S4).

For the Asteraceae specific models, we found a significant positive relationship for greater seed weight with greater Shannon index H' and bee species richness (Figure 5 and Table 2). Neither of the models showed a significant difference between the habitat types (Figure 5 and Table 2). For the *S. pratensis* Shannon index H' model, we observed a significant positive relationship for the Shannon index H' and a difference between the habitat types with near-natural habitats again outperforming wild flower strips (Figure 5 and Table 2). Similar results were obtained for the *S. pratensis* species richness model (Figure 5 and Table 2).

Significant differences were also found between habitat types for both *S. arvensis* models, with plants on wild flower strips performing better than on near-natural habitats (Figure 5 and Table 2). Nevertheless, only the Shannon index H' was significantly positively correlated to seed weight, whereas species richness was not (Figure 5 and Table 2).

4 Discussion

The examined study locations showed an overall high wild bee diversity, which resulted in high seed sets in four wild plant species that are important host plants of wild bees. We found significant differences across the habitats of near-natural grasslands and flower strips and the effects of bee species richness and Shannon index H' on the seed weight but did not find such an effect of bee abundance. The results suggest that the wild bee diversity in a habitat influence

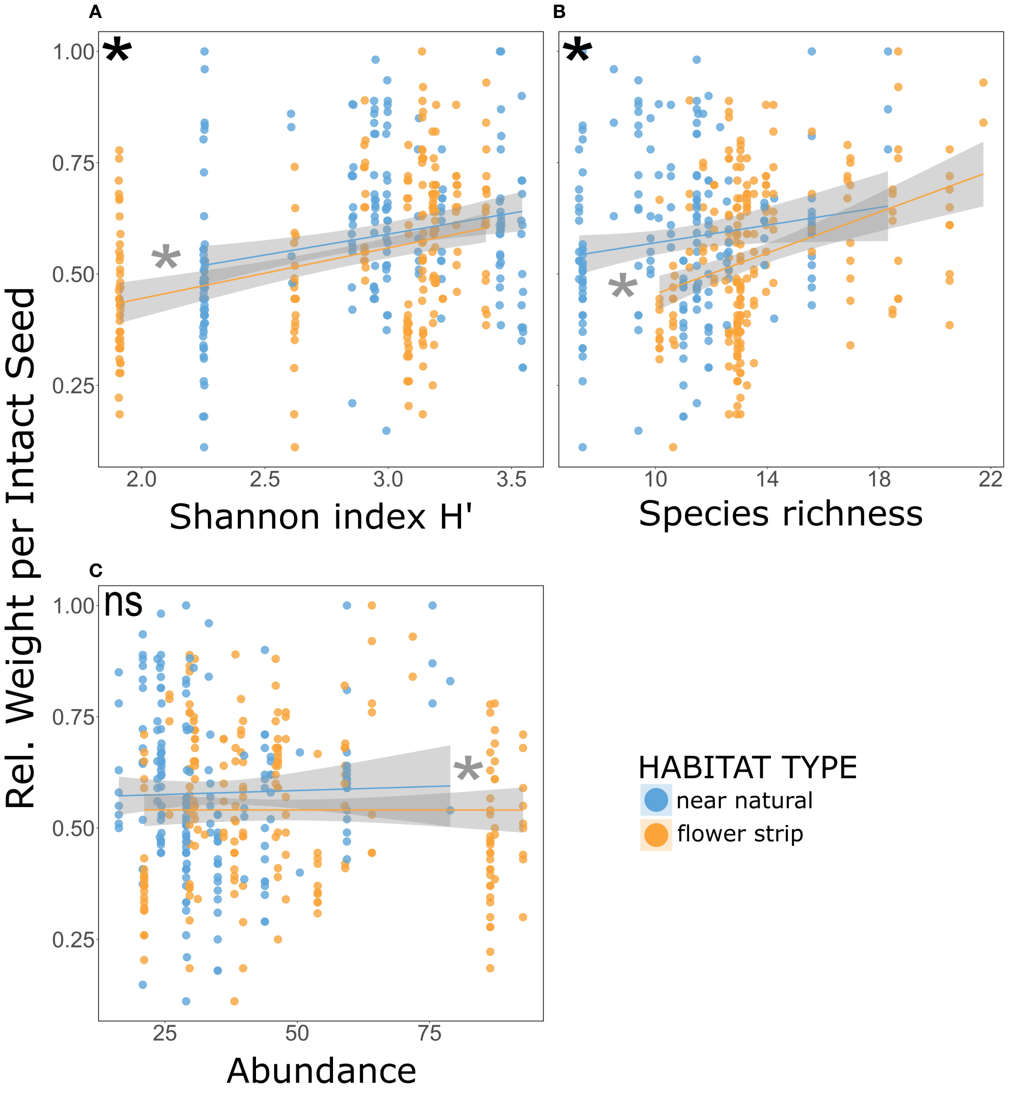

FIGURE 4
Correlation between the relative weight per intact seed on the two habitat types and the Shannon index H' **(A)**, the species richness **(B)**, and abundance **(C)**. Within each global model, black asterisks indicate a significant effect for the bee variable, and gray asterisks indicate a significant effect of the habitat type (GLM, p<0.05). Non-significant differences are indicated by 'ns' (p>0.05).

the seed set of native plant species and consequently influence the reproductive success of these plants.

4.1 Increased seed sets in near-natural habitats

The study locations of our pollination experiments hosted a high bee diversity and abundance. Higher species richness was found on near-natural grassland. Permanent habitats such as near-natural grasslands are normally rich in flowers and also provide diverse nesting sites for wild bees, thus explaining the high bee diversities (Requier and Leonhardt, 2020). In comparison, wild flower strips generally had a higher bee abundance while being inhabited by fewer species. Despite these differences, the Shannon index H' was not significantly different over the two habitat types and across all study sites. The relatively high Shannon index H' indicated the high proportions of intermediate and rare species (Peet, 1974). The wild bee monitoring data and previous analyses of the bee diversity at the study locations (Neumüller et al., 2020) confirmed the occurrence of rare species that are often threatened according to the German Red List of wild bees (Westrich et al., 2011). We also found a substantial overlap of bee species between both habitats. These findings indicate that the artificially created flower strips were highly attractive for wild bees and can be considered as a successful conservation measure for improving the availability of floral resources within a region. Many commercially available seed mixtures with high proportions of annual non-native plants often only increase the abundance of a few abundant bee species (Albrecht et al., 2020). In contrast, the floral resources of the examined flower strips were sustainably relatively flower-rich over several years because of an effective mowing regime and the use of a species-rich seed mixture (Neumüller et al., 2021).

TABLE 1 Results of the three initial models.

Model	Independent variable	sum sq	mean sq	f	p-value
Species richness	Species richness	0.33	0.33	12.03	< 0.001
	Habitat type difference	0.56	0.56	20.74	< 0.001
	Plant species	0.98	0.33	12.05	< 0.001
Shannon H'	Shannon H'	1.09	1.09	41.91	< 0.001
	Habitat type difference	0.11	0.11	4.29	0.04
	Plant species	1.03	0.34	13.14	< 0.001
Abundance	Abundance	0.01	0.01	0.42	0.52
	Habitat type difference	0.13	0.13	4.84	< 0.05
	Plant species	1.61	0.54	19.71	< 0.001

Each model used standardized seed weight as a dependent variable and is referred to by using the bee-independent variable.

The perennial flower strips still provided valuable food resources including important pollen hosts of wild bees (Kuppler et al., 2023), and the high flower cover resulted in a high bee abundance. Nevertheless, permanent habitats such as near-natural grassland hosted the highest numbers of bee species. These habitats, which were extensively managed, were highly diverse in flowers and also provided diverse nesting sites for wild bees, factors that explain high bee diversities (Requier and Leonhardt, 2020).

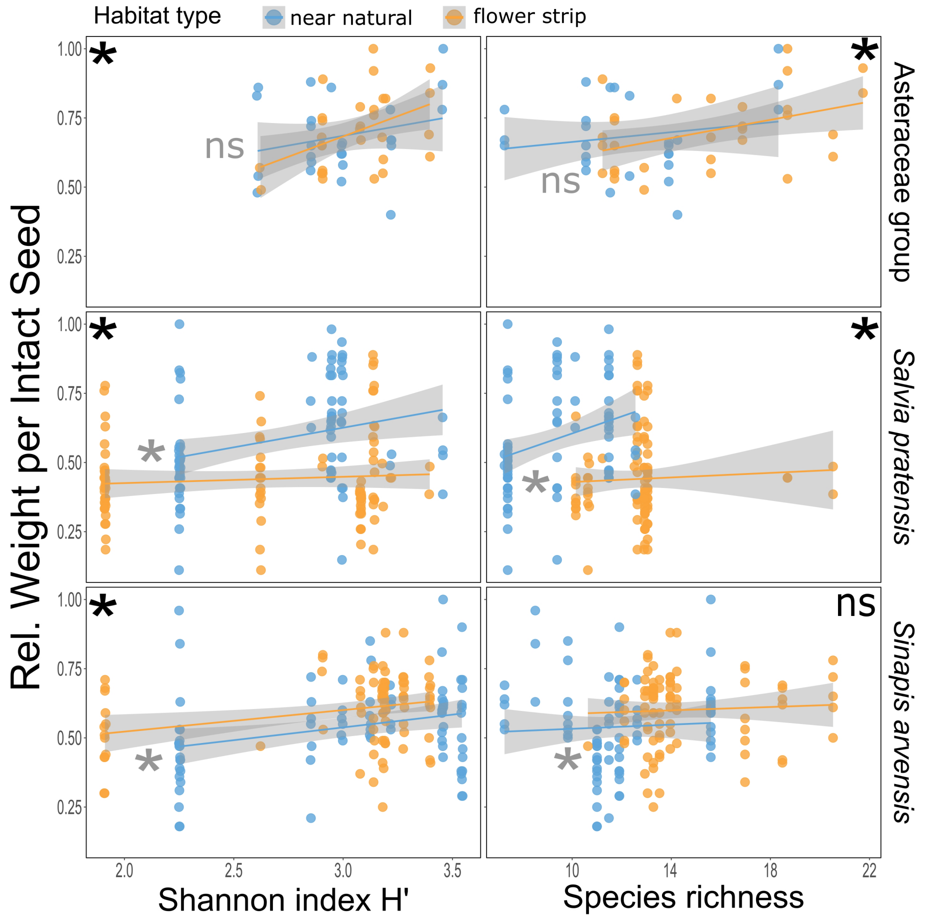

FIGURE 5
Comparison of relationships between bee diversity (Shannon index H' for the entire season left, species richness for experimental day right) and seed weight between the plant taxa (Asteraceae group (*Centaurea jacea* and *Cichorium intybus*), *Salvia pratensis*, and *Sinapis arvensis*). Within each model, black asterisks indicate a significant effect of the bee variable, and gray asterisks indicate a significant effect of the habitat type (GLM, p<0.05). Non-significant differences are indicated by 'ns' (p>0.05).

TABLE 2 Results of the six species-specific models (two per taxa).

Plant taxa	Model	Independent variable	est.	std. error	t-value	p-value
Asteraceae group	Species richness	Species richness	0.01	0.01	2.48	0.02
		Habitat type difference	-0.24	0.04	-0.62	0.54
	Shannon H'	Shannon H'	0.20	0.08	2.61	0.01
		Habitat type difference	0.003	0.04	0.08	0.94
Salvia pratensis	Species richness	Species richness	0.02	0.01	2.34	0.02
		Habitat type difference	-0.20	0.03	-5.67	<0.001
	Shannon H'	Shannon H'	0.06	0.03	2.14	0.03
		Habitat type difference	-0.14	0.03	-5.35	<0.001
Sinapis arvensis	Species richness	Species richness	0.24	0.12	2.01	0.50
		Habitat type difference	0.24	0.12	2.01	0.05
	Shannon H'	Shannon H'	0.38	0.10	3.79	< 0.005
		Habitat type difference	0.28	0.10	2.86	0.005

Each model used standardized seed weight as the dependent variable and is referred to by using the bee-independent variable.

The high numbers of bee species found in near-natural grasslands might explain the significant influence of the habitat type on the seed setting rates. We found a significant influence of the habitat type, with higher seed setting rates in near-natural grassland compared with those on flower strips. Previous studies have shown that structure-rich landscapes have a positive effect on bee diversity (Kennedy et al., 2013; Neumüller et al., 2020) and, consequently, on seed set (Albrecht et al., 2020). Nevertheless, increasing distances to pollinator-friendly habitats have a negative effect on plant reproductive success (Steffan-Dewenter and Tscharntke, 1997; Steffan-Dewenter et al., 2001), and high proportions of arable land in a landscape, often combined with decreased structure richness, can negatively affect the number of produced seeds (Söderman et al., 2018; Herbertsson et al., 2021; Ammann et al., 2024). In contrast to these previous studies, we have not analyzed effects at the landscape scale, as the two habitat types were in close proximity at a study site and therefore were surrounded by the same landscape within the flight distance of most wild bee species (Steffan-Dewenter et al., 2002). In our study, the bee community was determined on 0.3 ha plots established within different habitats. Although the previous studies mentioned above did not directly monitor bee diversity in the surrounding landscape elements, we can draw similar conclusions from our results. We conclude that both the preservation of near-natural habitats as a reservoir of wild plant species diversity and the conservation of reproduction-assuring pollinators are of great importance for seed setting.

4.2 Bee diversity affects seed set

In our pollination experiments, we found increases in seed set with greater wild bee diversity (species richness and Shannon index H') across habitats and study sites. Although the bee species richness was calculated for the experimental day and specific plot, the Shannon index H' represents the bee diversity of the entire season. We thus compared two bee parameters and included two different time-scale approaches. We were able to show that both parameters significantly influenced the seed weight, as greater species richness and a greater Shannon index H' resulted in greater seed set, and both seemed to be a suitable measure for seed set prediction. Both parameters allowed conclusions to be made from monitoring data without the performance of time-consuming pollination experiments and direct observations of bee visits. The studies reviewed by Garibaldi et al., 2013 and the meta-analysis by Woodcock et al., 2019 have especially particularly highlighted the important role of wild bees in pollination and have shown that the visits of diverse wild bee species, in particular, explain the pollination success. For example, distinct bee assemblages increased the seed set of *Helianthus anuus* by up to 45% (Mallinger et al., 2019).

Wild bee diversity highly depends on the structure of the habitat, but the effects of the habitat type on pollination success and its dependency on wild bees have previously often been measured only indirectly as effects of surrounding landscape elements. For example, the seed set of *Raphanus sativus* is increased by flower strips in the surroundings (Albrecht et al., 2007) and, for the seed set of *Sinapis arvensis*, by near-natural habitats. Although these previous studies have not directly monitored the wild bee community of the habitats, as carried out in our study, the results support our findings: habitats that naturally host or are established to promote high bee diversities increase the seed set in wild plant species. Concurrently, pollinator diversity, in addition to bees and thus resulting niche complementarity, has been shown to impact fruit set positively (Albrecht et al., 2012; Magrach et al., 2021), but this was not a focus of our study.

As the chosen plant species benefit from cross-pollination by bees and are highly attractive to generalists and specialist bees, we assume that the higher seed weights are attributable to cross-pollination by diverse bee species. Seed weight is particularly linked to the initial growth of the plantlet (Lamont and Groom, 2013). In this phase, the fitness of the plantlet in its surroundings is crucial for its survival. Survival is assured, for example, by its genotypic characteristics such as higher heterozygosity presumably arising from cross-pollination, adaptability resulting from cross-pollination, and its fast growth as a competitive advantage (e.g., competition for light by out-growing other plants). We conclude that the high bee diversities of our habitat types provides the necessary pollination services to maintain the next generations of study plant species, which are important host plants of diverse bee species.

4.3 High bee abundance does not increase seed set

In addition to bee diversity, a greater bee visitation rate has been reported to result in a higher seed set (Herbertsson et al., 2021). As a high bee abundance leads to more potential flower visits, we expected to observe this effect in our experiments. However, this was not confirmed by our study. The bee abundance at the study sites was mostly driven by a few widespread bee species that occurred in high numbers, such as the bumblebees *Bombus lapidarius* and *B. terrestris*. An effective seed set thus seems not to be strongly affected by abundant bee species. More specialized visitors that are often part of species-rich wild bee communities can, in contrast, greatly improve pollination (Mallinger et al., 2019). Similarly, we found an increase in pollination via higher bee diversity, which can largely explain the seed sets in the studied plant species. The foraging behavior and functional traits of intermediate or rare bee species are more important than high abundancies of common bee species. An alternative explanation for the non-significant effect of bee abundance might be that a saturation in pollination occurs (Morris et al., 2010). This means that at least the minimum bee abundance needed for pollination was assured in both our habitats. On the other hand, over-pollination attributable to an excess of bee visits did not seem to be a factor in our experiments, as this would have resulted in a decreased seed set (Sáez et al., 2014; Garratt et al., 2021).

4.4 Differences in seed set between plant species

The pollination experiments revealed that the bee diversity differently impacted the seed set of the four studied wild plant species. In all represented taxa, the seed set was positively correlated with greater Shannon indices H' and, in two models, also to bee species richness, although the effects depended, in some of the plant species, on the habitat type.

4.4.1 Sinapis arvensis

Sinapis arvensis plays an important role as a floral resource for wild bees in spring (Kuppler et al., 2023) because of the limited availability of flowering herbaceous plants early in the season. Although the nectar reward lies relatively deeply within the flowers, the petals are flexible, and the nectar and pollen is easy to exploit regardless of bee morphology. This result in visits by a broad variety of bee species including widespread ones that are often abundant in agricultural landscapes. We found that the seed set in *S. arvensis* was only slightly influenced by greater bee-species richness and the Shannon index H' indicating sufficient pollination events, even by a few bee species occurring in sufficient numbers. This also supports our finding that *S. arvensis* performs better in wild flower strips, which have been shown to exhibit higher bee abundances compared with the flower strips in our rarefaction analyses.

The effective pollination of *S. arvensis* flowers by bees has also been demonstrated in previous studies. *Sinapis* plants are annuals and easy to breed probably explaining the use of this native plant species in contrast to others frequently used in pollination experiments. Previous studies have shown landscape effects with decreasing seed set as a result of increasing distances to near-natural grassland (Steffan-Dewenter and Tscharntke, 1997; Steffan-Dewenter and Tscharntke, 1999). Moreover, these studies have shown that wild bee abundance is a better predictor for *S. arvensis* seed weight per plant than that of honey bees alone (Steffan-Dewenter and Tscharntke, 1999). Other members of the *Brassiceae*, i.e., the widely cultivated *Brassica napus* is highly dependent on bees for pollination. *Osmini* mason bees, *O. cornifrons*, and *O. lignaria* have been shown to increase seed set in flight cage experiments (Abel et al., 2003). Not only analyses of bee visitor identity, but also the determination of the pollen deposition of visiting species are needed to identify the most effective pollinating species of *S. arvensis* and other Brassicaceae species.

4.4.2 *Centaurea jacea* and *Cichorium intybus*

The Asteraceae species *Centaurea jacea* and *Cichorium intybus* bloom during peak bee activity in high and late summer and might be crucial resources for nectar and pollen for a broad spectrum of bee species. Based on the ranking of bee visits analyzed by Kuppler et al., 2023, *C. jacea* has the highest visitor richness of the four wild flower species used in this study. High numbers of visiting bee species suggest that the flowers have a more generalist pollination system (with several bee species as effective pollinators) and do not restrict access to floral rewards to a small visitor subset. Asteraceae species are also among the most important host plants for oligolectic bees (Zurbuchen and Müller, 2012), which are often specialized on host plants that are frequently visited by other bee species as reliable food sources. Our results indicate that Asteraceae are the only group without a habitat-specific effect, and thus, we assume that they are the least affected by specific bee species compositions because of their overall high attractiveness for bees. Although the Shannon index H' did not appear to play a crucial role, seed set for both plants was higher with greater bee diversity. Again, the results emphasize that bee-diverse habitats are needed to ensure effective pollination and to conserve plant diversity.

In agreement with our findings, an effect of landscape complexity, which normally coincides with high bee diversities, has been shown to affect seed set in *C. jacea* (Steffan-Dewenter et al., 2001). However, other studies on the pollination efficiency in *C. jacea* and *C. intybus* are rare. The florets of *Crepis sancta*, another Asteraceae species with a similar morphology, lie closer to the center of the inflorescence and have been demonstrated to be more prone to fertilization by homogenic pollen, with the resulting seeds therefore being not as well adapted for dispersal as seeds from the outer florets (Cheptou et al., 2001). This results in certain intra-floral and intra-plant differences of seed traits, which should be considered in future experiments, e.g., by only evaluating outer seeds to measure seed set.

4.4.3 *Salvia pratensis*

The seed set of *Salvia pratensis* was most strongly affected by habitat types, with near-natural habitats performing significantly better than the experimental plots located on wild flower strips. *Salvia pratensis* attracts fewer bee species compared with the other study plants (Kuppler et al., 2023). Instead, the pollination system of *Salvia* is described as being specialized for large bees, mostly bumblebees (Moughan et al., 2021). The exploitation of *Salvia* flowers requires a distinct body size for entering the flowers, with small bees being unable to trigger the floral mechanism, and a sufficient tongue length for reaching the nectar in the deep corolla (Claβen-Bockhoff et al., 2003; Reith et al., 2007). We have observed high numbers of bumble bee individuals in both habitats, a result that seems to contradict the significant effects of habitat type. However, the seed set in *S. pratensis* not only depends on the number of visiting bumblebees, but also on bee traits (Zhang and Claßen-Bockhoff, 2019), again indicating that some bee species or individuals are more effective than others. In addition to bumblebees, *Anthophora* spp. or *Lasioglossum xanthopus* are, for example, regular *S. pratensis* visitors, both having a large body size. Interactions between *S. pratensis* and these bee species and the higher diversity of *Bombus* species have only been found in the near-natural grassland in the examined study locations. Thus, the pollinator requirements of *S. pratensis* seem to be more specific than expected.

5 Conclusion

In this pollination study, we have determined the effects of local bee communities, recorded on the habitat scale, on the reproduction of four wild plant species that are known to be attractive to wild bees. We have shown that high-quality habitats, particularly near-natural grasslands, with a (resulting) high bee diversity have a positive effect on the reproductive success of all tested plant species. Perennial flower strips can promote diverse bee species in agricultural landscapes, although near-natural grasslands host the highest bee diversities resulting in high seed sets. We conclude that the preservation of diverse wild bee communities and suitable wild bee habitats is indispensable for the indirect promotion of native plants that have suffered severe declines over the last few decades.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

KH: Writing – original draft, Formal analysis, Investigation, Methodology, Visualization. MA: Conceptualization, Supervision, Writing – review & editing. HB: Conceptualization, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1343885/full#supplementary-material

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Neonicotinoid contamination in conservation areas affects bees more sharply than beetles

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The neurotoxic insecticide class of neonicotinoids has become one of the most widely used groups of pesticides globally. Their long half-lives and high water solubility increase their potential to linger and affect numerous organisms long after application. A prominent concern associated with residual contamination is the negative impact that neonicotinoids can have on beneficial arthropods such as bees and certain groups of beetles. Many studies have looked at the effects neonicotinoids have on arthropod communities in lab settings; however, comparatively few studies have looked at these groups in neonicotinoid-contaminated restored prairie habitats. These habitats are often restored from or located near agriculture and are almost ubiquitously contaminated with neonicotinoids. Our one-year manipulated field study compared native bee nesting rates and beetle community assemblages between paired clothianidin-contaminated and non-contaminated restored prairie plots. Native bee nesting probability and nesting abundance increased by 46% and 172%, respectively, in sites contaminated with clothianidin. Conversely, we observed no significant differences in beetle family assemblages, abundance, or richness between clothianidin-contaminated and control sites. These results suggest that neonicotinoid contamination of natural habitats can have numerous environmental consequences for arthropods and that these effects are not always consistent between taxa. Understanding how neonicotinoid contamination affects beneficial groups such as bees and arthropod community assemblages is crucial for characterizing the risks these chemicals pose to ecologically imperative taxa.

KEYWORDS

ground-nesting bees, beetle feeding guilds, clothianidin, restored prairie, agricultural contamination

1 Introduction

Insects account for three-quarters of global animal and plant species, occupy a vast array of ecological niches (Chapman, 2009), and support countless ecosystem functions, such as nutrient cycling, soil formation, decomposition, water purification, and pollination, which have an outsized impact on the global economy. As insects decline, ecosystem structure and overall human well-being are expected to be adversely affected (Ameixa et al., 2018). The pervasive use of pesticides, specifically neonicotinoids, which is the most commonly used class of pesticide, is considered a major contributor to the decline of insects due to the impact that they have on non-target organisms (Godfray et al., 2014; Pisa et al., 2014; Hladik et al., 2018; Wagner et al., 2021). Yet, we still lack a fundamental understanding of how neonicotinoid contamination broadly affects non-target arthropods, as most neonicotinoid studies have focused on managed insect species that are not representative of the larger insect community.

Neonicotinoids have become ubiquitous in agricultural, industrial, and urban landscapes because of their low mammalian toxicity, application versatility, and tendency to contaminate adjacent habitats (Jeschke et al., 2011). The most prominent application method for neonicotinoids are seed coatings on agricultural commodities such as cereal grains and oilseeds (Jeschke et al., 2011). This method was developed to provide more targeted pest control, as neonicotinoids can be systemically incorporated into growing plants (Bonmatin et al., 2015). The incorporation of neonicotinoids into plant tissues has led to concerns about non-target exposure to pollinators in pollen and nectar (Rundlöf et al., 2015), but the proportion of the pesticide absorbed by target plants is small, ranging from 0.7-20% in several crop species (Sur and Stork, 2003). The remainder of the pesticide usually ends up in the soil, where it can persist for long periods of time. Clothianidin, the neonicotinoid with the longest environmental persistence, exhibits a half-life between 148-6931 days (Rexrode et al., 2003). This contamination can negatively impact the beneficial arthropods that natural habitats foster (Main et al., 2020; Kuechle et al., 2022). As neonicotinoids move into natural areas embedded in agroecosystems, these habitats could unintentionally attract beneficial insects to locations contaminated with harmful neonicotinoid insecticides.

Two beneficial insect groups that are often targeted in restoration efforts for their role in providing arthropod-mediated ecosystem services (AMES) (Isaacs et al., 2009) are bees and beetles. Both bees and beetles generally exhibit increases in richness and abundance in these restoration settings compared to agricultural fields (Purvis et al., 2020); however, due to differences in life history traits, bees and beetles are likely differentially affected by neonicotinoid contamination in these habitats. While numerous groups of beetles (Pfiffner and Luka, 2000) and the vast majority of bee species are ground-dwelling (Harmon-Threatt, 2020), the feeding guilds that they occupy vary (Losey and Vaughan, 2006). A majority of bee species are considered pollinators, while beetles occupy comparatively more feeding guilds including predators (Labrie et al., 2003; Menalled et al., 2004), pollinators (Young, 1986; Maia et al., 2013), detritivores (Wicklow et al., 1988; Topp et al., 2008), omnivores (Wäckers et al., 2005; Blubaugh et al., 2016), and herbivores (Alyokhin et al., 2008; Gray et al., 2009). The abundance and composition of these feeding guilds can have drastic impacts on ecosystem structure and function (Whiles and Charlton, 2006), including plant composition and biomass (Mulder et al., 1999), nutrient cycling and soil health (Stanton, 1988), and pest suppression (Moran and Hurd, 1997). Because these functional groups have evolved due to different evolutionary pressures in their ecological niche and have different routes of exposure to contamination, they are likely to respond differently to neonicotinoid exposure, therefore potentially shifting ecosystem structure and services.

Numerous studies have shown that neonicotinoid exposure can have negative consequences on cognitive and motor function (Alkassab and Kirchner, 2017; Tooming et al., 2017), reproduction and development (Alkassab and Kirchner, 2017; Wu-Smart and Spivak, 2018; Feng et al., 2019; Fortuin et al., 2021), and longevity (Alkassab and Kirchner, 2017; Feng et al., 2019). However, most neonicotinoid bee and beetle studies have been conducted in a lab setting with managed species. Because these managed species have either different social organization or nesting habits than most native ground-nesting species, potential effects and routes of exposure should not be broadly applied to all bees (Mayack and Boff, 2019). Furthermore, neonicotinoid studies rarely compare responses to insects in other orders, which would provide a more thorough community-level response. By looking at ground bee nesting and beetle functional group abundances in response to neonicotinoid contamination, this study will provide a more comprehensive picture of how beneficial insects are utilizing restorations from agriculture and the potential exposure risks for each group. Findings from this study could also be used to provide a more realistic account of the proposed benefits to beneficial insect communities associated with habitat restoration initiatives. The objectives of this study are to (i) evaluate differential ground bee nesting rates and (ii) beetle feeding guild assemblages between clothianidin-contaminated and non-contaminated soils of natural areas intended to augment conservation biological control systems.

2 Materials and methods

2.1 Study sites

Five fields located in Champaign and Vermilion Counties, IL, were utilized in the study. Each field site was separated by at least 500 m to ensure site independence. All field sites were previously in row crop agriculture but were removed from production for at least 17 years (Supplementary Table S1). Within each field site, a pair of $100m^2$ plots separated by 50m were established and assigned as either control or neonicotinoid treatment.

In May of 2018, one of the paired plots at each site was treated with the granular, clothianidin-based insecticide Arena 0.25G (Valent U.S.A. Corporation, Walnut Creek, CA) at a rate of 80g of active ingredient per acre. This application rate was chosen based on manufacturer recommendations for row crops. Because neonicotinoid levels in restoration habitats are notoriously heterogeneous and rates of persistence are dependent on other environmental variables (Felsot et al., 1998; Donnarumma et al., 2011; Sharma et al., 2014; Fletcher et al., 2018), we selected an application rate to reflect a worst-case scenario of clothianidin soil contamination in field margins or prairies recently restored from conventional agriculture; areas that are designed to attract and be a refuge for beneficial insect communities (Lagerlöf et al., 1992; Winfree, 2010). This application rate yielded soil contamination rates higher (Supplementary Table S4) than some studies in the neonicotinoid soil contamination literature (Hladik et al., 2017; Main et al., 2020). These higher rates were chosen to prevent treatment effects from being masked by higher variance typical of field-based studies, ultimately providing more confidence in the directionality and intensity of the treatment effect. While not traditionally used in row crop agriculture, Arena 0.25G was chosen as a delivery method to mimic pesticide soil deposition associated with seed coatings. It was selected over alternatives such as killed, treated seeds due to the ease of application and control of confounding variables. As most coated seeds contain other pesticides and the physical seed represents a carbon addition, Arena 0.25G was an appropriate application technique to control for clothianidin accurately.

All sites were sampled for arthropods, bare ground, floral abundance, and floral richness during June, July, and August 2018 as detailed below.

2.2 Bee and beetle sampling

During each sampling event, nine emergence tents (BugDorm, Taichung, Taiwan; model BT2006) were deployed in each plot (18 per site, 9 in control and 9 in treated plots) in a three-by-three grid with adjacent tents separated by 2m. Tent corners were staked down, and soil was packed on the edges of tent flaps to prevent insect movement in or out of the tent. A collection jar, located at the top of the tent at the end of a mesh funnel, was filled with soapy water to collect any insects emerging from the soil and vegetation beneath the tent. Tents were installed between 1800 and 2000 when diurnal insect movement decreases and retrieved after 72 hours, which was previously found to be sufficient to maximize captures of actively nesting female bees (Pane and Harmon-Threatt, 2017). Captured specimens were removed and placed into 70% ethanol. Bees were identified to species using keys created by Michael Arduser (unpublished, 2015) and Discover Life (Orr et al., 2021). These data were used to generate two separate response variables - bee abundance and bee nesting probability - in the models described below. Beetles captured were identified to at least family using American Beetles Volume II (Thomas et al., 2002), Beetles of Eastern North America (Evans, 2014), and A Field Guide to the Beetles of North America (White and Peterson, 1998). Feeding guilds (predator, herbivore, omnivore, and detritivore) for each beetle were assigned using the same resources. From these data, beetle richness, beetle abundance and abundance of each feeding guild were determined and used as responses in models described below.

2.3 Environmental covariate quantification

Environmental characteristics that influence ground bee nesting (O'Toole and Raw, 1991; Potts et al., 2005) and beetle abundance (Woodcock et al., 2008b; Diehl et al., 2012; Egerer et al., 2017) were quantified during each sampling session. Quantification was conducted using 16 independent 0.25 m^2 quadrats, evenly spaced within each plot in a four-by-four grid and separated by 2m. Bare ground cover (exposed soil), floral abundance, and floral richness were recorded for all quadrats. For each sampling period, all 16 quadrat observations made within the same plot were averaged to provide more representative plot-scale metrics as model covariates.

2.4 Statistical analysis

All statistical modeling was conducted in R v4.3.1 (R Core Team, 2023). Generalized linear mixed effects models (GLMMs) were fitted using the *glmer* function in *lme4* (*v1.1-2* Bates et al., 2015) to establish global models for model selection. Average bare ground cover, average floral abundance, and average floral richness were considered as covariates in the model selection process. Site was included as a random effect in all models to account for the paired nature of the experimental design. Beetle abundance and richness data were pooled across months to deal with issues associated with low abundance for certain feeding guilds, heteroskedasticity, and model overfitting. Bee abundance and nesting probability did not have these issues and therefore were not pooled.

A model selection process utilizing AICc (Akaike information criterion with correction for small sample sizes) comparisons was used to identify the most predictive model(s) for bees and beetles. Models that had a delta AICc less than two were included as potential candidate models. Candidate models for bee nesting probability, bee abundance, beetle omnivore abundance and beetle detritivore abundance were used to create model averages using the *model.avg* function in the *MuMIn* package (*v1.47.5* Bartoń, 2023) in order to account for numerous candidate models falling within our delta AICc cutoff of two (Johnson and Omland, 2004). Multicollinearity among independent variables was assessed by calculating variance inflation factors (VIF). VIF scores from all models showed low correlation between predictor variables, indicating that our covariates were sufficiently independent. Residuals from all models were assessed visually and via Shapiro-Wilk tests of normality. Heteroskedasticity was assessed visually and via Breusch-Pagan tests for all models.

GLMMs with binomial distributions were used to assess bee nesting probability. The probability of bee nesting was designated as the number of tents that captured one or more bees divided by the total number of tents. Because many ground-nesting species exhibit varying degrees of sociality and have been found to gregariously nest (Eickwort, 1975; Wcislo, 1992; Wuellner, 1999; Smith et al., 2003), analyzing bee nesting as tent success accounts for conspecifics that may otherwise be double counted. GLMMs with Poisson distributions were used to assess nesting bee abundance. Unlike the previous model, bee abundance is comprised of all captured females, therefore accounting for potential size variations in nest aggregations. In both bee nesting probability and bee abundance models, male and above-ground nesting bees (Harmon-Threatt, 2020) were omitted from analyses as they do not participate in nest construction (Antoine and Forrest, 2021). Due to low capture rates common with this sampling method, bee richness measures were not evaluated.

Generalized linear mixed effects models (GLMMs) with Poisson distributions were used to assess total beetle richness and abundance, as well as abundances for predator, herbivore, omnivore, and detritivore feeding guilds. In addition to environmental variables, models looking at individual feeding guilds included all other feeding guilds as possible covariates. These parameters were included in order to account for interspecific interactions. All model covariates were scaled in order to account for large eigenvalues observed during the model selection process. Residuals for the omnivore abundance models were not normally distributed and the issue could not be resolved using other model family residual methods. Furthermore, numerous beetle models exhibited symptoms of model overfitting. As a result, model predictions were tested using predicted residual error sum of squares (PRESS) and predictive R^2 cross validation (Mediavilla et al., 2008). These methods showed that beetle herbivore and omnivore abundance models were drastically overfitting the data and therefore were not very predictive (Table 1). These models were therefore not used for further data interpretation.

3 Results

3.1 Bee response to clothianidin

We caught 50 ground-nesting bee females from 11 species across the five sites and three sampling periods. A greater number of bees were seen in clothianidin-treated plots (8.6 ± 2.874) compared to control plots (1.4 ± 0.510), as seen in Figure 1B. Similarly, the average tent capture success was greater in clothianidin-treated plots (1.33 ± 0.187) than in control plots (0.47 ± 0.192) (Figure 1A).

Four candidate models were similarly predictive for estimating the probability of bee nesting at the tent level. The averaged model included the independent variables clothianidin ($Z = 2.326$, $P = 0.020$), floral abundance ($Z = 1.216$, $P = 0.224$), floral richness ($Z = 1.061$, $P = 0.289$), and average bare ground ($Z = 1.049$, $P = 0.294$). (Table 2). Full model selection and estimates can be found in Table 2 and Supplementary Table S2, respectively.

Likewise, four candidate models were similarly predictive of bee abundance and were averaged. The averaged model included the independent variables clothianidin ($Z = 3.912$, $P < 0.001$), floral abundance ($Z = 2.099$, $P = 0.036$), floral richness ($Z = 1.799$, $P = 0.072$), and average bare ground ($Z = 2.011$, $P = 0.044$) (Figures 1B–D). Full model selection and estimates for bees can be found in Table 2 and Supplementary Table S2, respectively.

3.2 Beetle response to clothianidin

We captured 2,613 beetles from 34 families across the sites and samples. Beetle abundance by family was dominated by *Staphylinidae* (792) and *Chrysomelidae* (652). Other prevalent families included *Latridiidae* (139), *Carabidae* (130), *Mordellidae* (118), and *Phalacridae* (111). Average (± SE) beetle abundance per site was similar between control plots (268.8 ± 71.639) and clothianidin plots (313.4 ± 82.622). Despite clothianidin not being a significant predictor of pooled beetle abundance, it was frequently present as a covariate in our top candidate models based on AICc

TABLE 1 Summary of model selection parameters and goodness of fit for evaluating overall beetle abundance, richness, and feeding guild models.

Model Dependent Variable	Model Ranking	Independent Variables	AIC_c	ΔAIC_c	*df*	W_i	Conditional R^2	Adjusted R^2	Predicted R^2
Beetle Abundance	*1*	average bare ground + floral abundance + floral richness	129.1	0.00	5	0.739	0.985	0.642	0.602
Beetle Family Richness	*1*	no model covariates	67.1	0.00	2	0.639	0.555	0.000	0.000
Beetle Predator Abundance	*1*	floral abundance + floral richness	104.4	0.00	4	0.933	0.985	0.614	0.891
Beetle Herbivore Abundance	*1*	detritivore abundance + omnivore abundance	110.8	0.00	4	0.583	0.989	0.645	0.000
Beetle Detritivore Abundance	*1*	average bare ground + omnivore abundance	92.1	0.00	4	0.391	0.944	0.851	0.973
	2	average bare ground	92.8	0.70	3	0.276	0.941	0.888	0.998
Beetle Omnivore Abundance	*1*	herbivore abundance	70.6	0.00	3	0.275	0.731	0.317	0.000
	2	no model covariates	71.7	1.11	2	0.158	0.583	0.000	0.000
	3	clothianidin	72.5	1.93	3	0.105	0.640	0.138	0.000

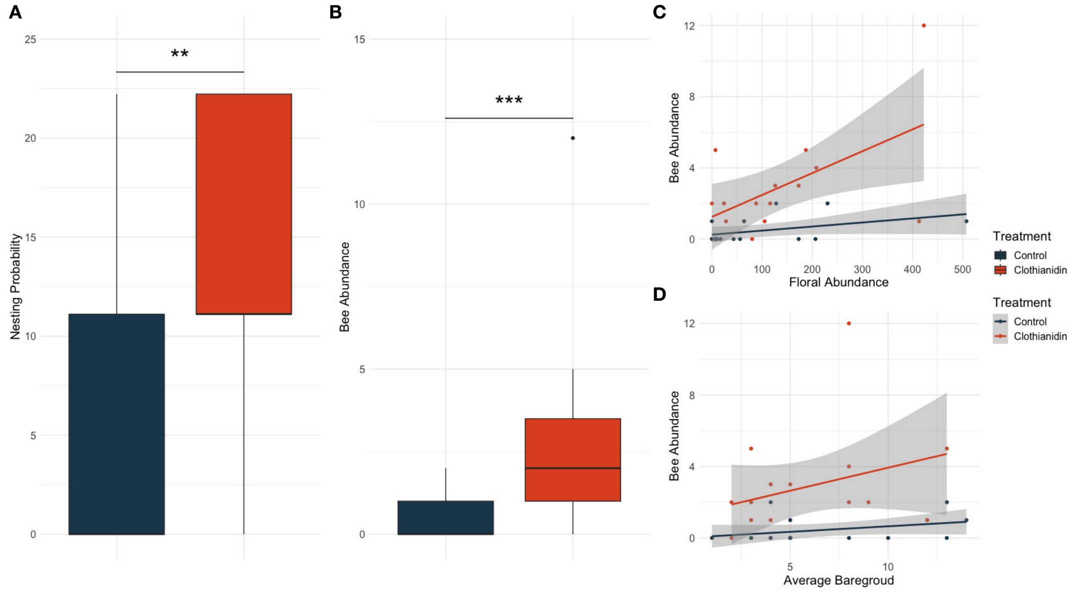

FIGURE 1
Significant predictors of the averaged top models for bee nesting probability **(A)** and bee abundance **(B–D)** in prairie restorations. Non-significant predictors that were present in our top models can be found in Table 2 and Supplementary Table S2. Asterisks indicate significance levels with two asterisks highlight *p*-values <0.01 and three asterisks highlighting *p*-values <0.001.

comparisons. Full model selections and estimates for beetles can be found in Table 1 and Supplementary Table S3, respectively. Top model dependent variables and regression coefficients are compared visually using incident rate ratios and confidence intervals in Figure 2.

Our most predictive model for beetle abundance included the scaled explanatory variables: floral abundance (Z = 5.876, P = <0.001), floral richness (Z = -4.678, P = <0.001), and average bare ground (Z = 3.491, P = <0.001). Our most predictive model for estimating beetle family richness did not include any model covariates. Significant predictors from top models are depicted in Figure 3.

Predacious beetles were highly abundant across sites and treatments with a total of 963 individuals across six families captured. A single predictive model of the abundance of predacious beetles included floral abundance (Z = 10.685, P = <0.001) and floral richness (Z = -5.657, P = <0.001) as explanatory variables. Significant predictors from any of the top models are depicted in Figure 3.

Beetle detritivores had a total of 554 individuals from 17 families. Two candidate models were averaged and include the explanatory variables: average bare ground (Z = 5.747, P = <0.001) and omnivore abundance (Z = 1.962, P = 0.050)Herbaceous beetles were also very common across sites and treatments with a total of 919 individuals from twelve families and omnivorous beetles had a total of 116 individuals. Both models showed symptoms of overfitting and were therefore not used for further interpretation.

4 Discussion

The results from our study indicate that high levels (Supplementary Table S4) of clothianidin in the soil of natural areas can have a profound yet inconsistent effect on the insect taxa found in those habitats. Ground bee abundance and nesting probability models showed a strong positive correlation with clothianidin contamination, while clothianidin contamination did not have an effect on beetle abundance, richness, or feeding

TABLE 2 Summary of model selection parameters for evaluating bee nesting percentage and bee abundance.

Model Dependent Variable	Model	Independent Variables	AIC$_c$	ΔAIC$_c$	df	W_i
Bee Nesting Probability	*1*	clothianidin	71.2	0.0	3	0.269
	2	clothianidin + floral richness	72.3	1.15	4	0.152
	3	clothianidin + floral abundance	72.3	1.16	4	0.151
	4	clothianidin + average bare ground	72.7	1.49	4	0.128
Bee Abundance	*1*	clothianidin + floral abundance	95.0	0.0	4	0.420
	2	clothianidin + floral abundance + floral richness	96.6	0.85	5	0.192

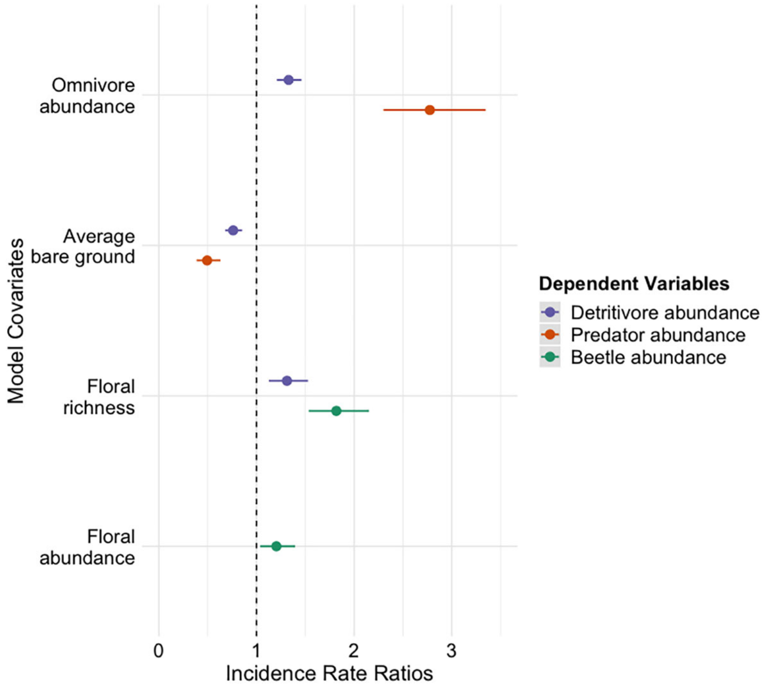

FIGURE 2
Top model dependent variables and regression coefficients are compared visually using incident rate ratios and confidence intervals (95%). Incident rate ratios provide a multiplying coefficient to describe direction and intensity of the effect that regression coefficients have on model dependent variables. Values in between zero and one indicate a negative relationship and numbers more than one indicate a positive relationship. Only models that are not overfit are shown.

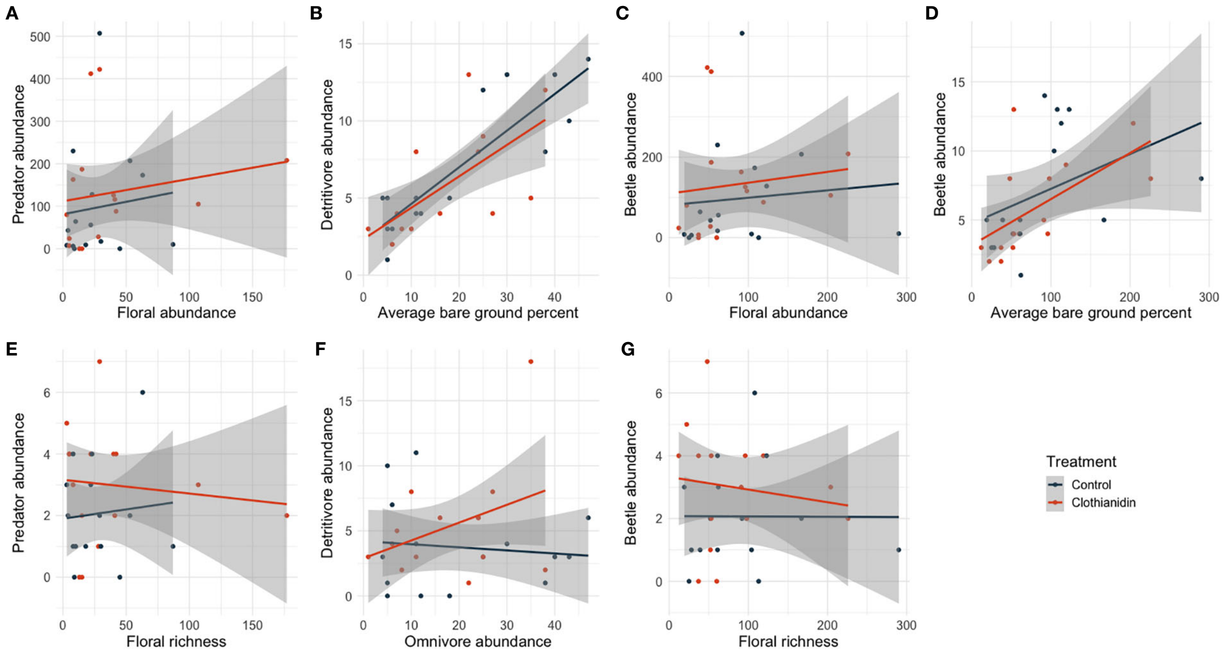

FIGURE 3
Significant regression coefficient predictors of overall beetle abundance **(C, D, G)**, beetle predator abundance **(A, E)**, and beetle detritivore abundance **(B, F)** in prairie restorations. Significant predictors were taken from all candidate models and not just model averages, which are often more conservative. Non-significant predictors that were present in our top models can be found in Table 1 and Supplementary Table S3.

guild abundances. Instead, beetle metrics were far more influenced by environmental factors. These differences outline the disproportionate effect that clothianidin contamination can have on insect communities in restoration ecosystems.

To our knowledge, this is the first study looking at ground bee nesting rates relative to clothianidin soil contamination in a restoration field experiment. These results contradict the findings of Willis Chan and Raine (2021), which showed a significant decrease in the nesting rates of the hoary squash bee (*Eucera pruinosa*) when exposed to different systematic insecticides in a manipulated agricultural setting. It is of note that herein we applied a single high dose of insecticides to restored prairies and examined immediate responses in active nest initiation and excavation, whereas in the Willis Chan and Raine (2021) study, different neonicotinoids were applied in a variety of application methods, and at different time points throughout the growing season. These differences in experimental design may influence the disparity in ground bee nesting rates in response to neonicotinoid contamination. Regardless, it suggests that many factors can contribute to differences in bee responses to contamination, including differences in insecticide type and application rate, experimental setting (agricultural vs. prairie restoration), or taxa (no bees from the genus *Eucera* were collected in our field experiment). In a follow-up study looking at bee emergence the year after application, so few bees were caught that data analysis could not be conducted (Tetlie and Harmon-Threatt unpublished work). This indicates that there could be high variability year to year and highlights the need for longitudinal work looking at bee communities over time in relation to neonicotinoid contamination.

While our results did not align with the only other nesting study on bees, they did have similarities with studies on oral exposure to neonicotinoids, which found that managed or semi-managed species do not avoid food sources containing neonicotinoid insecticides (Kessler et al., 2015; Arce et al., 2018). Furthermore, Kessler et al. (2015) found that honey and bumble bees consumed greater amounts of sucrose solutions that had been laced with neonicotinoids than sucrose alone. Similar results were seen by Singaravelan et al. (2005), who found that free-flying honey bees prefer to collect sucrose solutions containing low nicotine concentrations, the plant phytochemical from which the neonicotinoid class of insecticides is derived. The increases in feeding behavior from previous studies and the increase in nesting behavior seen in our data can likely be attributed to the mode of action of neonicotinoids themselves. Neonicotinoids target nicotinic acetylcholine receptors (nAChRs) throughout the brain, including the mushroom bodies required for learning and memory (Dupuis et al., 2011; Palmer et al., 2013). Sublethal doses of these neonicotinoids may provide an associated positive stimulus, therefore incentivizing congruent behaviors. It is however important to note that bee attraction to neonicotinoids is not ubiquitous (Kang and Jung, 2017; Fortuin and Gandhi, 2021); further highlighting the importance of additional variables which could augment bee behavior.

The increase in ground bee nesting behavior in contaminated soils that we have seen in our study and the affinity of various bee species to feed on neonicotinoid-laced foods could have significant negative consequences on bee communities. Previous work has shown that chronic exposure to neonicotinoids can affect larval mass, development speed, sex ratios, fecundity, and adult longevity in a variety of bee species (Laycock et al., 2012; Anderson and Harmon-Threatt, 2019; Strobl et al., 2019; Willis Chan and Raine, 2021). This is particularly concerning as many conservation efforts have focused on converting conventional agricultural fields and adjacent margins into pollinator habitats (M'Gonigle et al., 2015; Williams et al., 2015; Harmon-Threatt and Chin, 2016). Therefore, pollinator restorations can become ecological traps (Robertson and Hutto, 2006). Furthermore, sublethal doses of neonicotinoids have been shown to negatively interact with other factors connected to bee declines, such as pathogens and viruses (Alaux et al., 2010; Doublet et al., 2015), meaning that there could be compounding adverse effects associated with neonicotinoid exposure.

In contrast to bees, beetle abundance, richness, and feeding guild abundances were driven by environmental factors and not clothianidin contamination. These findings are contradictory to previous work indicating a negative impact of clothianidin on arthropod abundance (Main et al., 2018), beetle herbivores (Dembilio et al., 2015; Harmon et al., 2023) and predators (Pisa et al., 2017; Harmon et al., 2023). It is important to note that very few studies examine the effects of neonicotinoids on feeding guilds in restoration habitats – many being conducted in laboratory settings – and most studies focus on a specific family or species and not the broader community. That being said, numerous studies have shown that neonicotinoids can have negative effects on behavior (Kunkel et al., 2001; Moser and Obrycki, 2009; Tooming et al., 2017) and reproduction (Smith and Krischik, 1999; Papachristos and Milonas, 2008; Khani et al., 2012). While declines resulting from neonicotinoid contamination in overall beetle and feeding guild abundances were not observed in this study, sublethal exposure could lead to declines in subsequent years. Interestingly, the absence of an effect of clothianidin seen on detritivores in this study, is consistent with previous work (Main et al., 2018). While it is possible that sublethal effects could be seen in future years, some work indicates that detritivores are far more influenced by fungicides (Sánchez-Bayo et al., 2016), highlighting the importance of looking at multiple factors and the broader insect community when assessing the environmental impacts of agricultural inputs.

In their 2023 arthropod community-level study, Harmon et al. (2023)saw a reduction in arthropod herbivore and predator biomass in response to clothianidin contamination in a prairie restoration. These reductions in herbivore and predator biomass were inconsistent with our findings, but they could be indicative of trends that were not captured in our study. In the Harmon et al., 2023 study, insect sampling was done two years after the sites were restored to prairie from row crop agriculture and in both years prior to sampling, the sites were treated with clothianidin. This repeated exposure, could be causing negative generational effects on the arthropod community. Furthermore, the reduction in biomass could be a result of decreased body mass rather than reduced abundance; an observed phenomenon in numerous insect-neonicotinoid studies (Shi et al., 2017; Wu et al., 2021). Additional factors that could explain this discrepancy in findings include differences in the scope of taxa being analyzed (beetles vs. Arthropods) and differences in sampling technique (sweep netting vs. emergence tent sampling). Regardless, these differing results highlight the complexity of these study systems and the need for further community-level analysis in the neonicotinoid-arthropod literature.

Overall beetle abundance and detritivore abundance were significantly positively influenced by bare ground cover. These positive effects could be a symptom of the sampling method (i.e. the more bare ground present under a sampling tent, the less obscured the collection jar), however numerous studies indicate that beetle abundance and richness are positively influenced by habitat management practices such as periodical burns and grazing (Reed, 1997; Woodcock et al., 2008a). While not equivalent, these management practices create disturbance and temporarily increase the amount of bare ground. It is possible that a similar phenomenon is being observed in our study.

Overall beetle abundance and predator abundance were influenced by both floral abundance and richness. In both cases, floral abundance had a significantly positive effect on beetle and predator abundance, and floral richness had a significant negative effect. While positive associations between beetle and floral abundance are well represented in the literature (Miller, 2021; Killewald et al., 2023), the observed reductions in overall beetle and predator abundance in relation to increased floral richness is contradictory to much of the existing literature (Varchola and Dunn, 1999; Jonsson et al., 2009; Cook-Patton et al., 2011), however these findings are not unprecedented (Koricheva et al., 2000; Zou et al., 2013). It is also important to note that we measured flowering plant richness and not total plant richness. Not all beetle species have floral associations so this metric may not have been representative of the plant community diversity as a whole.

Despite their prophylactic application and ubiquity of use, the efficacy of neonicotinoid seed coatings on common pests of cereal crops, such as the western corn rootworm (*Diabrotica virgifera*) on corn (*Zea mays*), is limited. Studies by Boetel et al. (2003); Witmer et al. (2003), and Furlan et al. (2006), have shown that prophylactic neonicotinoid seed coatings do not manage or reduce corn rootworm population levels. While seed coatings have been effective in controlling other pest species on various crops (Krupke et al., 2017), the discrepancy in effectiveness against pests and the potential negative consequences to beneficial arthropod groups, brings the ubiquitous use of neonicotinoids as seed coatings into question. The findings from this study along with an abundance of neonicotinoid research, indicate that non-target organisms are differentially affected by neonicotinoids. Yet, very few studies examine these trends in field realistic settings and even fewer compare findings across taxa. The lack of consensus in the literature examining the negative effects of neonicotinoid contamination on beneficial arthropods, highlights the importance of field-based research, community level analysis, and longitudinal studies; which provide important environmental and long-term context. We believe that further examination of these factors is imperative to comprehensively assess the risks associated with neonicotinoid contamination of natural habitats and will allow for more informed management and policy decisions.

Data availability statement

The original contributions presented in the study are publicly available. Specimens collected in this experiment are available from the Illinois Data Bank: https://doi.org/10.13012/B2IDB-1762625_V1.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because research on insects typically does not require ethical approval. Special permitting is occasionally required, but only when the study involves an endangered species. This study did not involve any endangered species.

Author contributions

JT: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. AH: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1347526/full#supplementary-material

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Canopy specialist *Hylaeus* bees highlight sampling biases and resolve Michener's mystery

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Large parts of the Pacific were thought to host low bee diversity. In Fiji alone, our recent estimates of native bee diversity have rapidly increased by a factor of five (from 4 to >22). Here, we show how including sampling of the forest canopy has quickly uncovered a new radiation of *Hylaeus* (Hymenoptera: Colletidae) bees in Fiji. We also show that *Hylaeus* are more common across the Pacific than previously thought and solve one of Charles Michener's mysteries by linking the previously enigmatic French Polynesian *Hylaeus tuamotuensis* to relatives in Fiji. We use systematic techniques to describe eight new *Hylaeus* species in Fiji (*n* = 6), French Polynesia (*n* = 1), and Micronesia (*n* = 1), and discuss impressive dispersal events by this genus. These clades also double the number of *Hylaeus* dispersals out of Australia from two to four. Our discovery highlights the severe impact of bee sampling methods on ecological interpretations and species discovery, specifically that canopy sampling is needed to correctly assess forest bee diversity even where there is a very long record of sampling. It further highlights the potential for forests to host higher-than-anticipated diversity and conservation value. This has broad methodological and regulatory impacts for land managers seeking to make choices about pollination services and diversity. The new species are *Hylaeus (Euprosopoides) chuukensis* Dorey, Davies, and Parslow; *H. (Prosopisteron) albaeus* Dorey, Davies, and Parslow; *H. (P.) apertus* Dorey, Davies, and Parslow; *H. (P.) aureaviridis* Dorey, Magnacca, and Parslow; *H. (P.) breviflavus* Magnacca; *H. (P.) derectus* Dorey, Davies, and Parslow; *H. (P.) navai* Dorey, Davies, and Parslow; and *H. (P.) veli* Dorey, Davies, and Parslow.

KEYWORDS

Fiji, French Polynesia, Micronesia, Hylaeinae, sampling methods, *Lasioglossum*, Colletidae, dispersal

1 Introduction

A key parameter in island biogeography theory is the distance separating remote islands from potential source populations (MacArthur and Wilson, 1967). Dispersal distances can act as filters, with successively more remote islands experiencing ever-more strict species filtering. However, additional filters also operate, such as taxon-specific capacities for dispersal, similarity in the ecology of source and sink regions, and opportunities to escape local enemies and pathogens (Patiño et al., 2017). Documenting how insular species diversity varies with distance from source regions facilitates our understanding of the relative roles of these filters in the assembly of insular biota.

Until recently, bee diversity in the Southwest Pacific (SWP) was regarded as depauperate, especially eastwards of New Caledonia (Perkins and Cheesman, 1928; Michener, 1979b). This aligns with predictions of decreasing richness over successively increasing distances, moving eastwards, of South Pacific islands from Sahul—Australia, Tasmania, New Guinea, and the surrounding islands (Groom and Schwarz, 2011). However, discerning regional patterns in diversity relies on sampling and taxonomic effort, and studies on bees from the South Pacific have been scarce until very recent times, often comprising privately published or unpublished museum records.

Recent studies have greatly increased the number and diversity of recorded bee species from multiple families in New Caledonia (Pauly and Munzinger, 2003; Barry et al., 2013; Pauly et al., 2015; Zakardjian et al., 2023), which might be expected given the geographical proximity of the archipelago to Sahul. At the same time, 10 years of intensive field work in Fiji has increased the number of described *Lasioglossum (Homalictus)* Cockerell, 1919 (family Halictidae) species from 4 (Perkins and Cheesman, 1928; Michener, 1979b) to 13 (Dorey et al., 2019) with more than 9 species waiting to be described (Dorey et al., 2020b; Naaz et al., 2022). These recent New Caledonian and Fijian studies show that our understanding of regional insular fauna can radically change perceived biodiversity patterns as sampling efforts increase.

Up until the last decade, only three bee families, Apidae, Megachilidae, and Halictidae, were reliably or recently recorded from the South West Pacific eastwards of Vanuatu (Pauly and Villemant, 2009; Groom and Schwarz, 2011; Naaz et al., 2022). Genetic studies have since shown that all of the apid species, and most of the megachilid species, in this region have been introduced via human agency (Davies et al., 2013; Groom et al., 2014, 2015). Remarkably, there is only one record of an endemic colletid bee in the South Pacific east of Vanuatu, namely, *Hylaeus tuamotuensis* Michener, 1965 from French Polynesia. Recorded in the 1930s, the species' provenance was a mystery to Michener (1965), being over 4,000 km south of Hawaii and almost 6,000 km east of Australia. The large *Hylaeus* radiation in Hawaii is recently derived from a Palearctic ancestor, and not closely related to the Australian or South West Pacific taxa (Magnacca and Danforth, 2006). This dearth of colletid specimens is surprising given that Colletidae comprises the most abundant and diverse family of bees in Sahul.

The bee family Colletidae has a Gondwanan origin with centers of diversity in South America and Australia (Almeida et al., 2012). The colletid subfamily Hylaeinae has an Australian origin, and one molecular-based study (Kayaalp et al., 2013) suggests that a single dispersal event outside of Sahul led to an almost global distribution of the largest hylaeine genus, *Hylaeus* Fabricius, 1793 [764 species; Ascher and Pickering (2020)], with an additional dispersal to New Zealand. This is a remarkable case of geographical radiation, but limited taxon sampling in the Kayaalp et al. (2013) study does not allow us to understand how the various dispersal steps were taken, nor does it take into account what can be gleaned by examining distributional patterns.

Here, we provide the first rigorous evidence of endemic hylaeine bees in the South Pacific east of Vanuatu. We use morphological and mitochondrial DNA data to describe eight new species from Fiji (n = 6), French Polynesia (n = 1), and Micronesia (n = 1). Despite 10 years of intensive sampling on Fiji, this radiation of bees on Fiji was never described and was detected with uncertain provenance or forgotten in museum drawers. We show that canopy sampling techniques employed at only a few sites in Fiji rapidly revealed new species. We argue that the presence of colletid bees in the Pacific has been largely underestimated and recommend widespread canopy sampling regimes to correct this shortfall globally. We further highlight the massive and global potential for species discovery of bees in trees and the importance of this discovery for biogeographical understandings, forest management, and conservation.

2 Materials and methods

2.1 Specimen collections

2.1.1 Fiji samples

Hylaeus specimens were caught between April 2016 and October 2019 by sweep netting flowers of several plant species. For all but one specimen (2016), samples were only collected using canopy nets (5–11 m) and sweeping off of red-flowering plants.

2.1.2 French Polynesia samples

All contemporary samples were collected in August of 2017 near the summit of Mt Marau (Tahiti). Most specimens were collected on the flowers of the introduced *Solanum nigrum* L. (Solanaceae) and one was collected in a yellow pan trap that was set for a few hours nearby.

2.1.3 Micronesia samples

Samples were collected on a single day, 14 April 2014, via sweep netting of flowering vegetation. Samples were collected from the Weno (Xavier College Campus) and Fono Mu islands.

2.2 COI data generation

Tissue samples were taken from a single hind leg of each individual that was sequenced and then sent to the Centre for

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Abbreviations: BPBM, Bernice Pauahi Bishop Museum; SSW, Supraclypeal Suture Width; SSL, Supraclypeal Suture Length; SAMA, South Australian Museum.

Biodiversity Genomics. Mitochondrial DNA was extracted and sequenced there using the SEQUEL platform, using the methods described by Hebert et al. (2018). The resulting sequences were then checked against the National Center for Biotechnology Information (NCBI) BLAST database to exclude non-target sequences. We retrieved 21 in-group *Hylaeus* sequences and three out-group *Hyleoides* Smith, 1853 or *Meroglossa* Smith, 1853 sequences. Outgroup specimens were identified by OKD using Houston (1975).

2.3 COI analyses

We employed the package *bModelTest* version 1.2.1 (Bouckaert and Drummond, 2017) in the *BEAST2* version 2.6.6 (Bouckaert et al., 2019) package in order to determine the best partition schemes for our COI partitions, split into first (SYM/GTR+Γ+I), second (123324+Γ+I+x), and third (TN93+Γ+x) codon positions. Each codon position was assigned a relaxed log normal clock. We assigned three outgroup species—*Hyleoides concinna* (Fabricius, 1775), *Meroglossa impressifrons* (Smith, 1853), and *M. itamuca* (Cockerell, 1910)—and restricted them in the phylogeny according to Almeida and Danforth (2009). All tree priors were linked and assigned a Birth Death process in *BEAUti* version 2.6.6 (Bouckaert et al., 2019). We used *CoupledMCMC* version 1.0.2 (Müller and Bouckaert, 2020) with four heated chains, running for 100 million iterations, resampling every 20,000th iteration, and undertook four independent runs in *BEAST2* to ensure convergence—as defined by an effective sample size of >200 in *Tracer* version 1.7 (Rambaut et al., 2018). The log and tree files from these four independent heated runs were combined using *LogCombiner* version 2.6.6 (Bouckaert et al., 2019). The consensus tree was created in *TreeAnnotator* version 2.6.6 (Bouckaert et al., 2019) and visualized using *FigTree* version 1.4.4 (Drummond, 2016).

2.4 Species descriptions

To describe these bees, we used dissecting microscopes and entered data directly into *Lucid* version 4. We recorded measurements and converted these into ratios using *Excel* and then transcribed them into *Lucid*. Specimens were identified to subgenus using the keys made by Houston (1981) and Michener (2007) by JBD. We checked the availability of our names against the expanded *BeeBDC* bee taxonomy list (Dorey et al., 2023a; Dorey et al., 2023b) that was generated using Ascher and Pickering (2020). The key to the Micronesian *Hylaeus* was modified from Krombein (1950). Material is deposited in the Bernice Pauahi Bishop Museum (BPBM), Honolulu, Hawaii, USA, and the South Australian Museum (SAMA), Adelaide, South Australia, Australia.

2.5 Images

Images of Fijian and French Polynesian specimens were taken with a Canon EOS 5DSR using a Canon MP-E 65mm f 2.8 1–5x macro (dorsal, lateral, and rear), Leica m205 C microscope with a Leica DFC 500 camera, Nikon 4x plan achromat microscopic, and Nikon 10x plan achromat microscopic lenses. Male sterna 7–8 and genitalia were imaged using a Nikon eclipse 50i with the same camera attached. Images were then stacked using Zerene Stacker (Littlefield, 2017) and then cleaned using Adobe Photoshop and Photoshop Lightroom. Images at the BPBM were taken using a Leica M165c microscope, a DMC5400 camera, and the Leica automontage system. These images were stacked using Helicon Focus (HeliconSoft, 2023).

3 Results

3.1 Specimen collections

3.1.1 Fiji

Our initial Fijian *Hylaeus (Prosopisteron) albaeus* sp. nov. specimen was caught in April 2016 by sweep netting a single flowering *Metrosideros* sp. (Myrtaceae) tree at Rakiraki on the northern coast of Viti Levu (Figure 1A). That specimen was captured at a height of ~3 m. Further targeted low strata sampling in that area in the following 2 years did not yield more *Hylaeus* specimens, but cyclone Winston had removed much vegetation in the region. Our next successful collection of *Hylaeus (Prosopisteron)* specimens were during April of 2019 on the Fijian island of Taveuni and at 875 meters above sea level (m asl) under Des Voeux Peak, 22 and three samples of *Hylaeus (Prosopisteron) apertus* sp. nov. and *Hylaeus (Prosopisteron) veli* sp. nov., respectively, were collected on a single red-flowering *Metrosideros collina* var. *collina* (Forst.) A.Gray tree, where the lower-branches were sampled at heights of 4–7 m (Figures 1B, E). We obtained further samples of *Hylaeus (Prosopisteron)* in October 2019 from the telecom tower escarpments ~3 km west of Nadarivatu at 898–1,072 m asl, from sweeps of a few red-flowering mistletoes at a height of 3–7 m, *Decaisnina forsteriana* (Schult.) Barlow. Here, we collected eight and three specimens of *Hylaeus (Prosopisteron) derectus* sp. nov. and *Hylaeus (Prosopisteron) navai* sp. nov., respectively (Figures 1C, D). However, the *Hylaeus* were much less abundant than *Lasioglossum*. Additionally, a nearby small (2–3 m tall) flowering *M. c.* var. *collina* only hosted *Lasioglossum*.

3.1.2 French Polynesia

Only one successful collection event was made in French Polynesia, returning six *Hylaeus (Prosopisteron) aureaviridis* sp. nov. from a *Solanum nigrum* and one from a yellow pan trap (Figure 1G). An additional *Hylaeus* observation has been made on iNaturalist by davidfl22 on 30 July 2023 (https://www.inaturalist.org/observations/176048893), which was also observed on *Metrosideros collina*.

3.1.3 Micronesia

We collected three specimens (two male and one female) of *Hylaeus (Euprosopoides) chuukensis* sp. nov. from Chuuk, Micronesia (Figure 1I). A male was collected from the Xavier College Campus (7.447, 151.887) and a further male and a female were collected from Fono Mu Islet (7.362, 151.923).

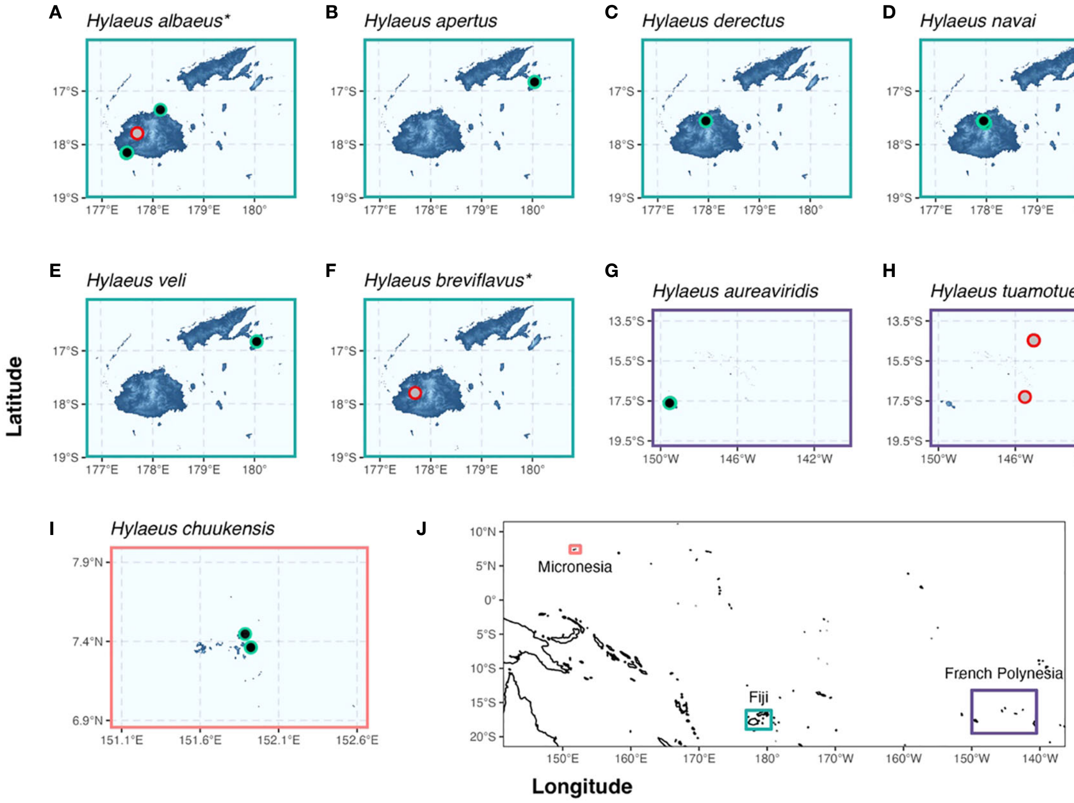

FIGURE 1
Collection locality maps of the examined *Hylaeus* species. The Fijian *Hylaeus*—*Hylaeus albaeus* sp. nov. **(A)**, *H. apertus* sp. nov. **(B)**, *H. derectus* sp. nov. **(C)**, *H. navai* sp. nov. **(D)**, *H. veli* sp. nov. **(E)**, and *H. breviflavus* sp. nov. **(F)**—are surrounded by green, the French Polynesian species—*H. aureaviridis* sp. nov. **(G)** and *H. tuamotuensis* **(H)**—are surrounded by purple, and the Micronesian species—*H. chuukensis* sp. nov. **(I)**—is surrounded by salmon. The inset **(J)** shows the entire study area. Asterisks, and gray and red points **(A, F, H)** indicate that at least some coordinates are georeferenced from general localities.

3.2 COI analyses

Our COI BEAST tree returned a well-supported phylogeny, where only a single node (between two Fijian spp.) had a posterior probability under 0.95 (Figure 2). Within-species variation was very low, and many nodes were quite deep relative to the base of the tree and the outgroup (Figure 2). While one clade contained only Fijian representatives, one was mixed with Fijian and French Polynesian representatives, and the Micronesian species formed its own clade (Figure 2).

3.3 Species descriptions

We provide brief species descriptions based on parts of the dichotomous key and full image plates (Figures 3–11). However, we also provide (i) a version of the manuscript with full-length descriptions embedded and an (ii) interactive Lucid key in our FigShare repository (https://doi.org/10.25451/flinders.24481231). There, we also share all data associated with the descriptions including (iii) all collection data (including georeferenced museum specimens), (iv) csv outputs from Lucid, (v) the R-code used to produce figures and manipulate data, (vi) BEAST2 run files and outputs, (vii) summary box plots of all measurements, and (viii) the GenBank submission file. While we do not provide written descriptions of male internal characters here (see FigShare), we do provide all images and note that they can be an excellent identification aid.

3.4 Fijian and French Polynesian *Hylaeus*

Family Colletidae Lepeletier de Saint Fargeau, 1841.
Subfamily Hylaeinae Viereck, 1916.
Genus *Hylaeus* Fabricius, 1793.
Subgenus *Prosopisteron* Cockerell, 1906.

3.4.1 Key to the Fijian and French Polynesian *Hylaeus (Prosopisteron)* males

1. Face with paraocular marks present … 2.

Paraocular area unmarked … 6.

2. Paraocular and clypeal marks contiguous, at least ventrally (Figure 9A); pronotal lobe yellow; mandible yellow; Tuamotu Islands … *H. tuamotuensis* Michener, 1965.

Paraocular and clypeal marks distinctly separated (Figures 3 and 5–7; pronotal lobe black; mandible variable … 3.

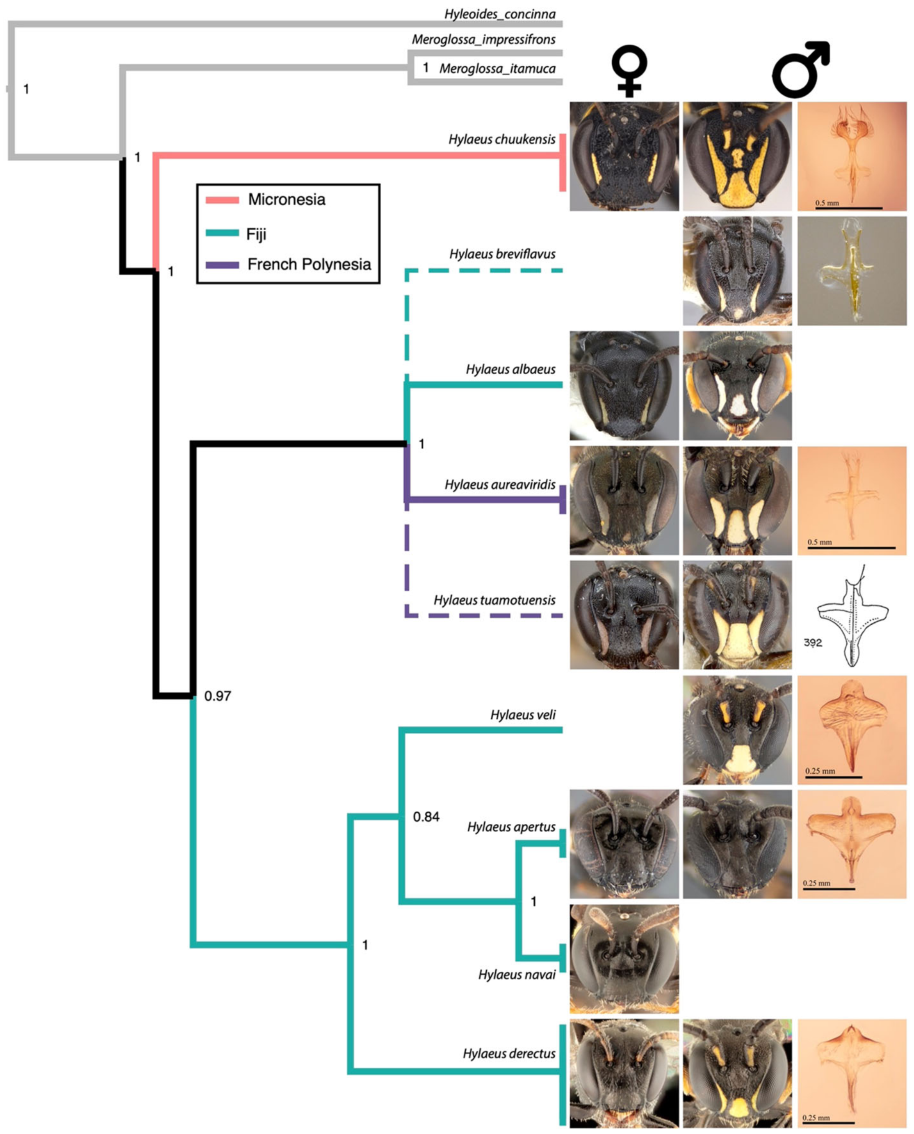

FIGURE 2
The phylogeny of the Micronesian (salmon), Fijian (green), and French Polynesian (purple) *Hylaeus*. The outgroup (gray) contains three Australian Hylaeinae from different genera, the Micronesian *Hylaeus* is of the subgenus *Euprosopoides*, while the remaining *Hylaeus* are of the subgenus *Prosopisteron*. Posterior supports are indicated at nodes, and dashed lines indicate inferred positioning from male genitalic characters. Images show the female faces (left), male face (middle), and male sternite 8 (right) for each species, where specimens exist. Note the bifurcation on posterior lobe (top) of sternite 8 for the middle Fiji–French Polynesia clade compared to the simple apex on the lower Fiji-only clade. Within-species genetic variation was essentially non-existent and so the terminals were flattened. The sternite 8 line drawing of *H. tuamotuensis* Michener, 1965 is reproduced from Michener (1965).

3. Head and mesosoma tinged with submetallic green; clypeal mark large, extending nearly to posterior clypeal margin (Figures 5A–C); Tahiti … *H. aureaviridis* sp. nov.

Head and mesosoma mostly black; clypeal mark small … 4.

4. Scape marked with yellow; supraclypeal area reticulate, without distinct striae; posterior margin of clypeus straight; face in profile strongly convex ventrally; metasoma without hair bands (Figures 7A–C); Fiji … *H. derectus* sp. nov.

Scape dark brown to black; supraclypeal area striate; face in profile flatter, not strongly convex ventrally; T1 with prominent apicolateral bands of white setae … 5.

5. Facial markings white; pronotal lobe white; gena sparsely punctured (Figure 3); Fiji … *H. albaeus* sp. nov.

Facial markings yellow; pronotal lobe brown; gena closely punctured (Figure 6); Fiji … *H. breviflavus* sp. nov.

6. Face, mandible, and pronotum black; scutum with open punctures; anterior third of dorsal propodeum weakly rugose (Figures 4A–C); Fiji … *H. apertus* sp. nov.

Face with a large clypeal mark, mandible yellow, and pronotal lobe with a yellow spot; scutum with close to dense punctures; anterior half or more of dorsal propodeum rugose (Figures 10A–C); Fiji … *H. veli* sp. nov.

3.4.2 Key to the Fijian and French Polynesian *Hylaeus (Prosopisteron)* females

1. Mask with two pale patches … 2.

Mask with zero or three pale patches … 3.

2. Pronotal collar black with two lateral yellow patches; scutellum reticulate with very fine punctures; T2–4 with translucent yellow margins and no apical bands of setae; mandible with an anterior stripe along its length (Figures 9F, G); Tuamotu Islands … *H. tuamotuensis* Michener, 1965.

Pronotal collar black; scutellum shinning with conspicuous close punctures; T2–4 margin not clearly differentiated; T1–2 with posterolateral fascia of white setae; mandible all black (Figures 3F, G); Fiji … *H. albaeus* sp. nov. or *H. breviflavus* sp. nov.

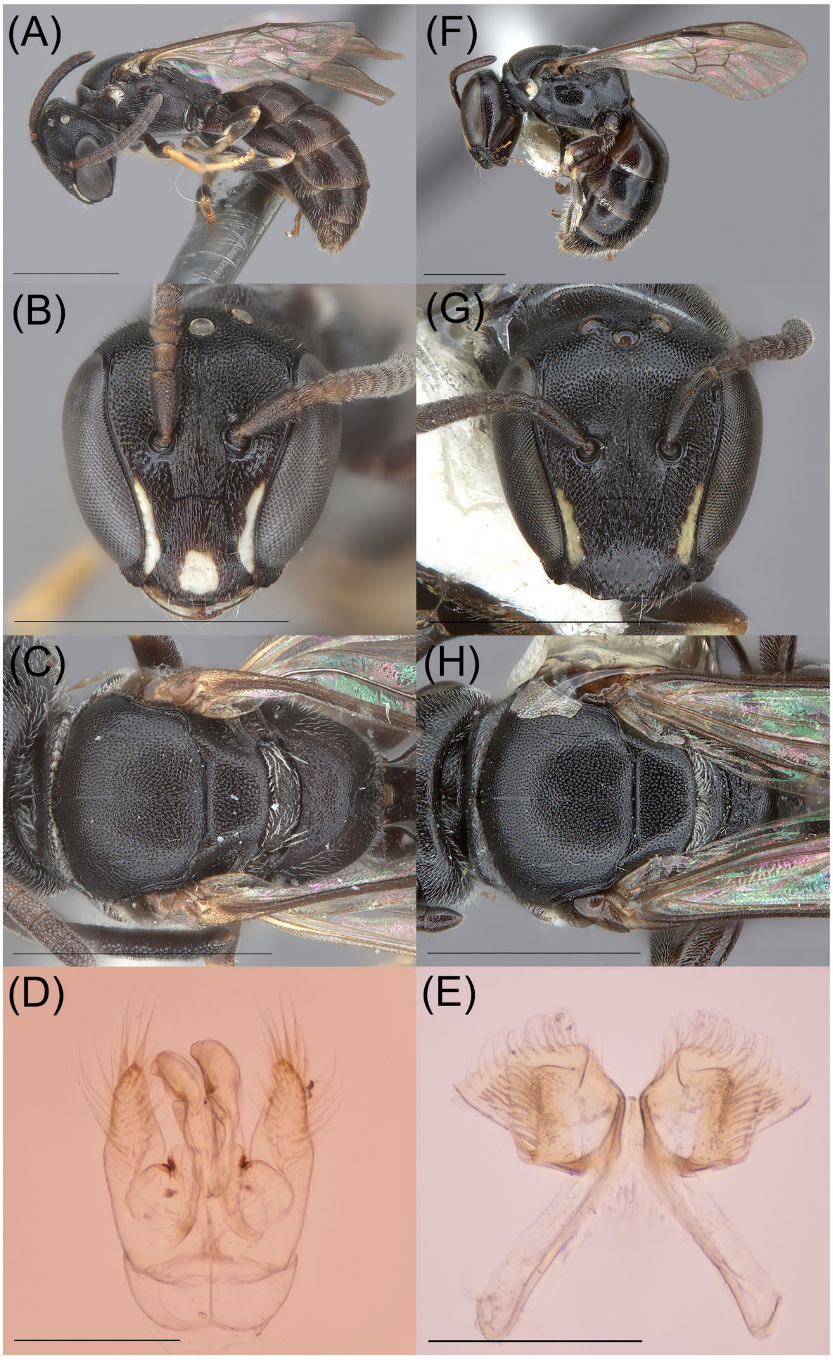

FIGURE 3
Hylaeus albaeus Dorey, Davies, and Parslow sp. nov. Male lateral habitus **(A)**, face **(B)**, dorsal mesosoma **(C)**, genitalia **(D)**, and sternite 7 **(E)**. Female lateral habitus **(F)**, face **(G)**, and dorsal mesosoma **(H)**. (Scale bar, **A-C**, **F-H** = 1.00 mm; **D**, **E** = 0.25 mm.)

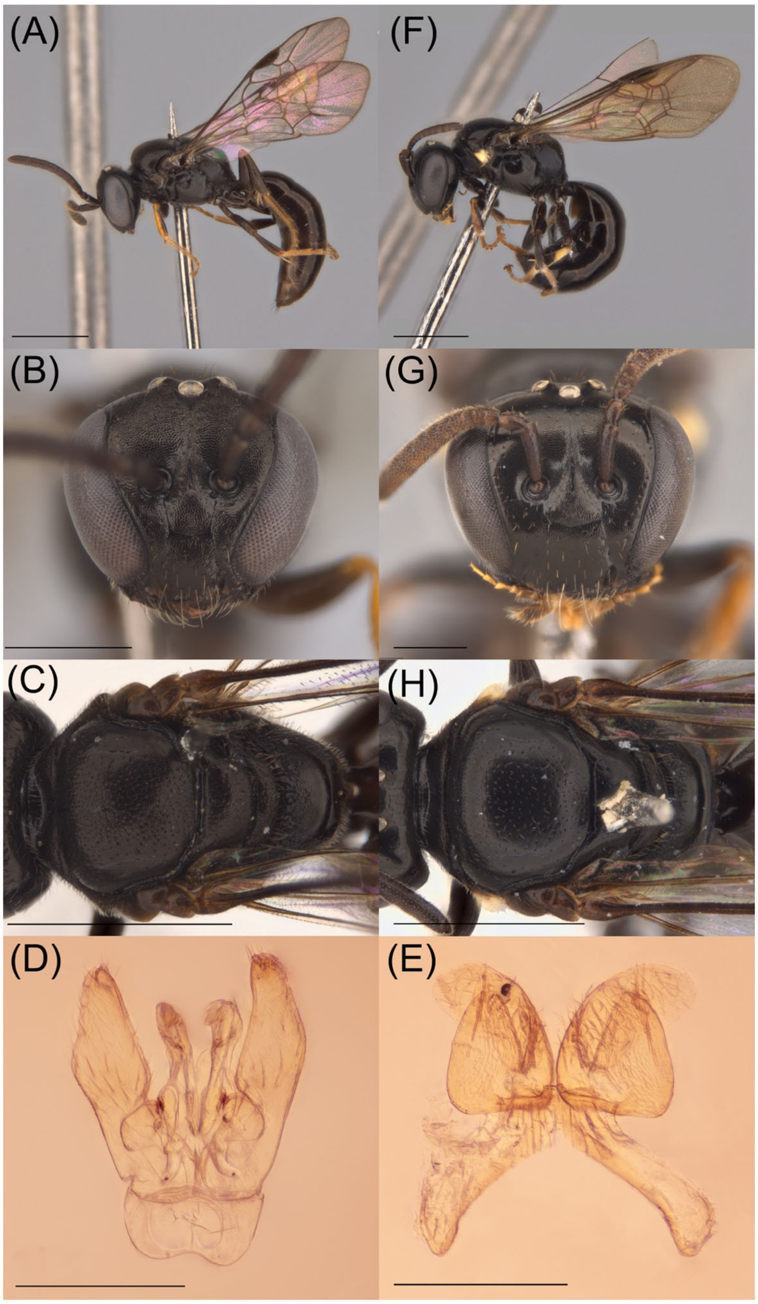

FIGURE 4
Hylaeus apertus Dorey, Davies, and Parslow sp. nov. Male lateral habitus **(A)**, face **(B)**, dorsal mesosoma **(C)**, genitalia **(D)**, and sternite 7 **(E)**. Female lateral habitus **(F)**, face **(G)**, and dorsal mesosoma **(H)**. (Scale bar, **A-C**, **F-H** = 1.00 mm; **D,E** = 0.25 mm.)

3. Mask with three patches; head and mesosoma mostly black with submetallic green tinge; posterior margins of tergites with a distinct and broad paler margin; scutum and scutellum with dense and short erect hairs (Figures 5F, G); Tahiti … *H. aureaviridis* sp. nov.

Face entirely black; head and mesosoma mostly black, no metallic tinge; posterior margin of tergites usually black or if there is a paler margin it is narrow; scutum and scutellum with close-open partly erect hairs … 4.

4. Propodeum dorsal face reticulate and anterior half or more rugulose; T2 reticulate, clypeus posterior margin straight (Figures 7F–H); Fiji … *H. derectus* sp. nov.

Propodeum dorsal face reticulate and only anterior third rugulose; T2 shining medially, clypeus posterior margin concave … 5.

5. Medial groove on frons is partly poorly defined before meeting median ocellus; supraclypeal suture width:length ratio ≥

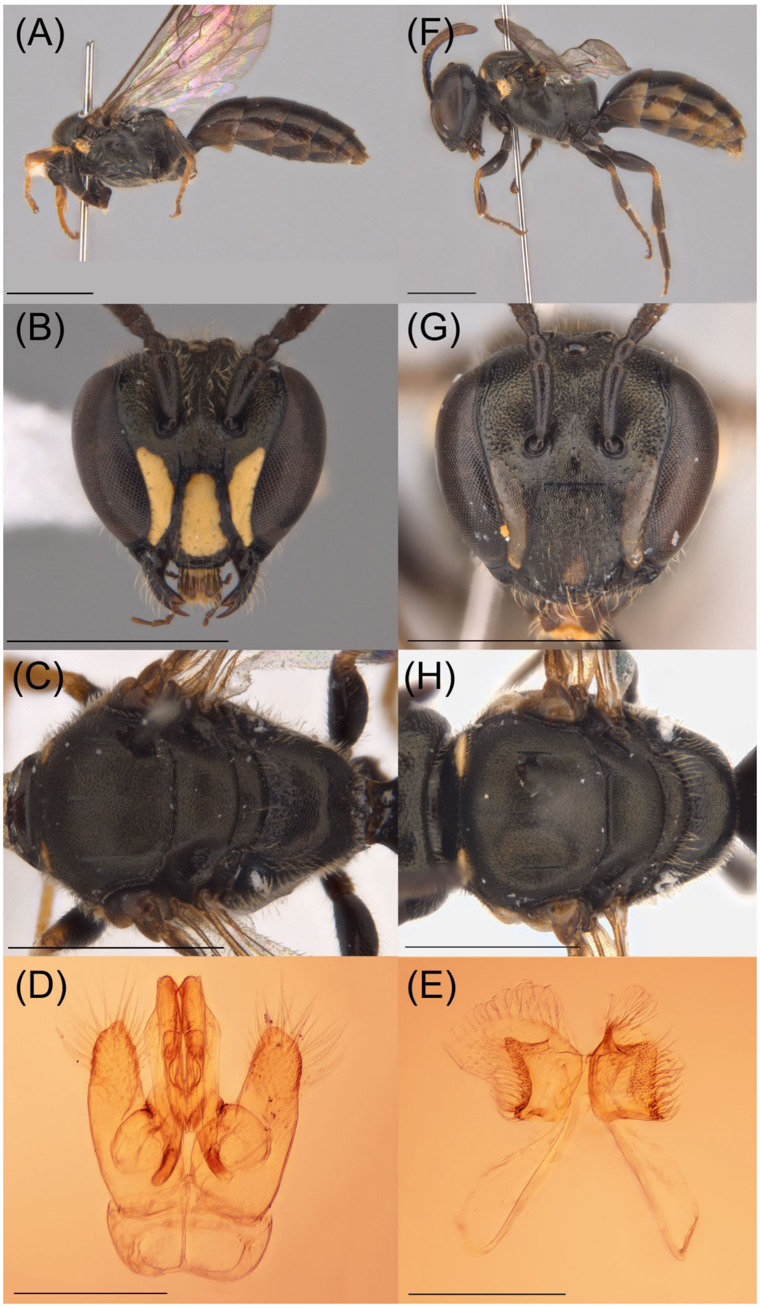

FIGURE 5
Hylaeus aureaviridis Dorey, Magnacca, and Parslow sp. nov. Male lateral habitus **(A)**, face **(B)**, dorsal mesosoma **(C)**, genitalia **(D)**, and sternite 7 **(E)**. Female lateral habitus **(F)**, face **(G)**, and dorsal mesosoma **(H)**. (Scale bar, **A-C**, **F-H** = 1.00 mm; **D**, **E** = 0.25 mm.)

13; gena reticulate but impunctate (Figures 8B–D); Fiji … *H. navai* sp. nov.

Medial groove on frons clearly meets median ocellus; supraclypeal suture width:length ratio ≤ 10; gena reticulate with sparse punctures (Figures 4F, G); Fiji … *H. apertus* sp. nov.

3.4.3 *Hylaeus albaeus* Dorey, Davies, and Parslow sp. nov.

(Figures 1–3).

Materials examined. Holotype 1♂ Rakiraki hotel, Viti Levu, Fiji, −17.3603, 178.1537, 3 m asl, 2016/04/01, MP Schwarz, swept from *Metrosideros collina* var. *collina*, CFJRR_NH9, (BPBM: 18008). Paratypes 1♀1♂ Sigatoka Prov., Sigatoka Sand Dunes N.P., Viti Levu, Fiji, −18.16, 177.5, 100 m asl, 2002/12/13, M Irwin, E Schlinger, M Tokota'a, Malaise trap, FJ-6B Malaise (BPBM: ♂ FBA 026760; ♀ FBA 026755); 1♂ 1♀ Sigatoka Prov., Sigatoka Sand Dunes N.P., Viti Levu, Fiji, −18.16, 177.5, 100 m asl, 2003/12/13, M Irwin, E Schlinger, M Tokota'a, Malaise trap, FJ-6C Malaise (BPBM: ♂FBA 035899; ♀FBA 035880); 4♀ Sigatoka Sand Dunes N.P., malaise 1.1 km SSW of Volivoli Vlg., Viti Levu, Fiji, −18.1694, 177.4847, 55 m asl, 2003/11/15, E Schlinger, M Tokota'a, Malaise trap, FJVL6b_M02_16 (BPBM:♀ FBA 063181, FBA 063184, FBA 063195, FBA 064760).

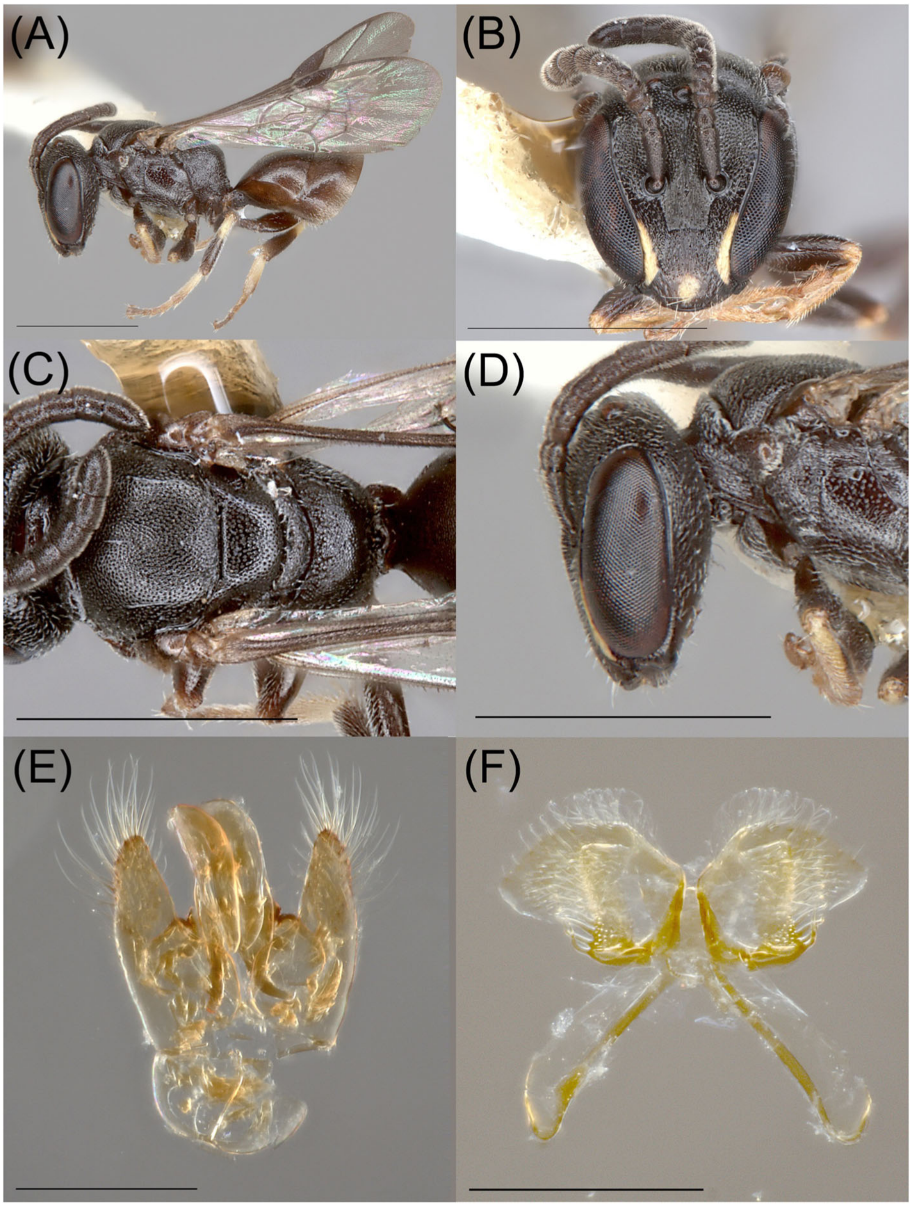

FIGURE 6
Hylaeus breviflavus Magnacca sp. nov. Male lateral habitus **(A)**, face **(B)**, dorsal mesosoma **(C)**, lateral head **(D)** (scale bar = 0.50 mm), genitalia **(E)**, and sternite 7 **(F)** (scale bar = 0.25 mm).

Male diagnosis. In combination, mask has three widely separated white marks; head and body are otherwise mostly black (not submetallic); supraclypeal area striate; and metasoma with distinct posterolateral setal bands on T1. Very similar to *H. breviflavus* sp. nov., distinguished by the white face marks and the scutum with moderately close puncture but with distinct interspaces, the surface reticulate and somewhat dull.

Male description. Head *mask* with three white patches, clypeal mark moderately small, not extending dorsally much over half length of clypeus, paraocular marks narrow and not or barely reaching ventral margin of antennal sockets; *scape* black; *mandible* mostly white, brown apex; *gena* reticulate, sparse punctures; *frons* densely punctured and rugulose and medial groove clearly meets median ocelli; *supraclypeal area* linear striae and small sparse punctures; *paraocular area* reticulate, sparse shallow punctures along eye margin or becoming punctured posterior of antennae; *clypeal posterior margin* convex; supraclypeal suture width: supraclypeal suture length (SSW : SSL) 7.39. Mesosoma *pronotal collar* black, yellow spot on pronotal lobe; *scutum* close-dense punctures and dense, very short, prostrate hairs, appearing velvety; *metanotum* with moderately dense, short, erect setae; *lateral propodeum* reticulate, close-open punctures; *dorsal propodeum* reticulate, anterior third weakly rugose. Metasoma *T1* black, *T2–4* black and posterior margin paler; *T5–6* dark brown or posterior margin paler; *T7* dark brown. *T2* distinctly more convex in lateral view than other terga. *T1* with a distinct fascia of white

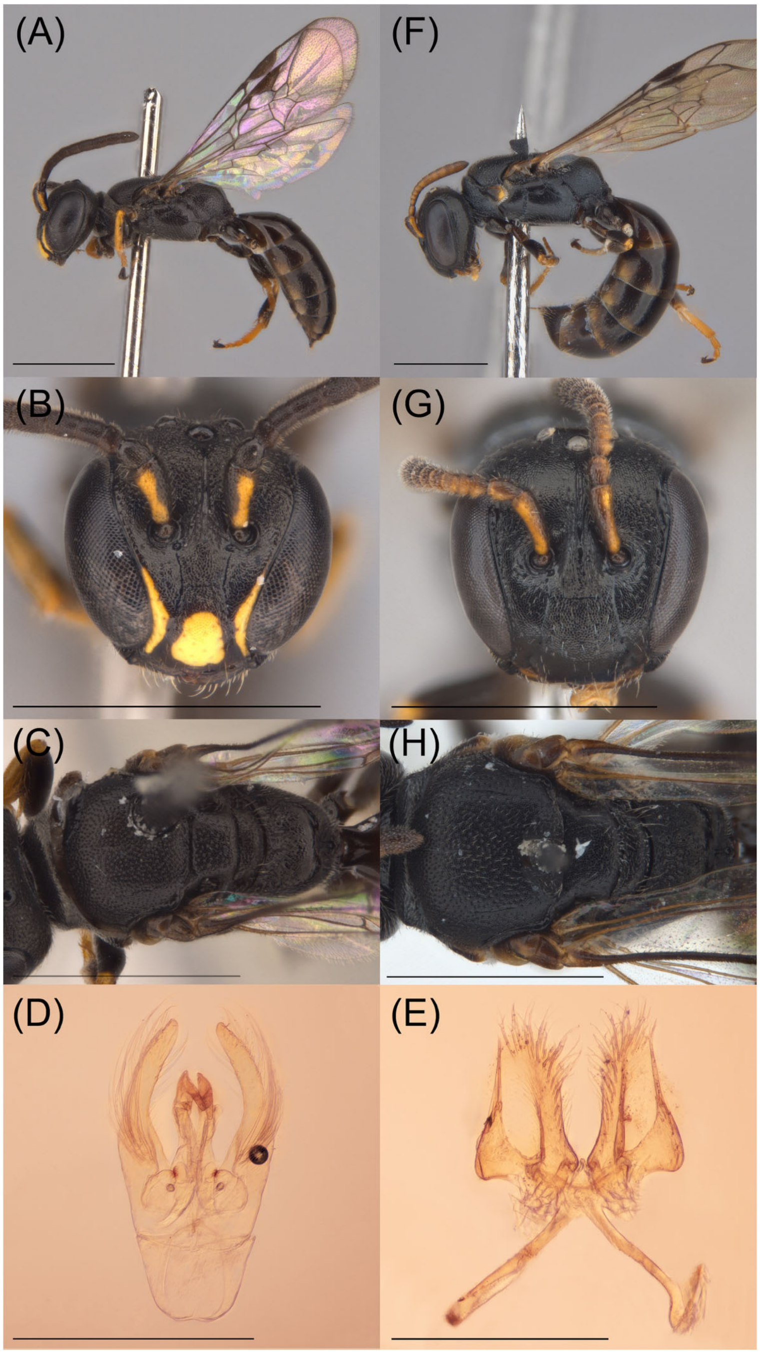

FIGURE 7
Hylaeus derectus Dorey, Davies, and Parslow sp. nov. Male lateral habitus **(A)**, face **(B)**, dorsal mesosoma **(C)**, genitalia **(D)**, and sternite 7 **(E)**. Female lateral habitus **(F)**, face **(G)**, and dorsal mesosoma **(H)**. (Scale bar, **A**–**C**, **F**, **G**, and **H** = 1.00 mm; **D** = 0.50 mm; **E** = 0.25 mm.)

setae laterally along posterior margin; *T2* with bands present but sparser, posterior terga lacking bands, with evenly spaced, moderately long erect setae.

Female diagnosis. Separated from other species here by the combination of two yellow face patches in the paraocular areas; pronotal collar lacking lateral yellow markings; and T1–2 with posterolateral seta bands. Not distinguishable from *H. breviflavus* sp. nov.

Female description. Head *mask* two patches consisting of narrow longitudinal stripes in paraocular area, not or barely reaching ventral margin of antennal sockets; *scape* and *mandible* black; *gena* closely punctured; *frons* close small punctures, smooth above, striate below and medial groove clearly meets median ocelli; *supraclypeal area* linear striae with small sparse punctures; *paraocular area* striate with dense, small punctures; *clypeal posterior margin* straight, *SSW* : *SSL* 1.6. Mesosoma *pronotal collar* black; *scutum* reticulate, small close

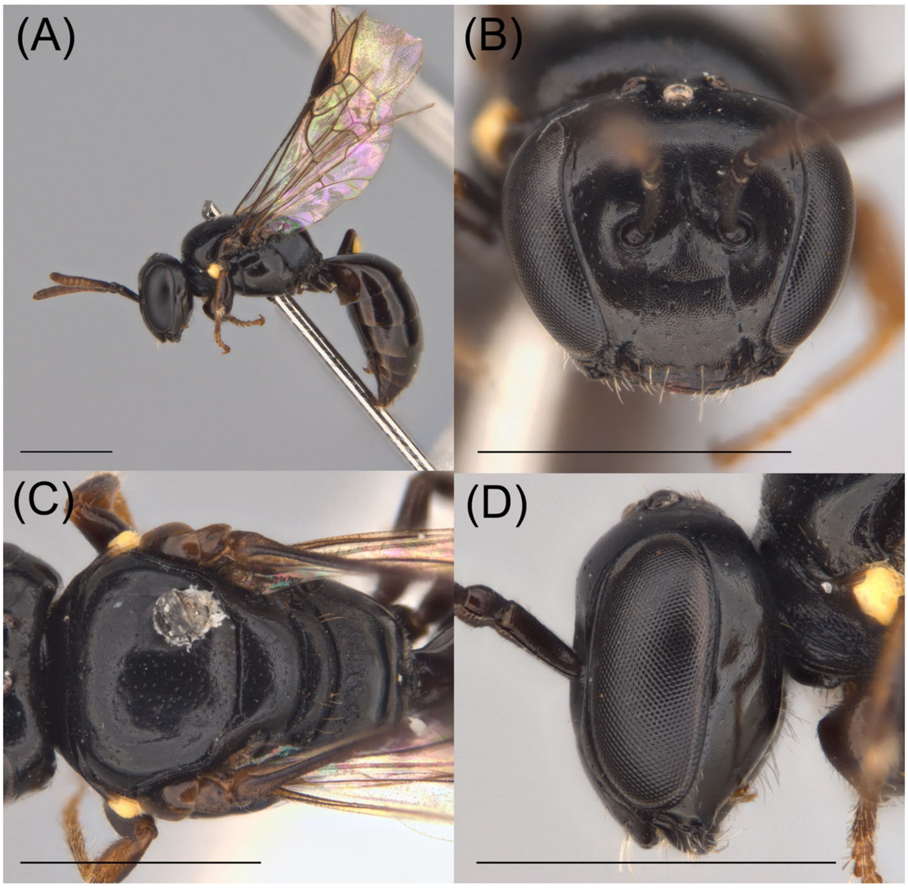

FIGURE 8
Hylaeus navai Dorey, Davies, and Parslow sp. Nov. Female lateral habitus **(A)**, face **(B)**, dorsal mesosoma **(C)**, and lateral head **(D)** (scale bar = 0.50 mm).

punctures; *lateral propodeum* reticulate, strigate-rugulose dorso-posteriorly; *dorsal propodeum* reticulate, anterior third rugose. Metasoma black. *T1* with a distinct fascia of white setae laterally along posterior margin; *T2* with bands present but sparser, posterior terga lacking bands, with evenly spaced, moderately long erect setae.

Etymology. This species is named after the distinctive white spots on the face of at least the male where *albaeus* is Latin for white. Hence, they are the white-spotted *Hylaeus*.

Distribution. Known from Rakiraki (3 m asl), and Sigatoka (100 m asl) in Viti Levu, Fiji (Figure 1A).

Remarks. This species is very similar to *H. breviflavus* sp. nov., and it is possible they may prove to be conspecific. However, face mark coloration is usually a consistent character within species of *Hylaeus*. They are also widely separated physically and ecologically, with *H. albaeus* sp. nov. taken at the coast and lowlands, and *H. breviflavus* sp. nov. at moderate elevations. Females are associated based on morphological similarities, such as a strong band of hair on the lateral edges of T1, and the collection of the specimens together. Females associated with the males of *H. albaeus* sp. nov. and *H. breviflavus* sp. nov. cannot be distinguished. Further collections of both are required and we raise the need for further sequencing efforts of these two species and both sexes.

3.4.4 *Hylaeus apertus* Dorey, Davies, and Parslow sp. nov.

(Figures 1, 2, 4).

Materials examined. Holotype 1♂ Des Voeux track, Taveuni, Viti Levu, Fiji, −16.83622, −179.97303, 872 m asl, 2019/04/29 13:12, JB Dorey, swept from *Metrosideros collina* var. *collina* (BPBM: 18009). Paratypes 4♂ 6♀ Des Voeux track, Taveuni, Viti Levu, Fiji, −16.83622, −179.97303, 872 m asl, 2019/04/29 13:12–13:42, JB Dorey, swept from *Metrosideros collina* var. *collina* (SAMA: ♂ 32-035991, 32-035992, 32-035993, 32-035994; ♀ 32-035985, 32-035990, 32-035986, 32-035987, 32-035988, 32-035989). Other materials 4♂ 7♀ Des Voeux track, Taveuni, Viti Levu, Fiji, −16.83622, −179.97303, 872 m asl, 2019/04/29 13:12–13:42, JB Dorey, swept from *Metrosideros collina* var. *collina* (BPBM: ♂ 19FJ54, 19FJ60, 19FJ65, 19FJ71; ♀ 19FJ55, 19FJ57, 19FJ64, 19FJ66, 19FJ69, 19FJ73, 19FJ75).

Male diagnosis. Punctation of the scutum is sparser laterally than medially (more or less even in most other species); the metasoma is predominantly smooth and polished with few setae; and, excluding legs, it is entirely black.

Male description. Head *mask* none; *scape* and *mandible* black; *gena* reticulate, sparse punctures; *frons* reticulate, open small punctures and medial groove clearly meets median ocelli;

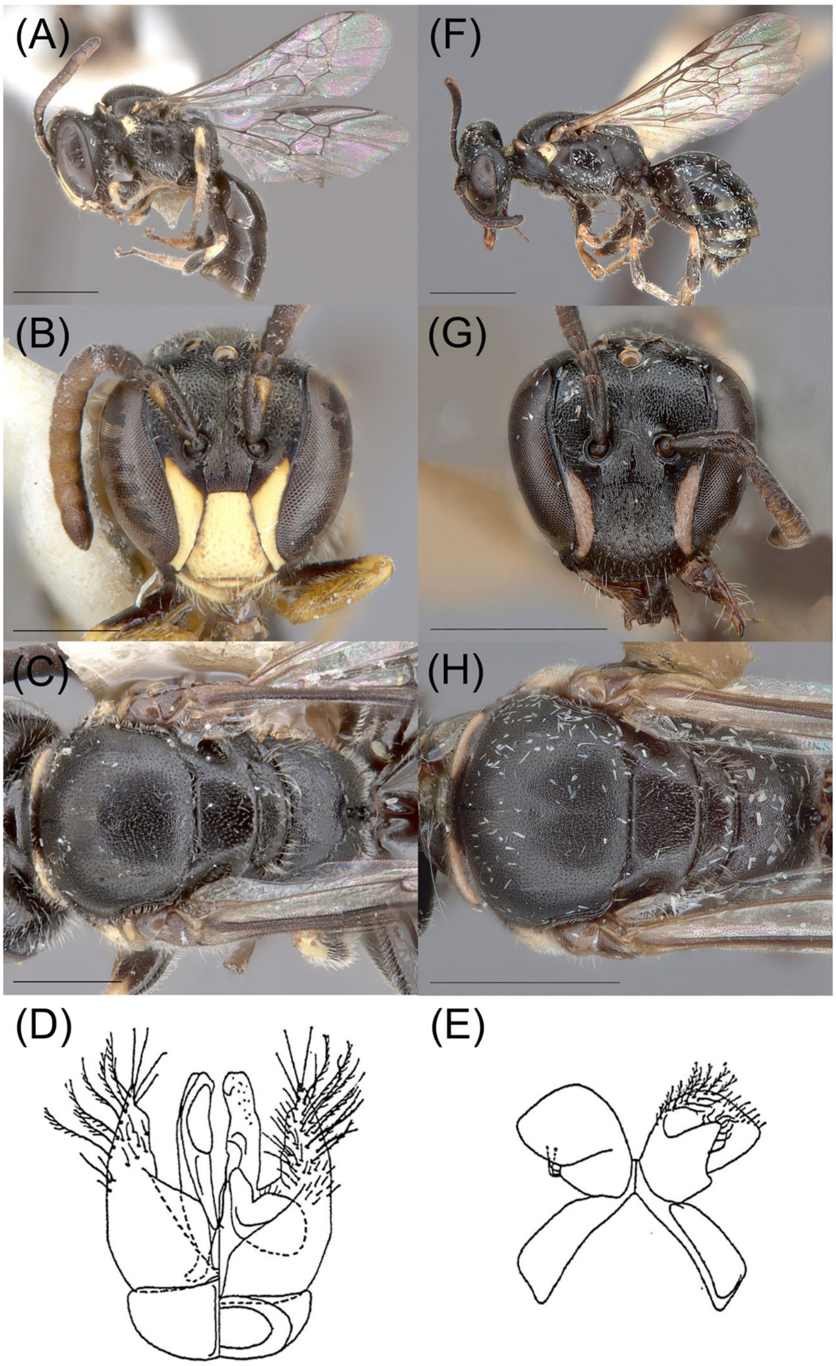

FIGURE 9
Hylaeus tuamotuensis Michener, 1965. Male lateral habitus **(A)**, face **(B)**, dorsal mesosoma **(C)**, genitalia **(D)**, and sternite 7 **(E)**. Female lateral habitus **(F)**, face **(G)**, and dorsal mesosoma **(H)**. [Scale bar, **A**-**C**, **F**-**H** = 1.00 mm; **D**, **E** are reproduced from Michener (1965) with no scale.]

supraclypeal area reticulate or reticulate-rugulose; *paraocular area* reticulate, sparse shallow punctures along eye margin; *clypeal posterior margin* straight or concave; *SSW : SSL* 7.5–38. Mesosoma *pronotal collar* black, some brown on pronotal lobe; *scutum* reticulate, large open-close punctures and close-open, short, partly erect hairs; *metanotum* with a posterior row of long simple hairs and short setae elsewhere; *lateral propodeum* reticulate and can have close-open punctures; *dorsal propodeum* reticulate, anterior third (sometimes weakly) rugose. Metasoma black or dark brown. *T2–3* with very faint lateral hairbands, nearly hairless medially.

Female diagnosis. In combination, has no face patches and medial groove on frons clearly meets median ocellus. The pronotal lobes are marked with yellow.

Female description. Head *mask* none; *scape* black; *mandibles* black, apex sometimes brown; *gena* reticulate, sparse punctures;

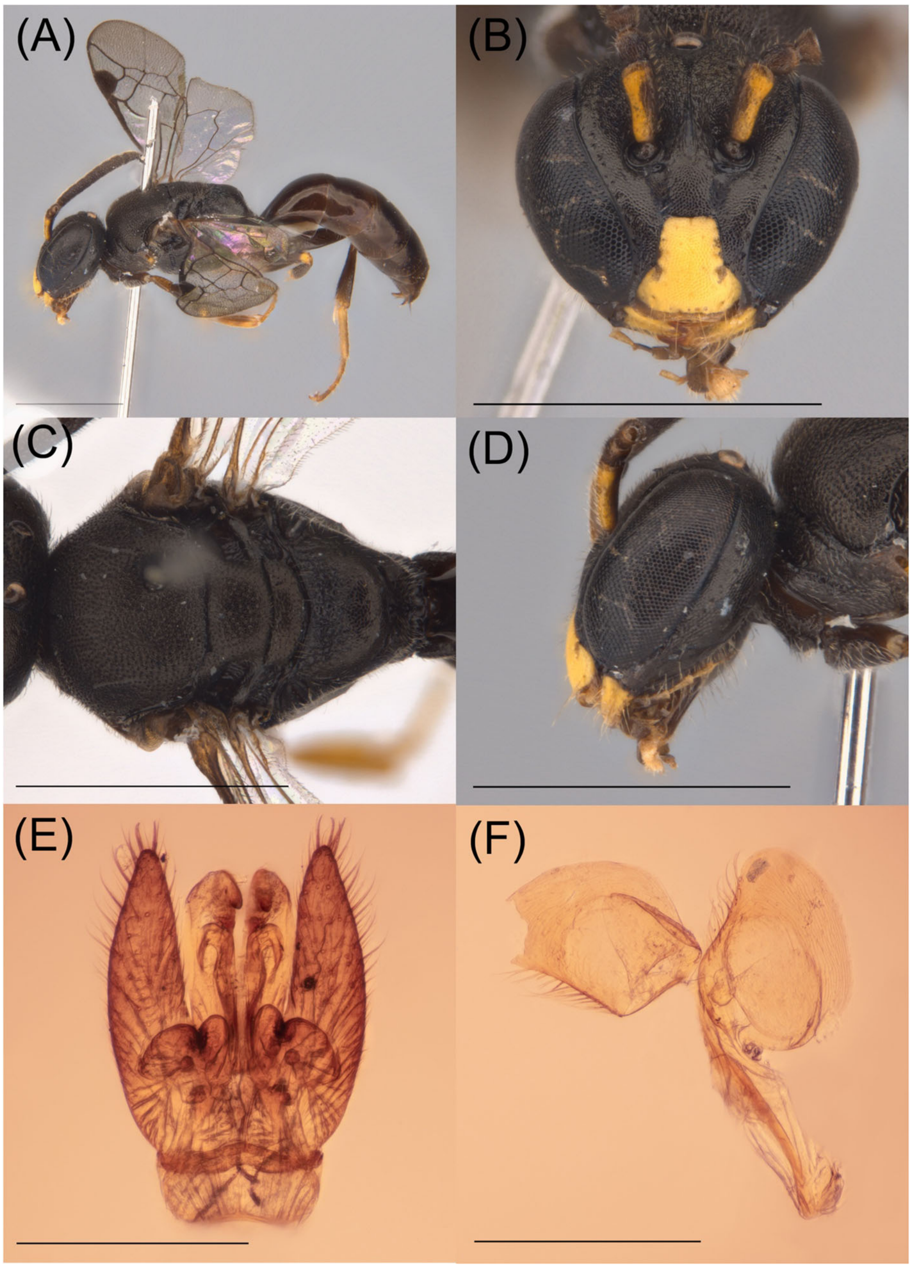

FIGURE 10
Hylaeus veli Dorey, Davies, and Parslow sp. Nov. Male lateral habitus **(A)**, face **(B)**, dorsal mesosoma **(C)**, lateral head **(D)** (scale bar = 0.50 mm), genitalia **(E)**, and sternite 7 **(F)** (scale bar = 0.25 mm).

frons reticulate, reticulate-rugulose, open-sparse small punctures and medial groove clearly meets median ocelli; *supraclypeal area* reticulate; *paraocular area* reticulate, sparse shallow punctures along eye margin; *clypeal posterior margin* concave, *SSW : SSL* 6.5–9.75. Mesosoma *pronotal collar* black, yellow patch on pronotal lobe; *scutum* reticulate, small open punctures and close-open, short, partly erect hairs; *metanotum* with a sparse posterior row of long simple hairs, nearly hairless elsewhere; *lateral propodeum* reticulate and can have close-open punctures; *dorsal propodeum* reticulate, anterior third (sometimes weakly) rugose. Metasoma *T1–3* black or dark brown; *T2–3* posterior margins of can be paler; *T4–7* black. *T2–3* with very faint lateral hairbands, nearly hairless medially.

Etymology. This species is named for the lack of a mask for both sexes. The name is derived from the Latin *apertus* (open), and hence, they are the open-faced *Hylaeus*.

Distribution. Only known from Mt De Voeux (875 m asl), Taveuni, Fiji (Figure 1B).

3.4.5 *Hylaeus aureaviridis* Dorey, Magnacca, and Parslow sp. nov.

(Figures 1, 2, 5).

Materials examined. Holotype 1♂ Near the summit of the Mt Marau, Tahiti, French Polynesia, −17.609041, −149.533164, 1,409 m asl, 2017/08/27, T Ramage, sweep net from *Solanum nigrum* or caught in nearby yellow pan trap, PFnG9Gm (BPBM: 18010). Paratypes 1♀ Tahiti, Near the summit of the Mt Marau, French Polynesia, −17.609041, −149.533164, 1,409 m asl, 2017/08/27, T Ramage, sweep net from *Solanum nigrum* or caught in nearby yellow pan trap, PFnG9Gf (SAMA: 32-036001); 1♀ Mt. Marau, Tahiti, French Polynesia, 1,300–1,400 m asl, 1984/08/28, G Paulay (BPBM); 1♀ Mt. Marau, Tahiti, French Polynesia, 1,409 m asl, 1977/06/29, PD Ashlock (BPBM); 1♂ 1♀ Fare Ata, Aorai Trail, Tahiti, French Polynesia, 1,800 m asl, 1977/03/09, WC Gagne (BPBM).

Male diagnosis. In combination, mask has three yellow patches (clypeus and paraocular areas); clypeal mark large; and head and body mostly black with faint tinges of submetallic green.

Male description. Head *mask* three yellow patches, clypeal mark extending nearly entire length and width, only narrow margins black, paraocular marks ventrally filling in area between eye and clypeus, dorsally extending nearly to ventral margin of antennal sockets; *scape* and *mandible* black; *gena* reticulate can have sparse punctures; *frons* densely punctured and rugulose and medial groove clearly meets median ocelli; *supraclypeal area* reticulate-rugulose or reticulate with distinct striae; *paraocular area* reticulate and sparse shallow punctures along eye margin or punctured posterior of antennae; *clypeal posterior margin* convex; *SSW : SSL* 0.95. Mesosoma *pronotal collar* black, yellow patch on pronotal lobe, *scutum* reticulate, small open or punctures, dense short erect hairs; *metanotum* with posterior row of branched hairs, can occur elsewhere; *lateral propodeum* reticulate or reticulate, strigate-rugulose dorso-posteriorly; *dorsal propodeum* reticulate, anterior third weakly rugose. Metasoma black or dark brown. *T2–3* hairbands absent or very faint, sparse short hairs medially.

Female diagnosis. In combination, mask has three pale patches (paraocular stripes and a small spot at clypeal apex) and head and body are mostly black with submetallic green reflections.

Female description. Head *mask* three small pale patches, paraocular marks moderately narrow, extending dorsally about to ventral margin of antennal sockets, clypeus with a small ventral mark (probably sometimes absent); *scape* and *mandible* black; *gena* reticulate, sparse punctures; *frons* open to densely punctured and rugulose and medial groove clearly meets median ocelli; *supraclypeal area* reticulate-rugulose; *paraocular area* reticulate, sparse shallow punctures along eye margin or open small punctures; *clypeal posterior margin* straight or convex; *SSW : SSL* 2.75. Mesosoma *pronotal collar*, yellow patch on pronotal lobe; *scutum* open-close punctures and dense short erect hairs; *metanotum* with sparse, elongate branched setae, can occur in a posterior row; *lateral propodeum* very finely reticulate or reticulate; *dorsal propodeum* reticulate, anterior third weakly rugose. Metasoma dark brown, posterior margins paler. *T2–3* hairbands absent or very faint, sparse short hairs medially.

Etymology. This species is named for both its yellow face patches and submetallic green sheen. Hence, we combine the Latin *aurae* (golden) and *viridis* (green) to become the golden-green *Hylaeus*.

Distribution. Known from Tahiti, near the summit of the Mt Marau and Fare Ata, Aorai Trail (1,300–1,800 m asl), French Polynesia (Figure 1G).

Remarks. The metallic coloration is faint but distinct, especially on the mesonotum. This character is unusual among *Hylaeus*, particularly extra-Australian species.

3.4.6 *Hylaeus breviflavus* Magnacca sp. nov.

(Figures 1, 2, 6).

Materials examined. Holotype 1♂ Nausori Highlands, Viti Levu, Fiji, 500–600 m asl, 1970/10/01, NLH Krauss (BPBM: 18011). Paratypes 2♀ Nausori Highlands, Viti Levu, Fiji, 500–600 m asl, 1970/10/01, NLH Krauss (BPBM).

Male diagnosis. Has three small yellow patches on its face where the clypeal mark is present only as a small spot, and supraclypeal area striate. Nearly identical to *H. albaeus* sp. nov. but the mask is yellow rather than white and the scutum has dense punctures without distinct interspaces, the surface microcarinulate and somewhat shiny. The clypeal mark is also smaller than any of the specimens of *H. albaeus* sp. nov., but only one male specimen is known.

Male description Head *mask* three small yellow patches, clypeal mark small, less than one-third length of clypeus, paraocular marks narrow and not or barely reaching ventral margin of antennal sockets, *scape* black; *mandibles* black and brown; *gena* closely punctured; *frons* densely punctured and rugulose and medial groove poorly defined before median ocelli; *supraclypeal area* linear striae and small close punctures; *paraocular area* striate, becoming punctured dorsal of antennae; *SSW : SSL* 0.95. Mesosoma *pronotal collar* black; *scutum* shining, small close punctures, dense, very short, prostrate hairs, appearing velvety; *metanotum* with dense, short, appressed tomentose setae; *lateral propodeum* reticulate, strigate-rugulose dorso-posteriorly; *dorsal propodeum* reticulate, anterior third rugose. Metasoma *T1* dark brown; *T2–4* dark brown and posterior margin paler; *T5–7* black. *T1* with a distinct fascia of white setae laterally along posterior margin; *T2* with bands present but sparser, posterior terga lacking bands, with evenly spaced, moderately long erect setae.

Female diagnosis and description. See *H. albaeus* sp. nov.

Etymology. This species is named for the small yellow patches on the male's face, particularly the little clypeal patch. The name is from the Latin *brevi* (small) and *flavus* (yellow); hence, they are the little yellow-spotted *Hylaeus*.

Distribution. Only a locality provided as "Nausori Highlands, Viti Levu, Fiji" (Figure 1F).

Remarks. See the remarks for *H. albaeus*.

3.4.7 *Hylaeus derectus* Dorey, Davies, and Parslow sp. nov.

(Figures 1, 2, 7).

Materials examined. Holotype 1♂ Near Nadarivatu, Viti Levu, Fiji, −17.568, 177.953, 904 m asl, 2019/10/19, JB Dorey, DE18 (BPBM: 18012). Paratypes 1♂ 3♀ Near Nadarivatu, Viti Levu, Fiji, −17.5682, 177.9527, 898 m asl, 2019/10/18 14:45, JB Dorey, sweep net from *Decaisnina forsteriana* (BPBM: ♂ 19JDFJ4ii; ♀ 19JDFJ5a, 19JDFJ5b, 19JDFJ5i); 1♂ 2♀ Near Nadarivatu, Viti Levu, Fiji, −17.5682, 177.9527, 898 m asl, 2019/10/14 14:28, JB Dorey, sweep net from *Decaisnina forsteriana* (SAMA: ♂ 32-035997; ♀ 32-035995, 32-035996).

Male diagnosis. In combination, mask has three patches; posterior margin of clypeus is straight; clypeus in profile strongly convex; scape marked with yellow ventrally; and scutum deeply and strongly punctate.

Male description. Head *mask* three yellow patches, clypeal mark large, extending approximately 2/3 distance to dorsal margin of clypeus, paraocular marks narrow and pointed dorsally, not reaching antennal sockets; *scape* yellow anteriorly*; mandibles* black with paler apex; *gena* reticulate, sparse punctures; *frons* densely punctured and rugulose and medial groove clearly meets median ocelli; *supraclypeal area* reticulate or reticulate-rugulose; *paraocular area* reticulate, becoming punctured posterior of antennae; *clypeal posterior margin* straight; *SSW : SSL* –15. Mesosoma *pronotal collar* black, yellow spot on pronotal lobe; *scutum* reticulate, large, deep open-close punctures and dense short erect hairs or close-open, short, partly erect hairs; *metanotum* with short setae medially and can have long setae in a posterior row, can be branched; *lateral propodeum* reticulate, close-open punctures; *dorsal propodeum* anterior half or more rugose. Metasoma black or dark brown, posterior margins can be paler. *T2–3* with faint lateral bands and nearly hairless medially.

Female diagnosis. In combination, mask has no patches (face is black); posterior margin of clypeus is straight; and clypeus in profile strongly convex.

Female description. Head *mask* none; *scape* brown, paler anteriorly; *mandibles* black and brown; *gena* reticulate, sparse punctures; *frons* reticulate-rugulose, sparse punctures, open small punctures and medial groove partly poorly defined before median ocelli; *supraclypeal area* reticulate-rugulose or reticulate, distinct striae; *paraocular area* reticulate, sparse shallow punctures along eye margin; *clypeal posterior margin* straight; *SSW : SSL* 46–76. Mesosoma *pronotal collar* black, yellow patch on pronotal lobe; *scutum* reticulate, close punctures, close-open, short, partly erect hairs; *metanotum* with short setae medially and can have long setae in a posterior row, can be branched; *lateral propodeum* reticulate, close-open punctures; *dorsal propodeum* anterior half or more rugose. Metasoma black or dark brown and posterior often margin paler. *T2–3* with faint lateral bands and nearly hairless medially.

Etymology. This species is named for the straight posterior margin of the clypeus in both sexes from the Latin *derectus* (straight). Hence, they are the straight-faced *Hylaeus*.

Distribution. Only known from near Nadarivatu (898–904 m asl), Viti Levu, Fiji (Figure 1C).

Remarks. The strongly convex clypeus is somewhat reminiscent of *H. crabronoides* (Perkins, 1899) of Hawaii, but the two are not otherwise similar.

3.4.8 *Hylaeus navai* Dorey, Davies, and Parslow sp. nov.

(Figures 1, 2, 8).

Materials examined. Holotype 1♀ Near Nadarivatu, Viti Levu, Fiji, –17.5682, 177.9527, 898 m asl, 2019/10/18 15:35, JB Dorey, sweep net from *Decaisnina forsteriana*, 19JDFJ7i (BPBM: 18013). Paratypes 2♀ Mt Nadarivatu, Viti Levu, Fiji, –17.576245, 177.935436, 1,072 m asl, 2019/10/19, JB Dorey, sweep net from *Decaisnina forsteriana* (BPBM: ♀ DE146; SAMA: ♀ 32-035998); 1♀ Naitasiri Prov., Navai Village, Viti Levu, Fiji, –17.616, –177.983, 700 m asl, 2003/07/15, E. Schlinger, FJ-11A Malaise, (BPBM: FBA 029757); 1♀ Cakaudrove Prov., Soqulu House in Soqulu Estate, Viti Levu, Fiji, –16.833, –180.000, 140 m asl, 2002/11/21, E. Schlinger, Malaise 1, (BPBM: FBA 099896); 1♀ Cakaudrove Prov., 5.3 km SE Tavuki Vlg. Mt. Devo, Viti Levu, Fiji, –16.841, –179.968, 1,064 m asl, 2002/11/17, Schlinger, M Tokotaʻa, Malaise 3, (BPBM: FBA 134592).

Female diagnosis. In combination, has no face patches; propodeum dorsal face reticulate and only anterior third rugulose; and medial groove on frons is partly poorly defined before meeting the median ocellus. The head is short and broad (wider than long), and the body overall has weak reticulate microsculpture and open punctation, thus appearing quite shiny.

Female description. Head *mask* none; *scape* and *mandibles* black; *gena* reticulate; *frons* reticulate, open small punctures and medial groove partly poorly defined before median ocelli; *supraclypeal area* reticulate; *paraocular area* reticulate, sparse shallow punctures along eye margin; *clypeal posterior margin* concave; *SSW : SSL* 13–26. Mesosoma *pronotal collar* black, yellow patch on pronotal lobe; *scutum* reticulate, small open punctures; *scutum* close-open, short, partly erect hairs, few much longer erect hairs or so few hairs as to appear hairless; *metanotum* with a posterior row of long simple setae, almost hairless medially; *lateral propodeum* reticulate; *dorsal propodeum* reticulate, anterior third weakly rugose. Mesosoma black. *T2–3* with faint lateral bands and nearly hairless medially.

Etymology. This species is named in recognition of the people of Navai village who have made a large contribution to the taxonomy and understanding of the Fijian bee fauna. Meli Naiqama has acted many times as our guide and helped collect bees, his family (especially his parents, Esira and Paulini Senimasi) has hosted and fed us over many trips, and the whole village has always made us feel very welcome! Hence, they are Navai's *Hylaeus*.

Distribution. Known from near Navai Village (700 m asl) and Nadarivatu (898–1,072 m asl) on Viti Levu, Fiji and Soqulu House (140 m asl) and Mt De Voeux (1,064 m asl), Taveuni, Fiji (Figure 1D).

3.4.9 *Hylaeus tuamotuensis* Michener, 1965

(Figures 1, 2, 9).

Hylaeus tuamotuensis Michener, 1965: 123.

Materials examined. Holotype 1♂ Tukuhora, Anaa I., Tuamotu Islands, –17.3, –145.5 [georeferenced], 1934/5/13, EC Zimmerman (BPBM). Other materials 10♂ 1♀ Teavaroa to Opakari, Takaroa Atoll, French Polynesia, –14.47, –145.04 [georeferenced], 0–2 m asl, 1984/06/29, G.A. Samuelson, mostly on *Euphorbia atoto* (BPBM); 1♀ Boring Bay, Hao Island, French Polynesia, –18.1, –140.9 [georeferenced], 1934/06/19, EC Zimmerman (BPBM).

Male diagnosis. In combination, mask has three yellow patches (clypeus and supraclypeal areas); head and body are otherwise mostly black (not submetallic); and the supraclypeal area has striae.

Male description. Head *mask* three yellow patches, clypeus completely yellow and paraocular areas mostly yellow, terminating around anterior margin of antennal sockets; *scape* black, lighter underside; *mandible* yellow, brown apex; *gena* reticulate; *frons* small close punctures, almost touching but not rugulose and medial groove clearly meets median ocelli; *supraclypeal area* faint sinuate striae; *paraocular area* striate, becoming punctured dorsal of antennae; *clypeal posterior margin* convex. Mesosoma *pronotal collar* black, yellow patch on pronotal lobe; *scutum* reticulate, small open punctures, dense short erect hairs; *metanotum* posterior row of long branched hairs, some hairs medially; *lateral propodeum* reticulate, strigate-rugulose dorsoventrally; *dorsal propodeum* reticulate, anterior third weakly rugose. Mesosoma black. *T2–3* lateral hairbands absent or very faint.

Female diagnosis. In combination, mask has two patches; metasoma is mostly black; and the pronotal colour has two yellow patches.

Female description Head *mask* two large pale patches almost reaching anterior margin of antennal socket; *scape* black, lighter underside; *mandible* black with yellow streak; *gena* reticulate; *frons* small close punctures, almost touching but not rugulose and medial groove clearly meets median ocelli; *supraclypeal area* faint sinuate striae, *paraocular area* striate, becoming punctured dorsal of antennae; *clypeal posterior margin* convex. Mesosoma *pronotal collar* black, yellow patch on pronotal lobe; *scutum* reticulate, small open punctures, dense short erect hairs, and scattered additional setae about twice as long; *metanotum* posterior row of long branched hairs, some hairs medially; *propodeum* reticulate, anterior third weakly rugose. Metasoma *T1–6* black and posterior margin paler; *T7* black. *T2–3* lateral hairbands absent or very faint.

Distribution. Known from Tukuhora, Anaa Island; Takaroa Island; and Boring Bay, Hao Island, Tuamotu Islands, French Polynesia (Figure 1H).

3.4.10 *Hylaeus veli* Dorey, Davies, and Parslow sp. nov.

(Figures 1, 2, 10).

Materials examined. Holotype 1♂ Des Voeux track, Taveuni, Fiji, −16.83622, −179.97303, 875 m asl, 2019/04/19 13:37, MI Stevens, MC Elmer, sweep net from *Metrosideros collina* var. *collina* (BPBM: 18014). Paratypes 2♂Des Voeux track, Taveuni, Fiji, −16.83622, −179.97303, 875 m asl, 2019/04/19 13:37, JB Dorey, sweep net from *Metrosideros collina* var. *collina* (SAMA: 32-035999; BPBM: 19FJ72).

Male diagnosis. Mask has one yellow patch (on clypeus); scutum and scutellum reticulate-rugulose; and mandible and anterior of scape almost all yellow.

Male description. Head *mask* one yellow patch, covering almost entire clypeus, only very narrow lateral and dorsal margins dark; *scape* yellow on ventral and medial surfaces; *mandible* yellow; *gena* reticulate, sometime with sparse punctures; *frons* reticulate, large close punctures and medial groove clearly meets median ocelli; *supraclypeal area* reticulate; *paraocular area* reticulate, sparse shallow punctures along eye margin or becoming punctured posterior of antennae; *clypeal posterior margin* straight or concave; *SSW : SSL* 8–34. Mesosoma *pronotal collar* black, yellow or brown spot on pronotal lobe; *scutum* reticulate-rugulose with close-dense punctures and dense short erect hairs or close-open, short, partly erect hairs; *metanotum* with a posterior row of long simple setae and moderate simple setae elsewhere; *lateral propodeum* reticulate or reticulate dorso-anteriorly, rugose ventro-posteriorly; *dorsal propodeum* anterior half or more rugose. Metasoma black or dark brown, posterior margins can be paler. *T2–3* with faint lateral hair bands, nearly hairless medially.

Etymology. This species is named for the *veli* of Fijian folklore who are powerful little people associated with forests. Accounts of the *veli* are varied and they were often seen in a positive light, but they could also be dangerous, for example, if you chopped down their favorite trees (Tomlinson, 2016). Hence, the name is meant to invoke a sense of responsibility for protecting these new forest-specialist species and their trees. Hence, they are veli's *Hylaeus*.

Distribution. Only known from De Voeux Peak (875 m asl), Taveuni, Fiji (Figure 1E).

3.5 Micronesian *Hylaeus*

Family Colletidae Lepeletier de Saint Fargeau, 1841.
Subfamily Hylaeinae Viereck, 1916.
Genus *Hylaeus* Fabricius, 1793.
Subgenus *Euprosopoides* Michener, 1965.

3.5.1 Key to the Micronesian *Hylaeus (Euprosopoides)*—modified from Krombein (1950)

1. Abdomen usually ferruginous in part or entirely; yellow markings more extensive than in other species, pronotal band complete, space between lateral margin of clypeus and inner eye margin entirely yellow, females with yellow spots on clypeus, scutum anterolaterally and axillae; almost all the punctures on scutum uniformly subcontiguous; Carolines (Yap) … *H. yapensis* (Yasumatsu, 1942).

Abdomen never ferruginous, occasionally dark brown on basal segments, but usually black with obscure metallic green or blue reflections; yellow markings much less extensive, pronotal band always interrupted in middle, space between lateral margin of clypeus and inner eye margin not entirely yellow (needs confirmation in *H. rotensis*), females without yellow markings on clypeus, scutum, or axillae; punctures of thorax separated (needs confirmation in *H. rotensis*) … 2.

2. Scutellum and metanotum entirely black; female unknown; Marianas (Rota) … *H. rotensis* (Yasumatsu, 1942).

Scutellum and metanotum with large yellow marks … 3.

3. Metasoma metallic blue or violet in both sexes; yellow mark on scutellum covering only the posterior third (male) or half (female); supraclypeal mark present in males; some punctation of thorax, at least proximal to parapsidal lines, separated by more than the width of a puncture (especially in females); Chuuk archipelago … *H. chuukensis* sp. nov.

Metasoma black, sometimes brownish anteriorly; yellow mark on scutellum covering posterior 60%–100%; supraclypeal mark present or absent in males; punctation of thorax separated by a little less than or as much as the width of a puncture … 4.

4. Male: upper margin of yellow mark on clypeus irregular, supraclypeal mark present; yellow mark on scutellum larger than on metanotum, the anterior margin of the mark on the former straight. Female: pronotal collar not produced above level of anterior part of scutum, scarcely notched in middle; yellow mark on scutellum covering the entire disk except narrow anterior margin. Marianas (Guam) … *H. guamensis* (Cockerell, 1914).

Male: upper margin of yellow mark on clypeus rounded, the supraclypeal mark absent ()?; yellow mark on metanotum as large as that on scutellum, the anterior margin of the mark on the latter with a median notch. Female: pronotal collar strongly produced above level of anterior part of scutum and with a broad, deep notch in middle; yellow mark on scutellum less extensive, covering only the posterior half or two-thirds of disk; anterior metasomal segments sometimes brownish; Carolines (Palaus) … *H. hirticaudus* Cockerell, 1939.

3.5.2 *Hylaeus chuukensis* Dorey, Davies, and Parslow sp. nov.

(Figures 1, 2, 11).

Materials examined. Holotype 1♂ Chuuk, Weno, Xavier College Campus, Micronesia, 7.447, 151.887, 39 m asl, 2014/04/14, SVC Groom, (BPBM: 18007). Paratypes 1♂1♀ Chuuk, Fono Mu Islet, Micronesia, 7.362, 151.923, 0 m asl, 2014/04/14, SVC Groom (SAMA: ♂32-38374; ♀ 32-38373).

Male diagnosis. Abdomen strongly metallic blue or violet; pronotal band incomplete; punctures on scutum dense, but interspaces often larger than punctures proximal to parapsidal lines; yellow patch on scutellum much wider than on metanotum and filling the posterior third. May be the only species with yellow patches anteriorly on the scapes. Falls out of Houston (1981)'s Australian *Euprosopoides* key at couplet #4 because it has a metallic blue abdomen and the first recurrent vein of forewing lacks a stub-like branch.

Male description. Head *mask* four yellow patches, clypeus yellow except narrow lateral and dorsal margins (touching paraocular marks ventrally), supraclypeal area with a separate mark, and paraocular areas broadly yellow, extending dorsal of antennal sockets, dorsally narrowing to a point; *scape* yellow anteriorly; *mandible* black, apex brown; *gena* closely punctured; *frons* large close punctures and medial groove partly poorly defined before median ocelli; *supraclypeal area* large open punctures, very faint striae; *paraocular area* large close to sparse punctures; *clypeal posterior margin* straight; *SSW : SSL* 33. Mesosoma *pronotal collar* black, yellow patch on pronotal lobe; *scutum* reticulate, open-close punctures and close-open, long, mostly erect hairs; *metanotum* posteriolateral row of long and branched setae, shorter branched setae elsewhere; *lateral propodeum* very finely reticulate; *dorsal propodeum* coarsely areolate, distinct posterior carina. Metasoma black or submetallic blue. *T2–3* hairbands absent but with short setae covering.

Female diagnosis. Abdomen strongly metallic blue or violet; pronotal band incomplete; punctures on scutum dense, but interspaces often larger than punctures proximal to parapsidal lines and medially; yellow patch on scutellum slightly wider than on metanotum and filling less than the posterior half; without clypeal marking; pronotal collar produced above the anterior part of scutum and deeply notched medially. Falls out of Houston (1981)'s Australian *Euprosopoides* key at couplet #4 because it has a metallic blue abdomen and the first recurrent vein of forewing lacks a stub-like branch.

Female description. Head *mask* two small linear yellow patches not reaching anterior margin of paraocular area but extending posterior to the anterior margin of the antennal sockets; *scape* and *mandible* black; *gena* shining with sparse to close punctures; *frons* large close punctures and medial groove clearly meets median ocelli; *supraclypeal area* large close punctures; *paraocular area* large close to sparse punctures; *clypeal posterior margin* indistinct or obscured. Mesosoma *pronotal collar* black, yellow patch on pronotal lobe; *scutum* large open-close punctures, open medially and close-open, short, partly erect hairs; *metanotum* posteriolateral row of long and branched setae, shorter branched setae elsewhere*; lateral propodeum* very finely reticulate; *dorsal propodeum* coarsely areolate, distinct posterior carina. Metasoma black or submetallic blue. *T2–3* hairbands absent or very faint but with short setae covering.

Etymology. Of the 12 already described species in *Hylaeus (Euprosopoides)*, 8 are Australian and 4 are found in the Pacific. The four Pacific species are *H. (E.) guamensis* (Cockerell, 1914) from Guam, Northern Mariana Islands; *H. (E.) rotensis* (Yasumatsu, 1939) from Rota, Northern Mariana Islands; *H. (E.) hirticaudus* Cockerell, 1939 from Palau; and *H. (E.) yapensis* (Yasumatsu, 1942) from Yap in Micronesia (Ascher and Pickering, 2020). Hence, we follow this tradition and the name *chuukensis* is from the island group where this species occurs in Chuuk, Micronesia. Hence, they are Chuuk's *Hylaeus*.

Distribution. The Chuuk archipelago (0–39 m asl), Micronesia (Figure 1I).

4 Discussion

By identifying and describing eight new species, we advance our understanding of this fascinating and speciose bee genus. We show that *Hylaeus* is more numerous in the Pacific than previously suspected and that more work in this region is urgently needed.

4.1 Hylaeus collections and biogeography

We show that Micronesia has at least one additional species, found in Chuuk (*Hylaeus chuukensis* sp. nov.), bringing the regional total to five *Hylaeus (Euprosopoides)* species, with no two from the same island group. With the use of canopy nets in 2019 in Fiji, we were able to collect four additional species from red-flowering plants, but only at heights of >3 m (even if known food plants occurred below this height). We describe these four species that form a monophyletic Fijian clade; two on the main island of Viti Levu (*H. derectus* sp. nov. and *H. navai* sp. nov.) and three on the island of Taveuni (*H. apertus* sp. nov., *H. navai* sp. nov., and *H. veli*

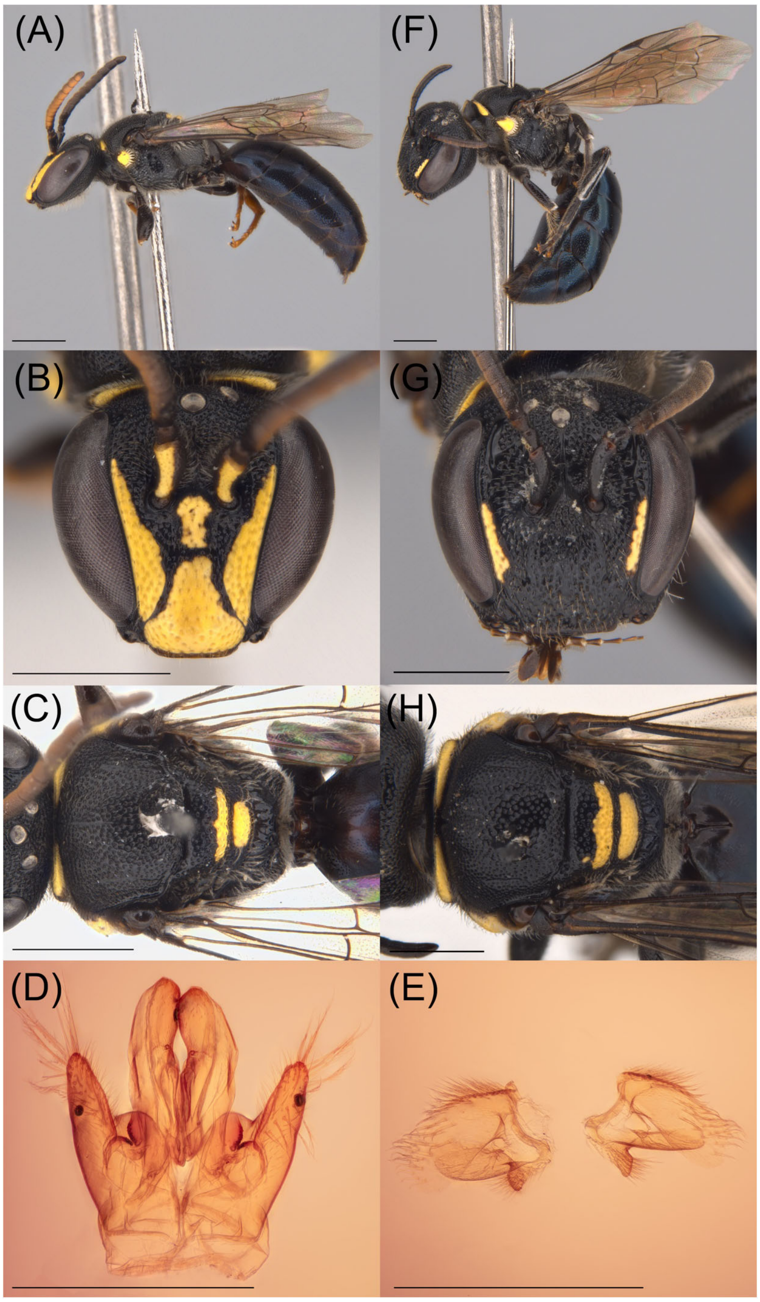

FIGURE 11
Hylaeus chuukensis Dorey, Davies, and Parslow sp. nov. Male lateral habitus **(A)**, face **(B)**, dorsal mesosoma **(C)**, genitalia **(D)**, and sternite 7 **(E)**. Female lateral habitus **(F)**, face **(G)**, and dorsal mesosoma **(H)**. (Scale bar, **A–C**, **F–H** = 1.00 mm; **D, E** = 0.50 mm.)

sp. nov.). On each island, we essentially collected these species on a single collection event and locality. However, *H. navai* sp. nov. was also collected using Malaise traps in 2002 and 2003. According to our phylogeny and bee dissections (especially the bifurcation of S8; Figure 2), one of our clades has two representatives in Fiji (*H. albaeus* sp. nov. and *H. breviflavus* sp. nov.), and two in French Polynesia (*H. aureaviridis* sp. nov. and *H. tuamotuensis*; Figure 2).

While the Micronesian and French Polynesian specimens were collected using standard methods, we only actively collected one Fijian *Hylaeus* specimen without a canopy net (*H. albaeus* sp. nov.). We could not relocate *H. albaeus* sp. nov. after its initial collection despite targeted, but standard, efforts over the following 2 years. However, this species has been collected in Malaise traps on five other occasions at two localities (~87 Malaise trap days). All of these collections were made in relatively cleared regions on the dry (western) side of Viti Levu and in regions that have been heavily sampled for *Lasioglossum* Curtis, 1833 in the past 10 years. We suggest that these Malaise collections, and possibly our 2016 collection, were of bees that were moving between stands of trees. Taken together, this indicates an extreme affinity of this *Hylaeus* clade for canopy life with only rare vagrants being collected at lower floral resources; despite a decade of targeted bee sampling in Fiji (Naaz et al., 2022).

Having two species in each of Fiji and French Polynesia might indicate natural long-distance dispersals between the two archipelagos, almost certainly via the intervening archipelagos (Figures 1, 2). This contrasts with assisted movement by the Austronesian peoples who used large ships for east–west return voyages that carried dozens of people, livestock, and plants for trading and settling of new territories (Thomas, 2021). This supports the idea that *Hylaeus* bees can be successful very-long-distance dispersers (many hundreds of kilometers at a time) and that Michener's mystery, *H. tuamotuensis*, most likely island hopped from Fiji (~3,000 km). The massive dispersal of this *Hylaeus* clade in the Pacific indicates that it is likely very widespread and speciose throughout the whole region.

Our findings also contrast with those by Poulsen and Rasmussen (2020) who suggested that, compared to mainland species, most island bees should be of moderate size (10–17 mm); however, their analyses were mostly restricted to non-endemic island species. In comparison, the Fijian (μ = 3.9 mm), French Polynesian (μ = 4.2 mm), and Micronesian (μ = 7.4 mm) *Hylaeus*, as well as the Fijian *Lasioglossum* (μ = 5.2 mm), are all minute to small bees and represent pre-human long-distance dispersals. Hence, our results support patterns observed by Michener (1979a) that smaller bees might be more easily dispersed by wind. Additionally, these *Hylaeus* are likely stem-nesters that could also disperse via rafting.

4.2 Potential for human impacts

The most abundant bee species in Fiji, *Lasioglossum (Homalictus) fijiense* (Perkins and Cheesman, 1928), has been shown to have undergone a massive and sudden population size increase following the arrival of humans on the archipelago (Dorey et al., 2021a). Because *L. (H.) fijiense* favors open ground for nesting and is a super-generalist pollinator, this expansion was attributed to the broad clearing and slash-and-burn agriculture of the Lapita and post-Lapita peoples (Dorey et al., 2021a). Prior to this time, Fiji was likely dominated by hardwood forest (Roos et al., 2016). Tropical hardwood forests in Fiji today have dense canopies with cool, dark, and damp understories that might not suit either ground-nesting (*Lasioglossum*) or cavity-nesting (*Hylaeus*) bees. However, by using forest canopies, *Hylaeus* might avoid the cool, moldy, and quickly decaying nesting substrates of forest understories. This might have additional benefits, such as easy access to early sunlight and nearby floral resources. Hence, we predict that the opposite pattern (population size decrease) might be observed in the Fijian *Hylaeus* and that they are likely vulnerable to both ancient and contemporary clearing of forests. This stressor is additional to the climate-change vulnerability that has been identified for the endemic *Lasioglossum* species (Dorey et al., 2020b).

In Fiji alone, the *Lasioglossum* diversity has increased from 4 (Michener, 1979b), to 13 (Dorey et al., 2019), to 22 (Dorey et al., 2020b), with current estimates from molecular data at ~30 species (unpublished data). We have only just started to scratch the surface of the *Hylaeus* radiation's true diversity in the Pacific. Our *Hylaeus* sampling efforts are incredibly sparse in Micronesia, French Polynesia, and even in Fiji. Between Fiji and French Polynesia, there are hundreds of islands and islets (e.g., the intervening archipelagos Tonga, Samoa, Cook Islands, Wallis, and Futuna). It is then reasonable to assume that there are many more *Hylaeus* species to be discovered and described across the Pacific. They need to be found and described before we can even consider conserving them.

4.3 Methodological implications

Perhaps our most important finding is related to the methods that are broadly used to sample bees around the world. We empirically show that a decade of sampling bias has led to a gross misunderstanding of a region's pollinator fauna. We provide evidence for the importance of forests for pollinators and that they can host a unique fauna not readily captured by standard sampling techniques (Ulyshen et al., 2023). Similar disparities have been observed in other studies. For example, sampling bias, canopy specialization, and even red-flower specialization has been shown in the very rarely collected, but widespread, hylaeine bee, *Pharohylaeus lactiferus* Cockerell, 1910, that was not collected for almost 100 years of Australian bee sampling until canopy sampling was employed (Dorey, 2021). Another study found that the American *Augochlora pura* (Say, 1836) (Halictidae) was 40 times more abundant in the canopy than understory, and even excluding this species abundance, richness and Shannon's diversity were all higher (Ulyshen et al., 2010). Additionally, Urban-Mead et al. (2021) found that between canopy and understory, (i) bee abundance did not differ (but this changed between years), (ii) richness did not vary, but (iii) Hill-Shannon diversity was higher in the canopy. In this study and Dorey (2021), active canopy sampling was employed while Ulyshen et al. (2010) used flight-intercept traps and all found strong indications of strata-dependent patterns. The weaker patterns found by Urban-Mead et al. (2021) may be due to the use of yellow, white, and blue bee bowls. That canopy-specialist *Hylaeus* appear to prefer red flowers deviates from the long-held belief that bees do not see, or often forage on, red-flowering plants (von Frisch, 1914). However, Horridge (1998) argued that "bees see red" and that red flowers would be particularly high-contrast on green backgrounds, as in a forest canopy.

Such sampling bias might have large impacts on biological understandings and land management. For example, Orr et al. (2021) undertook excellent modeling of global bee diversity patterns but had to control for forestation; otherwise, patterns of increasing net primary productivity and bee diversity were inverted. This indicated that forest cover might be bad for bee diversity on a macroecological scale. While we do not refute this finding, we do highlight that sampling bias away from canopy sampling has the potential to impact such a pattern, particularly as forest canopies can be almost inaccessible for sampling. Current evidence, especially from the northern hemisphere, suggests that open forests can be beneficial for wildflower and bee abundance (Hanula et al., 2016). However, this evidence likely stems from the almost exclusive use of understory sampling techniques that will be biased towards understory bee taxa—although we show here that, under the right environmental conditions, Malaise traps may detect some canopy vagrants. This has implications for thinning, clearing, and burning management techniques and recommendations that would otherwise ignore the importance of forest and canopy pollinators (Dorey et al., 2021b; Ulyshen et al., 2023). We add to a growing discussion about bee systematic sampling (Prendergast et al., 2020; Prendergast and Hogendoorn, 2021), temporal (Dorey et al., 2020a), and strata biases (Dorey, 2021).

4.4 Conclusions

Despite a decade of intensive and widespread low-strata sampling across Fiji, only one *Hylaeus* specimen was collected using standard active-sampling techniques until canopy sampling was employed. Firstly, we show that, including our *Hylaeus (Euprosopoides)* and *Hylaeus (Prosopisteron)*, there have been at least four dispersals of *Hylaeus* out of Australia instead of two as suggested by Kayaalp et al. (2013). However, greater work in the region is required and will allow a higher-resolution examination of hylaeine dispersal patterns. Secondly, in contrast to the Fijian *Lasioglossum (Homalictus) fijiense*, these bees are canopy specialists and are therefore expected to be vulnerable to both ancient and contemporary anthropogenic habitat destruction. We recommend that further sequencing and analyses are required on the demographic patterns of this new bee clade to assess possible impacts. We also postulate that, like the endemic *Lasioglossum* species, these tropical hylaeines might be vulnerable to changing climates. Finally, we highlight that much greater sampling and sequencing efforts in canopies across the South Pacific will lead to further discoveries. We demonstrate and argue the need for better application of canopy sampling and understory sampling methods.

Our understanding of the Pacific bee fauna as a whole continues to rapidly grow, to inform theory and conservation, and to surprise. We therefore emphasize the need for greater research funding in the region as a whole and for the training and support of local experts to continue and expand upon this work.

Data availability statement

All data and code associated with this article are made available via our FigShare — https://doi.org/10.25451/flinders.24481231 and our sequence data are additionally made available via GenBank — SUB13956663 (OR780414-OR780432; iii and viii on FigShare). Zoobank LSID urn:lsid:zoobank.org:pub:583AF470-5B12-41CF-8957-CE4971B68C59.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because ethics approval is not required for work on insects.

Author contributions

JD: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. OD: Conceptualization, Data curation, Methodology, Project administration, Writing – review & editing. KM: Conceptualization, Data curation, Methodology, Validation, Visualization, Writing – review & editing. MPS: Conceptualization, Funding acquisition, Supervision, Writing – review & editing. A-MG: Validation, Writing – review & editing. TR: Data curation, Validation, Visualization, Writing – review & editing. MT: Data curation, Resources, Validation, Writing – review & editing. SG: Data curation, Funding acquisition, Writing – review & editing. MIS: Funding acquisition, Writing – review & editing. BP: Conceptualization, Data curation, Methodology, Software, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Advancing bee conservation in the US: gaps and opportunities in data collection and reporting

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Introduction: Bee conservation in the US is currently hindered by challenges associated with assessing the status and trends of a diverse group of >3000 species, many of which are rare, endemic to small areas, and/or exhibit high inter-annual variationin population size. Fundamental information about the distribution of most species across space and time, thus, is lacking yet urgently needed to assess population status, guide conservation plans, and prioritize actions among species and geographies.

Methods: Using wild bee data from two public data repositories representing the contiguous US, we evaluated the availability and sufficiency of data for use in species assessments of wild bees. We also examined the number of bee species recorded in each US state and the proportion of species with recent records (2012–2021).

Results: Although efforts to monitor bees continue to grow, there remains a massive paucity of data. Exceedingly few records (0.04%)reported both sampling protocol and effort, greatly limiting the usefulness of the data. Few species or locations have adequate publicly available data to support analyses of population status or trends, and fewer than half of species have sufficient data to delineate geographic range. Despite an exponential increase in data submissions since the 2000s, only 47% of species were reported within the last decade, which may be driven by how data are collected, reported, and shared, or may reflect troubling patterns of local or large-scale declines and extirpations.

Discussion: Based on our analysis, we provide recommendations to improve the quality and quantity of data that can be used to detect, understand, and respond to changes in wild bee populations.

KEYWORDS

bee (Apoidea), conservation, species assessments, data quality, data quantity, geographic range, data standardization, trend

Introduction

Global evidence of wild bee declines has accumulated steadily over the last three decades. Although the conservation status for most of the world's roughly 20,000 wild bee species (Michener, 2007; Ascher and Pickering, 2017) has still not been assessed (Winfree, 2010; deMaynadier et al., 2023), the proportion of threatened species ranges from 12.5 to 45% of regional faunas among those groups that have been considered, such as the bumble bees (Cameron and Sadd, 2020; Bumble Bee Specialist Group, 2023) and a small proportion of other bee groups (NatureServe, 2023). Notably, certain bee groups, including pollen specialists with limited host plant associations, and species with larger body sizes (e.g., genus *Bombus*) and smaller phenological breadth (e.g., genus *Andrena*), appear particularly susceptible to decline (Biesmeijer et al., 2006; Bartomeus et al., 2013; Hofmann et al., 2019; Bogusch et al., 2020). The putative drivers of wild bee declines are overwhelmingly anthropogenic and include widespread loss, degradation, and fragmentation of suitable habitat; non-target effects of broadly-deployed pesticides, such as neonicotinoids; and climate change, which has both direct influences, such as exceeding thermal limits, and indirect effects, such as reducing floral resource availability (reviewed in Potts et al., 2010; Goulson et al., 2015). Bee conservation is now a formal priority on the part of both national (e.g., Pollinator Health Task Force, 2015) and international efforts (e.g., Promote Pollinators, 2023). This is in part because bee-mediated pollination services are paramount to human food security and ecosystem stability (IPBES, 2016) and also due to the widespread recognition of the intrinsic value of biodiversity.

In the United States, there are over 3000 wild bee species, with a number of endemic and highly specialized species, and particularly high diversity found in arid lands of the Southwest (Meiners et al., 2019; Orr et al., 2021; Chesshire et al., 2023). Conservation of threatened bee species is carried out through both regulatory and non-regulatory governmental policies, as well as through a patchwork of voluntary, non-governmental efforts. At the Federal level, nine bee species, all within the genera *Hylaeus* and *Bombus*, are currently protected under the Endangered Species Act (US Fish and Wildlife Service, 2016b, 2017, 2021a), with at least another five species being considered for listing (US Fish and Wildlife Service, 2023). At the state level, species can be protected under state endangered species acts in cases when these laws apply to insects, such as in California, where four species of bumble bee are candidates for listing under the California Endangered Species Act (Sanders, 2022). However, the level of protection afforded by state endangered species acts varies greatly by state. Species can also be designated as conservation priorities as Species of Greatest Conservation Need (SGCN) through State Wildlife Action Plans (SWAPs) (Mawdsley and Humpert, 2016; deMaynadier et al., 2023), or regionally as sensitive species on US Forest Service and Bureau of Land Management managed lands. State Natural Heritage Programs, operating as part of the NatureServe network, can assign species ranks according to threat level, and these assessments inform state and regional lists of at-risk species. Federal to local-level conservation incentives can also stem from species assessments completed using the International Union for the Conservation of Nature's Red List Criteria, although at present only bumble bee assessments have been completed (Bumble Bee Specialist Group, 2023). Large-scale efforts are currently underway by researchers and conservation organizations to evaluate the extinction risk of wild bees in the US Conservation action for rare and threatened pollinator species takes many forms, including a significant annual investment in pollinator habitat management and restoration, based on the premise that local pollinators are habitat-deficient and possibly declining. For example, a key goal of the US Pollinator Health Task Force (2015) was to create or enhance >7 million acres of pollinator habitat by 2020. However, without a solid understanding of which species are declining, what those species need, and how populations respond to restoration, it is unclear whether conservation investments are actually improving outcomes for declining bee species. In the end, the ability to assess population status and evaluate the effectiveness of management interventions relies upon having sufficient data across species, locations, and time.

Two of the greatest limitations to understanding the full extent of wild bee declines in the US are (i) widespread gaps in availability of (or access to) bee data (Orr et al., 2021; Chesshire et al., 2023), and (ii) lack of implementation of standardized collection protocols and practices, outside of their use for particular projects (Montgomery et al., 2020; Woodard et al., 2020; Montgomery et al., 2021). The lack of available bee data hinders our ability to adequately assess bee status and trends because there is a paucity of data for many species, regions, and time periods. Correspondingly, the extinction risk of most US wild bees is unknown, with only ~600 species, or <1/5 of the fauna, having been assessed according to criteria of the International Union for the Conservation of Nature (IUCN) or NatureServe, two of the most commonly used frameworks for species conservation status assessments. Among these 600 species, the ~50 species in the genus *Bombus* have been assessed most thoroughly (Bumble Bee Specialist Group, 2023). Moreover, when wild bee species are assessed, they are likely to be determined to be “Data Deficient” or “Unrankable” because only limited data are available, and only species with very small ranges and known threats within those ranges are likely to be considered imperiled. The wild bee data that are available were overwhelmingly collected using unstandardized data collection protocols, and thus they are largely not interoperable or are difficult to analyze together in meaningful ways (Potts et al., 2010; Montgomery et al., 2020; Woodard et al., 2020). This precludes performing some analyses that are critical for conservation decision-making, such as estimating species ranges with species distribution models (SDMs) or calculating extinction risk through population viability analyses (PVAs). For example, occupancy models, which can be powerful for detecting trends while accounting for some of these issues, have only recently begun to be developed for bee species (Graves et al., 2020; Otto et al., 2021, Otto et al., 2023; Boone et al., 2023a; Boone et al., 2023b), and the data needed to calculate these models are not often collected in routine field surveys. Recent research from other groups of insects (especially butterflies) highlights declines in broadly distributed, formerly abundant species (e.g., Wepprich et al., 2019; Forister et al., 2021; Van Deynze et al., 2022; Forister et al., 2023). If similar declines are occurring in the wild bee fauna, as available assessments suggest, they are potentially going unnoticed.

Ideally, wild bee data collection, especially when it is carried out with the goal of supporting species conservation, would be performed to best accommodate the needs of the conservation entities who use these data to assess statuses and trends (Nichols and Williams, 2006; Carroll et al., 2023). These entities have data needs that are largely overlapping, despite some differences in the analyses they employ (Table 1). Importantly, assessments can be carried out even when only minimal, unstandardized data are available; however, when high-quality data sets are available for assessments, this can lead to much more meaningful and informative status assessments, benefitting bee conservation. Evidence of this can be found in recent work on two bumble bee species, *Bombus occidentalis* (Federal ESA listing status: petition is under a 12-month finding) and *Bombus affinis* (Federal ESA listing status: endangered as of 2017). *B. occidentalis*, which once had a broad distribution across the western US (Milliron, 1971), now occupies only isolated pockets of its former range. Occupancy-based analyses for this species have leveraged both historical sampling efforts inferred from presence data and newly collected, standardized data. These analyses helped to both document the extent of decline (Graves et al., 2020) and identify the primary causes, particularly the role of neonicotinoid insecticides (Janousek et al., 2023). In the case of *B. affinis*, fully standardized surveys, where effort is known and not inferred, have been conducted in recent years to support occupancy modeling (Otto et al., 2023; Boone et al., 2023a; Boone et al., 2023b). This work has helped to optimize detection probabilities and ultimately improved monitoring program design, which is essential for efficient and effective monitoring. Both of these examples, in particular *B. affinis*, clearly demonstrate how data collection methods that are fully reproducible, and account for and report sampling effort and methods of data collection, empower wild bee conservation efforts.

We used publicly-available biodiversity data for wild bees to evaluate the quality and quantity of US bee data, specifically in the context of understanding data availability for higher-quality status assessments. With an eye towards reproducibility and the needs of conservationists who perform species assessments, we focused on the propensity to report much-needed metadata such as sampling methods (protocol and effort) for data collection. Several recent studies have examined the status of bee data at broad spatial (US and global) and taxonomic scales and used these data to detect trends in patterns such as data gaps, species richness, and species ranges (Orr et al., 2021; Zattara and Aizen, 2021; Chesshire et al., 2023). Our work complements these studies by extending the focus to the quality of these data with respect to reporting, reproducible data collection, and the interests of conservation decision-makers. Based on the recognition

TABLE 1 List of major entities/unions completing species assessments for conservation status for species located in the Us – International Union for Conservation of Nature (IUCN), Endangered Species Act by US Fish & Wildlife Service (ESA-FWS), and the NatureServe Network – and the source of data and information needs associated with each.

	IUCN	ESA-FWS	NatureServe
Region(s) of interest	Regional to global	United States	Regional to global
Source of data, relative to date of species assessment			
Data from past 2 or 3 years	Used, if available	Used, if available	Used, if available
Data from past 10 years	Used, if available	Required	Used, if available
All data are considered, regardless of years	Used, if available	Used, if available	Used, if available
Standardized data (observations with protocol and/or effort)	Used, if available	Used, if available	Used, if available
Information needs			
Number of individuals	Used, if available	Required	Used, if available
Vetted data (confirmed correct ID)	Required	Used, if available	Used, if available
Number of locations with presence	Used, if available[1]	Required	Used, if available[2]
Absence data (surveyed but not observed)[3]	Used, if available	Used, if available	Used, if available
Spatial spread as extent of occurrence (from convex polygon)	Used, if available	Used, if available	Used, if available
Geographic range as area of occupancy, from species distribution model	Used, if available	Used, if available	Used, if available
Geographic range as area of occupancy, from occupancy model[4]	Used, if available	Used, if available	Used, if available
Trend in population size	Used, if available	Used, if available	Used, if available
Threats[5]	Used, if available	Used, if available	Used, if available

[1] Number of locations for IUCN is defined as the number of geographically or ecologically distinct areas in which a single threatening event can rapidly affect all of the individuals of the taxon present.

[2] Number of locations for NatureServe is defined as the number of occurrences.

[3] Absence data are defined as a record with species, date, location, protocol, and effort, but with a count (number of individuals) of zero.

[4] Occupancy models consider multiple visits (at least two) to calculate detection probabilities and probability of species occurrence (Graves et al., 2020; Guzman et al., 2021; Janousek et al., 2023; Boone et al., 2023b). This is different from calculating the geographic range using "area of occupancy", i.e., the number of grid cells with presence data.

[5] While threat information is not assessed through this project, its information is used by all species assessment entities, when available.

that there are different levels and types of data quality, that data are often lacking for bees compared to many other taxa, and that species assessments are valuable even when performed with minimal available data, we used a flexible approach where we examined how many bee species would have sufficient quantity and quality of data to meet different analysis quality thresholds. We found that even with relatively relaxed criteria, there are major data and reporting gaps that hinder bee species status assessments, and thus are ultimately limiting bee conservation action in the US. In particular, information about sampling protocol and effort is very rarely reported in publicly available data sets, which limits the ability to replicate data collection methods and use data for more rigorous analyses to assess status and trends. In spite of these limitations, we detected a general pattern where more than half of US bee species have not been observed in the last decade of our dataset (i.e. from 2012 to 2021). These species are important candidates for future targeted data collection efforts and can serve as an initial list of bee species that may be of conservation concern for consideration by states in conservation planning (Supplementary Material S1; Figure 1). Moving forward, we provide suggestions for improving data reporting for bee conservation and provide resources to aid states and other conservation practitioners in their efforts to conserve bee species.

Materials and methods

We evaluated the extent to which the current state of bee data is sufficient to support rigorous assessments of species for conservation status based on population size, distribution, and trend analyses (Table 1). Species conservation status assessments (Master et al., 2012; IUCN Standards and Petitions Committee, 2022; US Fish and Wildlife Service, 2016a) are instrumental in prioritizing species for conservation action, and the data generated from them contribute to management and recovery plans (e.g., US Fish and Wildlife Service, 2021b). As such, we focus on data requirements to improve species conservation status assessments. Some of these requirements are not readily available and were identified through a series of communications with the various entities completing these assessments (see Acknowledgment section; Table 1).

Creation of dataset

We began our analyses with the bee dataset compiled by Chesshire et al. (2023), which was downloaded from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) and Symbiota Collections of Arthropods Network (SCAN; https://scan-bugs.org/) in February 2021. This dataset contains 1.9 million records observed from 1700 through early 2021. We then supplemented the Chesshire et al. (2023) dataset with 111,216 records observed in 2021 and downloaded from GBIF (GBIF.org, 2022) and SCAN (SCAN, 2022) in August 2022. We applied a series of filters to the 2021 dataset following the process performed by Chesshire et al. (2023). First, we confirmed the 2021 species validity through expert assessment; this included updating species names containing typographical errors or names that were taxonomically revised, and removing species lacking species-level identification or not reliably confirmed to be present in the US Next, we removed all records of honey bees (*Apis mellifera*) from the 2021 data, as this is a managed or feral species in the U.S, rather than a wild native species. Last, we removed records that were outside the contiguous US and those for which the uncertainty about a location exceeded 15 km. We recognize that some records with a high uncertainty may be rare species whose locations were obscured to protect their location. After filtration, the 2021 data contributed an additional 68,026 records, resulting in a total of 1,991,840 records. We would like to acknowledge the following institutions, whose data contributed to at least five percent of all records used in the analysis: American Museum of Natural History (Johnson, 2020), iNaturalist (iNaturalist contributors and iNaturalist, 2023), University of Kansas Biodiversity Institute (Bentley and Thomas, 2023), US Department of Agriculture (Ikerd, 2019), US Geological Survey (Droege and Maffei, 2023). All analyses were completed in R (R Core Team, 2023).

Data suitability for conservation status assessments

To evaluate the suitability of records in our dataset for conservation status assessments, we established two classes of records: (1) Complete records, which included detailed

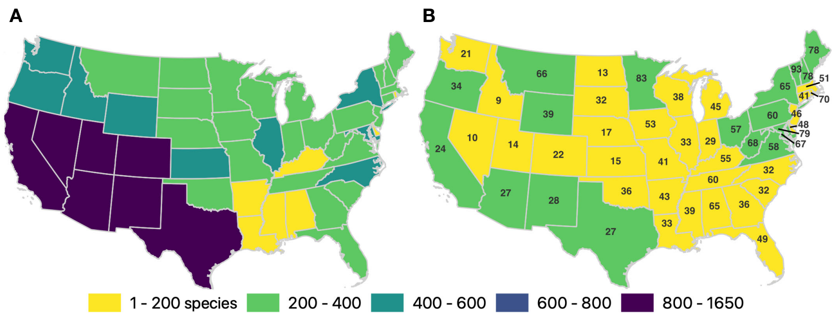

FIGURE 1
Number of species sampled per state and time period. **(A)** Total number of species observed across all years (1700–2021), per state **(B)** The colors represent the number of species observed from 2012 to 2021, and the numbers overlaid on each state represent the percentage of the total number of species known from each state that were observed during the recent time period. The data associated with these maps, including a list of the species that have been observed in each state but were not observed from 2012 to 2021, are available in the Supplementary Material S1.

information about species nomenclature, date (month, day, year) or range of sampling date (date and time start and date and time end), location (latitude, longitude, location uncertainty), count (number of bees per record), sampling protocol (e.g., trap type or protocol name), and sampling effort (e.g., number of traps/observers and sampling duration), and can be used to conduct population sizes and trend estimates, and (2) Partially complete records, which identified species and location within 15 km certainty but were missing other information. A record was determined to provide sampling protocol if it included any information about how the associated bee was collected. We categorized any provided sampling protocol information into the following groups: net (hand-netted), pan (pan trap), net and pan, malaise (malaise trap), or other traps (which included, for example, vane, pitfall, and light traps). Similarly, a record was determined to provide sampling effort if it had any information related to number of traps, number of collectors, and/or sampling duration.

Species summaries and data thresholds

To investigate the spatial patterns of bee occurrences across the contiguous US, we summarized the number of bee records within 25 km apothem (inradius) hexagon grid cells covering this region. We created species summaries by calculating the total number of records per species and the number of decades during which they were sampled. We also assessed the number of bee records per species from 2012 to 2021, the associated number of records per trap type, number of unique locations, and the number of records with sampling protocol and/or effort information. (Supplementary Material S2). The most recent ten-year window was selected because it represents a period of interest for several entities completing species assessments (Master et al., 2012; IUCN Standards and Petitions Committee, 2022) and aligns with the ten-year cycle of updating Species of Greatest Conservation Needs lists for State Wildlife Action Plans (Mawdsley and Humpert, 2016; deMaynadier et al., 2023).

Because species assessments typically include details about geographical spread and range, such as the extent of a species occurrence and area of occupancy, we established whether each species met a set of progressively more stringent hierarchical data thresholds. Each additional threshold allows for a more detailed assessment of the species distribution, most of which are performed, if possible, by the major entities that perform bee species status assessments (Table 1). The thresholds presented here are minimum requirements that are dramatically reduced relative to the norms used for vertebrate species (Mackenzie and Royle, 2005; Devarajan et al., 2020; Johnston et al., 2021); we have modified them to account for some of the additional challenges of collecting bee data and focus on the relative number of species for which it would be possible to complete each level of analysis. We tested the sufficiency of each species' data for the following thresholds using the 2012–2021 dataset:

1. Convex polygon requirements: three unique locations, which is the minimum requirement for this calculation.
2. Minimum species distribution model requirements: 30 records and 30 unique locations (Stockwell and Peterson, 2002; Wisz et al., 2008; Luan et al., 2020).
3. Low-resolution occupancy model requirements: Using a 100 km hexagonal cells grid (Jackson et al., 2022), we selected all cells with at least two visits, where a visit was defined by a unique combination of date and location. All species present in at least 30 cells satisfied this threshold.
4. Higher resolution occupancy model requirements: Using a 10 km hexagonal cells grid (Janousek et al., 2023) and records containing protocol (trap type) information, and selecting all cells with at least two visits. All species present in at least 30 cells satisfied this threshold.

Occupancy models, when completed using best practices, provide a more accurate assessment of a species distribution because they consider imperfect detection (Graves et al., 2020; Guzman et al., 2021; Janousek et al., 2023; Otto et al., 2023; Boone et al., 2023a; Boone et al., 2023b). Their creation requires information about surveys where species were detected or not detected (i.e., absence data where the individual count is zero), and multiple visits at the same site. Though there are cases where a multi-species occupancy model may provide more precise inference than single-species occupancy models (Broms et al., 2016) – particularly when species have similar patterns of detectability or occupancy – the appropriate situations for which use is warranted as well as data requirements are poorly understood. Therefore, for this paper we are only assessing the criteria for single-species occupancy models.

State-specific analyses

To assess the number of bee species for each state in the contiguous US over time, we summarized our dataset over all years (1700–2021) and in recent decades (1972–1981, 1982–1991, 1992–2001, 2002–2011, 2012–2021). We determined the number of bee species ever observed in each state and decade for the past 50 years. We assessed if more species were observed in the recent decade (2012 – 2021) compared to previous decades (1972 – 2011). We also identified the species in each state that had been previously recorded at least three times but were not observed from 2012 to 2021 (Supplementary Material S1).

Results

Availability of US bee data

Data downloaded from public repositories including GBIF and SCAN often require extensive data cleaning for analytical purposes, substantially reducing the amount of data available for conservation-related analyses, such as species assessments (Chesshire et al., 2023; this paper). Nearly 25% of the records in the Chesshire et al. (2023) dataset were discarded because they lacked species or location (personal communication, Paige

Chesshire). Bee record quality and quantity have improved over the years, particularly since the 2000s (Figure 2). Yet, only a small fraction of publicly available records were complete and contained information about protocol and effort (n = 733, or 0.04% of all records; Supplementary Material S2); all of these records were from 2021. Most records (92%) collected from 2019 to 2021 were submitted through iNaturalist and lacked sampling protocol and effort information. Complete records provide the data required to estimate population size and trend, as they enable comparisons of bee abundance and richness over time and space.

With respect to data availability per species, particularly for species assessments, only 33% of the 3,219 species recorded in the contiguous US had sufficient data to describe their geographic spread using convex polygons (Table 2; Supplementary Material S2). Few species had sufficient data to generate distribution models (11%), lower-quality occupancy models (6%), or higher-quality occupancy models (5%).

Spatial distribution of bee data

Summarizing our dataset within 25 km hexagon grid cells revealed a greater availability of data on the west and east coasts, with sparse coverage in many parts of the interior US (Figure 3). The percentage of grid cells without bee records, represented by the white surface in Figure 3, ranged from 6% across all years combined, to 23% from 2012 to 2021. The majority of grid cells contained fewer than 100 records, whether across all years (57%) or from 2012 to 2021 (86%).

Of the 3,219 bee species in the contiguous USA (Supplementary Material S3), 2,811 were recorded at least three times before 2012. Among these, only 53.5% were observed between 2012 and 2021. (Table 2; Supplementary Material S2). Merely, five states had >75% of their known US bee species recorded between 2012 and 2021, whereas 30 states had fewer than half (Supplementary Material S1; Figure 1), despite the fact that most states (n = 28) have their highest number of species per number of records in the recent decade (Supplementary Material S1). Most species (2,449 species) that had been observed at least three times prior to 2012 were no longer observed between 2012 and 2021 in at least one state in which they historically occurred.

Discussion

As populations of wild bees continue to decline, a broad community of scientists, practitioners, and members of the public have begun to galvanize around the need to better track species status and trends and take action to conserve bee populations (National Research Council, 2007; Pollinator Health Task Force, 2015; Mawdsley and Humpert, 2016; Inouye et al., 2017; Woodard et al., 2020; deMaynadier et al., 2023). Because the availability of high-quality data remains a limiting factor to conservation, we evaluated the extent to which publicly available data are sufficient to support species-level assessments of population status and trends. Based on the most minimal data standards (e.g., specifying location, sampling protocol, effort), we found that only a small fraction of data records are suitable for use in species assessments.

Our analysis points to a striking paucity of complete records in public data repositories for wild bees, and this greatly limits our ability to assess population status and trend for most species. Many records were excluded because species and/or location information was not provided or was not precise enough, often because the records originated from older collections or, in terms of location uncertainty, because data providers chose to not make this information publicly available. Most recent data (92% of records

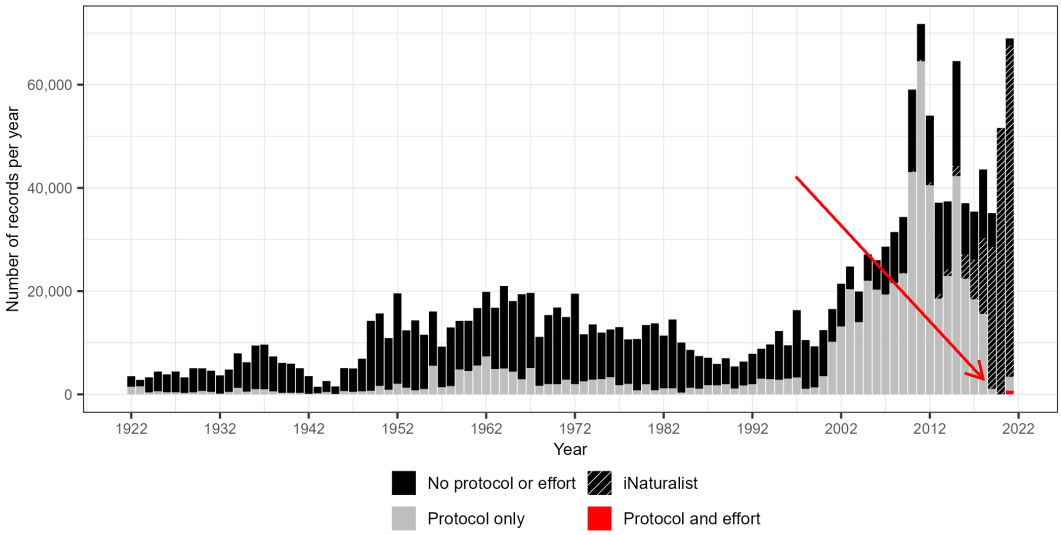

FIGURE 2
Number of bee records per year, for 1922 to 2021 (few records exist prior to 1922; n = 73,695), where the black bar section represents the number of records without protocol (trap type) nor effort (duration and/or number of traps/volunteers), gray represents records with only protocol information, and red represents *complete* records containing both protocol and effort information.

from 2019 through 2021) come from iNaturalist, which is a publicly available platform to which volunteers can submit photograph-based observations, often opportunistically-obtained. iNaturalist data are heavily biased with respect to their geographic distribution and photographed species, with more records from areas of higher human habitation or use and representing larger bee species (Chesshire et al., 2023). iNaturalist records were also seldom complete because they failed to include information on sampling effort or protocol, which may reflect how the screens to enter sampling information are not obvious to an observer. While incomplete iNaturalist records are not amenable for use in species assessments, they may provide valuable information on rare or uncommon species with few records. It is also appreciated as a source of information collected using non-lethal sampling (Lövei and Ferrante, 2024), something that is increasingly valued by members of the scientific community and public (Drinkwater et al., 2019). Whether from citizens or monitoring and research programs, and despite improving submission rates and record completeness over the last two decades, our ability to collect complete data on wild bees continues to fall short of what is sorely needed by the scientific and conservation communities. Case in point, information about sampling protocol and effort was reported for only 0.04% of records in the dataset. All complete records are from 2021, the last year represented in our dataset. Based on our species-specific examination, we also found a striking lack of data that met the core criteria for species assessments, outlined in Table 1. Insufficient data existed to describe geographic spread (67% of species), generate distribution models (89%), and support either lower- (94%) or higher-quality (95%) occupancy models.

TABLE 2 The number and associated percentage of bee species for which we have records from 2012 to 2021 and meet the data thresholds for four geographical range analyses.

Time period or analysis	Threshold	Number of species	Percent of species
2012 to 2021	Number of species for which we have at least one record from 2012 to 2021. Percentage uses total number of species with at least three records prior to 2012 (2,811 species).	1,528	53.5%[1]
Convex polygon – Records from 2012 to 2021	Number of species with at least 3 unique locations	1,070	33.2%
Species distribution model – Records from 2012 to 2021	Number of species with at least 30 records and 30 unique locations	369	11.5%
Lower-quality occupancy model – Records from 2012 to 2021	Selected 100 km grid cells with at least two surveys. Number of species present in at least 30 grid cells.	194	6.0%
Higher-quality occupancy model – Records from 2012 to 2021	Selected 10 km grid cells with at least two surveys, using only records with trap type information. Number of species present in at least 30 grid cells.	148	4.6%

[1] Percentage goes down to 47.4% if we consider the total number of species with at least one record (3,219 species).

Total number of species considered when calculating the “Percent of species” is 3,219 for all rows besides the first one.

“Threshold” refers to the minimum data needs for the analysis listed.

Our focus was specifically on understanding what proportion of publicly available bee data are complete with respect to reporting information, such as protocol and effort, that is required for many analyses of species status and trends. We note, however, that there are special considerations for bee data collection and curation that influence the quantity and quality of available data. The bee data collection community faces obstacles such as the complexities of sampling a diverse group of small and highly mobile species, taxonomic challenges that are exacerbated by lack of funding and support (Gonzalez et al., 2013; Woodard et al., 2020), and bee identification and digitization backlogs. These challenges are being met (Cobb et al., 2019; Seltmann et al., 2021; Chesshire et al., 2023; Dorey et al., 2023) but have almost certainly contributed to a relative lack of data to date. We also note that some major efforts to collect bee data across the US, such as through the USGS Native Bee Inventory and Monitoring Program, have only recently uploaded a complete version of their records, while others, such as state atlas projects, will yield more, and higher-quality, data in the coming years.

One worrisome finding was that most bee species in the US in our data set were recorded only prior to 2012. Despite an exponential increase in bee data collection since 2012, more than half of bee species have not been recorded, at least based on data housed within major public repositories. Moreover, 30 states in the contiguous US had fewer than half of their bee species recorded in the past 10 years, an especially alarming pattern for states in which bees have been intensively monitored. Important to note is that, in some cases, high proportions of species detected in recent years may be an artifact of states that had little sampling prior to 2012 rather than increases in species richness. One explanation for the low resighting rates on bees over time is that local extinctions of species have gone unnoticed in well-surveyed areas. More broadly, this would be consistent with the idea that more bee species are declining than are currently recognized (Zattara and Aizen, 2021), and certainly more than are currently being protected at the state and Federal levels. An alternative explanation is that these species have been observed since 2012, but these records are not housed in major public biodiversity data repositories but instead in privatized data collections; in some cases, these collections may even be especially likely to contain data for at-risk species. These species may have also been observed in recent surveys, but these data are simply not yet publicly available. This highlights the need, when possible in light of restrictions in data sharing, for statewide wild bee atlases and other bee data collection efforts to fully share their data on public repositories. This facilitates data sharing, openness, and reproducibility, and allows for species assessments and other analyses to be performed by the broader bee

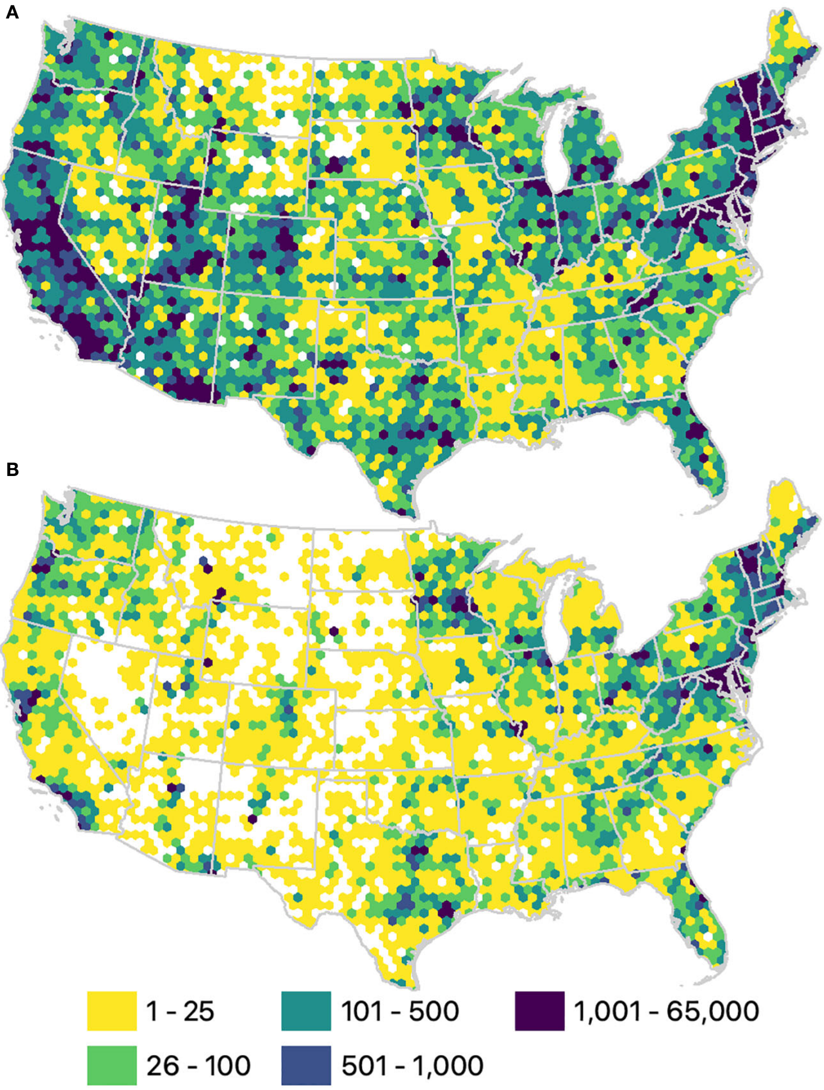

FIGURE 3
Number of bee records per 25 km hexagon grid cell. **(A)** Total number of records available since 1700 (n = 1,991,840). **(B)** Number of records from 2012 to 2021 (n = 464,845).

research and conservation communities, to the overall benefit of bee conservation. Regardless of whether species declined or data are not available, we recommend that species that have not been observed in our data set in the most recent decade (2012–2021; see lists by state in Supplementary Materials S1, S2) be candidates for more targeted data mining and collection. This list of putatively "missing" species, if they are confirmed absent in all available data sets, may also be used to inform statewide conservation planning. This could include their placement on lists of Species of Greatest Conservation Need (Mawdsley and Humpert, 2016; deMaynadier et al., 2023), as the bee species that have not been recently observed may indeed be of great conservation concern. Without improvements, the incompleteness of bee data, particularly in the interior US, is likely to continue limiting our overall understanding of species occurrence, persistence, and decline (Chesshire et al., 2023).

Moving forward, we see several actions that could improve the quality of wild bee data, many of which center on greater standardization of data collection, reporting, and management. Data standards, if they have been applied at all, have been applied differently across the myriad bee survey efforts that have taken place over the past two decades (Montgomery et al., 2020; Woodard et al., 2020; Montgomery et al., 2021). Concrete data standards and best practices would help ensure that we have data we need to complete robust, accurate assessments. We suggest encouraging data collection that adheres to an existing standard (e.g., Darwin Core) and promotes FAIR (findable, accessible, interoperable, reusable) data sharing principles (Wieczorek et al., 2012; Wilkinson et al., 2016). We further suggest defining a standardized vocabulary of accepted entries for each data variable collected, as was proposed by Montgomery et al. (2021). Tangible suggestions, including a formalized wild bee data standard generated by members of the bee monitoring community, are forthcoming from the US National Native Bee Monitoring Research Coordination Network (Woodard et al., 2020). This will facilitate data sharing, interoperability, and use, as the terms and the corresponding entries will align across multiple datasets. We provide a list of suggested terms in the Supplementary Material S3 that describe the date, location, count, species nomenclature, sampling protocol, and sampling effort associated with the data. The significant gaps we, and others (Chesshire et al., 2023), have identified in wild bee data and the potential for wild bee species declines or losses compel us to request that wild bee data collectors consider integrating our suggested changes in data collection and reporting into their current and future inventory, survey, and monitoring efforts. Recommendations include uploading all data collected, including metadata such as protocol and effort, with the bee records in the public repositories. Doing so would contribute to the creation of quantitatively supported, sound wild bee conservation policy and practice, which is critical in the protection of these species. Combined, the protocol and effort fields allow us to compare bee abundance and richness across time and locations, which is essential for estimating accurate trends. Data collected now using these methodologies would enable calculation of trends in just a few years.

Conclusions

Despite the accumulation of decades worth of wild bee data in public repositories, we found that the quality of available records is often insufficient to support the rigorous estimation of range/distribution, population size, trends, or other information needed for species assessments. This is a pattern that is generally observed for invertebrates, not only bees. The shortcomings that we outline in this paper can be readily addressed with improvements in data collection and reporting, along with the use of more standardized protocols. With coordinated outreach and education to improve data quality, we can build capacity in the broad network of scientists and practitioners working to identify species most in need of conservation, elucidate potential drivers of decline, and guide strategic action to halt wild bee declines.

Data availability statement

Publicly available datasets were analyzed in this study, available from the following sources: 1) Chesshire, P. R., Fischer, E. E., Dowdy, N. J., Griswold, T. L., Hughes, A. C., Orr, M. C., et al. (2023). Completeness analysis for over 3000 United States bee species identifies persistent data gap. Ecography n/a, e06584. doi: 10.1111/ecog.06584, 2) GBIF.org (2022): GBIF Occurrence Download available at: https://www.gbif.org/, and 3) SCAN (2022): Available at: http://scan-bugs.org/portal/index.php. The codes used in this analysis are available at: https://zenodo.org/records/10783956.

Author contributions

JR: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing, Project administration, Software. SW: Conceptualization, Methodology, Writing – original draft, Writing – review & editing. SJ: Conceptualization, Methodology, Writing – original draft, Writing – review & editing. BC: Writing – original draft, Writing – review & editing. AJ: Conceptualization, Methodology, Writing – review & editing, Funding acquisition. BD: Data curation, Writing – review & editing. AR: Conceptualization, Funding acquisition, Writing – review & editing, Supervision.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1346795/full#supplementary-material

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Sampling the understory, midstory, and canopy is necessary to fully characterize native bee communities of temperate forests and their dynamic environmental relationships

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Introduction: Native bee communities of temperate forests are conventionally sampled from the understory, yet there is growing evidence that bee assemblages in forest canopies are distinct from those in the understory. Therefore, conventional approaches to quantify forest bee–habitat relationships may not comprehensively characterize forest bee communities.

Methods: To examine this, we sampled bees 1–26 m from ground level at 5-m increments at 47 locations in forests located in western Massachusetts, USA. We evaluated bee abundance and species richness responses to a suite of environmental factors measured in the understory with linear and segmented regression comparing four bee sampling strategies: (1) understory sampling only, (2) understory and midstory, (3) understory and canopy, and (4) all strata combined.

Results: We found that not sampling higher strata underestimated bee abundance and species richness, and linear models had less ability to explain the data when bees of higher strata were included. Among strategies, responses analyzed linearly differed in magnitude due to overall differences in abundance and species richness, but segmented regressions showed relationships with understory characteristics that also differed in slope, which would alter interpretation.

Discussion: Collectively, our findings highlight the value of including vertically stratified sampling strategies throughout the flight season to fully characterize native bee and other pollinator communities of forests.

KEYWORDS

sampling strategy, native bee, vertical gradient, nonlinear analysis, forest strata, closed-canopy forest

1 Introduction

Native pollinators and their pollination services are critical in supporting ecosystems worldwide (Klein et al., 2007; Winfree et al., 2007, 2008; Ollerton et al., 2011; Kennedy et al., 2013; Rodger et al., 2023). Evidence that many pollinator species are experiencing population declines (Biesmeijer et al., 2006; Cameron et al., 2011; Bartomeus et al., 2013; Burkle et al., 2013; Koh et al., 2016) has raised alarm among conservationists and the public. In response, there has been a rapid increase in research aimed at understanding basic habitat associations at community and species levels to inform pollinator conservation efforts (Williams et al., 2010; Tonietto and Larkin, 2017; Neumüller et al., 2020; Milam et al., 2022). To date, research within the temperate zone suggests that native bees tend to be more abundant and diverse within open and early-successional communities (Taki et al., 2013; Hanula et al., 2015; Roberts et al., 2017; Wagner et al., 2019; Milam et al., 2022; Ulyshen et al., 2022). As a result, the bulk of native bee research in the interest of pollinator conservation has focused on early-successional plant communities over other natural communities such as closed-canopy forest (herein referred to as 'forests'; Ulyshen et al., 2023).

Limited research addressing native bee communities within forests has primarily focused on the understory (e.g., Rodríguez and Kouki, 2015; Roberts et al., 2017; Smith et al., 2019; Rivers and Betts, 2021; Eckerter et al., 2022; reviewed in Ulyshen et al., 2023). This sampling strategy, although accessible and convenient, is potentially problematic since the understory contains only a fraction of the vertically distributed resources available to bees (Saunders, 2018; Smith et al., 2019; Requier and Leonhardt, 2020; Urban-Mead et al., 2021). Indeed, field experiments that sampled at heights reaching beyond the understory have firmly established that bees are well distributed throughout temperate forest canopies (Ulyshen et al., 2010, 2020; Campbell et al., 2018; Cunningham-Minnick and Crist, 2020; Simon et al., 2021; Urban-Mead et al., 2021; Allen and Davies, 2022; Milam et al., 2022; Cunningham-Minnick et al., 2023), sometimes at significantly greater abundances than in the understory (Ulyshen et al., 2010; Campbell et al., 2018; Urban-Mead et al., 2021). Thus, sampling approaches that rely on understory sampling alone (e.g., Roberts et al., 2017; Harrison et al., 2018; Wagner et al., 2019) are informative but may not sufficiently characterize the full breadth of the forest bee community, although the magnitude and meaningfulness of this bias – from both a statistical and conservation perspective – remains uncertain. Further research in forests from a broader geographic range are necessary to gauge the extent to which vertical sampling affects the characterization of forest bee communities.

Milam et al. (2022) addressed the concern that only sampling forest understories may bias results and influence conclusions when comparing forest and early-successional communities in restored barrens. This study demonstrated how sampling the forest canopy does not change the conclusion drawn when comparing bee communities of the forest understory to the restored barrens: bee communities in barrens were more abundant and diverse. Though not the focus of their study, the authors also found significant differences in bee species composition between the forest understory (1.0 m) and canopy (8.6 m) in stands ~20 m tall, yet did not compare abundance or species richness between strata. Similarly, Ulyshen et al. (2010) sampled the forest understory at 0.5 m and canopy at 18.8 m near trees with an average height of 31.7 m and found a unique canopy assemblage with greater abundance, species richness, and diversity than the understory. Urban-Mead et al. (2021) sampled at 1.0 m and 22.5 m in a stand with an average maximum canopy height of 25 m and also found that the bee community was more diverse in the canopy but only more abundant for one of the three sampling years. Though regional differences (e.g., landscape composition or configuration; bee or plant species) may explain variation in vertical stratification of species among studies, the interaction between trap positioning and vegetation height may play an important role in the distribution of native bee communities (Geroff et al., 2014; Roberts et al., 2017; Ulyshen et al., 2023). Thus, the variation in results among these studies could also be due to differences in the maximum canopy height of these forests, which may affect the accessibility of canopy resources, or differences in the relative position of bee traps relative to the canopy, which could affect the proximity of the traps to different resources (e.g., canopy flowers, dead wood, alternative food sources; Cunningham-Minnick and Crist, 2020; Urban-Mead et al., 2021; Ulyshen et al., 2023). Of course, the maturity (size and flowering) and life histories of the tree species that comprise the forest community are likely to determine the availability of preferred resources throughout the canopy and thus the presence of particular bee species at different strata (Cunningham-Minnick and Crist, 2020; Urban-Mead et al., 2023). These points raise the question of whether the vertical stratification of bee communities can be better predicted from height above the ground or in relation to the height of the canopy. The inconsistency in findings across studies highlights the issue of how authors define each stratum, which complicates comparisons among studies and is exacerbated by studies that sampled at three (Ulyshen et al., 2020), four (Cunningham-Minnick et al., 2023), or more (Cunningham-Minnick and Crist, 2020) heights. Ulyshen et al. (2020) reconciled this issue with their recommendation of sampling at 5 m above the forest floor following findings that the bee assemblages at 1 and 15 m above the ground were distinct in composition while the assemblage at 5 m was not statistically different from either. Still, the variation in canopy height among forest types and forest composition based on geographic locations suggests the need for a more standardized approach that can account for these differences.

The goal of this study was to understand the extent to which sampling at different forest strata influences how forest bee communities might be characterized, and in turn, its implications for understanding broader environmental relationships. We vertically sampled a total of 47 forest sites for one year (17 sites in 2020; 30 sites in 2021) at 5-m increments from the understory into the upper reaches of the canopy to compare the effects of four potential sampling strategies on the characterization of the vertically stratified bee community: (a) understory sampling only, (b) understory and midstory sampling, (c) understory and canopy sampling, and (d) understory, midstory, and canopy sampling. Specific objectives were to: (1) determine if vertical stratification is best described in terms of absolute height above the ground or in relation to the height of the canopy, (2) compare abundance and diversity among these sampling strategies, and (3) examine whether sampling strategy has the potential to influence conclusions about relationships with the environment (e.g., microhabitat).

2 Methods

2.1 Study area

This study took place in western Massachusetts within heavily forested areas of three ecoregions in 2020 and 2021 (Figure 1). The Connecticut Valley ecoregion includes central and transition hardwood as well as floodplain forests in relatively rich soils due to thick outwash and alluvial deposits with a largely sedimentary geology while the Worcester/Monadnock Plateau and Lower Worcester Plateau/Eastern Connecticut Upland ecoregions include transition hardwood forests at southern sites of lower elevations on stratified deposits of sand, gravel, and silt as well as hardwood forests and forested wetlands with scattered monadnock relics from glaciation events, which are typically colder in temperature due to their higher elevation (150–425 m) on a shared gneiss, schist, and granite geology (Griffith et al., 2009). All study sites comprised closed-canopy forests with an average maximum canopy height of 24.6 m (range: 19–31 m); dominate species include *Pinus strobus* and *Quercus rubra* and codominant species *Acer rubrum*, *Betula lenta*, and *Tsuga canadensis* that reached the canopy ceiling while intermediate species included scattered *Betula alleghaniensis*, *Betula papyrifera*, *Fagus grandifolia*, *Pinus rigida*, *Quercus alba*, and *Quercus montana* depending on the forest type. The understory consisted largely of *Amelanchier* spp., *Hamamelis virginiana*, *Kalmia latifolia*, *Vaccinium corymbosum*, and snags, as well as immature *Castanea dentata*, *F. grandifolia*, and *P. strobus* trees, with an herbaceous layer primarily of ferns, seedlings, *Vaccinium* spp., and scattered *Monotropa uniflora*, *Panax trifolius*, *Trientalis borealis*, and *Viola* spp. on a groundcover of leaf litter, *Maianthemum canadense*, and *Mitchella repens*. These forests do not generally support spring ephemerals characteristic of mesic forests with rich soils.

2.2 Bee sampling

Bees were sampled at 17 sites in 2020 (April 29–October 14) followed by a different suite of 30 sites in 2021 (March 25–August 25) across nine forests (Figure 1) for a total of 47 sites that were each sampled for one year (Supplementary Table A1). Sites were established along a distance gradient from the edge of a managed opening and into the forest interior up to 640 m within each forest to represent the multidimensional aspect of a forest (Figure 1). Since some bee species have the capacity to forage long distances (Zurbuchen et al., 2010), and to include a variety of forest types and management histories into our study, we addressed potential spatial autocorrelation among sites within a forest through our statistical approach. The shortest distance between sites within a forest averaged 351 m (SD: 162 m; range: 157–973 m) and the shortest distance between forests averaged 3.1 km. We sampled bees at each site by attaching Blue Vane Traps (BanfieldBio Inc.$^{\text{TM}}$) to one central rope that reached from the forest floor to a branch high in the canopy (herein 'trap line') as in Cunningham-Minnick and Crist (2020). Tree species targeted for trap lines varied depending on the tree composition of the site and branch availability for a trap line, but included all aforementioned canopy species. Traps were vertically spaced five meters apart at 1, 6, 11, and 16 m on each trap line, though we included traps at heights of 21 and 26 meters if

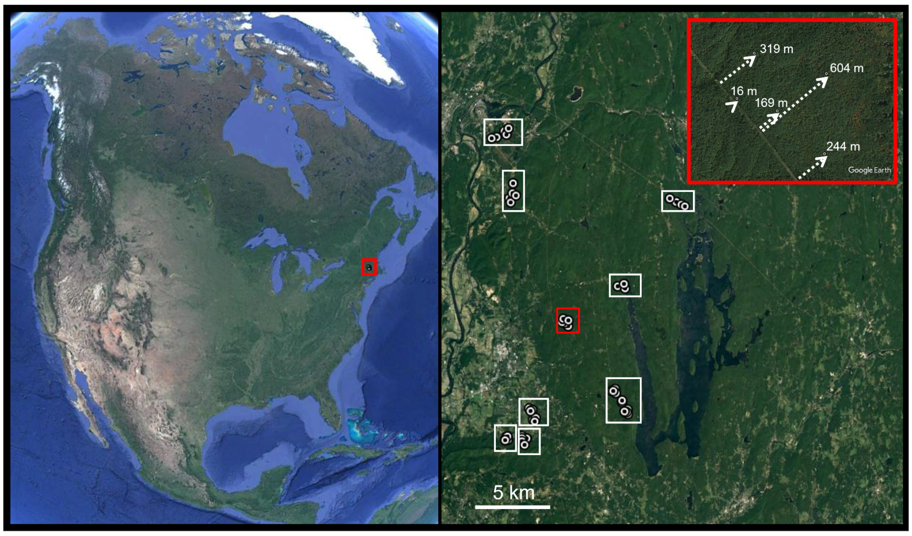

FIGURE 1
Sites were located in the northeastern United States in a forested landscape of western Massachusetts. Within each forest, or Wildlife Management Area, a series of sites were established that collectively represented a distance gradient from an opening, often a powerline right-of-way, managed for wildlife (see inset for an example).

branches in the high canopy were strong enough, for a total of 4–6 traps per site. Soapy water was placed in traps to reduce surface tension and capture specimens. Sampling was continuous over time; the contents from traps were emptied and traps reset with fresh soapy water roughly every two weeks (Supplementary Table A1). Bees were taken back to the lab, pinned, and identified to species by JM using published keys (Mitchell, 1960, 1962; LaBerge, 1973, 1980, 1986, 1989; Gibbs, 2011; Gibbs et al., 2013) and the online source Discoverlife.org (Ascher and Pickering, 2020). Seven *Nomada* bees were lumped as *Nomada bidentate* group due to unresolved taxonomy. Voucher specimens are currently being held in the research collection of JM.

2.3 Vegetation sampling

2.3.1 Not tree-associated

To understand local environmental factors that may affect the bee community, including available nesting and food resources, we measured multiple aspects of the vegetation community. At each site, we recorded the ground substrate at 20 randomized locations (angle and distance up to 20.0 meters from trap line) as either bare soil, dead wood, duff, leaf litter, moss, or rock. Since 95% of the 340 randomized locations sampled were leaf litter, we did not include this as a predictor in our models. We converted the presence of coarse woody debris (>4 cm diameter) on the ground and herbaceous plants at each location into separate variables as proportions to represent relative availability of food and nesting resources. To address potential negative effects of vegetation density on the presence of bees in the understory, we took detailed measurements of understory structure including the highest contact point less than 1, 2, and 3 meters on a 3-m pole for a total of 60 measurements per site (Roberts et al., 2017). This information was used to create variables of the overall understory structure (proportion of potential contact points touched by vegetation), the average maximum vegetation height, and the coefficient of variation in the max height of vegetation at each site.

2.3.2 Tree-associated

To develop variables that are likely to influence bees at strata above the understory, we measured the diameter of each snag (dead standing tree) and mature tree (>8 cm diameter at breast height) within 11.3 m of the site center, chosen to account for the breadth of tree crowns, of the trap line and calculated the mean diameter at breast height, as well as total basal area, of the site for snags, coniferous trees, and deciduous trees as separate variables. We also qualified the presence of foliage and deadwood (estimated >4 cm diameter) above the ground and binned to distances above the ground that corresponded to the height of each trap (0–3.5 m for trap at 1 m, 3.6–8.5 m for trap at 6 m, etc. that corresponded with the understory stratum) at nine locations (site center and 5-m and 10-m in each cardinal direction) and converted the data into a proportion for predictor variables representing food (floral resources on live twigs near foliage in spring) and nesting (dead wood) sources.

2.3.3 Seasonality and edge-effects

Since the expected use of forest floral resources by bees is seasonally dependent on floral resource availability (Smith et al., 2019), yet some studies have found many bees in the forest late in the summer (e.g., Ulyshen et al., 2010; Milam et al., 2022; Cunningham-Minnick et al., 2023), we created a variable of 'season'. Cunningham-Minnick et al. (2023) found that the bee community composition shifted among forest strata based on tree leaf phenology. Therefore, we categorized our seasons as 'early spring', 'late spring', and 'summer' based on the changes in canopy cover. We converted pictures taken of the forest canopy at the center of all sites in 2021 (Samsung Galaxy S10e camera at 1.0x zoom) at different times of the year into black and white contrasts using the imageJ software (Schneider et al., 2012), then graphed the proportion of pixels representing canopy cover as a function of the day of year and estimated changes in slope at May 8 and June 20 which represented the onset and completion of the forest leaf phenology and corresponded with season (Supplementary Figure A2). Finally, we accounted for potential edge effects by including distance to the nearest opening (powerline rights-of-way, road edges and managed barrens) as a covariate in all model building procedures.

2.4 Statistical analyses

2.4.1 Deriving forest strata

To determine if vertical stratification is best described in terms of absolute height above the ground or in relation to the height of the canopy (Objective 1), we built generalized linear mixed effects models. Specifically, we compared the fit of models with a single predictor of either the relative height of the trap to the mean height of the canopy (relative mean canopy height), relative height of the trap to the maximum height of the canopy (relative max canopy height), or height above the ground (absolute height) to each response (bee abundance and species richness). We employed a rangefinder to measure the canopy height at nine locations within 11.3 m of each site center, from which we extracted the mean and maximum heights (Figure 2). We allowed the model intercept to vary with year to account for interannual differences, as well as site nested within forest to account for the different forest types and effects of previous management, the repeated sampling of each site, and any imbalance in the sampling design due to lost traps due to extreme weather events and wildlife tampering; thus, our analysis differentiated between zeroes and NAs. Finally, to account for additional sampling effort in strategies with pooled strata (number of traps deployed) as well as traps that were deployed for more or less than fourteen days (e.g., we did not collect samples during storms), we included an offset of the number of days each trap was deployed (logged to be compatible with the log-link in models). We performed likelihood ratio tests of each single-predictor model against a null that only included the error terms for each response, for a total of four likelihood ratio tests and directly compared single-predictor models with AICc (Mazerolle, 2023). Since relative mean canopy height was a better predictor of bee abundance and species richness (Table 1), we binned relative

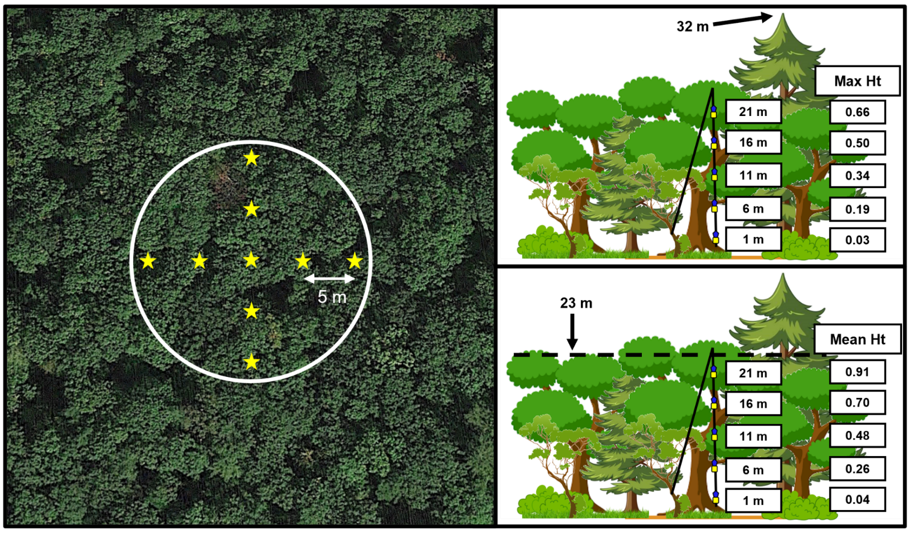

FIGURE 2
Sampling design as it relates to trap height above the ground (i.e., 1, 6, 11, 16, and 21 meters) relative to canopy height. Canopy height was measured at nine locations (stars) at each 11.3-m radius site (*left*) with a rangefinder, including at the trap line as well as 5 m and 10 m in each cardinal direction. Trap height relative to the maximum canopy height (top-right) was then calculated as the proportion of the height of each trap relative to the tallest measurement taken (32 m in figure). Similarly, trap height relative to the mean canopy height (bottom-right) compared trap heights above the ground to the average of all nine measurements (23 m in figure).

mean canopy heights into three simple strata based on the growth forms of the vegetation including understory (herbaceous and shrub layer: relative height ≤ 0.167), midstory (midstory and immature trees: 0.167 < relative height < 0.640), and canopy (large mature trees: relative height ≥ 0.640) for all other analyses.

2.4.2 Comparing responses among strategies

To compare abundance and diversity among sampling strategies (Objective 2), we built generalized linear mixed effects models for each strategy. Bee abundance and species richness were response variables and represented pooled bees from each stratum included within each strategy. For instance, bee abundance for the strategy of sampling the understory and canopy was the sum of the bee abundances for those strata while species richness was the total number of species within the pooled assemblages of those strata. In all linear models, we tested the inclusion of distance to forest edge (continuous) and season (categorical based on change in canopy cover; Supplementary Tables A2, A3). Distance to forest edge rarely occurred as an interaction term with focal model covariates and will not be discussed further (Supplementary Table A2). The error structure was identical to the models comparing height variables.

TABLE 1 Comparison of models to determine the best approach for stratum classification, including Chi-squared (χ^2) statistics, associated p-values, and change (Δ) in Akaike Information Criterion corrected for small sample size (AICc) of single-predictor generalized linear mixed effects models (CVAR) compared against the null, as well as change in AICc compared to best model (italicized) for bee abundance (unshaded) and species richness (shaded) responses.

Var	χ^2	P-value	$\Delta AICc_{NULL}$	$\Delta AICc_{VAR}$
Height (m)	18.21	< 0.0001	−16.19	11.13
Relative Mean Height (%)	*29.33*	*< 0.0001*	*−27.32*	*0.00*
Relative Max Height (%)	21.04	< 0.0001	−19.02	8.30
Height (m)	10.87	< 0.001	−8.85	6.47
Relative Mean Height (%)	*17.34*	*< 0.0001*	*−15.32*	*0.00*
Relative Max Height (%)	11.48	< 0.001	−9.45	5.87

Strategy models were fit with the glmmTMB function in the glmmTMB package (Mollie et al., 2017) term-by-term, including two-way interactions, with a suite of variables representing potential environmental associations of the understory with bees, including vegetation structure as well as food and nesting resource availability that were categorized as associated with mature trees (e.g., basal area of mature woody plants) or not (substrate on soil surface; vegetation cover and structure). If an additional term increased model fit >2 AICc units, then that term was added. This process was continued until all resulting models were >2 AICc units less than the simplified model, at which point the simplified model was considered the best model for that strategy and response. From each of the eight best models (two responses each for four sampling strategies), we calculated 95% CIs of the y-intercept representing the expected number of bees or bee species within each sample and determined strategies to be different if confidence intervals did not overlap.

2.4.3 Comparing bee ecology among strategies

To determine whether sampling strategy has the potential to influence inferences of forest-bee ecology (Objective 3), we considered linear and segmented (nonlinear) regression models. First, we determined the explanatory power of the environmental covariates by examining differences in coefficients of determination (R^2) – a metric describing how well the model explains variation in the response data – between the marginal effects (fixed explanatory variables) of best models derived for Objective 2 with only the predictors of distance to forest edge and seasonality with the r.squaredGLMM function in the MuMIn package (Bartoń, 2023). This allowed us to calculate how much variation in the response was explained by the environmental factors within the model. We also calculated the proportion of all variation explained by each model due to captured environmental variation as the quotient of the marginal R^2 of environmental predictors and the conditional R^2 of the entire model. To determine if model variation explained by understory variables not associated with higher strata (non-tree) changed among strategies, we repeated the comparisons of R^2 with marginal R^2 calculations for models without non-tree variables.

We then determined if the relationship of each response differed per predictor among strategies by fitting single-predictor models of linear (as previously described) and nonlinear models and comparing the 95% CIs of fitted slopes. We considered predictors that were most often included in best models to linear fits. To examine potential nonlinear relationships between bee abundance and species richness to environmental factors, we employed a segmented, or broken-stick, regression model for each environmental variable examined in linear models across strategies with the segmented package (Muggeo, 2008). To ensure all strategies had the exact same breakpoints, we included all strategies within each model fit (Muggeo, 2003). We chose the number of breakpoints to use in a model through AICc comparison of models fit with one to five breakpoints. Once breakpoints were identified, we fit each strategy with a segmented regression and included an offset term for the total sampling duration of traps. We extracted the slopes from the summary output of the model (summary function) and calculated the 95% confidence interval of each slope as the slope plus or minus the square root of the sum of the variance–covariance matrix of included terms multiplied by 1.96. All plots were created with the ggplot2 package (Wickham, 2016) and all analyses were performed in R (R Core Team, 2023).

2.4.4 Bee community composition

The community composition among strata were statistically compared with PERMANOVA using the adonis function and differences among different combinations of season and stratum were determined with the pairwise.adonis function in the pairwiseAdonis package (Arbizu, 2017). Overall expected species richness of the community for each strategy was estimated with the estimateR function in the vegan package. We report 95% confidence intervals for Chao1 estimates, which calculate the number of unobserved species based on the observed number of singletons and doubletons, as well as ACE estimates, which employ a coverage-based estimator of rare (10 individuals or less) versus common (>10 individuals) species (Chao and Chiu, 2016).

3 Results

Traps sampled a total of 4,765 bees of 109 species, including 258 specimens that could not be identified to species due to body damage and unresolved taxonomy; for instance, 131 unidentified specimens were of the subgenus *Lasioglossum* (*Dialictus*), a taxonomically difficult group. The specific composition of this community and close examination of its ecological relationships is outside the scope of this study and will be published separately.

Generalized linear mixed effects models demonstrated that variation in the vertical distribution of bee abundance and species richness was better explained by the height of the trap in relation to the mean canopy height than relative height in relation to the maximum canopy height and the absolute height from the forest floor (Table 1; Figure 2). Subsequent model selection of strategies with the relative mean canopy height covariate showed that bee abundance and species richness were highest when all strata were considered followed by the strategy that included only understory and midstory strata, while abundance and species richness were lowest when only the understory was sampled (Figure 3). This pattern was also observed when comparing species richness estimates among strategies that considered sample coverage (Table 2) and collectively demonstrates that unique species occurred within each stratum.

The predictor of herbaceous cover was included within the best model for all strategies of the abundance response, as well as strategies modeling the richness response (Table 3; Supplementary Table A2). Herbaceous cover was the only environmental predictor in best models for abundance not associated with mature trees, though coarse woody debris on the ground was included species richness models. The explanatory power of herbaceous cover for variation in bee abundance data was highest for the strategy only including understory bees (0.147) and lowest when bees in all strata were pooled (0.046), demonstrating a bee in the midstory or canopy is much less affected (< 33%) by resources offered by herbaceous plants than a typical bee found in the understory (Table 3). This pattern was also apparent when considering only variation explained by the model (understory: 53%, all strata: 23%), affirming this difference in relationships with herbaceous cover among strategies is due to biological responses of bees at different strata and not a modeling artifact (e.g., differences in covariates among models, unmeasured covariates; Table 3). The same pattern was found when considering both tree- and non-tree-associated predictors (Table 3). Modeled strategies explaining species richness also demonstrated a decrease in explanatory power of the dataset and model with the addition of bees in higher strata, meaning that variables in the model were explaining the occurrence of bees in the canopy poorer than bees in the understory. However, the strategy including all strata explained more variation in the data when all understory predictors were considered compared to the strategy of understory plus canopy. Further, sampling all strata showed that non-tree-associated factors (coarse woody debris on the ground and herbaceous plants) played a larger role in explaining the bee community than strategies including the understory and just one higher stratum (Table 3).

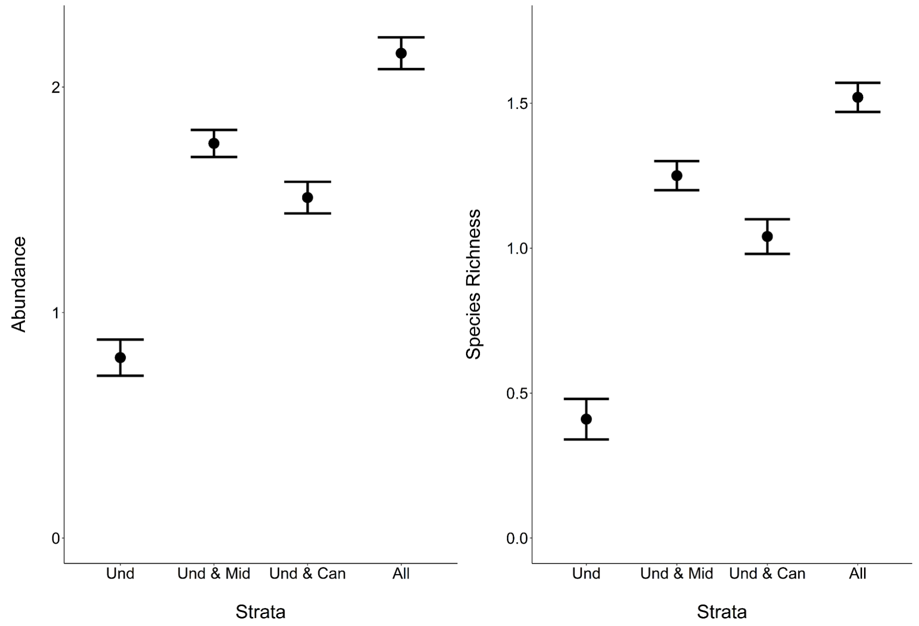

FIGURE 3
Comparing the interpretation of bee metrics with different strategies. Mean and 95% CI of fitted bee abundance (left) and species richness (right) per sample per site (two weeks of trap deployment) from generalized linear mixed effects models for each sampling strategy (Und, understory; Mid, midstory; Can, canopy; All, all strata).

Slopes of linear relationships between response variables and predictors did not vary among strategies with the exception that the understory and midstory sampling strategy in early spring in response to tree foliage was not significant, while the other strategies responded positively (Figures 4, 5; Supplementary Table A3).

A segmented modeling approach revealed that relationships between bee abundance and each predictor included negative and positive slopes for most strategies, demonstrating that the relationship was not linear (Figure 4). Furthermore, there were differences in segment slopes within most strategies both in direction and magnitude (mean or confidence interval on the positive or negative side of zero, respectively). Relationships of bee species richness via segmented regression similarly showed variability in direction and magnitude of fitted slopes among strategies and covariate values (Figure 5). Notably in the understory, there was high uncertainty that the slope of all segments across some predictors (i.e., foliage cover, basal area of deciduous trees) was different from zero; meaning that bees sampled in the understory were not responding consistently negatively or positively to environmental variables of the understory (Figure 5). Among strategies and within covariate values, there were many occurrences of non-overlapping confidence intervals, indicating that interpretation of the bee–environment relationship will differ by sampling strategy. Finally, bee community composition differed among all strata by season combinations except the midstory vs canopy in the early spring and summer, as well as the understory vs canopy and midstory vs canopy in the late spring (Supplementary Table A4).

TABLE 2 Confidence intervals (95%) of bias-corrected species richness estimates that base the number of unobserved species on the number of singletons and doubletons (Chao1) and sampling completeness (ACE).

Strategy	Chao1	ACE
Understory	70.7–111.4	84.2–103.8
Understory and Midstory	100.5–146.7	116.9–138.7
Understory and Canopy	87.3–132.9	101.4–122.0
All Strata	110.4–158.8	130.1–155.1

4 Discussion

Our findings highlight that study design approaches, including sampling strategies and their analysis, can change how forest-bee communities are characterized. We demonstrate that not sampling higher strata may lead to poor estimates of forest bee community metrics and potentially misrepresent forest bee habitat associations. We discuss these issues as well as how they are likely to bias our understanding of bee communities within forests and the conservation value of closed-canopy forest systems.

4.1 Ignoring vertical strata underestimates community metrics

We encountered bees in all strata, which is consistent with other studies that sampled at least three strata (e.g., Cunningham-Minnick and Crist, 2020; Ulyshen et al., 2020; Cunningham-Minnick et al., 2023) indicating that sampling more strata increased the number of individuals and species that are expected

TABLE 3 Change (Δ) in coefficient of variation (R^2) between all marginal effects (including distance to forest edge and season) of the best model and the marginal effects of the simplified model excluding all environmental factors measured in the understory (ΔR^2_{Under}), as well as the associated change in the proportion of the marginal variation to total variation explained in the model expressed as a percent in abundance (unshaded) and species richness (shaded) models.

Response	Strata Included			ΔR^2_{Under}	$\Delta R^2_{Non\text{-}Tree}$	Non-Tree Vars	Tree Vars
	Und	Mid	Can				
Abundance	Y			0.187 (66.30%)	0.147 (52.79%)	Herbaceous Cover	Dead Wood Above Ground Deciduous Basal Area Foliage
Abundance	Y	Y		0.092 (42.56%)	0.069 (31.62%)	Herbaceous Cover	Foliage
Abundance	Y		Y	0.079 (36.33%)	0.050 (23.68%)	Herbaceous Cover	Foliage
Abundance	Y	Y	Y	0.071 (35.42%)	0.046 (23.17%)	Herbaceous Cover	Foliage
Richness	Y			0.148 (75.20%)	0.112 (58.95%)	Herbaceous Cover CWD_{Ground}	Dead Wood Above Ground Foliage Deciduous Basal Area Snag Basal Area
Richness	Y	Y		0.049 (41.08%)	0.019 (8.44%)	Herbaceous Cover	All Trees Basal Area Mean Tree DBH Snag Basal Area Mean Snag DBH Foliage
Richness	Y		Y	0.028 (26.07%)	0.019 (19.38%)	Herbaceous Cover	Foliage
Richness	Y	Y	Y	0.033 (34.56%)	0.026 (28.27%)	Herbaceous Cover CWD_{Ground}	Dead Wood Above Ground Deciduous Basal Area Foliage

Change in R2 due to the removal of environmental predictors that are associated with mature trees ($\Delta R^2_{Non\text{-}Tree}$) and the associated proportional change in variation explained by the marginal effects. Sampled strata include the understory (Und), midstory (Mid), and canopy (Can). Covariates included coarse woody debris in contact with the soil (CWD_{Ground}), as well as tree and snag size measured as diameter at breast height (DBH).

to occur within forests. Our findings confirm that sampling the understory, midstory, and canopy will lead to abundance and species richness estimates that are greater than the expected values modeled from understory sampling alone. It follows that not including higher strata within the sampling design will underestimate community metrics and consequently the pool of pollination service potential that forests provide (Blaauw and Isaacs, 2014). Considering the importance of closed-canopy forests in pollinator conservation discussions (reviewed in Ulyshen et al., 2023), our study suggests future work is needed to characterize the temporal component – particularly following leaf-out – of these communities in the understory, midstory, and canopy to provide the most accurate understanding of native bee distribution in forests.

The finding that sampling the understory, midstory, and canopy provides a different interpretation of bee community metrics than other sampling strategies is likely a direct consequence of the unique composition of bee assemblages at each strata, albeit season dependent. However, Cunningham-Minnick and Crist (2020) and Cunningham-Minnick et al. (2023) found that community composition did not differ among understory, midstory, and canopy strata, while Ulyshen et al. (2020) found that bee community composition differed between understory and canopy assemblages, which is consistent with other studies that examined two strata (i.e., Ulyshen et al., 2010; Milam et al., 2022). Since most other studies did not evaluate how species composition changed across the three strata considered in this study throughout the temperate seasons, it is difficult to discern if our approach of employing relative height with respect to the mean canopy height for binning traps within strata is responsible for the observed differences with previous studies. It also remains unclear if division of the vertical gradient into three discrete strata is the best approach to describe a community of organisms that presumably move freely in and out of strata when resource availability changes seasonally (Bertrand et al., 2019). For instance, bee composition of the understory differed from the canopy between early spring and summer, but notably the midstory composition differed from that of the understory across seasons yet was never statistically different from the canopy. This clear seasonal shift in composition among strata indicates that forest-bee communities are spatially and temporally dynamic, and highlight the possibility for seasonal-dependent stratum specialists (Dorey et al., 2024). Further investigation into the local factors responsible for the occurrence of species along the vertical gradient of resource availability within the forest will surely provide insight into how many strata need to be considered in sampling strategies, or if vertical sampling is better approached as a continuum. Nonetheless, our findings collectively highlight that sampling the understory, midstory, and canopy strata of closed-canopy forests provide a more informed understanding of the bee community than other sampling strategies when strata are based on the trap height relative to the mean height of the canopy and sampling includes the entire flight period of native bees.

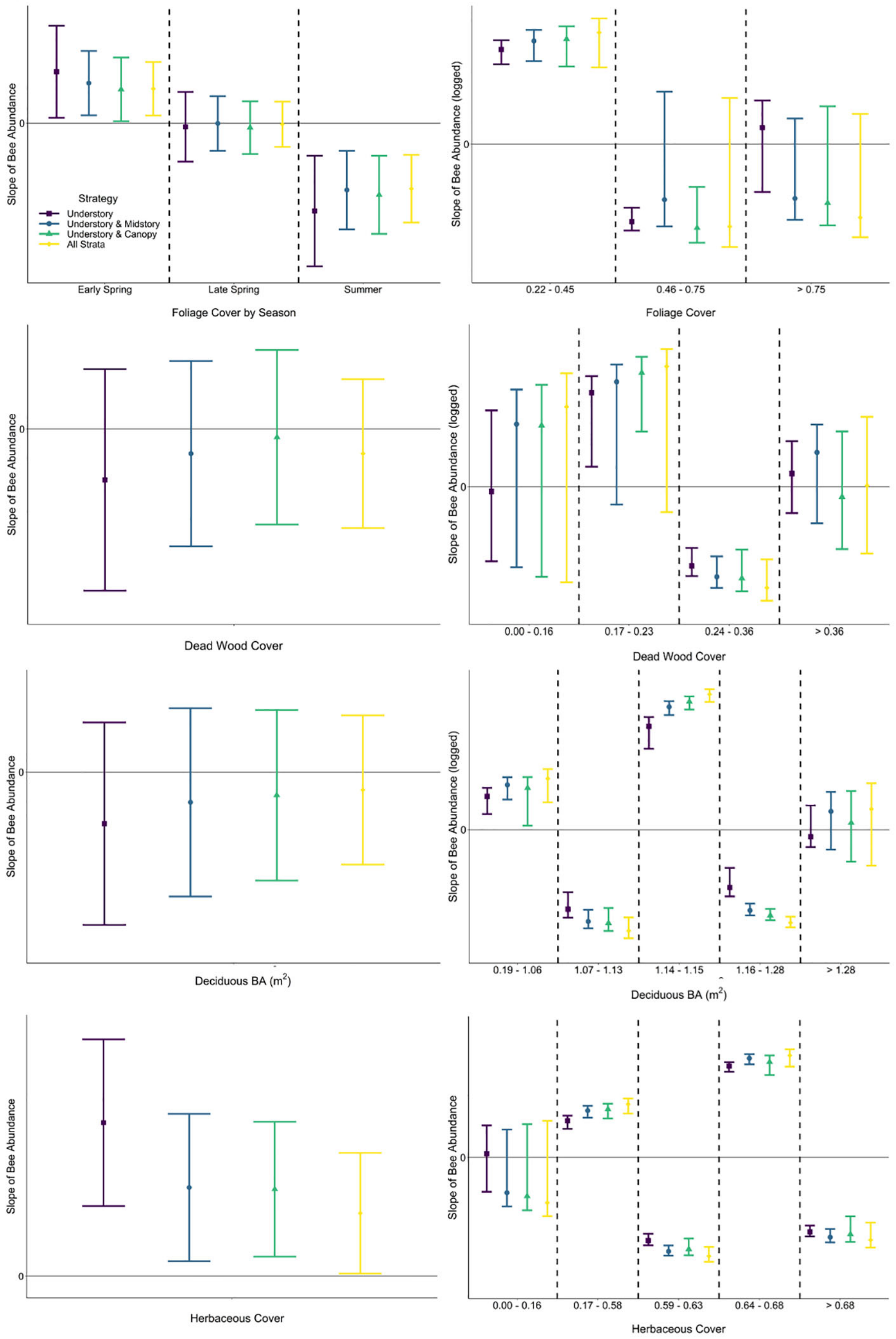

FIGURE 4
Comparison of slopes (with 95% CIs) of fitted single-predictor relationships (first row: foliage cover, second row: dead wood cover above the forest floor, third row: basal area of deciduous trees, fourth row: herbaceous cover) explaining bee abundance within generalized linear mixed effects (left column) and segmented regression (right column) for each strategy. Foliage cover was modeled with season interaction in linear regression. Among strategies, slopes with 95% CIs that do not overlap would be interpreted differently, as would slopes with 95% CIs that cross zero (not statistically significant) versus those that do not.

4.2 Bees respond at heights relative to the canopy

To our knowledge, we present the first analysis of bee community responses to forest strata in temperate forests described in terms of relative canopy height. The fact that relative mean canopy height was a better predictor of bee abundance and species richness than height above the ground suggests future work on forest bees should consider this metric in their analyses. Note that trap height relative to the maximum canopy height performed poorly and on par with height from the forest floor in models. Considering that the bee community extends above the forest

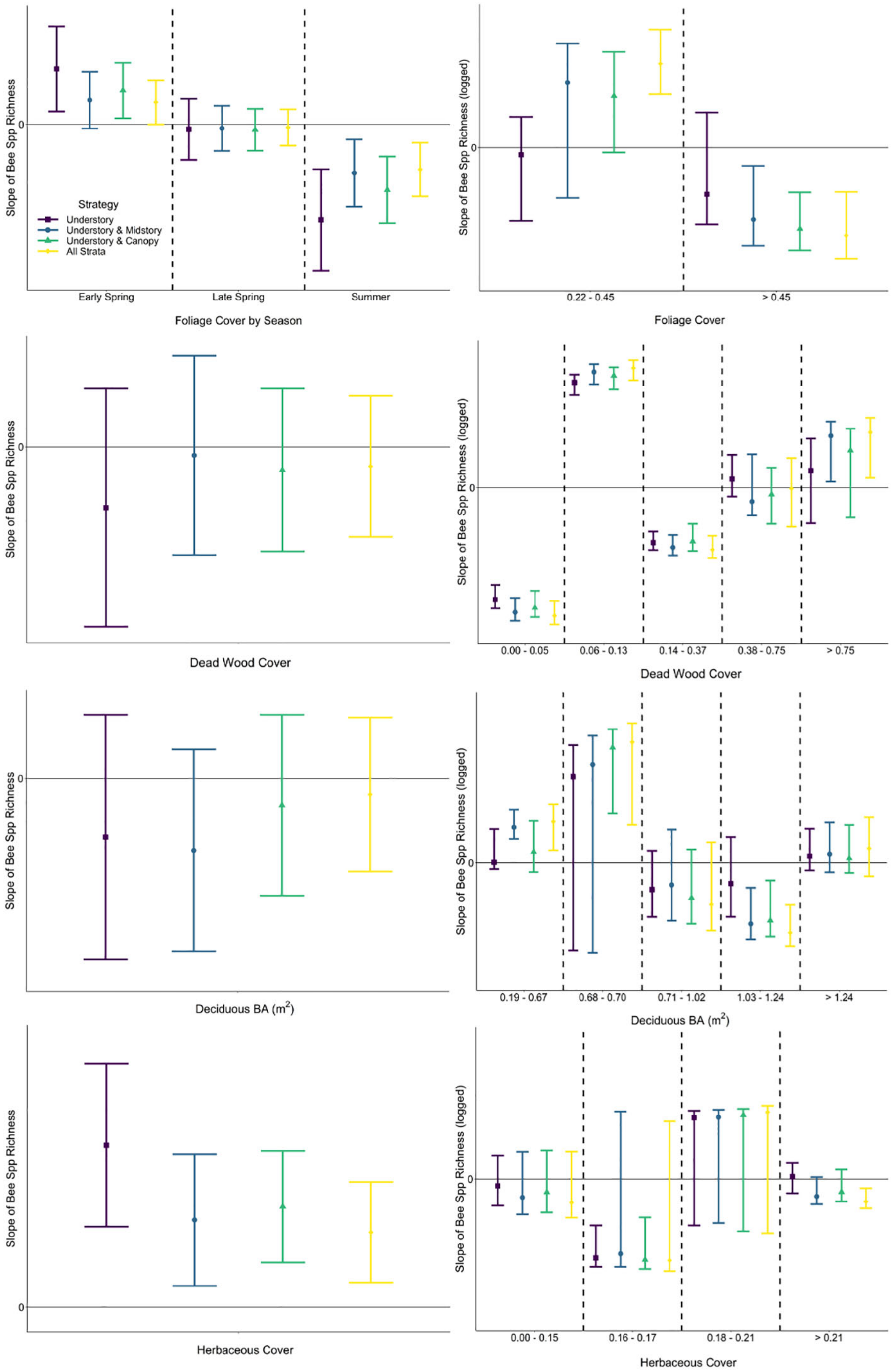

FIGURE 5
Comparison of slopes (with 95% CIs) of fitted single-predictor relationships (first row: foliage cover, second row: dead wood cover above the forest floor, third row: basal area of deciduous trees, fourth row: herbaceous cover) explaining bee species richness within generalized linear mixed effects (left column) and segmented regression (right column). Among strategies, slopes with 95% CIs that do not overlap would be interpreted differently, as would slopes with 95% CIs that cross zero (not statistically significant) versus those that do not.

canopy (Cunningham-Minnick et al., 2023), our findings highlight the potential importance of canopy topography, or variation in height among neighboring emergent trees, in affecting the distribution of forest bees. Thus, instead of considering the mean canopy height as a physical boundary for bees, it should be recognized as an important scaling point from which to describe the vertical distribution of the forest-bee community. There are likely many questions and exceptional situations pertaining to the degree of variability in mean canopy height of different forest types and geographic locations of varied topography (Rahman et al., 2022) that need to be addressed to validate the improved fit of bee community metrics to relative mean canopy height within analyses.

Nonetheless, researchers adopting this consideration of trap height relative to the mean canopy height in their design and analyses will improve our understanding of forest bee communities and help standardize sampling.

4.3 The role of vertical strata in forest bee ecology

Our study demonstrates that the interpretation of ecological relationships between forest-bee communities and local forest characteristics change with sampling higher strata. Specifically, our findings highlight how the prediction ability of local factors present only in the understory (i.e., herbaceous cover, woody debris on the ground) is limited in describing the bees in higher strata. Combined with the overall decrease in the proportion of bee data explainable by all understory variables measured, our findings suggest there are important resources for forest bees associated with mature trees and snags in the midstory and canopy across seasons. Quantifying the relationships between bee community metrics and local forest factors or the conservation implications of these findings is outside the scope of this study; however, while foundational studies have identified important roles of canopy resources for bees in early spring (Smith et al., 2019; Cunningham-Minnick and Crist, 2020; Simon et al., 2021; Urban-Mead et al., 2023), more field studies are needed to identify and investigate mechanisms responsible for bee presence in the canopy throughout the rest of the year (Dorey et al., 2024).

In addition to changes in the magnitude of ecological relationships, we also found that the slope of these relationships with local forest factors were dependent on the included strata. Importantly, this was not the case when responses were analyzed with linear regression. Our results from segmented regressions demonstrated clear differences between strategies and suggest that relationships between common bee community metrics and local factors are not linear when additional strata are considered. The changes in slope directions among segments suggest that greatest bee abundance and species richness occurs at optimal values of each covariate rather than the 'less or more' situation associated with linear regression, which has been demonstrated when relating landscape composition to bee community metrics (Roberts et al., 2017). Therefore, analyzing bee abundance and species richness with linear regression may provide a false understanding of how the bee community responds to resources (e.g., food and nesting) within forest habitat. This warrants further investigation into nonlinear analysis techniques to describe bee ecological relationships, as it will be important for conservation practitioners to know that too much or too little of a particular resource may foil their efforts to meet pollinator conservation objectives. We also caution that we only modeled local forest factors as measured in the understory and were only interested in the slopes of these relationships. Thus, it remains unclear if these patterns will hold when covariates that include measurements at other vertical strata are employed in analyses. Further, the covariates used in segmented models were chosen based on optimal fits in linear regression models and thus did not undergo the same model selection process which would be needed to formally demonstrate these differences. If these patterns hold in future studies, their implications on forest-bee conservation will extend towards management of forests to meet optimal local conditions for an abundant and species rich bee community.

Though the methodology employed in this study demonstrates clear patterns, forest-bee researchers should keep in mind several factors that could, simply due to a lack of testing, result in a different interpretation. For instance, our study design included many blue vane traps in close proximity that were employed continuously. In bee habitat different than closed-canopy forest, these traps have been suggested to place some populations at risk due to their high catch-rates and potential oversampling (Gibbs et al., 2017). We based our sampling effort on previous experience with these traps in forest systems (e.g., Cunningham-Minnick and Crist, 2020; Milam et al., 2022; Cunningham-Minnick et al., 2023) and our total specimen count suggests that oversampling was likely not an issue, as each of our 47 trap lines (4–6 blue vane traps each) sampled an average of roughly 100 bees throughout the experiment. Nonetheless, employment effort of other trap types used in forest systems (e.g., Ulyshen et al., 2010; Campbell et al., 2018; Urban-Mead et al., 2021) may require a different design to avoid oversampling, which if present would interfere with data interpretations during multiyear studies and be counterproductive to conservation research efforts.

5 Conclusion

The current approach to most forest-bee studies largely limits 1) sampling of the bee community and environmental factors to the understory in the spring before leaf-out and 2) analyzing relationships of bee communities with environmental covariates using linear relationships. We demonstrate that only sampling bees and resources within a single season and stratum, or even two strata, does not represent the vertical stratification and seasonal dynamism of the forest bee community. Therefore, to prevent underestimation of the abundance and richness of forest-bee communities, we recommend that future studies of native bees in forests consider the bees occurring in at least the canopy, midstory, and understory in respect to the mean canopy height throughout a greater part of the year. We further urge researchers to consider analyzing the relationships between bees and local forest conditions at these strata using non-linear methods. Doing so will allow forest scientists and land managers to better evaluate the role of forests in conserving native bee communities. Notably, the implications of these recommendations may complicate the feasibility of land managers to survey or monitor forest-bee communities at this level; however, the sampling strategy we have selected should facilitate the discovery and description of mechanisms shaping the distribution of forest bees and other pollinator taxa, and modifications will likely be needed with additional research characterizing forest-pollinator communities. Following the guidelines presented in this paper will more broadly increase our understanding of the role of closed-canopy forests across forest types in supporting native pollinators, help standardize sampling and monitoring efforts of native bee and other pollinator communities, and further contribute to a deeper understanding of the currently undescribed mechanisms explaining forest pollinator distribution and conservation needs.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

MC: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Project administration, Software, Visualization, Writing – original draft, Writing – review & editing. HR: Conceptualization, Data curation, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. JM: Data curation, Investigation, Methodology, Resources, Writing – review & editing. DK: Data curation, Funding acquisition, Investigation, Methodology, Resources, Writing – review & editing.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1352266/full#supplementary-material

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Local factors influence the wild bee functional community at the urban-forest interface

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Introduction: Urban forests provide necessary habitat for many forest-associated bee species amidst development and fragmentation. These forest fragments provide a variety of important floral and non-floral resources for bees that encompass a diversity of functional guilds characterized by size, diet breadth, nesting, sociality, origin, and seasonality. The relative importance of forest edge vs. interior habitats to these organisms is not well understood.

Methods: Here, we compare bee communities between forest edge and interior locations at eight locations in Athens, GA, USA. We also explore the effects of stand structure, tree composition, ground cover type, and the presence of snags and downed wood on these organisms.

Results: We found bee abundance and richness to be higher at the forest edge than interior with distinct community compositions at both locations. Canopy cover, invasive shrub cover, ground cover, and tree diversity influenced the observed community composition. We also determined that the most impactful functional traits influencing bee community structure in urban forest fragments were nesting substrate, origin (native or exotic to North America), sociality, and diet breadth.

Discussion: Our findings will help establish the effects of local forest characteristics on the community composition, diversity, and abundance of wild bees and further our knowledge of the conservation value of urban forests for preserving wild bee communities.

KEYWORDS

wild bees, fragmentation, functional diversity, urban forest, diversity

1 Introduction

Wild bee communities have complex responses to anthropogenic landscape alterations that convert natural habitat into development or agricultural matrices (Harrison and Winfree, 2015; Baldock, 2020; Wenzel et al., 2020). While some land use change can enhance habitat complementarity in ways that can be beneficial to flower-visiting insects, semi-natural habitats such as forests play a critical role in maintaining the full complement of species endemic to an area. Extensive land use changes filter the taxonomic and functional diversities of bees (Ayers and Rehan, 2021), and high levels of deforestation can result in forest-dependent bees being replaced by habitat generalists or species adapted to open habitats (Harrison et al., 2018). Remnant forest patches therefore provide critical refugia to specialized groups of endemic species, including kleptoparasitic and early-emerging bee species, that do not have the necessary habitat features (i.e. forage and nesting requirements) to persist in other land use types (Harrison et al., 2018; Smith et al., 2019).

As more and more forests are lost to development, remaining forest patches are becoming increasingly degraded. For example, urban forests are characterized by encroachment of invasive plant and insect species. Exotic plants such as Chinese privet (*Ligustrum sinense*, Lour.*)* decrease floral resource availability and pollinator abundance near the forest floor and prevent regeneration of overstory trees (Ulyshen et al., 2010). Meanwhile, introduced bees, e.g., *Osmia taurus* Smith, 1873 and *Osmia cornifrons* Panzer, 1806, pose threats to native pollinators through competition for pollen and nesting resources and disease transmission (Potter and Mach, 2022; LeCroy et al., 2023).

While simplification of overstory tree composition, as commonly seen in planted or disturbed forests, may also have negative implications for pollinators, native tree diversity is beneficial for forest associated bee species (Ulyshen et al., 2023). Traylor et al. (2022) detected a positive correlation between bee diversity and flowering tree diversity in southeastern U.S. forests, suggesting that bees require compositionally diverse canopies. Further, many native bee species are detected in greater abundances in canopies dominated by insect-pollinated broadleaf species rather than conifer dominated canopies (Traylor et al., 2024). Wind-pollinated tree species such as oaks (*Quercus* spp.) also provide wild bees with invaluable pollen resources, which may be more nutritious than some herbaceous plant pollens (Wood et al., 2021).

Additionally, forest fragmentation from urbanization can increase the amount of edge habitat between developed and forested areas. Haddad et al. (2015) found that 70% of global forests lie within 1 km of an edge. Increased edge diminishes the biodiversity in mature forest habitat. However, this edge habitat increases connectivity between open and forested habitat which may be beneficial for bee diversity and abundance (Griffin and Haddad, 2021). Previous work suggests forest edges may increase pollinator network robustness (Ren et al., 2023).

Functional diversity protects habitats from further pollination network dissolution by maintaining resilience (Burkle et al., 2013). Maintaining functional diversity, or functional redundancy, ensures that ecosystem services are preserved by species occupying the same functional role as biodiversity is lost. Functional traits describe the ecological niche an organism occupies. These characteristics describe morphological, physiological, and phenological traits that elucidate an organism's life history and infer its role in the environment (Violle et al., 2007). Wild bees occupy a diverse array of functional guilds encompassing nesting, sociality, diet breadth, size, and seasonality (Fortuin and Gandhi, 2021; Braman et al., 2023).

Estimates from northeastern US suggest that roughly 32% of bee species are forest associated, and an additional 31% of bees are habitat generalists which may use forests in some capacity (Smith et al., 2021). While we do not have estimates of forest-associated species within the southeastern US, recent studies within the same geographical area (Athens-Clarke, Co., Georgia, USA) suggest that forest cover impacts bee diversity at small and large spatial scales (Janvier et al., 2022; Traylor et al., 2022; Braman et al., 2023). We were interested in further determining species and functional diversity at the urban-forest interface. We first determined what bee species and functional groups are present in urban forest fragments. We then assessed local forest structural metrics including tree community, invasive shrub cover, ground cover type, etc. for their effects on wild bee community composition, diversity, and abundance at forest edge and interior. We anticipated local factors to have functional-group specific trends on the bee communities distinct to forest edge and interior.

2 Material and methods

2.1 Study sites

This study took place in the Southeastern United States, a region that was extensively forested prior to colonization by Western European countries. Forest cover was greatly reduced for cotton production in the 1800s before expanding in area following the abandonment of the cotton industry. Currently, forest cover is declining again due to urbanization and development (Miller, 2012). All sites were located in Clarke County, Georgia, within or nearby the city of Athens. Athens is the 5th largest city in the state with a population of over 127,000 people that is expanding at a rate of 0.5% per year. (World Population Review, https://worldpopulationreview.com/us-cities/athens-ga-population). Within the county, eight forested sites were chosen that were at least 1 km from each other to minimize autocorrelation (Osborne et al., 2008; Greenleaf et al., 2007). Forests were hardwood-dominated at all eight locations with common genera including *Quercus*, *Carya*, *Acer*, *Fraxinus*, *Liquidambar*, and *Populus.* There was also a minor pine component at all sites. All eight locations were situated near rivers or streams. Six sites were part of recreational parks or gardens, one site bordered a residential community while the eighth site bordered an organic farm. Sites (Figure 1; Supplementary Table 1) were chosen as typical representatives of mature, regenerated forest remnants typical of the southeastern U.S. piedmont.

All sites consisted of a forest and edge location. Edge traps were placed within 1m of literal edge line demarcation between forested and open adjacent land cover. Since selected sites were small forest

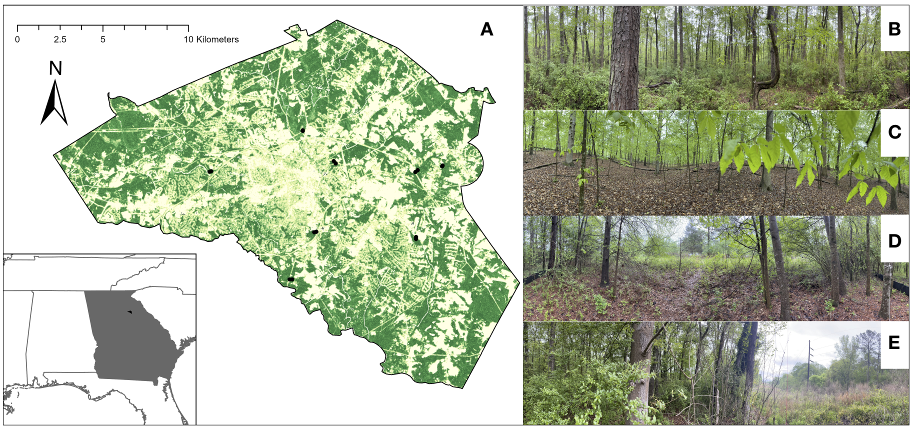

FIGURE 1
Sample sites and locations. **(A)** Forest cover and sampling sites indicated by black dots within Athens-Clarke, Co. USA. Examples of interior locations are shown in **(B)** and **(C)**. Examples of edge locations are shown in **(D)** and **(E)**.

patches, each interior location was chosen at least 100 m from the edge to ensure interior locations were distinct from any edge.

2.2 Passive sampling

Two methods of passive sampling were employed to collect the pollinator community at each forest interior and edge: colored pan traps and blue vane traps. A colored pan trap set consists of blue, white, and yellow colored bowls containing soapy water (Dawn$^{\text{TM}}$ dish soap). Each bowl was placed on a wire stand which held the pan traps approximately 30 cm off the ground. The bowls were oriented in a 3 m transect with a bowl at each meter mark. The bowls were placed in a random color order for 48 hours and collected weekly.

Along with the pan traps, we placed blue vane traps at the exact forest edge and 100 m to interior. Blue vane traps are a type of passive trap that consists of a yellow-painted collection container fitted with a fluorescent blue plastic funnel and vane. The collection container is filled with a preservative to prevent specimen decay. In 2022, we used a saltwater solution (Morton$^{\circledR}$) for the traps; however, we switched to propylene glycol for 2023. Blue vane traps ran continuously with their contents collected weekly. All traps were deployed in late February of 2022 and 2023. Sampling concluded in mid-August both years.

2.3 Bee processing and identification

All samples were stored in 75% ethanol until they could be processed. Bees were separated from the rest of the by-catch, placed in organza bags, and dried in a compact clothes dryer. Once dry, bees were pinned for identification.

Bees were identified to species using a variety of available resources (Discover Life keys; Mitchell, 1960, 1962; Gibbs, 2011; Gibbs et al., 2013). Honeybees (*Apis melifera*) were retained with wild bees for floral resources despite not necessarily being a part of the wild bee community as they are interacting and potentially competing.

Bees were designated to functional guilds. In the present study, we consider the following functional traits of wild bees per (Danforth et al., 2019; Fortuin and Gandhi, 2021; Braman et al., 2023; Brasil et al., 2023).

1. Nesting: Nesting substrate is separated into cavity, litter, softwood, soil, and occupied. Cavity nests are built in pithy stems and dead wood. Litter nests are built in leaf litter, grass, the organic layer above soil, or vacated rodent dens. Softwood nests are built in wood that has been heavily decayed but still holds shape. Occupied nests are not built, but rather, the maternal bee lays her egg in another bee species' nest (kleptoparasitism).
2. Sociality: Wild bee sociality is classified as solitary, communal, eusocial, and kleptoparasitic.
3. Size: Size is divided into 3 groups based on intertegular width (mm): small (<2mm), medium (2.1–3mm), and large (>3mm).
4. Seasonality: Peak flight season can be separated into early (February-April), mid (May-July), and late-season (August-November).
5. Diet breadth: Bees may either be oligolectic (specializing on a single plant species or family) or polylectic (generalists).
6. Origin: Native or exotic to North America (Russo et al., 2021).

2.4 Habitat assessment

Environmental parameters measured are summarized in Table 1. At each location, we established a 0.1 ha circular plot centered around the passive traps (Supplementary Figure 1). Every tree within the plot was identified to species and diameter at breast height (DBH) was measured. Only mature trees with a DBH above

TABLE 1 Summary of measured environmental parameters.

Environmental parameters	
Location	Edge or interior of forest
Canopy cover	Percent overstory coverage
Invasive shrub density	Density of *Ligustrum sinense* and *Elegnus umballata*
Hill indices for total tree community	Species richness, Shannon diversity, and Simpson diversity for trees within a 0.01 ha radius
Median tree diameter	Median diameter of trees within a 0.01 ha radius
Total basal area of tree cover	Area occupied by trunk of trees within a 0.01 ha radius
Hill indices for insect pollinated trees	Species richness, Shannon diversity, and Simpson diversity for trees that require insect pollination within a 0.01 ha radius
Total basal area of insect pollinated trees	Area occupied by trunk of trees that require insect pollination within a 0.01 ha radius
Ground cover (bare ground, leaf litter, dead wood, and vegetation)	Approximate coverage of ground cover types used by various nesting functional guilds

20 cm were considered. Trees were recorded as "insect pollinated" if known to have nectar producing flowers for insect pollinators (as per Traylor et al., 2022). While wind-pollinated trees are visited by bees for pollen, these trees do not require bees for pollination and reproduction (MacIvor et al., 2014; Ollerton, 2021). Tree community included species in the genera *Pinus, Quercus, Nyssa*, Liriodendron*, Prunus*, Liquidambar, Celtis*, Acer*, Ulmus*, Carya*, and *Pyrus** (*denotes insect-pollinated). Median diameter and total basal area were calculated for both total and insect tree community. Canopy cover was measured at each trap using a densiometer and averaged at each location.

Ground cover, downed wood, and invasive shrub cover was assessed along two intersecting 40-m transects centered around the passive traps. At every 10 m, we placed a quadrat and determined dominant ground cover type (leaf litter, wood, bare ground, or vegetation) at the four corners of the quadrat. Leaf litter depth was also measured at every quadrat corner with leaf litter present.

Along the entire length of the transect, we quantified invasive shrub cover and downed wood. For invasive shrub cover, we counted every stem of privet (*Ligustrum sinsense*) and autumn olive (*Elaeagnus umbellata*) above one meter on either side of the transect. We focused on these two species which dominated understory shrub community within our study sites.

Downed wood was quantified by measuring every piece of wood 5 cm in width or greater that intersected the transect. For each piece of wood, we measured total length and diameter of wood, Volume was calculated using the formula for a tapering cylinder. We also determined decay class for each piece of downed wood using the USDA Forest Inventory (United States Department of Agriculture, Forest Service, 2016). Each occurrence of downed wood was ranked on scale of 1 to 5, where 1 indicated the wood was recently downed and 5 indicated nearly decayed.

2.5 Statistical analysis

Statistical analyses were performed in R (R Core Team, 2022). Since sampling occurred with the same timeframe, sites, and passive sampling scheme, we combined 2022 and 2023 data for all analysis.

Tree and bee diversity for each site and location was calculated using Hill numbers as diversity indices (Chao et al., 2014) using the 'hill_taxa' function from the hillR package (Li, 2018). For trees, these calculations were made for all trees as well as for insect pollinated trees. Hill numbers serve as proxies for species richness (q=0), Shannon diversity (q=1), and Simpson diversity (q=2) (Roswell et al., 2021). Hill numbers were calculated for each location at each site using the. Estimated species richness was calculated using the Chao1 estimator using the 'chao1' function of the rareNMtests package (Cayuela and Gotelli, 2022).

Generalized linear mixed effect models (GLMMs) were constructed to test the effects of location and environmental parameters on each of the three Hill numbers (species richness, Shannon diversity, and Simpson diversity), abundance, and Chao1 estimator. The continuous environmental variables were first checked for independence from the categorical location variable. Secondly, they were assessed for multicollinearity using the 'VIF' function from the package car (Fox and Weisberg, 2019). We accepted variables with the VIF threshold less than 5 as a conservative measure. This left tree Shannon diversity, invasive shrub cover, and percent bare ground as our environmental variables. GLMMs were constructed with the 'glmer' function from the lme4 package (Bates et al., 2015). Each GLMM was created with the fixed effects as location, tree Shannon diversity, invasive shrub cover, and percent bare ground, the response variable as one of the Hill numbers, abundance or Chao1 estimator, and site as a random effect. Species richness and abundance were fit to a Poisson distribution, while Shannon diversity, Simpson diversity, and Chao1 estimator were fit to a Gaussian distribution. *Post hoc* tests were performed with the package emmeans (Lenth, 2023).

To describe bee community composition at forest edge and interior, we conducted non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarities of locations with the metaMDS() function from the vegan package. The data was transformed using a Hellinger transformation to reduce the weight of rare and hyperabundant species. This transformation is appropriate for skewed ecological data (Legendre and Gallagher, 2001). A multiple regression using the envfit () function determines correlation of environmental parameters with NMDS axes (Oksanen et al., 2022). Significance of environmental parameters was assessed with 9999 permutations. Permutational analyses of variance (PERMANOVAs) compared Bray-Curtis dissimilarities between sample sites to determine if bee communities differed by forest location (edge vs. interior). PERMANOVAs were performed with the adonis2() function of the vegan package using 10000 permutations. We then performed indicator species analysis using the 'multipatt' function of the *indicspecies* package to determine which species were associated with edge or interior locations (De Cáceres and Legendre, 2009).

To determine how functional groups interplay with community composition and environmental variables a double canonical correspondence analysis (dCCA) was performed following Götzenberger et al. (2021). The dCCA first constrains species data by environmental parameters in a canonical correspondence analysis (CCA) determines how species respond to gradients of environmental variables. This CCA is secondarily constrained by functional traits to show how species respond to their environment based on their traits. First, we constructed a "trait free" CCA using the 'dudi.coa' function from the *ade4* package to assess which environmental variables had the greatest impact on species community (Dray and Dufour, 2007). A permutation-based ANOVA determined which environmental factors were significant. For the dCCA, we secondarily constrained the species CCA from above with the functional traits (origin, diet breadth, nesting, seasonality, and sociality) using the 'dbrda' function written by Kleyer et al. (2012). This produces an ordination where environmental and functional traits are vectors scaled by effect size. A cluster analysis identified optimal species clusters based on functional designations and environmental parameters using the 'hclust' function of the stats package (Murtagh and Legendre, 2014; R Core Team, 2022).

While the CCA and dCCA tell us which environmental variables influence bee diversity, it does not give the direction of the effect. To extrapolate the direction of the effect of environmental parameters on functional trats, the meaningful environmental parameters for significant functional traits were used to generate linear models using the geom_smooth function (method = "lm").

3 Results

During 2022 and 2023, we collected 3,770 individual bees. These bees belong to 122 described species of 28 genera within five families: Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae. Forty-one species were unique to forest edge, 13 species were unique to forest interior and 70 species were found at both locations. The 122 species were placed into functional guilds for nesting, origin, sociality, diet breadth (lecty), sociality and size (Figure 2; Supplementary Table 2). Nesting functional groups describe 30 species as cavity nesting, 6 species as litter nesting, 66 species as soil nesting, and 22 as occupied nesting. Origin describes 4 species as exotic and 122 as native. Sociality describes 21 species as eusocial or primitively eusocial, 71 species as solitary, and 22 species as parasitic. Diet breadth describes 10 species as specialists and 114 as specialists. Size functional groups were divided into 55 species as small, 43 species are medium, and 22 species as large. Seasonality functional groups encompass 67 early-season species, 55 mid-season species, and 4 late-season species.

3.1 Bee abundance and diversity

Bee abundance and diversity responded to location (edge vs. interior) and environmental variables differentially (Table 2). Location had a negative effect on abundance, a marginally negative effect on species richness, but a positive effect on Shannon diversity and Simpson diversity. Tree Shannon diversity had a negative effect on abundance but positive effect on the Chao 1 estimator. Invasive shrub cover had a marginally positive effect on abundance, but a marginally negative effect on Shannon diversity. Bare ground was positively associated with species richness and Chao1 estimator, but a marginally negative effect on Simpson diversity.

3.2 Bee community composition

NMDS ordination visually identified distinct community composition at forest edge and interior (Figure 3). The multiple regression of environmental variables with NMDS axes revealed significant interactions with the following variables and NMDS axes: location (r^2 = 0.4153, p=0.041), tree Simpson diversity (r^2 = 0.4058, p= 0.033), insect pollinated tree species richness (r^2 = 0.4058, p=0.033), canopy cover(r^2 = 0.4813, p=0.009), and percent bare ground (r^2 = 0.5408, p=0.007); see Supplementary Table 3. PERMANOVA confirmed distinct communities at both forested locations (F= 2.0549, p= 0.0107). Indicator species analysis revealed three species associated with edge habitat: *Hoplitis truncata* (Cresson, 1878) (F=0.866, p= 0.007), *Ptilothrix bombiformis* (Cresson, 1878) (F=0.858, p= 0.010), and *Bombus pensylvanicus* (DeGreer, 1773) (F=0.828, p= 0.019). No indicator species were solely associated with forest interior.

Canonical correspondence analysis of community composition grouped species by environmental preferences (Supplementary Figure 2). Environmental parameters explained 32.7% of the species diversity (adj R^2 = 0.326586). The greatest predictor of community composition was canopy cover (F= 2.416, p=0.001, df=1). Invasive shrub cover (F= 2.085, p= 0.002, df=1), tree Simpson diversity (F= 2.056, p= 0.003, df=1), location (F= 1.952, p= 0.004, df=1), insect associated tree Shannon diversity (F= 1.674, p= 0.011, df=1), and percent bare ground (F= 1.737, p= 0.017, df=1) also had significant effects on bee community composition.

3.3 Functional diversity

The cluster analysis revealed that the bee community separated into 32 groups when species diversity, functional diversity, and environmental parameters were considered (Supplementary Figure 3). Linear regressions suggest origin, nesting, diet breadth, and sociality all had significant effects on clusters. Origin (p<0.01, F= -0.004117), nesting (p<0.001, F= -0.04928), and sociality (p<0.01, F=-0.023436) had negative effects on clusters in the ordination space. Diet breadth (p<0.01, f=0.006824) had a positive effect within the ordination. Seasonality and size showed no significant effect. The dCCA shows species grouped into the 32 clusters overlayed with vectorized effects of functional traits and environmental parameters (Figure 4).

Linear models of meaningful environmental parameters on significant functional groups indicated by the cluster analysis revealed interactions between canopy cover, invasive shrub cover,

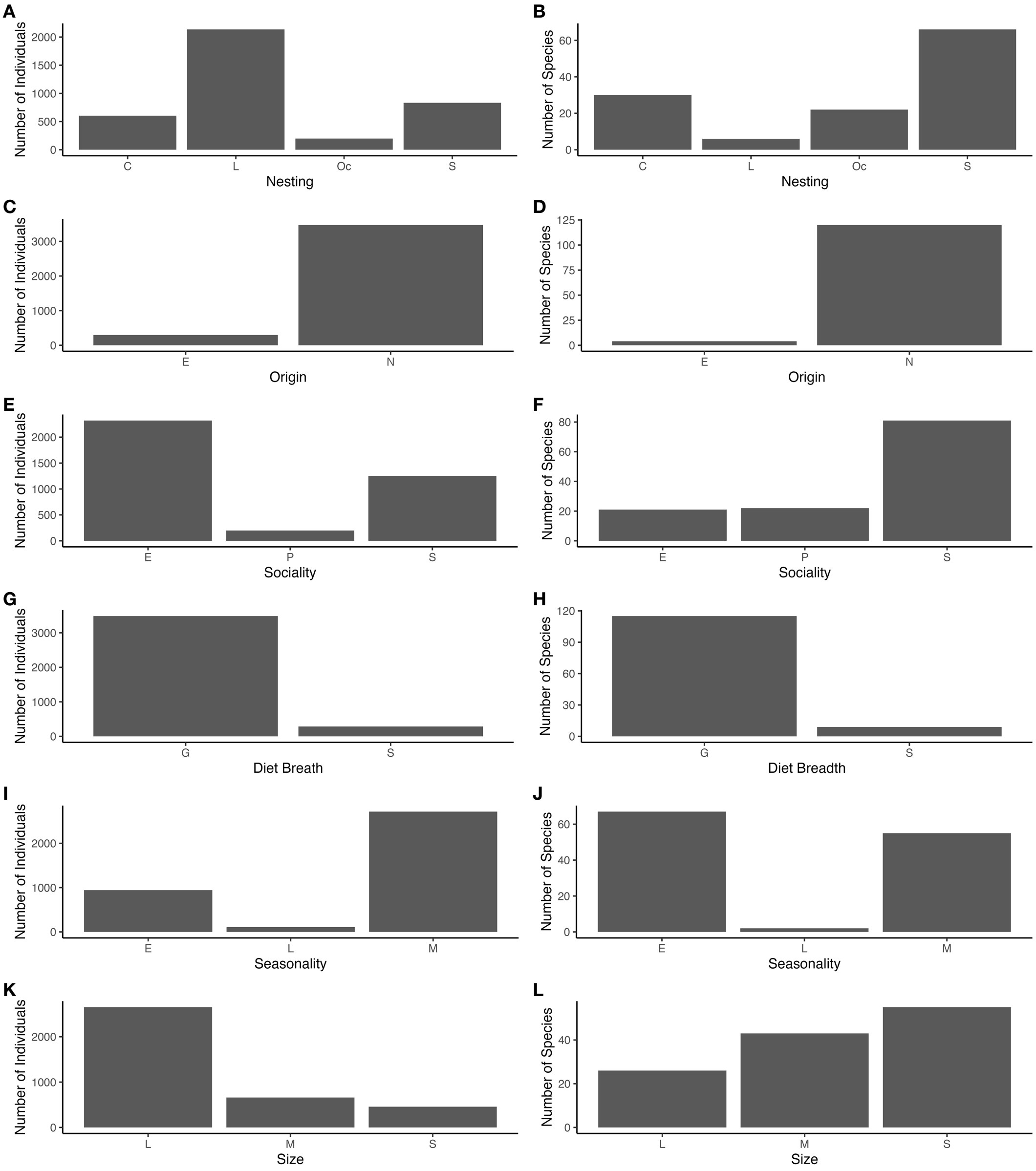

FIGURE 2
Total numbers of individuals **(A, C, E, G, I,** and **K)** and species richness **(B, D, F, H, J** and **L)** collected in the following functional groups: nesting (C=cavity, L=litter, O=occupied, S=soil); origin (E= exotic, N=native); sociality (E=eusocial, P=kleptoparasitic, S=solitary); diet breadth(G=generalist, S=specialist); seasonality (E=early, L=late, M=middle); size (S=small, M=medium, L=large).

Simpson diversity of all trees, Shannon diversity of insect-pollinated trees, and percent bare ground on nesting, origin, sociality, and diet breadth (Supplementary Figures 4-8).

4 Discussion

Here, we determined local drivers of bee community composition and functional diversity in urban forest fragments. Species and functional diversity revealed different insights into the communities at the interior and edge of urban forests. The 122 sampled species represent 22% of the 542 bee species recorded in Georgia (Native Bees of Georgia, https://native-bees-of-georgia.ggc.edu/?page_id=28). We found greater abundance and species richness at forest edge than interior, and bee community composition was distinct between edge and interior locations (Figure 3). This community composition was largely driven by local environmental factors including canopy cover, invasive shrub cover, bare ground, and tree diversity. The bee community in urban forest fragments exhibits a diverse assemblage of functional traits (Figure 2). The functional community response to local environmental factors was largely influenced by origin, nesting, diet breadth, and sociality (Figure 4). While most of the species richness can be categorized as small, solitary, early-season, soil-

TABLE 2 Generalized linear mixed effect model coefficient, t value (or z value for abundance and species richness) for each predictor (location, tree Shannon diversity, invasive shrub, and percent bare ground) of bee diversity and abundance.

Response	Predictor	Estimate	S.E.	t value	P value
Abundance*	Intercept	6.61	0.38	17.48	< 0.001 *
	Location	-0.77	0.24	-3.20	0.0014 *
	Tree Shannon diversity	-0.37	0.11	-3.44	< 0.001 *
	Invasive shrub	0.01	0.01	1.94	0.052.
	Percent bare ground	-0.20	1.21	-0.17	0.865
q=0=species richness*	Intercept	3.54	0.20	17.66	< 0.001 *
	Location	-0.17	0.11	-1.66	0.096.
	Tree Shannon diversity	-0.05	0.06	-0.82	0.41
	Invasive shrub	0.002	0.002	1.07	0.284
	Percent bare ground	1.53	0.58	2.62	0.009 *
q=1= Shannon diversity	Intercept	2.52	0.39	6.44	< 0.001 *
	Location	0.41	0.13	3.24	0.001*
	Tree Shannon diversity	0.02	0.11	0.19	0.852
	Invasive shrub	-0.007	0.003	-1.92	0.055.
	Percent bare ground	-0.54	1.03	-0.53	0.598
q=2= Simpson diversity	Intercept	2.04	0.46	4.48	< 0.001 *
	Location	0.51	0.15	3.44	< 0.001 *
	Tree Shannon diversity	0.02	0.13	0.16	0.870
	Invasive shrub	-0.01	0.004	-1.55	0.120
	Percent bare ground	-2.12	1.20	-1.77	0.077.
Chao1 estimator	Intercept	3.39E+00	2.11E-01	16.084	< 0.001 *
	Location	-4.57E-02	1.37E-01	-0.334	0.739
	Tree Shannon diversity	1.53E-01	6.05E-02	2.527	0.012 *
	Invasive shrub	5.78E-05	2.48E-03	0.023	0.981
	Percent bare ground	2.18E+00	5.26E-01	4.148	< 0.001 *

Significant p-values are indicated by the asterisk (*).

nesting, native, generalists, abundance favored large, social, mid-season, litter-nesting, native, generalists. This discrepancy between richness and abundance largely is due to the hyperabundance of *Bombus impatiens* and *Bombus bimaculatus*.

Of the local environmental factors assessed, canopy cover is known to negatively impact bee abundance and richness as light availability is associated with greater diversity (Kilkenny and Galloway, 2008; Williams and Winfree, 2013). Here, canopy cover was found to be multicollinear with leaf litter. We found that more bare ground availability was associated with greater bee abundance and diversity. While over three-fourths of all bee species globally nest in the soil (Antoine and Forrest, 2021), over half of all species sampled in the present study were soil nesting species. Open areas and clearcuts support soil nesting bees (Fortuin and Gandhi, 2021). Ground cover generally has a negative impact on these, as they require open swaths of bare ground for nesting. Development may offer opportunities for exposed ground. However, a recent study indicated that closed canopy forests with frequent disturbance to leaf litter may be beneficial to ground nesting bees (Ulyshen et al., 2023).

While the cavity nesting functional guild was the most second most diverse group, we did not detect dead and downed wood as a predictor of bee community composition. However, deadwood in the canopy may have a greater contribution to nesting resources for cavity nesting bees (Urban-Mead et al., 2021; Milam et al., 2022). Alternatively, neighboring developed, and residential areas provide a plethora of wooden and stone structures such as walls and porches that offer alternative nesting substrates for cavity nesting bees.

Origin of bee species explained some of the relation between functional community and environment. While majority of bees sampled were native, *Osmia taurus* and *Apis mellifera* were the most abundant exotic species. *Peponapis pruinosa, Xenoglossa*

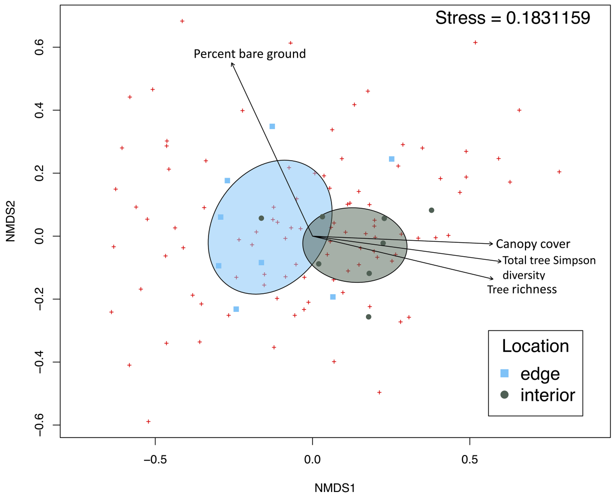

FIGURE 3
Non-metric multidimensional scaling ordination of bee community composition at forest locations. Points representing bee community at each location are plotted based on Bray-Curtis distances. Ellipses show standard deviation from centroid for each location cluster. Vectors show significant environmental parameters with p<0.01from the *envfit()* multiple regression.

strenua, and *Megachile sculpturalis* were also documented within the present study. *Osmia taurus* is native to east Asia and was first documented in Georgia between 2018 and 2020 (Gutierrez et al., 2023). This species is suspected to directly compete with and spread disease into native *Osmia* populations (LeCroy et al., 2023). We detected a slight positive association between invasive shrub cover and exotic bee abundance in the present study. This is consistent with a 2022 study that found more exotic than native bees on exotic woody shrubs in an urban setting (Potter and Mach, 2022). Previous studies suggest that nonnative shrub cover decreases bee diversity, particularly at the forest floor (Ulyshen et al., 2020).

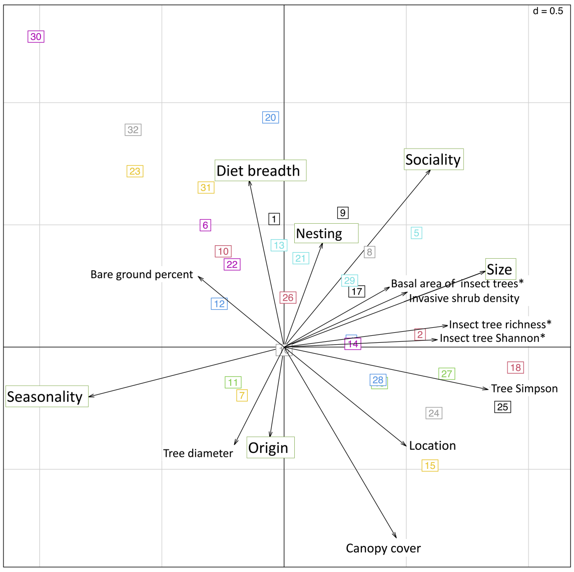

FIGURE 4
Double canonical correspondence analysis shows the relationship between functional trait size, seasonality, nesting, origin, sociality and diet breadth with local habitat parameters. Numbers in boxes depict functional response clusters from hierarchical cluster analysis of bee species responding similarly to environmental parameters.

Kleptoparasitic bees, as indicated by the occupied nesting and parasitic sociality functional guilds, are distinctly recognized as disturbance sensitive taxa that are associated with forested land cover (Sheffield et al., 2013; Harrison et al., 2018). These species tended to be small to medium in size; often emerging early (Supplementary Table 2). The highest kleptoparasite diversity captured lies within the genus *Nomada.* We also documented kleptoparasites in the genera *Malecta, Holcopasites, Sphecodes*, and *Heriades* in urban forests. While kleptoparisitc bees do not provision their own nests with pollen, they still rely on flowers for nectar and thus remain pollinators. Bees that fit into the occupied nesting functional group are more abundant in managed hardwood; compared to pine and clearcut stands (Fortuin and Gandhi, 2021). However, the presence of these bees depends on the presence of host species and whether they are cavity or soil nesting taxa. Due to their dependence on other bee taxa and sensitivity to disturbance, it has been proposed that kleptoparasites could be used a indicators of bee community health (Sheffield et al., 2013; Odanaka and Rehan, 2019). However, hosts species of these kleptoparasites are poorly understood. Future studies should focus efforts to further understand life history of kleptoparisitic species.

We did not find a significant relationship with bee community composition and size or seasonality. Several studies have found no difference in body size between forest types or with development (Fortuin and Gandhi, 2021; Braman et al., 2023). In a 2020 meta-analysis of functional traits in urban areas, body size again offered mix results where 8 studies found a positive relationship while others had none (Buchholz and Egerer, 2020).

Our finding of no relationship with seasonality and functional diversity groupings is unusual as previous studies suggest that forests are particularly beneficial for early season bees (Harrison et al., 2018; Urban-Mead et al., 2021). It is plausible that the abundance of mid-season bees (e.g. *Bombus* spp.) obscured the relationship between seasonality and habitat parameters. However, the lack of a relationship between seasonality and the observed bee community may also suggest that forest fragments support bees across seasons. While floral resources at the forest interior proliferate in spring with overstory tree bloom (Schemske et al., 1978; Heinrich, 1976), forests also provide non-floral resources including nesting materials for a bees across nesting functional guilds, honeydews for non-floral sugar sources, resins for nest building, and the physical structure of the forests can buffer bees from weather and climate change (Ulyshen et al., 2023).

The indicator species analysis revealed three species associated with forest edge: *Hoplitis truncata, Ptilothrix bombiformis*, and *Bombus pensylvanicus*. *H. truncata* is a small bee in the Megachilid family. While literature documents little on this species' natural history, this bee is active early in the season and presumably builds nests in cavities or pithy stems as is common for species within the Megachilidae family. *H. truncata* likely formed the association with forest edges which provides abundant natural stems for the bees to create their nests. *P. bombifomis* is a large, mid-season, mallow specialist. These bees build turret-style nests from exposed mud and water (Rust, 1980). Their edge association is likely attributed to their diet breadth and nesting biology where both the flowers on which they specialize, and nesting substrates are found at edge into open areas. *B. pensylvanicus* is a large, generalist, social bee. *B. pensylvanicus* is an open area associated species, as they nest in grass and vacant rodent dens. The IUCN Redlist considers *B. pensylvanicus* as a vulnerable species (Hatfield et al., 2015). These three species can serve as a benchmark for future studies monitoring value of urban forest fragments.

These findings add to the growing body of literature suggesting that forest cover benefits bee diversity. The local environment created by forested ecosystems favors a variety of floral resources and nesting substrates (soil, leaf litter, cavities) that support wild bees within a variety of functional guilds. It is important to consider the interactions of different bees with varied functional traits and their environment when managing forest fragments to support diverse bee communities. Management should focus on augmenting forage and nesting resources. Diverse tree canopies provide pollen and nectar resources for early season bees (Urban-Mead et al., 2023; Wood et al., 2021). Insect-pollinated genera including *Acer, Prunus, Liriodendron* and wind-pollinated *Quercus* prove to be valuable pollen and nectar sources. Tree diversity further creates nesting opportunities, where tree roots create gaps of exposed soil for ground nesting species, and leaf litter provides materials for litter dwelling species. Fallen tree root balls expose bare ground, as well, and subsequently provide substrates for cavity nesting bees as the tree decomposes. While invasive plants may offer floral resources for native pollinators, their removal has been shown to bolster pollinator communities by increasing native flora while offering nesting opportunities in bare ground, leaf litter, or dead wood cavities (Ulyshen et al., 2020).

In habitats already fragmented by urbanization, further loss has negative effects on bee abundance and diversity (Winfree et al., 2009). While mature hardwood forests support a functionally diverse assemblage of wild bees (Fortuin and Gandhi, 2021), urban development provides unique avenues for pollinator conservation (Braman and Griffin, 2022). Protecting forest fragments amidst development ensures retention of functional diversity of wild bees. While recent pollinator monitoring has focused efforts on maintaining trees for bees, many gaps remain on what tree community structure and extent of forest is necessary for bee conservation. Undoubtedly, continued deforestation and landscape simplification may extirpate forest-associated species from their native landscapes.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

ME: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. MU: Conceptualization, Data curation, Supervision, Writing – review & editing. SB: Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1389619/full#supplementary-material

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Characterization of the bee community and pollination network in a southeastern U.S. pine savanna

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Although the fire-maintained pine savannas of the southeastern U.S. Coastal Plain are recognized for their plant diversity, pollinators associated with these ecosystems remain comparatively understudied. Here we present the results from a season-long effort to record bee-flower interactions at a single site in Florida. We collected 93 bee species (out of an estimated 117) from 79 flower species, with a total of 446 unique interactions. Bee richness and the number of interactions exhibited a bimodal pattern, dipping in mid-summer before an estimated peak in October. The most important floral resources changed throughout the season as did the composition of bees, with the spring and fall periods being particularly distinct. We found that pollen specialists (that collect pollen from a single family of plants) and pollen generalists accounted for a similar proportion of bee species over the entire season. However, pollen generalists outnumbered pollen specialists in the spring and summer before reversing in the fall. Pollen specialists visited significantly fewer plant species and families than pollen generalists and many were collected exclusively from their host family. This was particularly the case for aster specialists active only during the fall. We estimate that between 18.3-25.8% of the local bee fauna depends directly on the overstory trees for nesting habitat including dead wood and resin. Two management recommendations can be made based on these results. First, because fall is the period of peak floral abundance and bee richness, including many late-season aster specialists, it is probably the least favorable time for prescribed fire. Second, considering that a significant proportion of native bees depend on dead wood for nesting, it is important to retain standing dead trees and fallen wood whenever possible.

KEYWORDS

Apoidea, flower visitors, fire-adapted, forest-dependent, saproxylic, shortleaf pine

Introduction

The pine savannas of the southeastern U.S. support an outstanding diversity of endemic species. These ecosystems are highly fire-adapted, requiring a return interval of about two years to maintain pine dominance, open stand conditions, and diverse understory vegetation. Pine savanna ecosystems, dominated by longleaf pine (*Pinus palustris* Mill.) with smaller components of shortleaf pine (*P. echinata* Mill.), slash pine (*P. elliottii* Engelm.), and other fire-tolerant tree species, came to dominate the southeastern Coastal Plain 7500-5000 ybp in response to a warming climate, frequent lightning ignitions from convective thunderstorms, and anthropogenic burning (Van Lear et al., 2005). Whereas pine savanna ecosystems covered 370,000 km^2 within this region prior to colonization by western European countries, they currently occupy a small fraction of their historical range (Frost, 2006) and many remain degraded from a history of agriculture and other soil disturbance, fire exclusion, logging, or invasion by exotic or off-site species. Ongoing efforts to preserve and restore native pine savannas are critical for conserving such iconic and vulnerable species as the red cockaded woodpecker, gopher tortoise, venus flytrap, and many others.

Southeastern pine savannas are recognized for their understory plant diversity which can reach up to 40 species per m^2 and include many endemic taxa (Peet and Allard, 1993; Walker, 1993). Roughly three quarters of plant species in these systems are pollinated by insects (Folkerts et al., 1993). Pollinator communities of Coastal Plain savannas are distinct from those of other southeastern ecoregions (Ulyshen et al., in press) and have been the focus of numerous studies, ranging from the creation of species checklists (Bartholomew et al., 2006), efforts to better understand the life histories of focal species, comparisons among land use histories (Ulyshen et al., 2020; Dixon et al., 2022), and investigations into the effects of management activities (e.g., prescribed fire, thinning) (Breland, 2015; Moylett et al., 2019; Odanaka et al., 2020; Ulyshen et al., 2021, 2022). However, even some of the most basic questions about these communities remain unanswered. For example, although several studies have recorded pollinators visiting particular species of flowers (Deyrup and Menges, 1997; Hamon et al., 2018), efforts to document entire pollination networks are lacking. Similarly, the specific resource requirements of species comprising pollinator assemblages remain largely unestablished. Such basic descriptive information is of critical importance to fully understanding the nature of these communities and how best to conserve them.

Two topics concerning pollinator resource requirements are of particular relevance to managers. The first involves the diet breadth of bees. While Folkerts et al. (1993) suggested most bees associated with the longleaf pine ecosystem visit a wide range of floral hosts for either nectar or pollen (termed polytropic), the proportion of bees that specifically collect pollen from many vs. few hosts (polylectic vs. oligolectic, see Robertson, 1925) remains unknown. Observations of floral visitation alone may overestimate polylecty as some bees are known to visit more species for nectar than for pollen (Pekkarinen, 1997). Many bees are adapted to the pollen of particular plant lineages and cannot develop on pollen from unrelated plants (Praz et al., 2008). Efforts to estimate pollen specialization are challenged by the fact that sufficient data to make such designations are available for less than 5% of bee species globally (Wood et al., 2023). However, the North American fauna is better understood and predictive models that take into account flower visitation, occurrence, and phylogenetic data show promise (Smith et al., 2024). Because pollen specialists are inherently more sensitive to any alteration in resource availability, efforts to identify such species, and to understand which plant species they require and at what time of year, can be beneficial to managers. For example, pollinator species may be more sensitive to prescribed fire at certain times of year if it results in a phenological mismatch between when they are active and when their preferred floral resource is available.

The second topic of particular importance to mangers concerns utilization of tree-derived resources by bees. A large fraction of bees found in broadleaf forests are likely forest dependent (Smith et al., 2021), meaning they require a resource restricted to forests at some point during their life cycle. Such resources can include the nectar or pollen produced by broadleaf trees or dead wood used by many species for nesting. There is growing evidence that eastern deciduous forests of the U.S. provide important floral resources to bees in the canopy (Urban-Mead et al., 2021, 2023), and recent work from southeastern forests suggests that forest bee diversity increases as the diversity of flowering trees increases (Traylor et al., 2024). By contrast, forest bee diversity within the Piedmont has been shown to decrease as the amount of pine in the surrounding landscape or as a proportion of local basal area increases (Traylor et al., 2024; Ulyshen et al., in press). Such patterns raise questions about the value of pine trees to bee assemblages. Although pines probably do not provide useful floral resources to these insects (Pernal and Currie, 2000), they do provide nesting resources in the form of dead wood and resin. However, no previous effort has been made to estimate what proportion of the bee fauna in pine savannas depend on tree-derived nesting resources.

Here we characterize the bee community and pollination network (i.e., bee-flower interactions) based on direct sampling from flowers throughout the growing season in a native pine savanna in Florida. We aim to 1) identify which plant species support the greatest diversity of bees and how this varies throughout the year, 2) determine what proportion of native bee species are pollen specialists vs. generalists and how consistent observed floral visits are with pollen specialization, 3) document seasonal changes in pollinator networks, including changes in bee species richness, the number of interactions between bees and flowers, and the relative species richness of pollen specialists and generalists, and 4) estimate what proportion of bee species requires tree-derived resources for nesting.

Methods

Study area

The study area and sampling methods used in this study are described in Ulyshen et al. (2023). Briefly, we worked in an area of pine savanna measuring less than half a square kilometer on Tall Timbers Research Station in Leon County, Florida (Supplementary

Figure S1). The site has no known history of plowing or other agricultural disturbance. The site has high plant species richness, with an average of 75 species per 100 m^2 (KR and CD unpublished data). The open savanna-like conditions have been maintained by biennial prescribed fire since 1990 when the research station first acquired the property. Although the overstory trees consisted primarily of mature shortleaf pine (*Pinus echinata*), bee sampling mostly took place within eight 0.4 ha blocks where longleaf pine was planted in the 1990s and is mixed with shortleaf pine in the canopy. In 2019 each block was subdivided into four 0.1 ha square plots that had been randomly assigned to one of four season of fire treatments: winter (January), spring (March-April), summer (June), or fall (September-October). Although testing the effects of season of fire on bee communities was the original purpose of our sampling, the resulting dataset offers a special opportunity to study the pollinator network in a southeastern U.S. pine savanna.

Sampling

As detailed in Ulyshen et al. (2023), two collectors followed a standardized protocol to net bees off flowers once a month from February to November 2022. During this period, prescribed fires were applied to the 0.1 ha plots according to the schedule described above, with winter plots being burned about one month before the study began. Nearly all plants in the community are perennial and rapidly resprout and often flower soon after burning in late winter through summer, so well-developed vegetation was always present in at least three of the four plots within each block. Only specimens judged to be actively foraging for pollen or nectar (based on observed behavior) were collected, and flowers were identified on site or from photographs and field notes. Sampling took place only during favorable weather (sunny or partly cloudy skies) between the hours of 9:30 am to 5:30 pm. Each collector spent 20 min (Feb, Mar, Aug, Oct, and Nov) or 25 min (Apr, May, Jun, Sep) sampling bees in each plot. In July, due to stormy weather, the plots within half the blocks were each sampled for a total of 40 min while the others were sampled for only 30 min. In November, only one collector visited the plots. Finally, some additional opportunistic sampling took place near the plots and we include those data in the current network analysis for completeness. In total, the data presented here resulted from more than 220 person-hours. Sampling took place on the following dates: February 22–24, March 20–21, April 19–29, May 16–18, June 13–15, July 13–14, August 6–10, September 12–15, October 19–21, and November 7–8. Bees were identified to species using published (Mitchell, 1960, 1962; Gibbs, 2011) and online (discoverlife.org) keys as well as an established reference collection. Voucher specimens are deposited in the first author's research collection.

Bee species were classified as pollen specialists (i.e., species that consume pollen from only a single family of plants), generalists, or parasites, based on information from the literature when available. For other species, diet breadth was predicted using a random forest model based on trait, phylogenetic, and visitation data compiled for 682 bee species native to the United States (Smith et al., 2024).

Analysis

All analyses were performed in R (Team, 2022). We pooled data by month to examine seasonal changes in bee-flower networks, including the number of interactions, the number of bee species, and the relative number of pollen specialist and generalist bees. Because our goal was to record the pollination network as completely as possible, data from the opportunistic sampling outside the main study plots were included in this analysis. To adjust for differences in sampling effort among months, we calculated the Chao1 richness estimator using the rareNMtests package (version 1.2) (Cayuela and Gotelli, 2014) for each month separately. We used the same method to estimate the total number of bee species present at our study site after combining data from all months. Chao1 adjusts the observed number of species based on the number of taxa represented by just one or two specimens. We used the bipartite package (version 2.19) to create figures showing interactions between the different bees and flowers for each month separately.

To investigate how bee community composition changed throughout the season, we performed non-metric multidimensional scaling (NMDS) on a Bray-Curtis distance matrix using the vegan package (version 2.6.4) (Oksanen et al., 2007). We only included the data collected from the season of fire plots in this analysis. We grouped data by month pairs (Feb-Mar, Apr-May, Jun-Jul, Aug-Sep, Oct-Nov), and bee abundance data were Hellinger-transformed (i.e., relativized by species maximum) prior to analysis. Then, to determine if any taxa were strongly associated with one or more of the month pairs, we performed indicator species analysis using the multipatt function in the package indicspecies (version 1.7.14) (De Caceres et al., 2016). This test produces values ranging from 0 (no association) to 1 (complete association).

Finally, we used the Wilcoxon ranked sum test to compare the number of hosts visited by pollen specialists and generalists. This test was performed separately for the number of flower species and families visited.

Results

We collected a total of 93 bee species (Supplementary Table S1) from 79 species of flowers (Supplementary Table S2), with a total of 446 unique bee-flower interactions. Based on Chao1, the total bee richness at our study site was estimated to be 117 species with a 95% confidence range of 101-165. We observed a distinct mid-summer dip in the number of bee-flower interactions as well as bee richness, with peaks occurring in April and October (Figure 1). Chao1 estimates of bee richness are generally in agreement with a mid-summer dip and with bee richness reaching a low point in July (Figure 1). The most important floral resources, in terms of the number of visiting bee species, varied from month to month (Table 1, Figures 2–4). In February, for example, most of the collected bee species and individuals came from *Gelsemium sempervirens* (L.) J. St.-Hil. whereas *Baptisia alba* (L.) Vent.

became the most important floral resource by March. Top species in April, May, and June were *Rubus cuneifolius* Pursh, *Tephrosia virginiana* (L.) Pers., and *Callicarpa americana* L., respectively. A variety of floral resources dominated later in the year, but, by October and November, members of Asteraceae (e.g., *Helianthus angustifolius* L., *Chrysopsis mariana* (L.) Elliot, *Pityopsis aspera* (Shuttlw. ex Small) Small) became the most visited flowers. Although the bee species observed visiting flowers of the most plant species also varied throughout the year (Table 1, Figures 2-4), several were commonly among the highest ranked species. For example, *Ceratina* sp. was either the first or second most interactive bee taxon from February through June. Similarly, *Lasioglossum reticulatum* (Robertson) was one of the top three most interactive species for five of the months.

Our NMDS ordination (stress=0.18) revealed distinct seasonal changes in bee composition, with the early spring (Feb-Mar) and fall (Oct-Nov) faunas being particularly distinct (Figure 5). Based on indicator species analysis, 37 bee species were strongly associated with one or more of the month pairs (Supplementary Table S4). Three species were associated with the earliest months (Feb-Mar) (*Eucera dubitata* (Cresson), *Habropoda laboriosa* (Fabricius), and *Osmia sandhouseae* Mitchell), whereas eleven were associated with the fall months (Oct-Nov). These were *Agapostemon splendens* (Lepeletier), *Andrena accepta* Viereck, *Andrena fulvipennis* (Smith), *Bombus bimaculatus* Cresson, *Melissodes boltoniae* Robertson, *M. dentiventris* Smith, *M. druriellus* (Kirby), *Paranthidium jugatorium* (Say), *Pseudopanurgus labrosiformis* Cresson, *P. solidaginus* Robertson, and *P. rugosus* Robertson (Supplementary Table S4). All but three of these fall-associated species are known to be pollen specialists of Asteraceae, and the others were either collected exclusively (*B. bimaculatus* and *P. jugatorium*) or mostly (*A. splendens*) from this family (Supplementary Table S3).

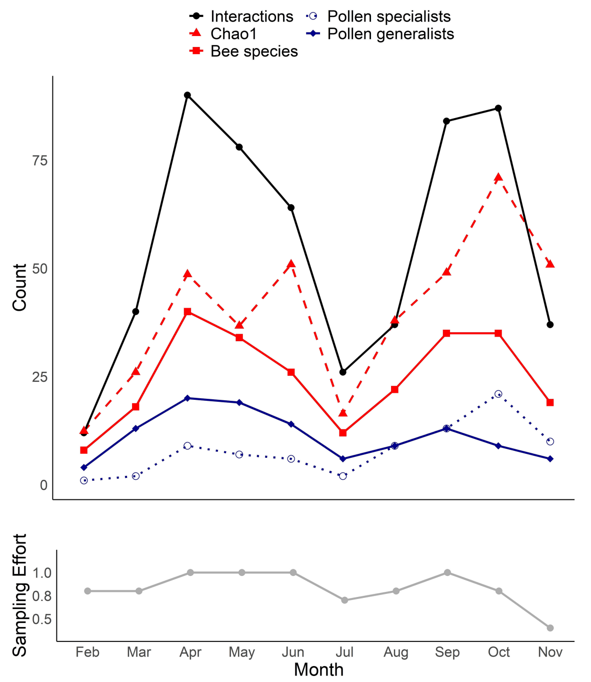

FIGURE 1
Total number of observed bee-flower interactions and the richness of all bees, pollen generalists, and pollen specialists by month. Chao1 estimates of bee richness are also shown. The lower graph shows changes in relative sampling effort over the same period of time.

Based on the literature and model predictions, 38 and 37 of the species collected in this study are pollen specialists and generalists, respectively. Of these classifications, 23 are model predictions. Another six species are parasitic and the remaining 12 species remain unclassified. Among the 25 species with known pollen specialization, 80% are specialists of Asteraceae (Supplementary Table S1). On average, species classified as generalists and specialists visited 6.2 ± 1.3 and 3.0 ± 0.6 species of flowers, respectively, a significant difference based on the Wilcoxon ranked sum test (W=920, p=0.02). The numbers of plant families visited by generalists and specialists were 3.7 ± 0.6 and 1.7 ± 0.2, respectively, also a significant difference (W=1025.5, p<0.001). Of the 50 most frequently captured bee species (represented by at least five specimens), twelve are known to be pollen specialists. Ten of these were captured exclusively from their known host family (Supplementary Table S3). Only one of these specialist species, *Svastra atripes* (Cresson), was captured more often on non-host families. We caught a greater number of pollen generalist species than specialists throughout the spring and much of the summer, but more specialist species were collected than generalists beginning in October (Figure 1).

Nearly three quarters of the sampled bee species nest either within the soil or at the ground surface (Supplementary Table S1). It is not possible to determine exactly how many species depend on trees for nesting, but at least 15 species (including a species of *Heriades*, ten species of *Megachile*, two species of *Osmia*, and two species of *Xylocopa*), and perhaps as many as 22, nest in dead wood. Additionally, two species of *Anthidiellum* are known to build nests out of resin collected from trees. Thus, between 18.3-25.8% of the local bee species collected in this study can be considered dependent on overstory trees for nesting.

Discussion

To our knowledge, this study represents the first effort to record species-level interactions between bees and flowers over an entire season in a southeastern pine savanna. We recorded 93 bee species (out of an estimated total of 117 species) within a sampling area measuring no more than half a square kilometer, showing that such savannas can support a high diversity of bees. Our observations likely represent only a small fraction of the bee-flower interactions that occur at our small study site (Chacoff et al., 2012), and network interactions are likely to vary considerably from year to year. For example, researchers previously reported that even species that appear to be restricted to a single host one year can function more like generalists over larger periods of time (Petanidou et al., 2008). Such findings suggest that many bees respond opportunistically to available resources and, as a consequence, pollinator networks may be less sensitive to disturbances than

TABLE 1 Top three most interactive bee and plant species by month with the total number of partner species (and total number of observations).

	Bees		Plants	
Feb	*Ceratina* sp.	3 (5)	*Gelsemium sempervirens* (L.) J. St.-Hil.	6 (43)
	Bombus impatiens Cresson	2 (2)	*Oxalis dillenii* Jacq.	4 (4)
	Lasioglossum reticulatum (Robertson)	2 (10)	*Crocanthemum carolinianum* (Walter) Spach.	1 (1)
			Pityopsis aspera (Shuttlw. ex Small) Small	1 (1)
Mar	*Ceratina* sp.	6 (8)	*Baptisia alba* (L.) Vent.	12 (179)
	Lasioglossum reticulatum (Robertson)	4 (9)	*Vaccinium virgatum* Aiton	7 (36)
	Augochloropsis metallica (Fabricius)	3 (11)	*Oxalis dillenii* Jacq.	5 (8)
	Bombus impatiens Cresson	3 (12)		
	Eucera dubitata (Cresson)	3 (126)		
	Osmia inspergens Lovell and Cockerell	3 (3)		
Apr	*Augochloropsis metallica* (Fabricius)	8 (24)	*Rubus cuneifolius* Pursh	22 (103)
	Ceratina sp.	8 (28)	*Tephrosia virginiana* (L.) Pers.	13 (42)
	Augochloropsis sumptuosa (Smith)	5 (17)	*Baptisia alba* (L.) Vent.	11 (18)
May	*Ceratina* sp.	7 (11)	*Tephrosia virginiana* (L.) Pers.	16 (111)
	Lasioglossum pectorale (Smith)	6 (9)	*Mimosa quadrivalvis* L.	12 (60)
	Megachile petulans Cresson	6 (38)	*Polygala polygama* Walter	8 (17)
Jun	*Ceratina* sp.	9 (21)	*Callicarpa americana* L.	9 (75)
	Augochloropsis metallica (Fabricius)	6 (51)	*Stylisma patens* (Desr.) Myint	8 (21)
	Halictus poeyi/ligatus	5 (28)	*Silphium asteriscus* L.	7 (26)
	Megachile petulans Cresson	5 (5)		
Jul	*Lasioglossum reticulatum* (Robertson)	5 (8)	*Silphium asteriscus* L.	8 (12)
	Megachile mendica Cresson	4 (6)	*Vernonia angustifolia* Michx.	5 (12)
	Halictus poeyi/ligatus	2 (3)	*Solidago altissima* L.	3 (7)
	Lasioglossum apopkense (Robertson)	2 (2)		
	Lasioglossum weemsi/leviense	2 (6)		
	Megachile georgica Cresson	2 (4)		
	Megachile petulans Cresson	2 (7)		
	Megachile texana Cresson	2 (4)		
	Melitoma taurea (Say)	2 (4)		
Aug	*Lasioglossum reticulatum* (Robertson)	4 (45)	*Rhus copallinum* L.	9 (106)
	Augochloropsis metallica (Fabricius)	3 (48)	*Chamaecrista fasciculata* (Michx.) Greene	3 (3)
	Lasioglossum apopkense (Robertson)	3 (11)	*Helianthus hirsutus* Raf.	3 (5)
	Melissodes comptoides Robertson	3 (4)	*Sabatia angularis* (L.) Pursh	3 (3)
			Silphium asteriscus L.	3 (6)
Sep	*Lasioglossum reticulatum* (Robertson)	9 (34)	*Pityopsis aspera* (Shuttlw. ex Small) Small	11 (29)
	Augochloropsis metallica (Fabricius)	8 (54)	*Sericocarpus tortifolius* (Michx.) Nees	11 (27)
	Lasioglossum apopkense (Robertson)	7 (17)	*Solidago arguta* Aiton	10 (36)
Oct	*Augochloropsis metallica* (Fabricius)	10 (41)	*Helianthus angustifolius* L.	21 (149)
	Bombus impatiens Cresson	9 (24)	*Chrysopsis mariana* (L.) Elliot	18 (88)
	Augochloropsis sumptuosa (Smith)	5 (11)	*Pityopsis aspera* (Shuttlw. ex Small) Small	9 (28)
	Bombus bimaculatus Cresson	5 (15)		
Nov	*Augochloropsis metallica* (Fabricius)	5 (14)	*Helianthus angustifolius* L.	11 (37)
	Augochloropsis sumptuosa (Smith)	5 (8)	*Chrysopsis mariana* (L.) Elliot	10 (57)
	Agapostemon splendens (Lepeletier)	4 (10)	*Pityopsis aspera* (Shuttlw. ex Small) Small	8 (17)

Note that more than three species are listed in the case of a tie.

once thought. Given such variability, the networks presented here should be viewed only as snapshots in time from a single location. However, several important insights into southeastern pine bee communities can be gleaned from these observations and are discussed below.

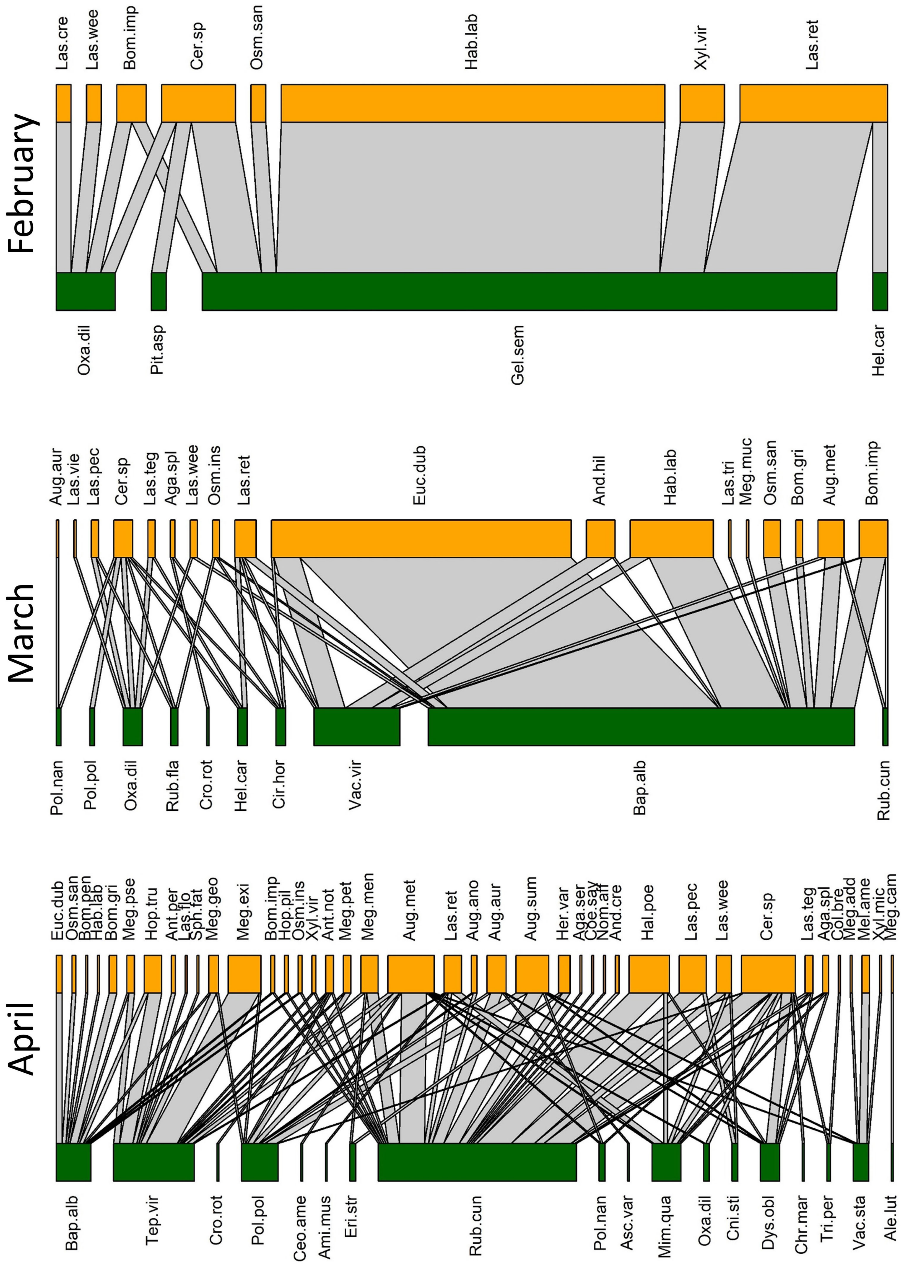

FIGURE 2
Observed pollination networks for February, March, and April 2022. See Supplementary Tables S1, S2 for species abbreviations.

The seasonality of southeastern pine savanna bee communities appears to be more complicated than previously understood, with the number of bee species and network interactions exhibiting peaks in both the spring and fall, with a dip in mid-summer. This bimodal pattern contrasts with the single June peak reported across multiple Coastal Plain forests and savannas by Ulyshen et al. (in press). There are several possible explanations for this discrepancy. First, sampling effort was not consistent across months in the current study and was somewhat lower in July and August than in the months before or after. This may have contributed to the observed mid-summer dip in the number of bee species and interactions (Figure 1). However, it should be noted that this dip was corroborated by our Chao1 richness estimates, which are less sensitive to differences in sampling effort. Another possibility is that our sampling under-represented bee diversity in mid-summer when high temperatures may have acted as a filter on the foraging bee assemblage. Although we did notice a marked reduction in mid-day bee activity on the hottest days in July and August, the fact that the downward trend began in May during milder conditions indicates that weather conditions alone cannot explain these patterns. Differences in sampling method may also have resulted in dissimilar observed seasonality patterns between studies. For example, the study by Ulyshen et al. (in press) involved pan traps which are known to under-sample certain taxa (Cane et al., 2000)

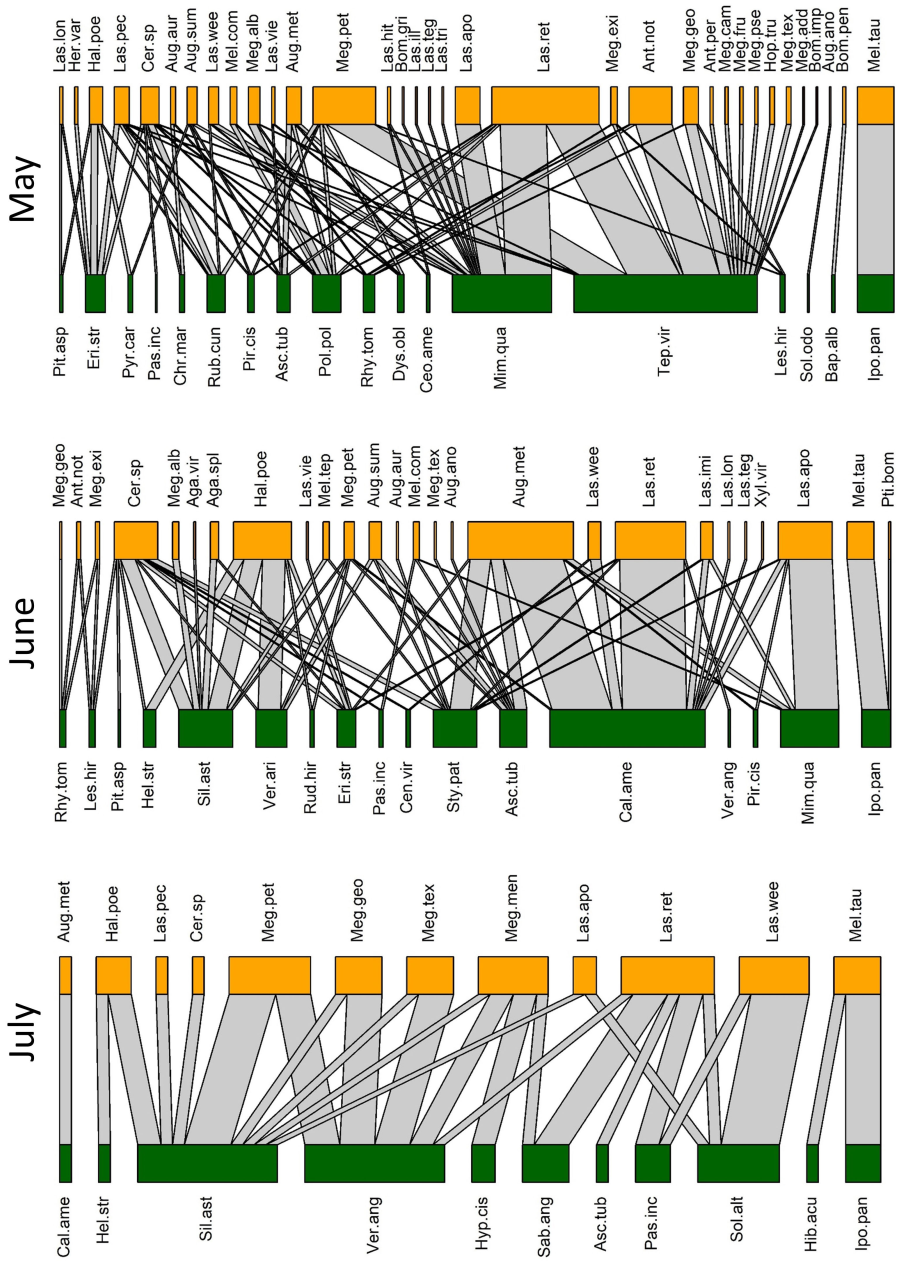

FIGURE 3
Observed pollination networks for May, June, and July 2022. See Supplementary Tables S1, S2 for species abbreviations.

and to be less effective during periods of high floral abundance (Baum and Wallen, 2011). Finally, that previous study did not extend beyond September and thus missed the peak fall blooming period. Whatever the explanation, the fact that October had the highest Chao1 richness estimate of all months, and eleven bee species were strongly associated with October and November, shows that fall is a particularly important time of year for bees in southeastern U.S. pine savannas.

Our findings suggest that pollen specialists may make up a larger proportion of bee species in pine savannas than previously thought (Folkerts et al., 1993). Based on published information as well as model predictions, we found bee species at our study site to be about equally divided between pollen specialists and generalists, with pollen specialists accounting for 50.7% of classified species. Although pollen specialists are known to often visit non-host flowers for nectar, they visited flowers of significantly fewer plant species and families than pollen generalists in the current study. Moreover, 83.3% of the most frequently captured pollen specialists were captured exclusively from their known host family (Supplementary Table S3). Consistent with previous studies (Pelletier and Forrest, 2023), we found the relative number of pollen specialists to increase later in the year. Of the eleven

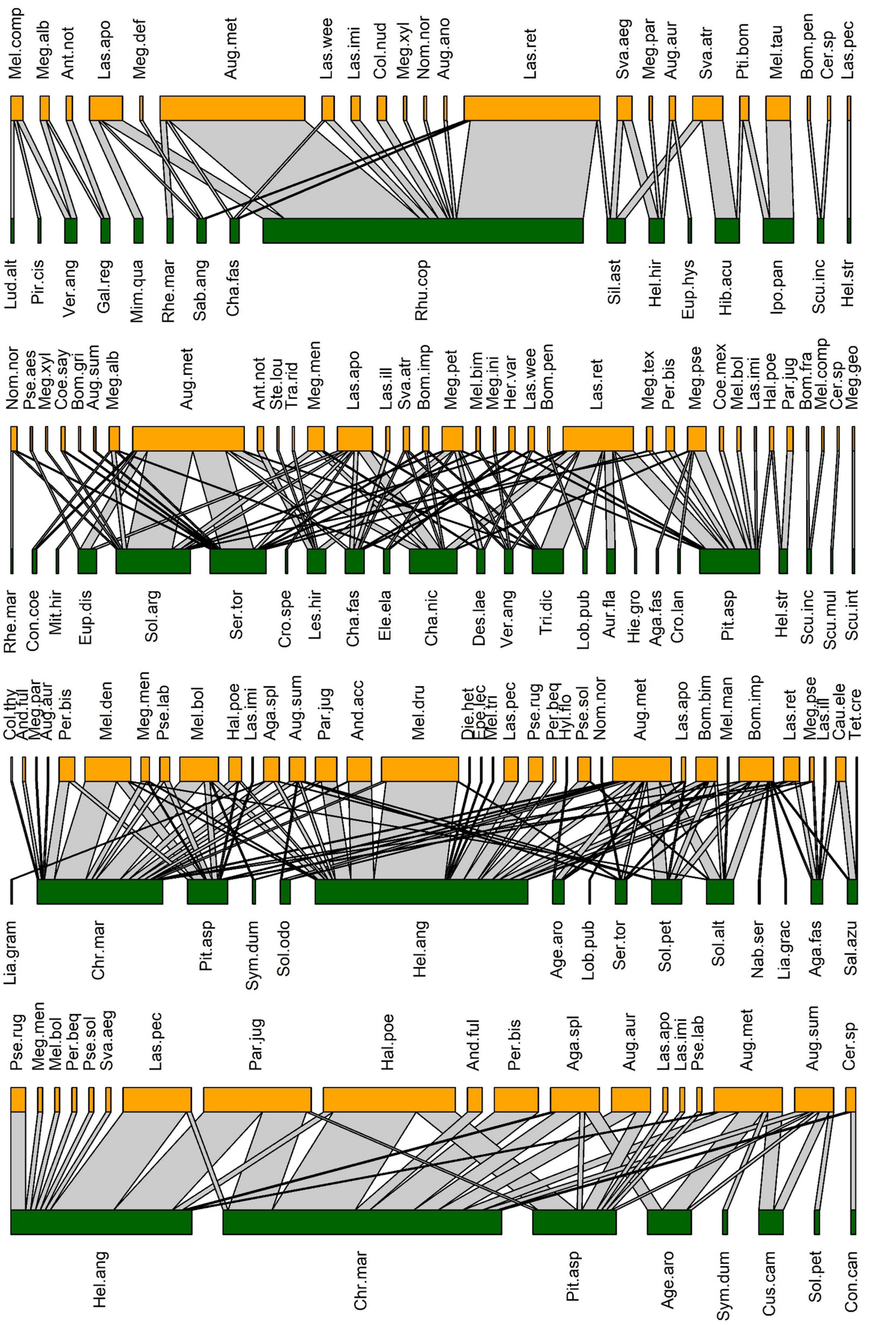

FIGURE 4
Observed pollination networks for August, September, October, and November 2022. See Supplementary Tables S1, S2 for species abbreviations.

species found to be strongly associated with October and November, eight were pollen specialists. All of these species are specialists of Asteraceae, which underscores the key role this family plays in shaping the fall bee community in southeastern U.S. pine savannas.

This study represents the first effort to quantify the importance of the pine overstory to savanna bee assemblages. Although the openness of pine savannas creates an almost grassland-like understory, and floral resources are almost entirely confined to this layer, it is clear from our results that the pine overstory is necessary for a large proportion of savanna bee species. We estimate that 18.3-25.8% of the bee species collected in this study depend on trees for nesting habitat (e.g., cavities in dead wood) or for resin used in nest construction. The upper end of this range is not much below the 32% of forest-associated bees reported from the deciduous forests of the northeastern U.S (Smith et al., 2021). Thus, even though pine trees do not provide floral resources beneficial to bees, they do provide many species with critical nesting resources. While beyond the scope of the current study, another potential benefit of the pine overstory to bees concerns the

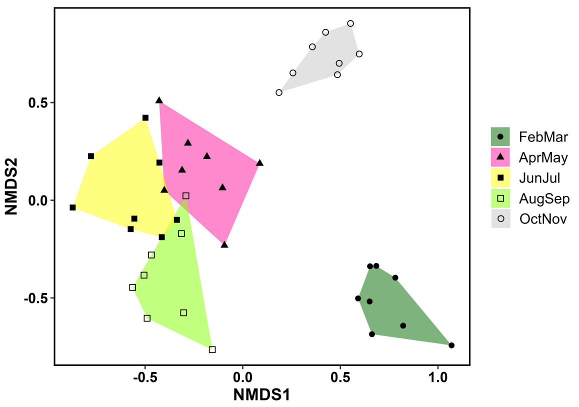

FIGURE 5
NMDS ordination depicting seasonal changes in bee composition.

role pine needles play as fuel for the fires so important to the maintenance of savanna plant diversity (Kirkman et al., 2007). It is probable that broadleaf trees, when present, provide further benefit to bees in this system. For example, the flowers of many broadleaf tree genera (including *Acer*, *Liriodendron*, *Quercus*, etc.) are known to be visited by bees, and bee diversity has been shown to be positively correlated with flowering tree diversity (Traylor et al., 2024). It is likely that riparian forests and other corridors or patches of hardwood trees provide an additional benefit to bees within Coastal Plain landscapes.

The results from this study have important implications for managers. First, it is clear from our results that fall is a particularly important time of year for bees including many late-season Asteraceae specialists. Thus, in terms of impacts on pollinators, fall may be the least favorable time of year for implementing prescribed burns, as suggested by a previous analyses of these data (Ulyshen et al., 2023). Our results also highlight the value of pine trees to savanna bee assemblages. We estimate that as much as one quarter of bee species may depend on trees for nesting purposes. Because most of these nest in dead wood, ensuring an adequate availability of standing and downed woody debris will benefit this fauna.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

MU: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing.KR: Conceptualization, Investigation, Writing – review & editing. SH: Investigation, Writing – review & editing. CD: Investigation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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Distance models reveal biases associated with passive trapping methods for measuring wild bee abundance

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Introduction: There is overwhelming evidence of declines in native bee populations and therefore a need for increased monitoring to track these declines and assist in conservation and restoration efforts. Bees can be sampled non-lethally through visual surveys (e.g., distance transects) or lethally through active (e.g., hand netting) or passive (e.g., traps that lure insects from afar) methods. These lethal methods suffer from imperfect detection that is difficult to account for and can confound inferences about habitat characteristics. Additionally, evidence suggests that lethal sampling methods can even invert habitat quality patterns such that high-quality sites yield fewer individuals and low-quality sites yield more individuals.

Methods: To study potential biases associated with imperfect detection, we used hierarchical density estimation with visual surveys to estimate density of bees within 40 young forest patches across Pennsylvania, USA. We surveyed bee communities non-lethally using visual surveys and lethally using blue-vane traps and bee bowls every two weeks between May and September 2019. We collected data on blooming flowers, vegetation structure, and weather during times of survey.

Results: We found that bee densities estimated from distance transects had a positive relationship with floral resource availability. In contrast, abundance measured via bee bowls and blue-vane traps had no relationship, or sometimes even negative trends with habitat quality, including floral resource availability. Raw bee counts within 2-m of the transect always correlated with modeled densities, showing that some methods do not share the biases of attractive traps.

Discussion: Our study demonstrates that failing to account for imperfect detection can impact the interpretation of pollinator surveys and adds to a growing body of literature that acknowledges the value of distance sampling for insects like bees to better understand species' habitat needs and to monitor populations for conservation.

KEYWORDS

bee, abundance, distance models, trapping methods, bias

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Introduction

Overwhelming evidence of declines in global native bee populations (Cameron et al., 2011; Koh et al., 2016; Jacobson et al., 2018) have spurred calls for biodiversity monitoring efforts to track these declines to inform their conservation and habitat restoration (Tepedino et al., 2015; Brown et al., 2016; Woodard et al., 2020). A critical aspect of bee population monitoring are those efforts that assess abundance and diversity; however, researchers employ a wide range of methods for quantifying abundance which makes direct comparisons across space and time difficult (Portman et al., 2020). Moreover, given that each method varies in its efficacy for producing meaningful data about bee abundance and diversity, there exists strong potential for inefficient use of limited monitoring resources (Tepedino et al., 2015; Tepedino and Portman, 2021). Even as entomologists coalesce around the development of standard monitoring practices (Woodard et al., 2020), there is a growing discourse around the ethics of some common methods (Montero-Castaño et al., 2022; Barrett et al., 2023; Klaus et al., 2024; Lövei & Ferrante, 2024). Thus, for researchers to ethically and effectively monitor the abundance and diversity of native bee populations, the relative value of common survey methods needs to be assessed and carefully weighed.

Among the most popular sampling methodologies used to generate metrics of bee abundance and diversity are: 1. pan traps or "bee bowls" (Wilson et al., 2008; Portman et al., 2020; Prendergast et al., 2020), 2. blue vane traps (BVT: Stephen and Rao, 2007), and 3. visual or netting surveys (Portman et al., 2020; Onufrieva and Onufriev, 2021). However, all three methods have biases and flaws. For example, capture rates from bee bowls can be impacted by the surrounding floral resource abundance at the time of deployment (Baum and Wallen, 2011; O'Connor et al., 2019; Kuhlman et al., 2021; Westerberg et al., 2021). Moreover, bee bowls only capture a small percentage of bees that are attracted to them (~19%; Hudson et al., 2020) and are ineffective at capturing large-bodied bees (Roulston et al., 2007; Joshi et al., 2015). In contrast, BVTs may over-sample insect communities (Gibbs et al., 2017) and unequally sample specific bee taxa (Halictidae and Apidae, Stephen and Rao, 2007; Portman et al., 2020). Furthermore, we know of no studies that have investigated what the area of effect around attractive traps is. Both bee bowls and BVT lure bees from an unknown distance, thus, the area "sampled" is highly ambiguous and may be context specific. Finally, visual or netting surveys are dependent on the skill of the observer (Portman et al., 2020; Onufrieva and Onufriev, 2021) and can introduce uncertainty by not accounting for the very low detection probability of bees (McNeil et al., 2019) which likely favors large-bodied and colorful species (Nielsen et al., 2011).

Detection probability is commonly defined as the probability of detecting an organism given that it is present at a given location (Mackenzie, 2006). Although some species may have detection probability near 1.0, most species exhibit imperfect detection variation in which can be explained by a wide variety of factors (Kellner and Swihart, 2014). For example, poor weather conditions (e.g., cold, rain) may preclude flight/foraging activity for ectotherms like bees (Ward et al., 2014), thus reducing their availability for detection (Gu and Swihart, 2004). Similarly, even when bees are active and available for detection, methodological issues may reduce detection probability including observer inexperience or secretive nature of some bee species (including small body size; Nielsen et al., 2011). However, among the most troubling detection issues facing bee researchers is that habitat characteristics can affect both abundance (i.e., the state variable of interest) and detection probability (MacKenzie et al., 2005; Zipkin et al., 2010). For example, vegetative dense cover may provide quality habitat for some bee species but also reduce observers' capacity to detect that species (McNeil et al., 2019). Thus, assessing habitat associations of wildlife without considering detection probability can lead to inaccurate inferences, which can be detrimental to our understanding of how animals distribute themselves across space and time (as in Mata et al., 2014). Current bee monitoring methods account for detection probability during the design phase but generally fail to consider it in the modeling phase. For example, it is assumed that placing traps or observing bees during optimal weather (e.g., only sample from 10a-5p in "good weather": Ward et al., 2014) is sufficient to overcome any effect of weather on bee behavior but weather parameters are then not included during modeling as covariates. Similarly, any inherent biases of trapping methodologies (e.g., related to floral bloom) and issues observing a very small organism flying quickly by an observer are also ignored.

One method that can account for low detection probability of insects while providing a density estimate is distance sampling (Buckland et al., 2015). Distance models are frequently employed to understand habitat associations and densities of vertebrate communities (Amundson et al., 2014), but recently have been used for bumble bees (*Bombus* spp.; McNeil et al., 2019; Keele et al., 2023) and whole bee communities (Mathis et al., 2021). They work by pairing animal counts with data on detection distances to generate a "detection function" that allows model-based accounts of imperfect detection by modeling the detection (p) and density (λ) processes separately (Buckland et al., 2015; Kéry and Royle, 2015). Importantly, covariates can be added to either component of the model (p or λ, or both) to assess important sources of variation in bee counts on surveys (Kéry and Royle, 2015; McNeil et al., 2019). The comparison of the resulting density estimate to raw counts from visual and trapping methodologies across the floral bloom spectrum can illuminate biases associated with these methods.

Herein, we monitored forested sites to compare density estimates derived from: 1) distance analyses from visual survey data, 2) counts of bees captured in BVTs, and 3) counts of bees captured with bee bowls. Building on the work of McNeil et al. (2019), we use hierarchical distance models (HDMs) to assess the biases of existing methodologies (BVT + bowl + visual) and investigate a known bias of floral resources against attractive traps (i.e., BVT + bowl; Kuhlman et al., 2021). It has been hypothesized that attractive trapping methods may be less effective when floral resources are rich (Joshi et al., 2015; O'Connor et al., 2019; Kuhlman et al., 2021; Westerberg et al., 2021), so we predicted that models fit with each kind of data would yield similar trends but dampened effect sizes for BVT and bee bowl data. We use the results of these analyses to inform bee monitoring methods that may improve conservation efficacy for this imperiled insect group.

Methods

Site selection

Site selection methods are already described by Mathis (2020) and Mathis et al. (2021). Sites were distributed across heavily forested portions of Pennsylvania and separated into three distinct ecoregions based on physiographic regions described by the Pennsylvania Geological Survey (Sevon, 2000): "Pennsylvania Wilds" (PAW), "Poconos" (POC), and "Ridge and Valley" (RV). We surveyed bees and associated vegetation communities on both private and public lands across all three study regions. Private lands consisted of those enrolled in the NRCS: Working Lands for Wildlife Golden-winged Warbler Partnership that aims to create and manage young forests for the golden-winged warbler (*Vermivora chrysoptera*; McNeil et al., 2020; Litvaitis et al., 2021). Golden-winged warblers are an early successional associate that benefits from a diverse forest landscape consisting of recent harvests adjacent to older forests to rear their young (Confer et al., 2020; Fiss et al., 2020). We also surveyed nearby public forest lands managed by the Pennsylvania Game Commission (State Game Lands) or Pennsylvania Department of Conservation and Natural Resources (DCNR; State Forests [SF]). Because native bees are abundant in young forests that regenerate after harvest (Mathis et al., 2021), this system provided an excellent context within which to study bee sampling methods.

In 2019, we monitored 40 timber harvests that experienced overstory removal in the stand initiation stage post-harvest (< 6 years post-harvest; 20 publicly owned, 20 privately owned). Using ArcMap 10.2 (ESRI, 2011), a random point was generated within the boundary for chosen harvests using the Create Random Points tool and a 66-m transect oriented N-S was centered on this point. The center of the sampling transects were at least 80m from the harvest edge to avoid potential edge effects; when this was not possible due to harvest size/geometry, the center of the transect was placed at the geometric center of the harvest. Our point placement protocol was identical to McNeil et al. (2019); McNeil et al. (2020) and additional details can be found therein.

Bee surveys

Bee survey methods were originally published by Mathis et al. (2021). We visited 40 young forest sites every two weeks in 2019 (n = 9 visits; 15 May – 15 September). On each survey, a single observer walked a 66-m North-South transect for 30 minutes counting all bees detected and estimating the perpendicular distance of each bee from the transect upon initial detection (Buckland et al., 2015; McNeil et al., 2019). We categorized bees to 6 morphogroups, but due to insufficient numbers in each group, they are pooled into one dataset for the analyses herein. At the time of each survey, we also recorded the following visit-specific variables that might impact detection probability: wind (Beaufort Wind Index, World Meteorological Organization, 1970), cloud cover (percent), and temperature. We did not conduct surveys in high winds (Beaufort Wind Index > 4), during rain, or when the temperature was< 15 degrees Celsius, as these conditions are not favorable to insect activity (Ward et al., 2014; Dibble et al., 2018) and would severely impact detection probability. In addition to our non-lethal transect surveys, we collected bees using bee bowls and blue-vane traps. All traps had approximately 2cm of water mixed with Dawn$^{\text{TM}}$ Ultra blue dishwashing soap (Procter & Gamble, Cincinnati, Ohio, U.S.) and were collected after 24-h. Because traps were not placed under consistent weather conditions, we used weather data collected from the Weather Underground (www.wunderground.com) to characterize conditions for each trap's active period, including average temperature (C), average humidity (%), average windspeed (mph), average atmospheric pressure, and total accumulated precipitation (cm). Note that we did not use netting in our bee surveys for several reasons. In addition to being explicitly compared to distance sampling by McNeil et al. (2019) already, many of our sites contained thick vegetation including brambles that were likely to damage nets and reduce the likelihood that we could swing nets in a systematic way across our sites. Species-level identifications are published in Mathis et al. (2021) and are available upon request.

Floral survey and vegetation surveys

Immediately following the visual bee surveys, we walked the same 66-m transect to estimate the floral resources available at the time of survey. We recorded all actively blooming flowering stems 1-m on either side of the transect to species and counted or estimated the number of individual flowers per stem within a 66x2m swath of habitat. We also measured structural vegetation at each location, once, in July. Briefly, we collected vegetation data along 3 radial transects (0 degrees, 120 degrees, and 240 degrees) that were 50-m in length. We used an ocular tube (James and Shugart, 1970) to record the presence of various plant strata, where only the strata that were within the "crosshairs" of the ocular tube were considered present. We collected presence data of plant strata every 10 m (for a total of 15 sampling locations per harvest). The vegetation strata included canopy cover, tall (>1m) saplings, short (<1m) shrubs, ferns, forbs, and grass. Distinctions between different vegetation classes were chosen as per McNeil et al. (2019). Full floral species list is available in Mathis et al. (2022) and is available upon request.

Statistical analyses

Prior to statistical analyses, we assessed pairwise correlations among all pairs of explanatory variables to confirm that they were not too highly correlated (Spearman's $\rho \geq 0.70$; Sokal and Rohlf, 1981). Additionally, we scaled all quantitative variables to have a mean of 0 and a standard deviation of 1 using the scale function in program R (R Core Team, 2020). Due to data-skew, we log-transformed floral density prior to analyses. We calculated floral diversity as the effective species unit variation of the Shannon-Weiner Diversity Index (eH'; Jost, 2006).

Hierarchical distance models for density estimation

To model bee distance data, we fit HDMs using the package "unmarked" in R (Fiske and Chandler, 2011; McNeil et al., 2019). These models have several important assumptions. We assume that all individuals are identified correctly (e.g., other insects are not incorrectly identified as bees), are detected at their initial location from the transect with an accurate distance estimated, and that detections are independent (Thomas et al., 2010). We modeled each sampling bout independently of the others (n=9) to investigate if floral characteristics varied within the year. For analysis, distances from the transect were binned into 5 bins: 0–1m, 1–2m, 2–3m, 3–4m, 4–5m. All observations beyond 5m were excluded from analysis (McNeil et al., 2019). We modeled both "site covariates" (characteristics describing the site such as floral abundance and floral diversity, fit to λ) and "survey covariates" (characteristics that varied among visits such as time of observation and wind index, fit to p). Specifically, we modeled the following site covariates: stand age (years since timber harvest), vegetation (% cover metrics), and floral resources (log-transformed floral abundance and diversity) and the following survey covariates: wind index, temperature, cloud cover, time of day, and ordinal date. We selected the key-function (hazard rate, half-normal, uniform, or exponential) and statistical distribution (Poisson or negative binomial) that best fit the data using the methodology explained by Kéry and Royle (2015). For more information on using HDMs for density estimation of insects, see McNeil et al. (2019).

We used a two-step model building protocol: step 1 assessed the most predictive detection covariates and step 2 assessed the most predictive density covariates. In step 1, we created univariate models for each observation covariate while holding λ constant (e.g., "p[wind], λ [.]" or "p[date], λ [.]") and ranked them in descending order of Akaike's Information Criterion adjusted for small sample size (AICc; Burnham and Anderson, 2004). We also ranked a null (intercept-only) detection model ("p[.], λ [.]"). Models were considered biologically meaningful if they had an ΔAICc > 2.00 compared to the null model, and β parameter 95% confidence intervals not overlapping zero. All variables within univariate biologically meaningful models were placed into a multivariate "global" model and backwards stepwise selection was used to determine the model with the lowest AICc value. For step 2, survey covariates within the top model from step 1 were used as covariates on the detection (p) component of all following models. For both steps, we created univariate and multivariate models for each habitat covariate and covariate pairs and applied the same information theoretic approach to assessing models. We ran a goodness-of-fit test using the function fitstats (Kéry and Royle, 2015) on the top candidate model to make sure that the final model was not over-dispersed ($\hat{c}$~1).

Generalized linear models

To investigate how structural vegetation, patch characteristics, and floral resources affected annual pollinator abundance across three methodologies (visual survey within 2-m of transect line, BVT, and bee bowl), we used linear mixed-effects models in R (lme4 package: Bates et al., 2015). To account for non-independence among visits to the same point location, site ID was included as a random effect, and all other variables (floral abundance [natural-log of count], floral diversity [effective species unit: eH': Jost, 2006], stand age [#growing seasons post-harvest], tall (>1m) saplings [% cover], short (<1m) shrubs [% cover], ferns [% cover], grass [% cover]) were treated as fixed effects. Additionally, we used negative binomial generalized linear models in R (glm.nb function: Venables and Ripley, 2002) to assess how associations with floral abundance and floral diversity varied by each sampling bout. For all linear modeling, every possible univariate- and bivariate combination of models was created and compared to a null model. Models were assessed using the same information theoretic approach mentioned above (see Hierarchical Distance Models for Density Estimation).

Results

Bee counts + weather effects on detection probability

We collected 1,253 total bees (n=544 bee bowls; n=709 blue-vane traps). During the 30-minute observational surveys, we observed 1,565 total bees within 2-m on either side of the transect line (considered visual survey "raw counts"), and 2,186 individuals up to 5-m away from the transect line (used in HDMs). Our models indicated that bee detection probability was impacted by all observation covariates (time of day, percent cloud cover, wind speed, temperature, date) at various times across our study. In our HDMs, wind and temperature were significant predictors of detection probability in 22% of all models, with higher wind speeds resulting in fewer bees observed and higher temperatures resulting in more bees observed. Additionally, 22% of models had detection probabilities that were affected by time of survey (positively), cloud cover (negatively), and ordinal date (positively). Bee detection was constant in only one model (sampling bout 4; late June-early July).

Predictions from different methodologies

When bee abundance values from each of our three alternative methods were compared to those derived from HDMs, the 2-m visual transect had the highest similarity to HDM estimates (adjusted R^2 = 0.48; Figure 1). In contrast, both trapping methods yielded bee counts that were very dissimilar to HDM-estimated densities (both adjusted R^2 ~ 0.01; Figure 1). Hierarchical distance models indicated a positive association between "% forb cover" and "% grass cover" and bee density, a result that was shared with the analysis of raw visual transect counts (Table 1). In contrast, while both BVT and bee bowl analyses had a covariate for "% forb cover" competing, they also had "% fern cover" with a positive beta parameter, a result that contradicts previous studies in our focal region (Mathis et al., 2021).

HDMs indicated that bee density was positively associated with both floral abundance and diversity, as commonly observed in many bee communities (Potts et al., 2003; Mallinger et al., 2016; Kuhlman et al., 2021; Table 2). Our analysis of visual transect data

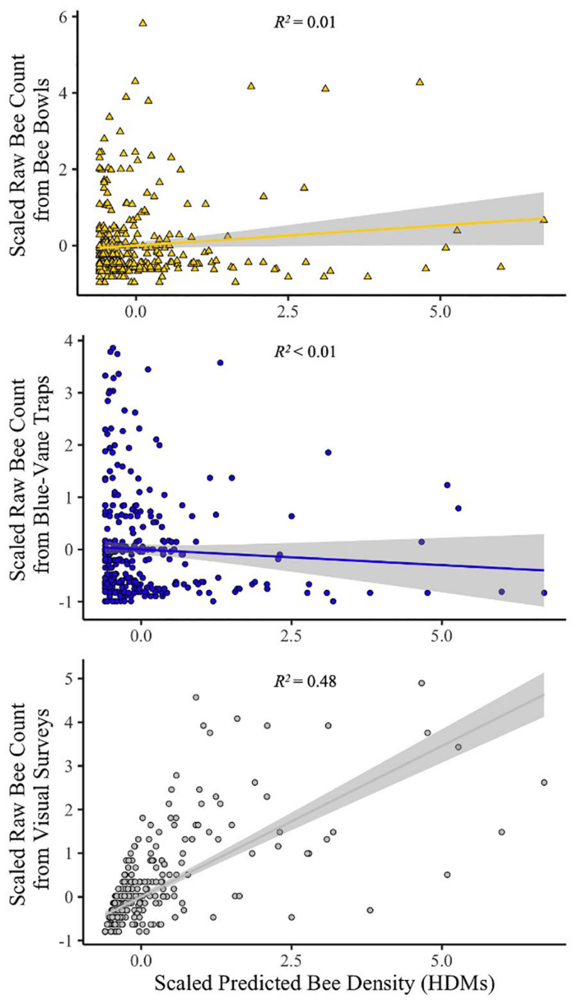


FIGURE 1
Regression lines for raw bee counts against predicted bee densities from HDMs with associated adjusted r-squared values. Gray areas surrounding regression lines are 95% confidence intervals.

aligned with the HDM predictions in that a positive relationship with both floral abundance and diversity was revealed (Table 2). In contrast, both trapping methods predicted a negative association between bee abundance and floral abundance. When we regressed the residuals of the regression lines against estimates of density derived from HDMs (Figure 2), we find that in times of low floral abundance, the trapping methods catch more bees than are observed in visual surveys and predicted in our models. Conversely, in times of high floral abundance, there are fewer bees captured in trapping methods than are observed and predicted in density estimates.

Within-season floral variation

Results from linear mixed-effects models using visual raw counts always aligned with the results of HDMs and exhibit a consistent positive association between bee abundance and floral abundance across the growing season (Figures 1–3). In contrast, models of blue-vane traps and bee bowls only indicated positive associations between floral abundance and bee abundance during the known floral dearth in late June + July (Mathis et al., 2022) and otherwise had no association (Figure 3).

TABLE 1 Results from models for habitat associations between HDMs and linear mixed-effects models for visual surveys, bee bowls, and blue-vane traps.

Model	K	ΔAIC_c	AIC_cWt	Beta (95% CI)
Hierarchical Distance Models				
Forb + Grass	9	0.00	0.42	Forb: 0.181 (0.159)
				Grass: 0.268 (0.165)
Grass	8	2.72	0.11	0.388 (0.125)
Visual Linear Mixed-Effects Models				
Forb + Grass	4	0.00	0.63	Forb: 0.241 (0.157)
				Grass: 0.244 (0.153)
Forb + Fern	4	3.51	0.11	Forb: 0.367 (0.123)
				Fern: −0.156 (0.125)
Bowl Linear Mixed-Effects Models				
Forb + Fern	4	0.00	0.66	Forb: 0.790 (0.171)
				Fern: 0.226 (0.157)
Forb + Short Sapling	4	3.79	0.1	Forb: 0.637 (0.176)
				Short Sapling: 0.162 (0.165)
Blue-Vane Trap Linear Mixed-Effects Models				
Forb + Fern	4	0.00	0.66	Forb: 0.447 (0.147)
				Fern: 0.201 (0.143)
Forb + Canopy	4	3.24	0.13	Forb: 0.368 (0.145)
				Canopy: −0.168 (0.149)

Results shown are the top competing models for each candidate set. K is the number of parameters, Δ AICc is the distance between the top model and the next model (with >2 Δ AICc representing a top model), AICcWt is the weight of the models, and beta parameters for each covariate are provided along with the 95% confidence interval.

Discussion

To our knowledge, our study is the first to critically analyze trapping methodologies commonly used to assess whole-

TABLE 2 Results from models for HDMs and linear mixed-effects models for visual surveys, bee bowls, and blue-vane traps.

Model	K	ΔAIC$_c$	AIC$_c$Wt	Beta (95% CI)
Hierarchical Distance Models				
Floral Abundance + Diversity	9	0.00	0.98	Abundance: 0.583 (0.145)
				Diversity: 0.214 (0.137)
Floral Abundance	8	7.68	0.02	0.724 (0.120)
Visual Linear Mixed-Effects Models				
Floral Abundance + Diversity	4	0.00	1.00	Abundance: 0.490 (0.140)
				Diversity: 0.265 (0.127)
Floral Abundance	3	13.88	0.00	0.668 (0.120)
Bowl Linear Mixed-Effects Models				
Floral Diversity	3	0.00	0.73	0.385 (0.157)
Floral Abundance + Diversity	4	2.04	0.26	Abundance: −0.007 (0.210)
				Diversity: 0.389 (0.194)
Blue-Vane Trap Linear Mixed-Effects Models				
Floral Abundance + Diversity	4	0	0.81	Abundance: −0.218 (0.180)
				Diversity: 0.291 (0.174)
Floral Diversity	3	3.02	0.18	0.184 (0.141)

Models are between bee density (HDMs) or raw bee counts (else) against floral abundance or floral diversity. Results shown are the top competing models for each candidate set. K is the number of parameters, Δ AICc is the distance between the top model and the next model (with >2 Δ AICc representing a top model), AICcWt is the weight of the models, and beta parameters for each covariate are provided along with the 95% confidence interval.

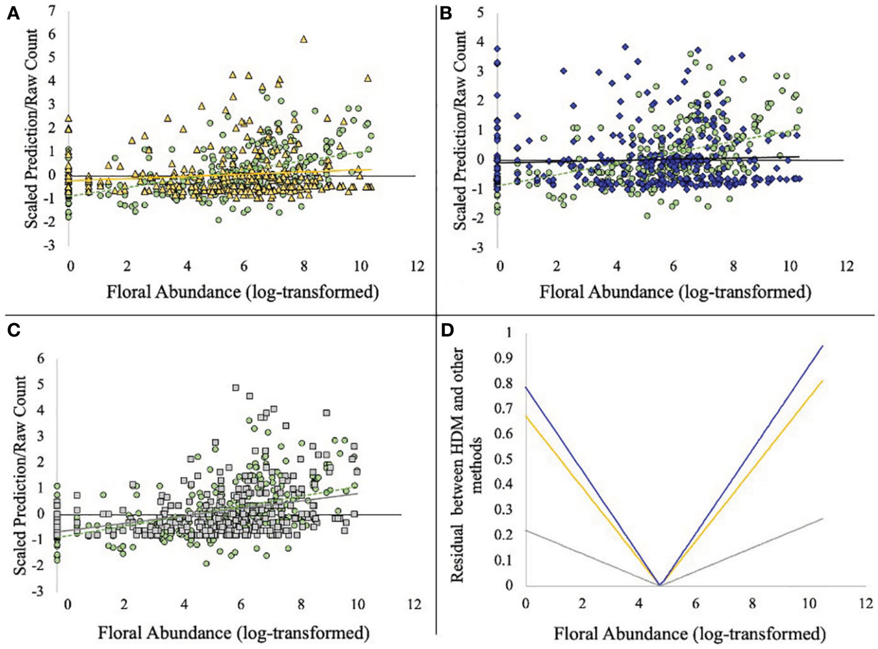
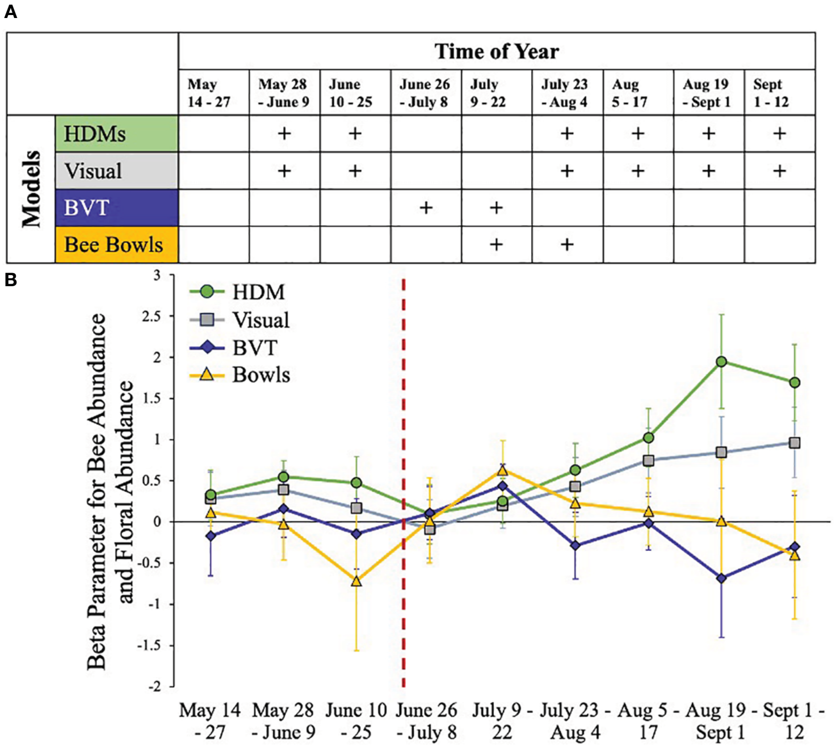


FIGURE 2
The residual between model predictions of bee density or raw counts along the floral abundance spectrum. In **(A–C)**, HDM prediction models are shown as green circles and the dashed regression line. **(A)** (top left): HDM prediction points and raw counts from bee bowls *(yellow triangles)* plotted simultaneously along a gradient of floral abundance (log-transformed). **(B)** (top right): HDM prediction points and raw counts from blue-vane traps *(dark blue diamonds)* plotted simultaneously along a gradient of floral abundance. **(C)** (bottom left): HDM prediction points and raw counts from visual survey *(gray squares)* are plotted simultaneously along a gradient of floral abundance. **(D)** (bottom right): The absolute residual between the regression lines in **(A–C)** when compared to the HDM prediction line, highlighting the magnitude of bias as a factor of floral abundance. Dark blue (top line) represents blue-vane traps; yellow (middle line) represent bee bowls; gray (bottom line) represents visual surveys.



		Time of Year								
		May 14 - 27	May 28 - June 9	June 10 - 25	June 26 - July 8	July 9 - 22	July 23 - Aug 4	Aug 5 - 17	Aug 19 - Sept 1	Sept 1 - 12
Models	HDMs		+	+			+	+	+	+
	Visual		+	+			+	+	+	+
	BVT				+	+				
	Bee Bowls					+	+			

FIGURE 3
Associations between floral abundance and model type across survey methods. Here, we consider HDMs to be a relatively unbiased assessment of habitat associations as they account for detection probability. **(A)** Graphic showing the sign of the associations between floral abundance and model type across the growing season. A plus sign is a positive association and a blank space is no association. **(B)** The beta parameters from the different models across time with standard error bars. The dashed red line indicates when leaf-out occurred on our sites.

community bee abundance against methods that account for imperfect detection (though see Briggs et al., 2022 for group-specific investigations). Given the growing need to develop consistent and rigorous methods for monitoring bee abundance (Tepedino et al., 2015; Brown et al., 2016; Klaus et al., 2024), it is imperative to assess candidate approaches for biases and adjust monitoring efforts accordingly. Our results demonstrate that two of the most frequently used survey methods, blue-vane traps and bee bowls, have critical biases in collection patterns that may make their data unsuitable for many applications. Moreover, the sampling biases, themselves, varied across the growing season such that trapping data provided a reasonable index of bee abundance at some time points (i.e., when floral abundance was “moderate”) but, at other points in the growing season, data were unreliable. Indeed, during times of low floral abundance, indices of bee abundance from trapping were over-inflated, while the reverse was true when floral abundance was high. Past studies have either acknowledged a potential bias (Baum and Wallen, 2011) or begun the work of understanding the biases (Kuhlman et al., 2021). Cane et al., 2000 suggested that flowers are more attractive than are the traps which may explain this pattern: when there are few flowers, traps are more visible and draw in more bees. Taken together, our results support the findings of Kuhlman et al. (2021), who asserted that attractive traps should be used cautiously and in conjunction with other survey methods like visual surveys or netting.

Beyond relationships with floral characteristics, our results suggest that structural vegetation may impact counts of trapped bees in ways that relate more to trap performance or visibility than bee ecology or abundance. Our models indicated that traps were more effective at capturing bees when forb density is high (though not when those forbs are in bloom), and when fern density was high. Previous research has shown that ferns negatively impact bee densities by outcompeting floral resources (Mathis et al., 2021, Mathis et al., 2022) and therefore result in a landscape with few understory flowers. This lack of flowers likely increases the attractiveness of traps (Baum and Wallen, 2011; Kuhlman et al., 2021), which could lead to an erroneous assumption that bees prefer sites with dense fern coverage (Mackenzie, 2006). Thus, while we believe our results support the use of attractive traps to study bee richness or presence/absence, they provide an ineffective – and, at times, misleading – index of bee abundance (Droege et al., 2010; Portman et al., 2020; Kuhlman et al., 2021). Given this, we stress that researchers should critically consider the use of attractive trapping methods (like blue-vane traps and bee bowls) and incorporate non-attractive methods (like visual transects) if density/abundance is of primary interest (as reviewed in Montero-Castaño et al., 2022).

Our results further highlight the value of using distance data to understand bee densities while accounting for detection probabilities within a site. While we used HDMs to investigate the bee community as a whole, these models can also be used for lower taxa (e.g., single genera/groups; Loffland et al., 2017; McNeil et al., 2019) or other arthropod orders (Lepidoptera: Mathis et al., 2021). Whether using HDMs or other statistical models, our results show the importance of accounting for variables that affect detection probability in the modeling stage, such as weather, vegetation density, or distance from observer. Even after only conducting surveys in "optimal weather" (as defined by the Xerces Bee Monitoring Protocol: Ward et al., 2014), we showed that weather was still a significant covariate that impacted detection in most sampling rounds. Finally, we acknowledge that HDMs provide our best approximation of bee density, but it is still not possible to know the true density of bees on a landscape and compare that to number of individuals in the traps. We used HDMs to understand trap biases, but there are promising equations on the horizon that may approximate insect abundance or density to trap catch (Onufrieva and Onufriev, 2021). The authors suggest a universal mathematical relationship that bridges absolute population density and trap catches. This is the first step towards being able to use statistical equations to approximate density from traps, which circumvents the need to account for detection probability. However, this research is still in its nascent stages and needs further testing, so we still believe that accounting for detection probability through modeling frameworks is an important consideration for studies seeking to understand bee abundance.

Future directions

Future studies could investigate the effectiveness of using HDM transects in conjunction with netting to obtain detection-adjusted density estimates (from HDMs) and species richness data (through netting). It is important to emphasize that some studies will still need to use passive trapping methodologies to provide species-level identification (as described in Westphal et al., 2008). One limitation of our sampling schema was the placement of bee bowls on the ground rather than elevating them; ground level traps are likely to under-represent bees that are foraging in the shrub or high forb cover (Cane et al., 2000). An investigation into whether elevating bee bowls to the height of surrounding blooming vegetation could alleviate some of the biases our data show is warranted, though further examination of other trapping methods that are not based on attraction would be more prudent. Future studies could investigate flight-intercept traps (as used in Ulyshen et al., 2010), which do not operate based on luring bees with an attractant but, instead, by intercepting the flight trajectory of flying insects (Hill & Cermak, 1997). A study using flight-intercept traps in conjunction with blue-vane traps and bee bowls could compare their efficacy and determine if captures vary taxonomically and seasonally. Moreover, it would be interesting to compare counts derived from flight-intercept traps to estimates from detection-adjusted methods. Finally, it is worth mentioning that the bycatch obtained when sampling bees with attractive traps (average of 63% of pan trap collections, Gonzalez et al., 2020) often goes unexamined (i.e., is wasted). A further consideration for increased use of trapping methods for bee monitoring would be to collaborate with experts of other taxa to most efficiently use non-target specimens. An investigation into what non-target specimens are captured in common bee trapping methods (blue-vane traps and bee bowls) is warranted.

Conclusion

As bee conservation is becoming a global priority, our need to increase monitoring efforts while assessing the biases of our current monitoring methods is paramount. By using hierarchical distance models, we were able to compare trap captures of bees to modeled densities and highlight the inherent biases of attractive traps. Our results illuminate the inconsistencies of trap efficacy depending on surrounding vegetation characteristics and floral resources, which could lead to erroneous understandings of bee abundance and habitat associations if taken at face value. We recommend that all bee surveys, even if they are conducted in optimal weather conditions, include model covariates of weather values (cloud cover, temperature, precipitation) and surrounding floral resource availability (floral abundance and richness) as proxies for detection probability. We caution against the use of attractive traps as an index for bee abundance and instead suggest alternative methods (netting, visual surveys, non-lethal surveys).

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

CM: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. DM: Conceptualization, Investigation, Methodology, Visualization, Writing – review & editing. MK: Conceptualization, Methodology, Visualization, Writing – review & editing. JL: Funding acquisition, Writing – review & editing. MS: Funding acquisition, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Native bee habitat restoration: key ecological considerations from recent North American literature

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Habitat loss is a primary driver of global biodiversity decline, negatively impacting many species, including native bees. One approach to counteract the consequences of habitat loss is through restoration, which includes the transformation of degraded or damaged habitats to increase biodiversity. In this review, we survey bee habitat restoration literature over the last 14 years to provide insights into how best to promote bee diversity and abundance through the restoration of natural landscapes in North America. We highlight relevant questions and concepts to consider throughout the various stages of habitat restoration projects, categorizing them into pre-, during-, and post-restoration stages. We emphasize the importance of planning species- and site-specific strategies to support bees, including providing floral and non-floral resources and increasing nest site availability. Lastly, we underscore the significance of conducting evaluations and long-term monitoring following restoration efforts. By identifying effective restoration methods, success indicators, and areas for future research, our review presents a comprehensive framework that can guide land managers during this urgent time for bee habitat restoration.

KEYWORDS

bee habitat restoration, pollination services, ground-nesting bees, floral resource availability, native bee monitoring

1 Introduction

Ecological restoration, or habitat restoration, is the process of aiding the recovery of an ecosystem that has suffered degradation, damage, or destruction (Society for Ecological Restoration, 2004) to re-establish native plants and animals. In restoration, it is a common practice to focus on planting native plants, with the assumption that this is sufficient to restore the community and ecosystem (Kimball et al., 2015; Miller et al., 2017; Hamilton et al., 2022), as well as to provide habitat for targeted species in conservation (Hamilton et al., 2022). Generally, it has been shown that there is a positive effect of habitat restoration on bee population abundance and diversity, even if bees are not specifically included in the restoration plan (Heneberg, 2012; Tonietto and Larkin, 2018; Esque et al., 2021). However, by directly targeting the needs of local native bee species, we can ensure that the habitat requirements and floral resources are available for the highest bee diversity possible, including local at-risk species such as specialist bees (bees that forage pollen from one family, genera, or species of plant) (Griffin et al., 2017; Tonietto and Larkin, 2018; Griffin et al., 2021; Bullock et al., 2022). We propose that bee-centric restoration can further enhance bee abundance and diversity, thus increasing plant-pollinator interactions, and supporting the long-term sustainability of both diverse plant and bee species within an ecosystem (Griffin et al., 2017; Tonietto et al., 2017; de Araújo et al., 2018; Fantinato et al., 2018; Tonietto and Larkin, 2018; Cariveau et al., 2020; Griffin et al., 2021; Purvis et al., 2021; Meldrum et al., 2023).

To assemble the literature on bee habitat restoration, we conducted a topical search on Web of Science using the following three keywords: bee, habitat, and restoration. This search captured publications that included all three words in the title, abstract, or list of keywords. We followed this with two additional combinatorial searches, the first using the terms “bee” + “nesting” + “restoration” and the second using the terms “bee” + “floral resource” + “restoration.” We then restricted our literature search to the years from 2010-2024, following the publication of “The Conservation and Restoration of Wild Bees” by Winfree (2010), which addressed the restoration of bee communities. Together, these searches yielded 391 distinct articles. We restricted our review to 125 articles by focusing on North America, as well as by excluding most studies related to agricultural and urban environments, and non-native bees (i.e., honey bees). A few studies were included outside of these criteria (i.e., neonicotinoid exposure to bees) if they were critical to our recommendations for effective restoration practices. Our review does not attempt to prescribe universal solutions for habitat restoration because factors such as the size of the site being restored, the geographical location, and the type of habitat present can significantly influence the execution and objectives of a restoration project. Habitat restoration can range in size from thousands of acres to small-scale projects of less than one acre. While recommendations from this review can be integrated into restoration efforts at any scale, we aim to provide insights that are especially applicable to smaller-scale restoration projects.

The articles we reviewed revealed a number of biases. Out of the 125 articles reviewed, only 22% (28 articles) targeted specific taxonomic or functional groups of bees (e.g., eusocial, solitary). Of these 28 articles, 75% (21) were focused on bumble bees. While the risk of population decline faced by bumble bees is high (Colla et al., 2006, Colla et al., 2012; Mola et al., 2021b), it is important to note that solitary bee species represent 85% of bee diversity globally (Batra, 1984). There was a notable lack of research targeting solitary bees, which was the focus of only 9 of the 28 articles (32%). The remaining articles focused solely on enhancing overall bee diversity and discussed general conservation or restoration strategies applicable to bees and other pollinators. Furthermore, only three of the 125 articles examined were focused on specialist bees. While some studies on specialists have been conducted in Europe (Exeler et al., 2010; Sydenham et al., 2014; Heneberg et al., 2019), there is a distinct lack of research focusing on North American specialists. Finally, the majority of the 125 studies that focused on a particular habitat or region were conducted in grasslands, prairies, and forests, with few studies conducted in desert, alpine, and scrubland environments.

Nearly 90% of angiosperm species rely on insects, especially bees, for pollination (Ollerton et al., 2011; Koh et al., 2016; Almeida et al., 2023). However, continued development, expansion of agricultural monocultures, the spread of invasive plant species, and pollution all pose risks to bee species diversity and abundance (Winfree, 2010; Lázaro and Tur, 2018; LeBuhn and Vargas Luna, 2021; Mola et al., 2021b). Native bee species and their associated host plants are experiencing local extinction and population decline due to human activities (Winfree, 2010; Goulson et al., 2015; Koh et al., 2016; Sánchez-Bayo and Wyckhuys, 2019; Raiol et al., 2021; Lima et al., 2022). Anthropogenic threats (summarized in Table 1) can reduce the quantity and quality of floral resources and suitable nesting habitats, exacerbating the stressors faced by native bees (Goulson et al., 2015; Goulson and Nicholls, 2016; Kline and Joshi, 2020; Olynyk et al., 2021) and highlighting the need for conservation and habitat restoration efforts to protect these species (Winfree, 2010; Drossart and Gérard, 2020; Hanberry et al., 2021).

The majority of bee species in North America are solitary bees, which are non-eusocial and typically build their nests in the ground (Danforth et al., 2019; Antoine and Forrest, 2020). The life history traits of solitary bees differentiate them from eusocial bees; solitary bees are usually smaller and produce fewer offspring per female than eusocial bees (Danforth et al., 2019; Antoine and Forrest, 2020; Lima et al., 2022). Focusing conservation and restoration efforts specifically on solitary bees is especially important as their needs may differ from the needs of eusocial species (Danforth et al., 2019). Currently, conservation initiatives focusing on solitary bees are limited due to a lack of data on their abundance, diversity, and extinction rates (Danforth et al., 2019; Kline and Joshi, 2020; Lehmann and Camp, 2021). Despite a recent increase of studies on solitary bees in restoration (Sydenham et al., 2014; Sexton et al., 2021), continued research is needed to determine the best practices to support these bees in a variety of habitats. Due to the preferential number of studies on bumble bees and limited information for the majority of bee species, implementing and consolidating precise, targeted restoration protocols for most bee species can pose significant challenges.

Our goal is to identify important steps for successful bee habitat restoration (Figure 1) and to demonstrate how the needs of bees can be considered and integrated at every stage. Our recommendations were developed by reviewing the literature using a rubric to identify effective restoration strategies, taking into account the specific habitat type and the focal bee species, including their unique biological traits such as nesting and social behaviors. We aim to promote interest in bee habitat restoration by targeting an interdisciplinary audience. Bee

TABLE 1 The effects of different anthropogenic factors on individual bee performance, bee diversity and abundance, and the plants on which bees rely.

Anthropogenic factor	Individual bee species' performance	Native bee diversity and abundance	Native plants on which bees rely
Invasive Bees	In the Mid-Atlantic US, when exotic species *Osmia taurus* and *Osmia cornifrons* were introduced, all native species showed substantial declines, resulting in a decrease of 76-91% catch rate when sampling (LeCroy et al., 2020).	Honey bee (*Apis mellifera*) presence was negatively associated with wild bee diversity in apple orchards regardless of local management strategies (Weekers et al., 2022).	Andean orchids *Brachystele unilateralis* and *Chloraea virescens* rely on non-native pollinators for reproductive success due to the disappearance of their primary native pollinator *Bombus dahlbomii* (Sanguinetti and Singer, 2014).
Pesticide/ Herbicide Exposure	Glyphosate exposure to wooden trap nests lowered the number of brood cells per nest for *Megachile* sp. in an agroecosystem in Panama (Graffigna et al., 2021).	In tropical agricultural landscapes, pesticide exposure was found to negatively influence bee diversity at the patch scale (100m) while a combination of factors (including pesticides) influenced bee diversity at the landscape scale (500m) (Basu et al., 2016).	A greenhouse study on the effects of a monocot-specific herbicide on non-target native plants in grasslands in northwestern North America found that native dicot species decreased seed production in response to the herbicide (Wagner and Nelson, 2014).
Climate Change	In a manipulation experiment in which heatwave conditions were mimicked, *Bombus impatiens* survival and health (antibacterial immunity) were reduced (Tobin et al., 2024).	The growing number of extreme heat days in North America and Europe are causing local extinction rates to increase and altering species richness for 66 bumble bee species (Soroye et al., 2020).	In a manipulation experiment, wildflowers under experimental warming scenarios decreased floral abundance by 40% and nectar availability by 60% in a Cereal Agroecosystem (Moss and Evans, 2022).
Pests, and Pathogens	In Ontario, Canada pathogen spillover from managed honey bees (*Apis mellifera*) caused increased disease in neighboring bumble bee populations (Colla et al., 2006).	The main cause of death and reduction in population for managed honey bee (*Apis mellifera*) colonies in Ontario, Canada was the pest *Varroa destructor* (Guzmán-Novoa et al., 2010).	Fungal pathogens such as *Ustilago violacea* affect flowering phenology in *Viscaria vulgaris.* The pathogen is transported by pollinators such as bumble bees (Jennersten, 1988).
Habitat Loss	Habitat loss, combined with increased pathogen exposure and climate change, is leading to *Bombus terricola* and *Bombus pensylvanicus* decline in North America (Liczner and Colla, 2020).	Loss of natural habitat reduced long-term population growth rates of *Bombus* sp. and rapid habitat change can have lasting effects on long-term population density (Iles et al., 2018).	In Texas savannahs, habitat loss is the leading factor impacting plant species richness over short periods (Alofs et al., 2014).
Invasive Plants	Generalist species *Bombus terrestris* was able to meet its nutritional needs by foraging off invasive plants, yet invasives likely disrupt plant-pollinator networks (Drossart et al., 2017).	Removal of invasive *Frangula alnus* led to a rapid shift in pollinator communities, and increased generalist bee diversity and abundance (Fiedler et al., 2012).	In North American grasslands, forb diversity was negatively associated with increased exotic grasses (Pei et al., 2023).

habitat restoration is a relatively new field and there is currently limited research on how to apply what is known about bee biology to ecological restoration efforts. In addition, we hope to offer insights that may be useful to land managers and to highlight future research directions in bee biology and ecology that can be integrated into ecological restoration practices.

2 Pre-restoration: planning and initial assessment

2.1 Establishing a baseline

Establishing ecological benchmarks using baseline data can be useful for assessing the impacts of habitat restoration by providing a reference point from which to measure change over time and setting realistic project goals (Hawkins et al., 2010; Downs et al., 2011). Baseline measures of pollinator diversity can be obtained through field sampling as well as by examining historical data from natural history collections (Lister, 2011; Breeze et al., 2021). Land managers can use this information to establish species-specific needs, prioritize the creation of habitat for targeted bee species by planting associated host-plant species, and provide suitable nesting habitat (Winfree, 2010; Danforth et al., 2019; Antoine and Forrest, 2020; Requier and Leonhardt, 2020).

During times of the year when bees are flying and plants are flowering, land managers can directly sample sites to determine species presence. Sampling relatively undisturbed areas nearby can aid in establishing realistic and site-specific goals for restoration projects (Curran et al., 2022), especially if these projects target habitat restoration towards species that are already occurring or nesting at nearby, undisturbed sites. Surveying sites before restoration is necessary to assess current bee diversity, identify existing nests for targeted conservation, evaluate available floral and non-floral resources, and devise strategies for managing invasive species (Ritchie and Berrill, 2020).

Historical specimen data from natural history collections, including those obtained from sources such as the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), are valuable for estimating local bee diversity, species distributions, species occurrence dates, and the floral resources visited by given bee species. When utilizing natural history collections, expanding searches to include specimen occurrences from adjacent sites can aid in identifying species that may be recruited from nearby regions, subsequently enabling their inclusion in targeted restoration efforts. In addition, natural history collections can be a critical tool for assessing species-specific flowering phenology and bee flight times (Ogilvie and Forrest, 2017), which may be used to select species of plants that are likely to form mutualistic relationships with bees in a given region or locality. For most species of plants and bees, specimens have not been collected equally across their ranges (Chesshire et al., 2023); in places where historical records do not exist, species distribution models may help to predict whether a location is suitable for a given plant or bee species. Researchers have used ecological niche modeling based on bee specimen records to estimate current and future species distributions (Carvalho and Del Lama, 2015; Beckham and Atkinson, 2017).

Determining targeted bee species nesting requirements is important when assessing the nesting conditions available at a given site. This can enable practitioners to find and protect bee nests before restoration or preserve nesting features (such as bare ground or woody debris; see Section 2.3.2 Nest Site Availability) that are already available on the landscape. However, for many bee species, these nesting requirements are unknown (Antoine and Forrest, 2020). Documentation of the nest site preferences (such as soil type or soil moisture) of different bee species in distinct environments is valuable so land managers can provide species and site-specific resources for nesting (Harmon-Threatt, 2020; Orr et al., 2022).

Recent community science efforts have been established to document the nesting habits of ground-nesting bees, such as when and where they nest (Liczner and Colla, 2019; Maher et al., 2019; Ground Nesting Bees, 2023). In the absence of species-specific nesting information, the nesting preferences of closely related congeners may be useful (Danforth et al., 2019). Contributions to shared databases can help correlate specific nesting conditions with bee observations, providing information for future bee conservation (Chesshire et al., 2023) and targeted bee habitat restoration.

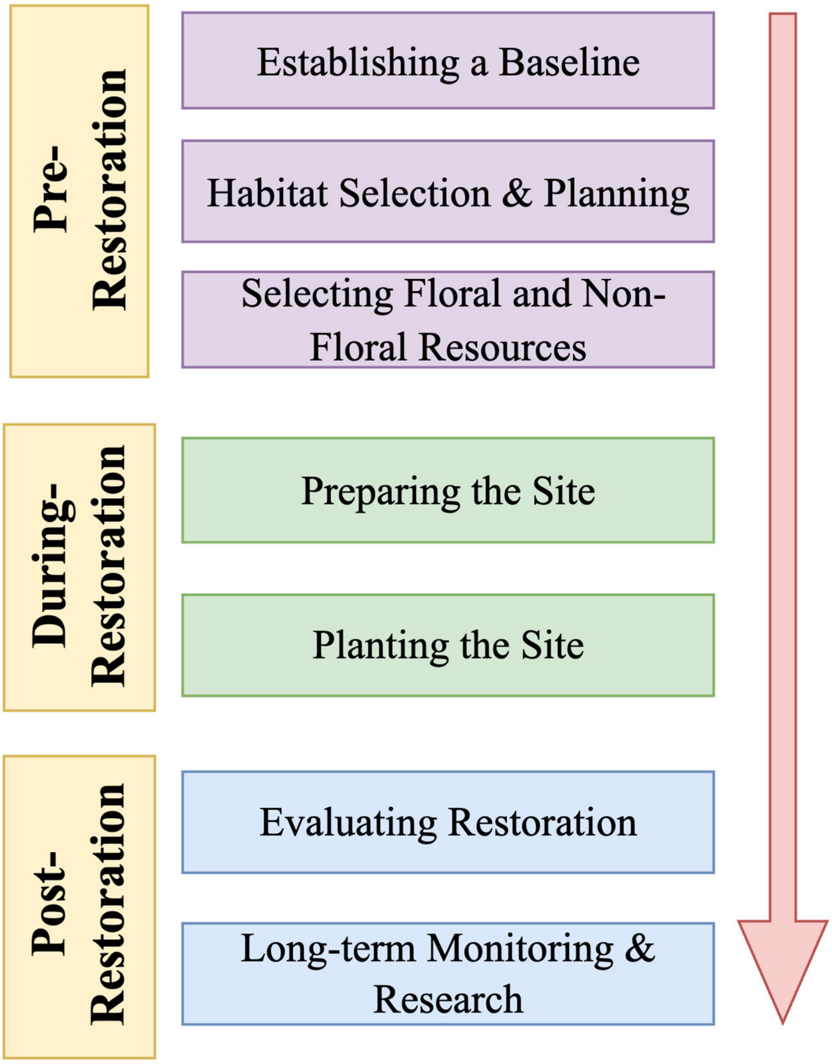

FIGURE 1
This paper provides a framework for integrating considerations of bees into each step of ecological restoration. While we chose this framework for clarity, it is important to note that the process is often non-linear. For example, results from post-restoration evaluations can prompt practitioners to revisit earlier stages of the restoration process such as planning, establishing new baselines, or continuing site maintenance.

2.2 Habitat selection and planning

Once ecological baseline data has been established, habitat restoration should create a detailed plan (Nilsson et al., 2016) which can include considerations of the needs of native bees. One approach is to begin by establishing baseline estimates that assess bee diversity, as well as the availability of floral and non-floral resources (such as materials for foraging and nest building) at or around the site. Based on information gathered from baseline surveys, specific plans can be developed for the bee species present or nearby. Consideration of floral and non-floral resources and nesting conditions for native bees can be included in these habitat restoration plans (Figure 2). Localized restoration initiatives, including small-scale habitat restoration projects, can provide floral resources and nesting habitats that support bee diversity and abundance (de Araújo et al., 2018; Phillips et al., 2019; Monasterolo et al., 2020; Phillips et al., 2020; Donkersley et al., 2023).

Unlike plant-centric restoration, where plants are introduced and established through seeds, cuttings, or outplanting entire individuals, the establishment of bee communities depends heavily on the natural recruitment of bee species from surrounding regions (M'Gonigle et al., 2015; Öckinger et al., 2018). The creation of suitable habitats and connectivity between habitats (corridors) can facilitate the movement and persistence of bee populations (Hanula et al., 2016; Keilsohn et al., 2018; Mola et al., 2021a), alter pollination services provided by bees (Mitchell et al., 2013), and affect the genetic diversity of founding populations (Bruns et al., 2024). For a review from 2013 on the relationship between landscape connectivity and ecosystem services, see Mitchell et al. (2013).

By identifying corridors between habitats in heterogeneous landscapes, restoration practitioners can better design projects that recruit diverse bee species to restored sites (Öckinger et al., 2018). Winsa et al. (2017) determined that trait composition (a trait-based approach for assessing bee diversity based on morphological, phenological, and behavioral traits) was positively correlated with connectivity to intact grassland habitat in restored pastures. Cusser and Goodell (2013) found as the distance to remnant habitat patches (areas from which bees would populate a restoration site) increased, bee diversity declined. However, they also observed that increasing floral richness promoted pollinator network stability, even at the sites furthest from remnant patches. Thus, Cusser and Goodell (2013) recommended prioritizing providing bee habitats that are diverse in floral resources far from remnant patches to increase pollinator network stability in new locations.

Proximity of restored landscapes to ecological threats can also impact bee communities. For example, numerous restoration projects are situated near roadways, raising the likelihood of bee fatalities resulting from traffic collisions (Keilsohn et al., 2018) and hurting more individual bees than they help (Keilsohn et al., 2018). Determining the optimal distance from roadways for bee habitat restoration sites (Keilsohn et al., 2018) and identifying the threshold of roadway activity that negatively affects bees are important goals for future research.

2.3 Selecting supplemental floral and non-floral resources

Consideration of floral and non-floral resources is important for bee habitat restoration (Requier and Leonhardt, 2020). Planting species representing a variety of growth forms (annual and perennial forbs and grasses, as well as shrubs and trees) can provide both floral and non-floral resources for native bees (Requier and Leonhardt, 2020), while also providing ecosystem functions such as shade and erosion control during restoration (Mitchell et al., 2022).

2.3.1 Supplemental floral resources

Enhancing flowering plant species richness at restoration sites can increase bee diversity and abundance (Fischer et al., 2016; Hanula et al., 2016; Purvis et al., 2020; Lane et al., 2022; Rubio et al., 2022; Beneduci et al., 2023) and bee visitation rates (Denning and Foster, 2018). A meta-analysis of observational studies by Kral-O'Brien et al. (2021) found that plant species richness was the strongest predictor of bee species richness. Other studies have reported comparable findings, indicating that vegetation type may significantly influence bee community assembly (Brooks, 2020; Novotny and Goodell, 2020). In addition, including high densities of flowering species through the implementation of seed mixes has also been found to increase the chances of pollination and reproductive success for some outcrossing plants (Cane et al., 2012), creating positive feedback loops between associated plant and bee species.

Nevertheless, the reintroduction or supplementation of appropriate combinations of native plant species at restoration sites may be difficult for several reasons. Seed mixes that represent local combinations of sympatric species are often unavailable, due either to their high cost in creating them, the difficulty of sourcing locally adapted genotypes, or challenges in producing seed mixes quickly enough (Nevill et al., 2018; Erickson and Halford, 2020). Nevertheless, carefully designed seed mixes that include seeds sourced from established "seed zones" (seeds from regions with similar environments; these seeds are considered the same in the context of locally adapted seed mixes; Erickson and Halford, 2020) can enhance bee diversity (Harmon-Threatt and Hendrix, 2015; Galea et al., 2016; Lybbert et al., 2022). Despite many benefits, seed zones are not defined for numerous important species in restoration (Johnson et al., 2023). Some research indicates that admixture seed sourcing (sourcing seeds from many different locations) can alter plant-arthropod interactions when flowering species richness is low (Hulting et al., 2024). However, there have been no studies examining the impact of admixture seed sourcing on pollination success or bee diversity.

Empirical tools can be beneficial for selecting plant species for bee habitat restoration (M'Gonigle et al., 2017; Esque et al., 2021; Purvis et al., 2021). M'Gonigle's genetic algorithm, which uses phylogenetic relatedness, bee visitation rates, and bee diversity, is an effective tool for designing seed mixes (M'Gonigle et al., 2017) and has been empirically tested and used in multiple restoration efforts (Williams and Lonsdorf, 2018; Campbell et al., 2019; Bruninga-Socolar et al., 2023). Continued testing of empirical tools designed to facilitate the

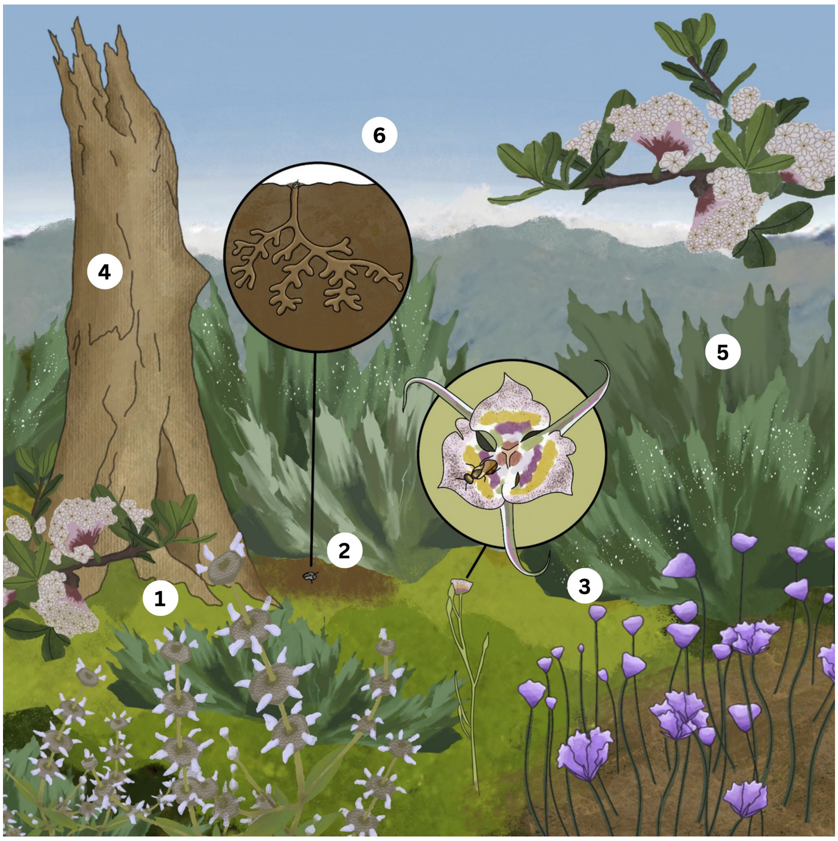

FIGURE 2
Key considerations for native bee habitat restoration planning in natural environments. (1) Plant native species that are nutritionally and phenologically diverse; (2) Implement restoration clearing and planting techniques that are bee-friendly, including the provision or protection of viable nesting sites; (3) Use empirical tools for optimizing pollinator species richness, including providing necessary host-plant species; (4) Provide non-floral resources for bee foraging and nesting; (5) Remove invasive plant species and replace with natives; (6) Increase bare ground and woody debris to enhance the availability of nesting habitat.

selection of plants that support generalist and specialist bee communities in different environments is needed.

2.3.1.1 Bee nutrition

The central focus of most bee-centric restoration efforts is to provide bees with ample floral resources to meet their nutritional needs (Winfree, 2010; Scheper et al., 2013; Image et al., 2022). The quality of these resources may be as important as their abundance (Vaudo et al., 2014). When foraging choices are insufficient, bee health and survival decline (Filipiak et al., 2022). High plant species diversity does not always guarantee nutritionally adequate pollen and nectar (Filipiak et al., 2022), which should be considered when designing bee conservation and restoration efforts (Vaudo et al., 2015, Vaudo et al., 2020; Crone et al., 2022; Filipiak et al., 2022). Moreover, bee microbiota is affected by the plants that bees forage, which can directly impact bee health (Nguyen and Rehan, 2023). Crone et al. (2022) recently published an extensive review of bee nutritional ecology, emphasizing the need to evaluate the diet preferences of all focal bee species. They also highlight the potential of emerging technologies (i.e., automated monitoring systems, DNA metabarcoding) to enhance bee habitat restoration for species of special concern in the future (see Section 4.2 Long-Term Monitoring & Research). Existing knowledge gaps include understanding the significance of macro and micronutrients for various bee species and discerning the nutritional requirements of specialist bees.

2.3.1.2 Plant and bee phenology

Phenology, or the biological timing of life events such as bee emergence or flowering time, is important for pollination success and bee survival. Plant reproduction and the availability of food for bee larvae largely depend on synchrony between plants and their associated pollinators (Kudo, 2014; Ogilvie and Forrest, 2017; Slominski and Burkle, 2021). A mismatch of just a few days can decrease bee fitness through increased mortality and decreased fecundity (Buckley and Nabhan, 2016; CaraDonna et al., 2018; Schenk et al., 2018). When selecting plant species for habitat restoration, seed mixes and propagules composed of species with overlapping and long bloom periods can benefit pollinator populations by decreasing the risk of a phenological mismatch and providing a long foraging season (Tilley et al., 2013; Havens and Vitt, 2016; Gross, 2017; Simanonok et al., 2022).

In restoration planning, practitioners should evaluate the distribution and diversity of floral resources throughout the flowering season, and ensure that both early and late-season floral resources are available (Curran et al., 2023). Gonzalez et al. (2013) found that bumble bee foraging areas shifted to different habitats throughout spring and summer based on the availability of floral resources in bunchgrass prairie habitats in the Pacific Northwest. Bees were supported by grasslands early in the flowering season and aspen stands in late summer. Providing variation in the flowering time of floral resources can establish alternate food sources for generalist bees during periods of scarce floral resources (Ogilvie and Forrest, 2017; Dibble et al., 2020).

2.3.1.3 Floral resources for specialist bees

Numerous studies have documented the advantages of providing supplemental floral resources for generalist bee species (Russo et al., 2013; Woodcock et al., 2014; Kremen and M'Gonigle, 2015; Eeraerts et al., 2019; Frankie et al., 2019; McCormick et al., 2019; Fuccillo Battle et al., 2021; Walston et al., 2023). However, there is a lack of research on specialist bees (Kremen and M'Gonigle, 2015; Fowler, 2016). Success in promoting specialized bee abundance and diversity in restoration efforts requires the inclusion of host plant species on which the local specialists rely (Frankie et al., 2009; Fowler, 2016; Brooks and Poulos, 2023). Additionally, many host plant species may depend on specialized pollinators for reproductive success (Page et al., 2019). Fowler (2016) emphasize the importance of host plants in habitat conservation for specialist bees in the Northeastern U.S., noting that approximately 15% of native bee species in this region specialize in pollen collection from a particular plant family or genus.

Similar research on specialist bees in other regions is needed, and focused restoration efforts could promote their conservation (Fowler, 2016). Sampling pollen loads carried by specialist bees can aid in identifying the plant species on which these bees rely (Kelly and Elle, 2021). Additionally, bee specimen data can provide insight into the floral resources historically associated with specialist bee species (Fowler, 2016). Recently available databases (Seltmann and Community, 2022; Wood et al., 2023) provide lists of plant-bee species interactions that may be used to improve bee-centric restoration efforts, while also facilitating data sharing and continued monitoring for a better understanding of the dietary requirements of these important pollinators.

2.3.2 Nest site availability

Although most bee-centric conservation plans focus on floral resources, the availability of nesting habitats should not be overlooked (Öckinger et al., 2018; Requier and Leonhardt, 2020). Bee nesting biology has been recently reviewed by Orr et al. (2022), and anthropogenic threats to bee nesting in wild bee communities have been reviewed by Harmon-Threatt (2020).

The majority of bee species, including both eusocial and solitary species, nest underground (Danforth et al., 2019; Liczner and Colla, 2019); for a review of ground-nesting bee biology, see Antoine and Forrest (2020). Different species create distinct nest architectures and prefer different microhabitat conditions (Danforth et al., 2019; Antoine and Forrest, 2020). In a study by Buckles and Harmon-Threatt (2019) in tall grass prairies, bee nesting was positively influenced by increasing floral resource abundance as well as increasing the availability of bare ground, low soil moisture, and warmer soil temperature (Purvis et al., 2020). However, some bee species (e.g., bumble bees) prefer increased litter over bare ground (Williams et al., 2019; Smith DiCarlo et al., 2020).

Studies of ground-nesting bees have assessed the effect of ground cover, temperature, texture, space, slope, soil compaction, and soil moisture on nest site selection (Cane, 1991; Xie et al., 2013; Sardiñas et al., 2016; Tsiolis et al., 2022). A multitude of studies have revealed that landscapes undergoing early successional stages, such as habitat restoration efforts, often provide nesting habitats that support diverse and specialized bee species (Rutgers-Kelly and Richards, 2013; Řehounková et al., 2016; Banaszak and Twerd, 2018; Seitz et al., 2019; Mola et al., 2020; Simanonok and Burkle, 2020; van der Heyde et al., 2022). Biotic factors, including plants, pathogens, parasites, predators, and conspecifics, can also influence the nesting density and nesting location at which bees choose their nesting sites (Potts and Willmer, 1997; Michener, 2000; Requier and Leonhardt, 2020). For example, in Hawaii, the nesting sites of *Hylaeus anthracinus* Smith, 1853 experience lower reproductive success due to invasive ants (Plentovich et al., 2021). Limited research has explored the biotic factors influencing bee nesting, such as soil microbial diversity.

Another group of bees is comprised of native cavity-nesting bee species, which require live or dead biotic material in which to nest. Studies have shown that areas with simplified vegetative structures have low cavity-nesting rates (Flores et al., 2018; de Araújo et al., 2019, de Araújo et al., 2021; Felderhoff et al., 2022). Many bee species are opportunistic nesters, choosing to nest in existing holes, stems, or downed woody debris (Galbraith et al., 2019; Davis et al., 2020; Foote et al., 2020; Glenny et al., 2023; Rappa et al., 2023). In addition, specific habitat types may be preferred as overwintering sites, such as forest habitats for many *Bombus* sp (Mola et al., 2021a). In sum, whether or not there is sufficient availability of nesting sites for the bees at a given locality will depend on the type of biotic material available, the complexity of the vegetation structure, the presence of existing holes and debris, and the prevailing habitat type, depending on the bee species' preferences.

2.3.2.1 Nest building materials

Including supplemental non-floral resources at a restoration site is important for providing bees with the materials they need to construct their nests (Requier and Leonhardt, 2020). Both eusocial and solitary bee species use leaves, bark, trichomes, or resin for nest building and to protect their brood cells (Shanahan and Spivak, 2021). Some native bees (Apidae, Meliponini, Centridini, Euglossini, Apini, some Xylocopinae, and some Bombini) use herbaceous material or coarse woody debris to build their nests (Michener, 2000; Danforth et al., 2019; Requier and Leonhardt, 2020). An example is the genus *Ceratina*, which creates nests in the stems of dried herbaceous material or woody branches (Danforth et al., 2019). Furthermore, the plant species that bees rely upon for nest building may not be their floral host plant species. For example, many *Anthidium* spp. depend on the trichomes of hairy plant species for lining their brood cells, while they collect pollen most frequently from other, glabrous, species (e.g., *Larrea* spp.; Vitale et al., 2017). Thus, providing floral resources alone would not be sufficient to support the genus *Anthidium*. Resin, another non-floral resource foraged from plants that some bee species rely on, can function like concrete, solidifying nesting structures and preventing bacteria from contaminating brood cells (Chui et al., 2022).

2.3.2.2 Non-floral resources for food

The importance of non-floral resources for solitary bees has only recently been recognized (Chui et al., 2022). Non-floral sugars, such as honeydew produced by scale insects, provide additional carbohydrates for some bee species. Meiners et al. (2017) observed 42 wild bee species, including many solitary and native species, visiting *Adenostoma fasciculatum* Hook. & Arn. to obtain honeydew, which may serve as a supplemental food source outside the flowering season. Preserving scale insects, which produce honeydew, could help to extend the seasonal duration of bee foraging, mitigating the negative effects of potential phenological mismatches (Gérard et al., 2020). Additionally, other symbionts can be important for bees. A study of the generalist solitary species *Osmia lignaria* found that bacterial and fungal symbionts increased larval developmental success (Westreich et al., 2023). Documenting and sharing these interactions can be useful for restoration managers. Continued research identifying symbionts associated with native bee species and their impact on bee health and determining the most effective strategies for incorporating these non-floral resources into bee habitat restoration efforts is needed.

2.3.3 Non-native plants

The role of non-native plants in bee conservation is highly debated. Parra-Tabla and Arceo-Gómez (2021) provide an extensive review of the influence of invasive plants on plant-pollinator networks, although bees were not a focus. While native plants are recognized for supporting a wide array of bee species (Discua and Longing, 2022), several studies have found that non-native plants can also promote bee abundance and bolster pollination networks (Severns and Moldenke, 2010; Gaiarsa and Bascompte, 2022; Kovács-Hostyánszki et al., 2022). However, most studies of non-native plants and bees focus on the floral resources that non-natives provide (typically in urban environments) and do not account for competition in bee visitation rates between non-native and native plant species (Aizen and Morales, 2020) or disruptions in ecosystem function (Parra-Tabla and Arceo-Gómez, 2021; Tallamy et al., 2021). Hanula et al. (2016) note that when non-native plants outcompete native plant species, this typically negatively impacts pollinator communities, including bees. Additionally, Mathiasson and Rehan (2020) observed that the decline of native bees (particularly specialists) was associated with the proliferation of non-native plant taxa in northern New England due to the loss of their associated host plants. Moreover, non-native plants may affect other aspects of bee biology and ecology, including reproductive success (Hanula et al., 2016), the availability of ground-nesting sites, the abundance of native plant species (Barron and Beston, 2022), as well as floral visitor communities (Denning and Foster, 2017). In some habitats, the removal of non-native plants during restoration increased bee abundance and species richness (Fiedler et al., 2012; Tonietto and Larkin, 2018; Ulyshen et al., 2020). Forb diversity is often negatively associated with non-native grass abundance (Drobney et al., 2020; Molinari and D'Antonio, 2020), high levels of which may cause declines in bee abundance, the simplification of bee communities (Pei et al., 2023), and the alteration of entire insect communities (Luong et al., 2019). Furthermore, non-native grasses create dense litter layers that may block nesting sites for ground-nesting bees (Pei et al., 2023). For example, Pei et al. (2023) observed a decrease in ground-nesting bee abundance at sites occupied by increased leaf litter and high densities of non-native grass *Poa pratensis* L. in the Northern Great Plains. Other studies have hypothesized that non-native grasses are responsible for a decline in both forb and pollinator diversity and abundance (Lybbert et al., 2022).

It is important to recognize that not all non-native plants are invasive, and some non-native species can provide floral resources to support bee abundance (Carson et al., 2016; Frankie et al., 2019; Gibson et al., 2019; Niemuth et al., 2021; Ulyshen et al., 2022). This is especially the case at the beginning and end of the flowering season, when non-natives may be less likely to disrupt native plant-pollinator networks (Staab et al., 2020). During restoration efforts, non-native plants may serve as temporary food sources for bees while native plants become established (Lybbert et al., 2022; Thapa-Magar et al., 2023). While non-native plant species may support generalist bee abundance in some habitats, prioritizing native plants is recommended as they provide habitat for a broader range of native insects and contribute to ecosystem function (Tallamy et al., 2021).

3 During-restoration: implementation

3.1 Preparing the site

Before undertaking habitat restoration, land managers are frequently required to remove debris, infrastructure, pollutants, or invasive species (Elmqvist et al., 2013). Different methods of vegetation removal have advantages and disadvantages for native bees (Table 2). For the effective execution of these strategies, they frequently require multiple iterations during and following the restoration process (Kimball et al., 2015; Oliveira et al., 2021; Keeley et al., 2023).

3.1.1 Mechanical and hand thinning

Heavy machinery used to move soil, water, or vegetation during restoration can affect soil structure (Schäffer et al., 2007; Nawaz et al., 2013). Many species of ground-nesting bees require specific soil characteristics to build their nests (Antoine and Forrest, 2020). Christmann et al. (2022) suggest that heavy machinery could threaten existing nesting sites for ground-nesting bees; however, no studies to date have looked directly at the effect of soil movement or compaction from heavy machinery on bee nesting success.

Mechanical thinning has been found to have several effects on bee communities. When Ealy et al. (2023) compared pollinator communities in old-growth forests with logged early seral forests, they detected negative long-term effects on the bee communities in clear-cut sites, including a decrease in specialist bees. However, when comparing clear-cut vs. young forests with dense understories, clear-cut forests have higher bee diversity, likely due to decreased canopy cover (Ealy et al., 2023). Odanaka et al. (2020) conducted an experiment measuring the effects of mechanical thinning on bee diversity and abundance in longleaf pine savannas compared to untouched remnant plots. They found that bee diversity and abundance were positively correlated with thinning and negatively correlated with canopy cover. Lettow et al. (2018) found thinning coupled with controlled burns significantly increased pollinator richness and abundance in oak savannas relative to unmanaged controls. Other studies observed similar results (Hanula et al., 2015, Hanula et al., 2016; Abella et al., 2017; Milam et al., 2018; Rivers et al., 2018; Glenny et al., 2022; Davies et al., 2023). These findings highlight that mechanical thinning can increase bee abundance and diversity in certain vegetation types such as forests.

Hand thinning offers the advantage of leaving woody debris on the landscape which can support cavity, stem, and opportunistic nesting bees (Rappa et al., 2023). The maintenance of structural heterogeneity to provide nesting sites for diverse bee species should be supported during and following bee habitat restoration (Antoine and Forrest, 2020; Image et al., 2022).

3.1.2 Prescribed fire

Some plant and animal communities in North America have adaptations that enable them to thrive when exposed to periodic wildfires (Simmons and Bossart, 2020). Prescribed fire (designed to mimic conditions of periodic low-intensity wildfires) can result in bare ground which provides nesting habitat for ground-nesting bees (Hanula et al., 2016; Sitters et al., 2016; Decker and Harmon-Threatt, 2019; Bruninga-Socolar et al., 2022; Brokaw et al., 2023). Ulyshen et al. (2021) examined the effects of frequent prescribed fires on bee abundance and species richness in southeastern U.S. forests. They found that bee abundances significantly increased in burned plots compared to unburned plots, although bee species differed in their tolerance to burn frequencies. Similar results were obtained following controlled burns of tallgrass prairies (Harmon-Threatt and Chin, 2016) and mixed conifer forests.

However, not all species benefit from controlled burns, particularly cavity and stem nesters such as *Bombus*, *Ceratina*, and *Osmia*

TABLE 2 Advantages and disadvantages of different methods used to clear restoration sites and to introduce plants during bee-centric habitat restoration. Continuous implementation of these methods may be necessary to maintain resources and achieve restoration objectives.

Protocol	Method	Advantages	Disadvantages
Clearing	Hand pulling	Preserves soil for ground-nesting bees; ability to leave native plants or snags on the landscape for bee nesting	Labor intensive and time-consuming; may not be as effective for some invasive species
Clearing	Weed whacking	Faster than hand pulling; preserves soil for ground-nesting bees; ability to leave native plants or snags on the landscape for bee habitat	Time intensive; may temporarily negatively affect bee abundance and diversity through loss of floral resources
Clearing	Controlled burning	Quick; can have positive impacts on bee diversity in some habitats	Narrow burn windows; negative public perception
Clearing	Mechanical clearing	Quick and effective; especially when working with large vegetative biomass	Compression of soil; may not be as effective for some invasive species; some equipment spreads invasive seeds
Clearing	Herbicide	Quick and effective; most effective for killing invasive plants; can specifically target either monocots or dicots with specific herbicides	Chemicals may affect the plants and wildlife present at the site; may temporarily negatively affect bee abundance and diversity; exposure to humans applying the chemicals
Clearing	Grazing	Positive impacts on bee diversity in some habitats; highly dependent on the habitat, site, and grazer	Negative impacts on bee diversity in some habitats, especially when floral resources are consumed
Clearing	Mowing	Quick and effective	May cause declines in bee abundance due to the removal of floral resources
Planting	Broadcast seeding	Time-efficient; fills the seed bank; great for annual wildflowers	Seeds may wash away; time delay before bees can visit
Planting	Hand planting	Deliberate placement of plants in areas where they will be most successful and beneficial to bees	Slow and labor-intensive
Planting	Hydroseeding	Quick; seeds stay in place and don't get washed away	Could disrupt ground-nesting bee species
Planting	Propagation	Deliberate placement of plants; can be fast depending on the method	Less genetic diversity; time delay before bees can visit
Planting	Transplanting	Able to provide bees with immediate floral and non-floral resources	Labor intensive; Risk introducing plants that are not locally adapted
Planting	Mulching	Seeds stay in place and don't get washed away; conservation of water; helps prevent weeds	Could disrupt ground-nesting bee species

(Galbraith et al., 2019). Bruninga-Socolar et al. (2022) determined that ground-nesting bee abundance and diversity responded positively to fire, while cavity-nesting bee abundance and diversity increased in the absence of fire, highlighting the importance of heterogeneity in fire regimes. Moreover, plant-pollinator interactions can be disrupted in certain habitats after fire due to the elimination of floral host plants (Love and Cane, 2019). Despite this, Cole et al. (2019) found that burn scars, which contribute to environmental heterogeneity in riparian environments, were positively correlated with bee diversity. Other studies have observed similar results in different habitats (Gelles et al., 2022). In addition, controlled burns have been found to reduce non-native grasses (Ditomaso et al., 2006; Weidlich et al., 2020) and to increase annual wildflower diversity (Peterson and Reich, 2008; Davies and Sheley, 2011; Decker and Harmon-Threatt, 2019; Lybbert et al., 2022; Gelles et al., 2023), which may lead to increases in bee abundance and diversity (Smith DiCarlo et al., 2019). In general, pyrodiversity (the variability in burn size, frequency, duration, and severity across a landscape), including some exposure to high-severity wildfires, has been found to increase bee species richness in fire-adapted regions (Galbraith et al., 2019). Creating a mosaic containing different burn histories will likely provide habitat and resources for the greatest diversity of bee species (Ponisio et al., 2016; Rodríguez and Kouki, 2017; Galbraith et al., 2019).

3.1.3 Mowing and grazing

Mowing is often used to manage weed and grass growth in restored habitats, especially during spring. Mowing has been found to promote forb diversity (Lybbert et al., 2022) but can have the opposite effect if done too frequently (Smith et al., 2018). Additionally, increased mowing frequency has been found to be negatively associated with bee species richness and abundance (Audet et al., 2021; Serret et al., 2022). The "No Mow May" movement has spread, in which residents are urged to reduce mowing during peak pollinator flight time (Andrews, 2023). This practice has been found to promote bee abundance on the US East Coast and elsewhere (Lerman et al., 2018), but it may require alterations when applied to other major geographic regions such as the western US, where peak pollinator foraging and flight times occur later in the season. Another method, such as the reintroduction of grazing animals such as wild horses, has been found to enhance forb diversity and boost bee abundance in habitats that historically evolved under herbivory from large ungulates (Garrido et al., 2019). Similarly, Bruninga-Socolar et al. (2022) found that the heterogeneity in vegetation cover caused by cattle grazing and controlled burns benefited ground-nesting bees by providing more bare ground, but implementation of specific grazing regimes is necessary to minimize soil compaction as well as providing habitat for stem and hole-nesting bees. In contrast, Stein et al. (2020) detected that grazing in grassland communities in the upper Midwestern United States led to a reduction in native flowering plant species abundance. In this study, body mass and lipid stores were also measured to assess nutritional health indicators in three sweat bees (*Agapostemon* spp.). It was found that in ungrazed sites, *Agapostemon virescens* (Fabricius, 1775) showed greater body mass compared to individuals sampled in grazed areas. Beckett et al (Beckett et al., 2022). determined that deer presence in British Columbia negatively affected bumble bee abundance indirectly by depleting floral resources, indicating a potential decline in colony success. For a review of the known roles of mowing and grazing in restoration as of 2016, see Tälle et al. (2016).

3.1.4 Herbicides and insecticides

The impacts of pesticide use on native bee health are poorly understood. Experimental studies on honey bees are frequently used to infer the effects of pesticides on all bee species (Franklin and Raine, 2019; Lehmann and Camp, 2021). The U.S. Environmental Protection Agency's Policy Mitigating Acute Risk to Bees from Pesticide Products states that protecting managed bees will "also protect native solitary and eusocial bees that are also in and around treatment areas" (EPA, 2015). However, honey bee sensitivity to pesticides may differ from the responses of native bees (Chan et al., 2019; Franklin and Raine, 2019). Because some solitary bee species are more vulnerable than honey bees to pesticide exposure, it is crucial to avoid relying solely on honey bees as the risk assessment model when observing the toxic effects of pesticides (Franklin and Raine, 2019). This increased susceptibility can be attributed to solitary bee consumption of fresher pollen and nectar, as well as increased exposure to pesticides through their nesting sites (Goulson, 2013; Chan et al., 2019; Franklin and Raine, 2019; Lehmann and Camp, 2021). In addition, solitary bees have a smaller body size than honey bees (Chole et al., 2019); thus, a dosage calibrated to honey bees could pose a significant risk to most wild bee species. This is particularly concerning as body size is one of the primary predictors of bee species' vulnerability to pesticides (Schmolke et al., 2021). Furthermore, honey bees are eusocial and thrive in large colonies, whereas native bees are typically solitary and relatively scarce across the landscape. This trait makes them particularly vulnerable to population declines if negatively impacted by pesticides (Straub et al., 2015; Sgolastra et al., 2019).

Herbicides can be useful for removing invasive plants during restoration, but their costs and benefits should be considered before implementation (Bennion et al., 2020). Whenever feasible, employing biological controls can be highly effective and bypass the hazards associated with herbicides (Auld, 1998; Peterson et al., 2020). However, biological control agents are not available for all plant species (Singh et al., 2020). In a review of 372 published articles, Weidlich et al. (2020) reported that 42.3% of the restoration projects used chemicals to eradicate invasive plants. Of these, 40% used glyphosate, an active ingredient in most herbicides (Weidlich et al., 2020). Glyphosate, marketed as Roundup$^{\mathrm{TM}}$, can be harmful and sometimes lethal to non-target pollinators including honey bees, bumble bees, and solitary bee species (Abraham et al., 2018; Battisti et al., 2021; Straw et al., 2021). When cavity nests were sprayed with glyphosate, solitary bee reproductive success declined due to reduced brood cell production (Graffigna et al., 2021). In an acute exposure experiment conducted under realistic field conditions, glyphosate exposure impaired fine-scale color recognition and long-term memory in bumble bees, which may disrupt their foraging behavior and lead to overall declines in colony success (Helander et al., 2023). Glyphosate use is restricted or banned in several European countries due to human and environmental concerns, including its negative effect on bee development, behavior, and survival (Kudsk and Mathiassen, 2020; Battisti et al., 2021). Further research is required to investigate the sublethal effects of glyphosate on native bee species observed in field settings, as noted by Battisti et al. (2021). While the effects of herbicides on bee health are considered in agricultural practices, these impacts have not been evaluated in habitat restoration efforts.

Although not commonly used in restoration, insecticides can occasionally be used to protect rare plants that are vulnerable to insect herbivores (Bevill et al., 1999; Flower et al., 2018). However, more commonly insecticides leach into native landscapes from neighboring agricultural fields or watersheds. Neonicotinoids, a class of widely used systemic neuro-acting insecticides absorbed by plants and spread throughout their tissues, are extremely harmful to bees (Alkassab and Kirchner, 2017). Transferred through pollen and nectar consumption, neonicotinoids cause bee mortality or have sub-lethal effects by altering bee communication, foraging behavior, or navigation (Fischer et al., 2014; Alkassab and Kirchner, 2017). Only two studies have investigated neonicotinoid exposure through soil contamination for ground-nesting bees, employing differing experimental designs and yielding conflicting results (Willis Chan et al., 2019; Tetlie and Harmon-Threatt, 2024).

While research on the effects of insecticides on native bee species has increased in recent years, more research is needed, especially on the sub-lethal effects of these chemicals (Dirilgen et al., 2023; Tetlie and Harmon-Threatt, 2024). Further research is needed to assess the impacts of pesticides on bee-centric restoration and to identify or discover practices that minimize negative outcomes. For instance, it has been shown that nighttime spraying is effective in reducing exposure to honey bees (Decourtye et al., 2023). Such studies will provide insights for practitioners to develop more informed, bee-friendly conservation and restoration strategies.

3.2 Planting the site

Various planting methods have been devised for bee habitat restoration (Leverkus et al., 2021), the pros and cons of which in relation to bee habitat restoration are summarized in Table 2. One planting technique that promotes annual plant species over time is continuous reseeding (Applestein et al., 2018). Ongoing research indicates that regular reseeding can boost wildflower populations (Barr et al., 2017; Applestein et al., 2018), and annual wildflowers may be replaced by a few perennial species over time without strategic, planned disturbance regimes (i.e. burning, mowing, or grazing) (Lybbert et al., 2022). Questions remain regarding the optimal frequency and density of reseeding to support bee species. Barr et al. (2017) highlighted that if land managers have to choose between prioritizing reseeding rates and plant species diversity when sowing seed mixes, prioritizing plant species diversity is best for improving restoration success in grassland habitats.

In addition to implementing bee-conscious planting techniques, the density and size of floral patches are important considerations in bee habitat restoration. Some research suggests that including corridors or gaps in vegetation for bees to fly through can provide bee-friendly habitat, especially in areas of dense woods or shrubs (Jackson et al., 2014; Hanula et al., 2016). Other research has found that distributing bee seed mixes at low densities increases nectar production per plant, providing higher-quality floral resources for bees (Neece et al., 2023). These results suggest that planting at lower densities could be strategic for bee habitat restoration.

Floral resources are often unequally distributed across a landscape, and patch size may influence bee foraging behavior, especially in fragmented habitats. Harmon-Threatt and Anderson (2023) found that bees in a naturally patchy Ozark Mountain glade ecosystem rarely traveled between patches, demonstrating the importance of nearby floral resources. Bumble bees and solitary bees respond to both patch size and isolation when foraging for resources (Fragoso et al., 2021; Fragoso and Brunet, 2023), and bumble bee foraging is considered particularly sensitive to habitat fragmentation (Osborne et al., 2008; Goulson et al., 2011). Fragoso and Brunet (2023) reported that *Bombus impatiens* Cresson, 1863 preferred larger, more closely spaced patches, while *Megachile rotundata* Fabricius, 1787 preferred patches located nearby their nests regardless of the patch size. Although bumble bees may prefer closely spaced patches, they can forage over greater distances than solitary bees. For example, an average-sized eusocial bee (intertegular distance = 2.5mm for a female foraging bee) has a foraging range of ~3,300 meters whereas a similarly sized solitary bee has a foraging distance of ~1,200 meters (Grüter and Hayes, 2022). Fragoso and Brunet (2023) determined that both solitary and eusocial bees use complex learning to determine which patches to visit. The composition of flowering patches may be expected to influence bees' foraging preferences. To our knowledge, however, no studies have investigated how a patch's plant diversity or the relative abundances of different species influence bee foraging distance or behavior in restored landscapes.

When establishing patches of floral resources, the provenance of seeds or plants can influence plant-pollinator interactions (Thomas et al., 2014; Bucharova et al., 2022; Höfner et al., 2022). For example, due to local adaptation, wild populations of plants differ with respect to flowering phenology, which in turn can affect bee foraging. If seeds or propagules are relocated for restoration, the flowering window of each plant species' population at the restoration site may differ from the window of the flight times of sympatric bee populations (Buisson et al., 2017). This could lead to a phenological mismatch between the flowering phenology of a restored site vs. its neighboring landscapes (Buisson et al., 2017; MacTavish and Anderson, 2022) increasing the risk of mismatches between plant species and their associated bees (see Section 2.3.1.2 Plant and Bee Phenology). Utilization of locally sourced seeds could potentially avoid this problem, but locally sourced seeds may not be physiologically adapted to changing climatic conditions (Bucharova et al., 2022). Managers should consider planting floral resources that are better suited for future climatic conditions (Oliver et al., 2016). Stephenson et al. (2020) found that in emergent wetlands, sites that were passively managed (allowing the establishment of native perennials through natural succession) after active restoration was completed had similar bee diversity and species richness compared to actively restored sites. No other studies within our review compared active and passive restoration methods.

4 Post-restoration: assessment & monitoring

Post-restoration refers to the assessment and monitoring that occurs after the initial steps of a project, but it does not necessarily signify the project's completion. Ecological restoration is an iterative process that requires continuous upkeep and evaluation to ensure that specific goals are achieved. Assessments and monitoring are beneficial at any stage of a project; however, they are particularly important for post-restoration evaluation.

4.1 Evaluating restoration for bees

To gauge the success of a restoration project, land managers must have specific, measurable outcomes and goals (Hallett et al., 2013). This may consist of setting targets that include specific biodiversity metrics, such as species richness, species diversity, or the presence of endangered species, which may be based on historical baselines (Michener, 1997). These metrics are possible to measure for small-scale bee habitat restoration initiatives; however, for larger projects that may take a rewilding approach (which involves allowing nature to reclaim a site rather than actively restoring it), other metrics may be more appropriate. Rewilding-focused strategies (Perino et al., 2019; Carver et al., 2021) emphasize the need to evaluate ecological complexity, which can be gauged by examining pollinator networks and redundancy (Elle et al., 2012; Bullock et al., 2022; Gawecka and Bascompte, 2023) as well as through the delivery of ecosystem services (Perino et al., 2019), which may be estimated by floral visitation rates, pollen transfer by bees (Plentovich et al., 2021), or the reproductive success of plants.

Assessing the success of restoration efforts should involve evaluating multiple ecological indicators (Prach et al., 2019); however, to date, bee diversity has not been commonly included in such assessments due to the difficulty and expense of monitoring (Bruninga-Socolar et al., 2023). Animals, particularly pollinators, can serve as excellent indicators of environmental health because of their interdependence with native plants (Buisson et al., 2017; Montoya-Pfeiffer et al., 2020) and their sensitivity to environmental toxins. Honey bee colony growth and performance have served as a useful bio-monitor for contaminants, pesticides, pathogens, and climate change (Quigley et al., 2019) and therefore may serve as useful indicators for assessing ecosystem health (CaraDonna et al., 2018; Herrera et al., 2023; Schenk et al., 2018; Willis Chan et al., 2019). Solitary bees are considered more sensitive to climate change and other anthropogenic factors than honey bees (Cunningham et al., 2022). Thus, solitary bees may be an even better proxy for ecosystem health, although no studies to date have tested this.

By utilizing multiple bee-capturing methods, sampling efforts can encompass bee species with different life histories (Begosh et al., 2020; Prendergast et al., 2020). For example, Sardiñas and Kremen (2014) employed emergence traps to estimate ground-nesting bee diversity, which differed from the composition of bee taxa estimated using aerial nets and pan trapping. Other, more indirect indicators of bee population health can be used to assess the long-term success of restoration projects. For example, native parasites (particularly brood parasites, found in bees' nests) indicate healthy populations that are able to sustain native parasitic species (Hudson et al., 2006; Dougherty et al., 2016; Araujo et al., 2018). Additionally, sex ratios can be used as an indicator of bee population health. In many species, including *Osmia rufa* Linnaeus, 1758, *Megachile apicalis* Spinola, 1808, and *Bombus* sp., bee sex ratios can be sensitive to resource availability and parasitism rates, both of which influence larvae provisioning (Bourke, 1997; Kim, 1999; Seidelmann et al., 2010). When larvae receive less food, there is a decrease in female offspring (Kim, 1999; Seidelmann et al., 2010). Female bees are primarily responsible for nest building and provisioning brood cells (Danforth et al., 2019); thus, when populations are female-limited, nest density and birth rates decrease, negatively affecting population size.

4.2 Long-term monitoring & research

Long-term bee monitoring at current restoration sites may help to improve future bee habitat restoration if used to identify practices that sustain native bee populations (see Section 2.2 Establishing a Baseline; Woodard et al., 2020; Droege et al., 2023). Sampling native bee species richness and estimating population abundances are useful metrics for evaluating restoration success (Williams, 2011; Tonietto and Larkin, 2018). Long-term monitoring of restored habitats is necessary to detect habitat and community changes over time, as short-term assessments (one to five years following the termination of a project) can provide incomplete or misleading indicators of a project's overall success (Herrick et al., 2006; Griffin et al., 2017; Onuferko et al., 2018; Sexton and Emery, 2020; Tang et al., 2023). For example, Abella et al. (2020) observed floristic quality (an index where plants are ranked by the commonality of a plant at a site) throughout 20 years, rather than just sampling at the beginning and end of monitoring. They found the difference observed across years better accounted for temporal fluctuations in vegetation growth and plant diversity. Thus, it may be meaningful to continuously assess the accumulation of restoration benefits considering the impacts of the restored landscape over time.

Long-term monitoring of bee populations and communities at a given location is challenging because observations can be sensitive to sampling methods (Portman et al., 2020; Bruninga-Socolar et al., 2023) and the costs associated with identifying bees and processing bee specimens can be high (Bruninga-Socolar et al., 2023). Surveillance monitoring, or broadly sampling bee communities to determine species presence, may provide measures of bee diversity. However, increased bee diversity does not guarantee that local populations of all bee species are sustainable; some populations may be thriving while others are not (Kammerer et al., 2021). Monitoring needs to occur across years; increased bee species occurrences across a season do not necessarily indicate an increase in population size (Portman et al., 2020; Woodard et al., 2020).

Alternatively, targeted monitoring is an emerging method for assessing bee populations. It is based on specifically monitoring certain bees or ecosystem functions that are the focal points of a given restoration project (Portman et al., 2020; Woodard et al., 2020). Tepedino and Portman (2021) contend that targeted monitoring is more effective than surveillance monitoring methods. Moreover, targeted monitoring is hypothesis-driven, which may facilitate the discovery of species-specific restoration practices rather than just observing broad trends (Tepedino and Portman, 2021). For example, targeted monitoring of rare plant reproductive success can benefit specialist bees because of their unique association with specialist pollinators (Motta et al., 2022). In addition, innovative techniques, such as using camera traps with deep learning technologies are emerging (Barlow and O'Neill, 2020; Spiesman et al., 2021; Bjerge et al., 2023). These approaches, which offer cost-effective and non-invasive methods for monitoring bee diversity, are expected to continue to improve in the near future (Bjerge et al., 2023).

Community science approaches can also provide cost-effective long-term monitoring strategies (Huddart et al., 2016; Edwards et al., 2018; MacPhail et al., 2020). Developing standardized protocols for community science efforts allows high-quality data to be obtained while educating the public about local environmental concerns (MacPhail et al., 2020). To assess bee abundance or diversity, community efforts could include catching and photographing specimens for identification, locating and counting nests, or quantifying floral resources and their phenology (Vilen et al., 2023). Moreover, new methods such as passive crowdsourcing can be a valuable screening tool for determining potential plant candidates for bee habitat restoration (Bahlai and Landis, 2016). Utilizing public resources such as iNaturalist and BugGuide for species identification can contribute to the growth of databases and more accurate distribution records (Orr et al., 2023). However, it is important to understand the strengths and limitations of community science data (Kosmala et al., 2016) and account for this when designing studies and analyzing data recorded by members of the public.

5 Discussion

Throughout this review, we provide insights for bee-centric habitat restoration through our pre-, during-, and post-restoration framework. We also emphasize promising directions for future research. Table 3 summarizes the most promising research areas needed to advance bee-centric restoration. Despite the limited knowledge of many aspects of bee habitat restoration, prioritizing the research gaps identified here can guide the application of restoration practices based on empirical evidence. Ultimately, bee habitat restoration aims to enhance native bee diversity and abundance, contributing to the persistence of bee populations, bee communities, and plant-pollinator interactions (Winfree, 2010; Tonietto and Larkin, 2018).

The effects of habitat restoration on native bee species diversity and abundance are currently data-limited but can be expanded through the open sharing of restoration plans and monitoring outcomes (Woodard et al., 2020). Throughout this review, we found the majority of studies reported an increase in bee abundance and diversity following restoration; however, we found only 21 studies that focused on species-specific responses of bees to restoration. Including species-specific responses in future studies can provide detailed information that can be used when restoring habitat for targeted bee species.

In the absence of species-specific data for most wild bee species, the best approach is to use strategies that will likely benefit a wide range of bee species. Implementing empirical tools such as M'Gonigle's Genetic Algorithm can aid in the selection of plant species to be used when restoring bee habitat (M'Gonigle et al., 2017). Despite significant gaps in our understanding of the specific nutritional requirements of native bees (Crone et al., 2022; Filipiak et al., 2022), a prudent approach would include planting phenologically overlapping floral resources (in which multiple related host plant species flower simultaneously), and augmenting floral resources both early and late in the flowering season in order to increase flowering duration at the community level. These approaches should consider plant nutritional variability when possible, increasing the chances that the nutritional requirements of most bee species will be met (Rowe et al., 2018). Additionally, including native keystone plant species that support a wide array of generalist bees and other insects should be a priority (James et al., 2014, 2016; Fantinato et al., 2018).

It is important to recognize that plant species that are important for bees may not always be bee-pollinated. For example, many bee species rely on willow (a wind-pollinated species) for pollen in riparian habitats (Mitchell et al., 2022). Moreover, not all sites may require the addition of supplemental floral resources. Many restoration projects can improve the habitat for native bees through the removal of non-native species and allowing the natural recruitment of native plants from nearby areas and from the existing seed bank (Hanula and Horn, 2011).

Nesting habitat can be provided by leaving dead plant debris at restoration sites and reducing the use of mulch to provide some bare ground for ground-nesting bees (Vaughan and Black, 2008; Eckerter et al., 2021; Rappa et al., 2023). If cavity nests are present during pre-site surveys, restoration efforts should be timed for spring to minimize net loss (when many cavity nesters are less likely to be overwintering). When applicable, care should be taken to reconstitute the original vegetation structure of the site using native plants. In addition, retaining dead piles of shrubs can increase nest site availability for bumble bees (Liczner and Colla, 2020). By providing nesting sites that attract bees and lead to high-quality nests, as well as by protecting existing nests, restoration efforts can contribute to the preservation of bee populations (Harmon-Threatt, 2020). Conserving existing nesting sites, however, is not the only option; occupied nests can be transplanted (Davison and Field, 2018), although the risks associated with this practice are unknown. Although no direct studies compare planting techniques for bee habitat restoration, implementing a mixture of techniques (e.g., transplanting, seed spreading, and propagation) to provide heterogeneity in habitat structure and plant diversity would likely best support bee habitat restoration.

Habitat loss and degradation are major factors driving insect declines (Wagner et al., 2021), and refocusing restoration practices on bees may help conserve native bee diversity and abundance.

TABLE 3 Research priorities that are critical for advancing the fields of bee conservation and habitat restoration.

Topic	Current knowledge	Research priorities
Bee foraging ranges	Bees use complex learning cues to determine where to forage.	Evaluate the influence of plant species diversity on bee foraging ranges.
Bee nutrition	The quality and quantity of floral resources impact bee health and survival.	Consider the effects of different micro or macronutrients. Establish databases for specialist bee nutrition.
Biotic factors and floral resources	Deer herbivory has caused a decline in bumble bee abundance in some systems.	Assess how biotic factors (i.e., herbivory) in other systems may impact bees.
Ground-nesting bees	Many factors influence ground-nesting bee behavior.	Evaluate the role of soil chemistry and soil microbial diversity for ground-nesting bees. Characterize nesting site attributes, evaluate nesting success under variable conditions, and share this information.
Non-floral Resources	Non-floral resources can be useful for native bee nesting and benefit bee health.	Assess the role of non-floral resources in bee habitat restoration. Characterization of non-floral resources, such as nesting material in shared databases. Increase inclusion of non-floral resources in bee host plant databases.
Non-native species	Non-native species can sometimes provide floral resources.	Assess whether non-native plants affect soils and ground litter, and determine how this impacts ground-nesting bees.
Pesticides & herbicides	Herbicides can be harmful to bees.	Establish sublethal effects of pesticides on native bees. Determine how herbicide use in restoration impacts native bee populations.
Plant patches	Bees prefer closer patches of floral resources for foraging.	Determine the quantity of floral resources necessary to support different types of native bees. Assess what patch attributes bees respond to when foraging.
Plant species origin	The provenance of seeds or plants can influence plant-pollinator interactions.	Compare the phenology of local and non-local plant provenance and determine if associated bees may be at risk for a phenological mismatch. Determine if non-local plant provenance has differing reproductive success than local plant genotypes.
Proximity to roadways	Roadways can cause declines in bee populations, and restoring sites near roadways can lead to ecological traps for bees.	Determine the optimal distance from roadways for implementing bee habitat restoration. Identify the threshold of roadway activity that negatively affects bees.
Seed mixes	Increasing plant diversity in seed mixes promotes bee diversity.	Determine how to best integrate phenology, taxonomy, and bee nutrition into affordable seed mixes. Establish a system to make site-specific seed mixes for a diversity of bee species and habitat types.
Solitary bees	Anthropogenic factors negatively impact the abundance and diversity of solitary bees.	Assess the extent to which solitary bees are declining and determine the role of restoration in preventing the local extinction of solitary bees.
Specialist bees	Host plants for specialist bees are well-documented for some species but not others.	Establish what host plants specialist bees rely on. Determine the quantity of floral resources needed to sustain a population of specialist native bees. Examine how we can aid the recruitment of specialist bees to newly restored sites.
Transplanting bee nests	Nests can be transported.	Assess the benefits and risks of transplanting native bee nests in bee habitat restoration.

Developing metrics for use as part of a rapid assessment protocol for bees is necessary to ensure clear quantitative and standardized outcomes of bee-centric restoration work across projects. If the establishment of metrics is widely adopted, this can provide specific information on the causes of successful or unsuccessful bee-centric restoration projects. Rapid assessment protocols are already employed in various restoration contexts (Obrist and Duelli, 2010; Collins and Stein, 2018). Similar protocols are currently being adapted to gauge the success of bee habitat restoration across ecological scales, from individual species to ecosystem functionality (Woodard et al., 2020). These protocols play a crucial role in providing standardized methodologies for evaluating the effectiveness of restoration efforts, facilitating the advancement of research, and promoting the implementation of bee-centric habitat restoration practices.

The restoration of bee habitats contributes to the overarching objectives of ecological restoration by increasing plant diversity and enhancing pollination services (Menz et al., 2011; Wratten et al., 2012; Wojcik et al., 2018; Cole et al., 2019). For example, restoring native plant communities to support bee populations can provide habitat and nutritional resources for a range of other species, including birds, mammals, and other invertebrates (Tallamy, 2020). Moreover, strategies that target the conservation of specialist bees can lead to the preservation of rare and endemic plant species, further contributing to the conservation of unique ecosystems (Motta et al., 2022). Restoring bee habitats within the framework of general restoration efforts can enhance pollination networks (Kaiser-Bunbury et al., 2017), promote ecosystem services, and improve plant and bee reproductive success (Albrecht et al., 2012; Danforth et al., 2019).

Author contributions

HP: Conceptualization, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. SM: Conceptualization, Supervision, Validation, Writing – review & editing. KS: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

Publisher's note

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Current trends in bee conservation and habitat restoration in different types of anthropogenic habitats

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Recent declines in bee populations and ranges have been cause for concern due to the valuable pollination service that they provide. Several factors have been proposed to contribute to these declines, including habitat loss, pathogen spread, and pesticide usage, so many pollinator conservation schemes have involved the addition of pollinator-friendly habitat through wildflower plantings and artificial nesting sites. Because of this, many efforts have been made to enhance bee populations across different landscape types, including natural, agricultural, urban, and industrial areas. Many of these schemes have focused on providing habitat for bees and other animal pollinators in agricultural landscapes, but other managed areas, such as cities, suburbs, and industrialized areas may have untapped potential for pollinator conservation. Available green space can be enhanced to provide healthy forage and safe nesting sites for pollinators. As these areas are also often frequented by human residents, the needs and perceptions of people, as well as the potential benefits for pollinators, must be considered to ensure the success of pollinator conservation on anthropogenic habitats.

KEYWORDS

wild bees, butterflies, wildlife, conservation, pollinator habitat, solar parks, roadside verges

1 Introduction

Bees, along with other flower-visiting insects and animals, provide the essential ecosystem service of pollination, which can benefit wild ecosystems, large-scale agricultural landscapes, and smaller residential gardens (Garibaldi et al., 2011; Ollerton et al., 2011; Lowenstein et al., 2015; Reilly et al., 2020; Allen-Perkins et al., 2022). Worldwide, around 85% of wild angiosperms are animal pollinated (Ollerton et al., 2011). In agriculture, over 75% of the leading food crops benefit from animal pollination, showing better yields and often larger, more appealing fruit when visited by pollinators (Foley et al., 2005; Klein et al., 2007; Sáez et al., 2020; Hünicken et al., 2021; Levenson et al., 2022). This pollination service improves the profits for growers, amounting to over $171 billion USD globally (Gallai et al., 2009). As well as providing pollination in natural and agricultural landscapes, bees and other animal pollinators can improve the fruit set of plants in residential gardens (Lowenstein et al., 2015; Reilly et al., 2020).

Despite their importance across these natural and anthropogenic landscapes, several native bee species of North America have had population and range declines in recent years, which can then lead to losses in the pollination services they provide. This has been best documented in the bumble bees (*Bombus* spp.) in North America (Colla and Packer, 2008; Grixti et al., 2009; Cameron et al., 2011; Jacobson et al., 2018), though in Europe, there is more documented evidence of similar declines in solitary bees (Rasmont et al., 2005; Fitzpatrick et al., 2006). In many regions, these declines have resulted in an overall loss in bee species richness and local pollinator populations (Turley et al., 2022; Nagamitsu et al., 2024), which are unable to meet the pollination requirements for dependent crops (Rucker et al., 2012; Degrandi-Hoffman et al., 2019). There have been several drivers implicated in these pollinator declines, including habitat loss, pesticide usage, parasites and pathogens, and climate change (Goulson et al., 2015; Belsky and Joshi, 2019; 2020).

The importance of bees and other pollinators, along with the concerns for their population declines, has led to an increasing need to mitigate risks and find ways to enhance pollinator populations across different landscapes (Alison et al., 2022; Glenny et al., 2022; Stout and Dicks, 2022; Duque-Trujillo et al., 2023). A growing trend in pollinator conservation has been the conversion and restoration of anthropogenic habitats, including cities, suburbs, and rights-of-way (ROWs) into pollinator habitat. Adding pollinator habitat to these managed areas, however, can increase human-pollinator interactions. Any pollinator habitat scheme on managed land cannot be for the benefit of the pollinators alone. Rather, for such schemes to be successful, they must rely on the support and enthusiasm of the human stakeholders who own or use the managed land. Here we discuss the potential benefits of developing pollinator habitat in these anthropogenic habitats, as well as the concerns for human health and safety that can arise from such schemes, in order to create more successful pollinator habitat schemes in human populated areas.

2 Enhancing managed landscapes in different habitats for floral resources

There are several managed lands with the potential to provide pollinator habitat and aid in pollinator conservation, including public parks, residential lawns, golf courses, solar parks, roadside verges, and powerline easements. Some of these areas already have semi-natural habitat that can be maintained and enhanced to provide pollinator forage, whereas others are degraded and would require more intensive conversion to provide adequate foraging and nesting sites for pollinators. These conversions could include seeding plots with native wildflowers, reducing pesticide spraying, or mowing less frequently at the sites (Muratet and Fontaine, 2015; Ramer et al., 2019). Any such conversions of developed areas would turn the land into multiple use sites and need to consider factors affecting the animal pollinators and human stakeholders in the area. These factors would include the original functionality of the site, the expense to implement and maintain pollinator habitat, the perception of the people who use it, and the benefit to local pollinator communities (Hopwood, 2008; Turo and Gardiner, 2019).

Currently, there is little national or international policy regarding habitat management for enhancing pollinator communities. In the United States, most policy implementation has occurred at the state or local level (Hall and Steiner, 2019; Bloom et al., 2022; DiDonato and Gareau, 2022; Pham et al., 2022; Campanelli et al., 2023). Increasing public awareness of pollination population declines and best management practices for improving habitat quality for these organisms, however, can increase local and regional scale improvements to pollinator habitat and populations in anthropogenic habitats.

2.1 Urban and suburban landscapes

Urban areas are often perceived as lacking in native wildlife populations, and many species decline in abundance as they move from natural to urban lands. Bees, however, have been shown to have fairly robust populations in many urban areas, especially when compared to intensive agricultural landscapes (Baldock et al., 2015; Samuelson et al., 2018; Guenat et al., 2019; Theodorou et al., 2020). With the proper management, urban and suburban landscapes are able to support a high diversity of bees and other pollinators (Baldock et al., 2015). Traditionally, most green spaces in cities and residential areas have mowed turfgrass lawns, herbicide applications for weed removal, and non-native ornamental plants (Aronson et al., 2017), which do not support as much pollinator richness and abundance as diverse floral plantings (Lowenstein et al., 2015). Additionally, most of the green spaces in urban areas are privately owned, leading to many individuals making management plans independently, rather than having a unified strategy (Aronson et al., 2017). Public perception of a habitat can also greatly influence the success of a conservation program, in both negative ways, including vandalism and protest, or positive ones, such as bringing in funding for the project (Turo and Gardiner, 2019). Any such programs, in order to be successful in urban and suburban areas, must consider the perceptions of the local residents, the expense and time to create and maintain the habitat, and the needs of the pollinators as well as opportunities for their conservation (Braman and Griffin, 2022).

Public parks are one type of urban green space with potential for creating bee habitat, either through planting low-growing flowers to replace turfgrass or through seeding areas of the park with wildflowers in order to create meadow patches. Surveys of park visitors in Minneapolis, MN reacted positively to the idea of enhancing turfgrass with low-growing forbs, such as lanceleaf coreopsis (*Coreopsis lanceolata*) and calico aster (*Symphyotrichum lateriflorum*), with over 95% of participants saying they would support the program (Ramer et al., 2019). Similarly, in a park in Saltdean, UK, 97% of park visitors supported management schemes to increase the abundance of wildflowers and insects

(Garbuzov et al., 2015). In spite of the support, several park visitors voiced concerns for schemes that would replace turfgrass with wildflowers. These included dislike of the "weedy" appearance of the wildflowers, fear of insects stings, and concerns that the flowers would take up usable park space (Garbuzov et al., 2015; Ramer et al., 2019). Insect stings can be medically relevant, with around 3% of adults that have systemic allergic reactions to them (Golden, 2017). These systemic reactions can result in anaphylaxis and even death in some cases, though occurrences tend to be low. In Europe, an average of 0.26 deaths per million people resulted from reactions to insect stings (Feás et al., 2022). Because of these concerns, any parks aiming to add pollinator habitat should keep areas well marked with signage and well maintained. Public outreach could also help inform people on the benefits of pollinators and keep them safer from stings (Ramer et al., 2019). Additionally, frequently mowed areas for recreation and sport should still be preserved in areas of the park.

In urban habitats, sections of residential lawns can also be converted from frequently mowed turfgrass into meadow patches to enhance pollinator populations, as frequent mowing can alter insect biodiversity (Proske et al., 2022). In an online national survey across the US, people in residential areas responded positively to the idea of adding wildflowers to their yards, though many cited concerns, such as "maintenance time" and "not knowing what to do" (Turley et al., 2020). In public outreach, then, conservation schemes should focus on residential programs that are simple, low maintenance, and relatively small scale (Turley et al., 2020). In addition to actively planting wildflowers, homeowners and renters can decrease mowing frequency to increase flower and pollinator abundance on their lawns (Lerman et al., 2018) and create pollinator friendly habitats in turfgrass systems (Billeisen et al., 2021).

Golf courses, which take up over 2 million acres of land in the US (Dobbs and Potter, 2015), offer another opportunity for pollinator habitat. By design, golf courses have mowed turfgrass fairways intermixed with woody areas and rough patches with taller grasses and other vegetation. These rough patches tend to have less intensive management than the fairways, with less mowing and reduced pesticide spraying, which makes them good candidates for bee habitats, as well as improving the aesthetics of the course (Dobbs and Potter, 2015). Enhanced golf courses with bee habitat can even host rare bee species, such as the three declining bumble bee species, *Bombus auricomus*, *Bombus pensylvanicus*, and *Bombus fervidus*, that were found on Kentucky golf courses after wildflower planting (Dobbs, 2013). Courses with wildflowers can also have greater bee abundance than those with turfgrass monocultures (Billeisen et al., 2021). As with the residential lawns, owners and managers of golf courses have voiced concerns over increased labor and maintenance for creating pollinator gardens (Bates et al., 2023). As such, any plantings should fit within the budget, labor, and time constraints of the golf course.

In cities, the proportion of impervious surfaces can impact pollinator abundance and species richness. Areas with high percentages of paved roads, parking lots, and buildings compared to green space provide smaller and more fragmented habitats for pollinators (Wenzel et al., 2020). Small-bodied pollinators, which fly shorter distances, in particular need more connected habitats to access resources (Zurbuchen et al., 2010). In city environments, green roofs have become more popular, and have several suggested benefits for the building and surrounding area, including reduced energy consumption, thermal regulation, improved air quality, and enhanced habitat in urban environments (Berardi et al., 2014). For bee pollinators, green roofs with flowering plants were able to support the same species richness and abundance as nearby fields (Colla et al., 2009). Building height, however, can limit the amount of pollinator species that are willing to fly up to the roof (Wu, 2019). Large- and medium-bodies bees were more commonly found on green roofs (MacIvor et al., 2015), so these roofs may not provide the same benefit to bees with shorter flight distances. The surrounding green space in the area can also impact the populations of bees on green roofs (Wu, 2019). Although cities can support numerous pollinator species, they often fail to provide suitable habitats for the rarest and most sensitive species with critical conservation status (Fauviau et al., 2024).

In the urban and suburban areas, where human residents are living and working in close proximity to these added pollinator habitats, the financial and cultural factors become especially important. For instance, pollinator habitats along footpaths and city roadsides, lacking signage, may appear overgrown and weedy to some residents, so improving public opinion of the sites can involve collaboration between ecologists, community leaders, landscape designers, and others, as well as adding "cues of care" to the habitats, signals to the residents that the areas are being maintained. As urbanization increases, finding successful ways to add pollinator habitat to urban and suburban areas can help maintain pollinator populations and pollination services (Derby Lewis et al., 2019). The interaction of bee habitats with the local human communities - not just the impact of humans on the habitat, but also the habitat on the community - is an important issue that is often overlooked in urban conservation schemes, but one that must be considered for their success (Turo and Gardiner, 2019).

2.2 Solar parks

As solar panels are becoming increasingly cost effective and solar photovoltaic energy one of the primary types of renewable energy, the land use dedicated to solar energy production is expected to increase (IEA, 2019; Blaydes et al., 2021). Though many people have installed solar panels on the roofs of buildings, widespread solar energy requires ground-mounted solar panels (Blaydes et al., 2021). Several solar energy companies have placed their ground-mounted panels in flat gravel-covered lots or fields of turfgrass, though some have put the land to agricultural use (Semeraro et al., 2022), by growing crops (Moore et al., 2022) or hosting livestock amongst the panels (McCall et al., 2023). Another proposed idea is to put in native prairie grasses and flowers, with low-growing, shade-tolerant plant species directly beneath the panels to provide habitat for pollinators (Davis, 2016) or to enhance population of certain bee species (Blaydes et al., 2022). Some solar parks have already established plantings of native perennial wildflowers and have had higher bee abundance compared to solar parks with only gravel or turfgrass (Randle-Boggis et al., 2020). Native prairie plants could have the additional benefit of improved erosion control and an even more environmentally conscious face for the solar companies (Briberg, 2016; Davis, 2016).

Some environmental and cost concerns have been raised for establishing native plantings in photovoltaic solar parks (Lafitte et al., 2022; McCall et al., 2023). The polarized light reflected off of solar panels can impact the movement and behavior of polarotactic insects, especially those that oviposit in aquatic environments. The solar panels may mimic the glare of sunlight on bodies of water (Horváth et al., 2010; Száz et al., 2016). Most studies have looked at insects with juvenile aquatic phases, such as Trichoptera, Ephemeroptera, and certain Diptera (Horváth et al., 2010; Száz et al., 2016). The area beneath the solar panels tends to be cooler and shadier than the surrounding environment, which can impact plant growth and pollination activity around the panels (Armstrong et al., 2016; Graham et al., 2021). While active pollination still occurred in the full shade regions below panels, the diversity and abundance of pollinators was lower in the full shade compared to partial shade and full sun areas (Graham et al., 2021). Pollinator gardens in solar parks would need to include shade-tolerant flowering plants in the areas under and directly around the panels. The addition of these gardens may provide the greatest benefit to more cold-tolerant pollinators, such as bumble bees (*Bombus* spp.) (Dehon et al., 2019). The implementation and first years management of native plantings can be more expensive and intensive than other solar park management options, such as sheep grazing, gravel lots, and turfgrass (McCall et al., 2023).

2.3 Rights-of-way: roadside vegetation

Roadside verges, the strips of land alongside roads, cover around 50,000 km^2 in the US, and provide a large area of land that could be used for wildlife habitat (Forman et al., 2003; Phillips et al., 2020). They tend to have more diverse plant species than many agricultural landscapes, including several early successional flowering plants (Hopwood et al., 2015; Phillips et al., 2020). Though roads themselves can cause habitats to become more fragmented, roadside verges can serve as corridors between habitats for insects (Hopwood et al., 2015), and these habitats have potential to support greater pollinator abundance (Dietzel et al., 2023).The conventional methods of maintenance of these sites include frequent mowing, use of non-native grasses, and herbicide spraying for weed control. Restored roadsides, those that have been seeded with native grasses and forbs can provide more flowering plants and support higher numbers and diversity of bees (Figure 1). There are concerns for the pollinators in providing habitat for them alongside roads (Meinzen et al., 2024). Management practices such as mowing of the roadside verges can impact pollinator community as well as their abundance. Similarly, proximity to roads can increase the incidents of vehicle collisions and the amount of automobile pollution, including heavy metals to which they are exposed (Phillips et al., 2020) and the contaminated roadside pollinator habitat (Shephard et al., 2022). Traffic intensity alongside road verges with pollinator habitat can also affect population of certain bee species such as bumblebee (Dániel-Ferreira et al., 2022). Verges alongside roads

FIGURE 1
Illustration showing establishment of pollinator habitats in roadside verges. These pollinator habitats can support diverse communities of pollinators as well as native plant species.

with less traffic and lower speed limits would likely provide the greatest benefit and lower risk for insect pollinators, though more research is need into the balance of potential hazards and benefits for pollinators in roadside verge habitats. Creating a mowed buffer zone directly alongside the road, with wildflowers planted at least 3 meters away from the edge of the road, may also reduce the risk of collision and contaminant exposure for pollinators (Meinzen et al., 2024).

The greatest human concern for roadsides is road safety, visibility, fire risk, and soil erosion prevention. Wildfires are becoming more common and more extreme in many areas, so the assessment of fire risk along roads is vital. The climate conditions of a region, the amount of dead plant matter, and the flammability of plant species can all impact the likelihood of ignition as well as the duration and intensity of a wildfire (Silva et al., 2014; Molina et al., 2019). Certain plant species are more flammable due to their moisture content and physical and chemical properties (Molina et al., 2019). Roadside design and maintenance can help reduce fire risk by properly assessing these factors and selecting lower risk plants for establishing in verges (Ree et al., 2015; Molina et al., 2019). In the United States, California has experienced frequent largescale wildfires in recent years, especially during drought conditions (Keeley and Syphard, 2021). Global regions like this, which are at high risk of drought conditions and wildfires, should prioritize fire safety near roadsides. Any added wildflower species for pollinators should be selected for low flammability. Mowing and removal of dead plant matter may also be required, which could increase labor costs of roadside maintenance. Though these verges have great potential for pollinator habitat the safety and usability of roads for humans has to be given priority.

2.4 Rights-of-way: powerline easements

Another right-of-way that has been proposed for habitat restoration is the land running along powerlines. In the US, powerline easements take up a sizeable area of land, around 5 million acres in total (Russell et al., 2005). These clearings can offer a different array of flowers and grass species than forested areas, and often a higher diversity of plant species. Instead of frequently mowing around powerline strips, the land along them could be converted into semi-natural grasslands (Eldegard et al., 2017) and pollinator habitat (Figure 2). Converted habitat around powerline easements can host early successional flowering plants and can have a greater diversity of pollinators than forested areas (Wagner et al., 2019) or other resource-poor landscapes (Du Clos et al., 2022), and can also support a diversity of species other than pollinators (Garfinkel et al., 2022). In Pennsylvania, nearly 30% of known bee species in the state were collected along a single powerline easement over a two-year study (Russo et al., 2021). Successful management for pollinator-friendly powerline easements would involve reduced herbicide usage, as well, as heavy usage of broad-spectrum herbicides correlated with lowered bee species richness in these habitats (Russo et al., 2021). It would be beneficial to add cues of care to such pollinator habitats, as well, to prevent the easements from seeming abandoned and unmaintained. These could include adding mowed borders around the tall grasses and flowers or adding signs that identify the area as restored prairie habitat for pollinators.

As with roadside verges, however, powerline easements can contribute to wildfire risk, especially in vulnerable and drought-prone regions. Powerline corridors are high risk areas for starting wildfires, as faults in the electrical grid, due to equipment failure or falling trees, can ignite surrounding vegetation (Arab et al., 2021).

FIGURE 2
Illustration showing converted land around powerline easements into pollinator habitat to support pollinator species diversity.

Most fire prevention schemes around powerline include removing trees from growing too close to the lines (Mitchell, 2013; Arab et al., 2021). Taller vegetation, like trees, pose the greatest risk of falling onto or against powerlines, and starting a wildfire. Conversely, trees and larger vegetation tend to only ignite at a higher temperature compared to smaller grasses, twigs, and leaves. As such, they are less likely to catch fire, but these canopy fires can be more devastating than surface fires over low growing grasslands (Jahn et al., 2022). When it comes to adding wildflowers and pollinator habitats to powerline easements, fire safety and prevention must remain a higher priority. Low growing, early successional plants pose little risk of interfering with powerlines or with increasing biomass within the easements (Clarke and White, 2008). In regions of high wildfire chance, low flammability species and ease of management should be prioritized, in order to maintain human and environmental safety.

3 Supplementing landscapes with nesting materials

Any conservation schemes to benefit pollinator populations must consider the habitat requirements of the bees in order to survive and successfully reproduce. Along with floral resources, bees need undisturbed nesting sites that are close to their foraging areas (Kline and Joshi, 2020). Several native bees, including many in the family Megachilidae, nest in existing cavities. Nest boxes or "bee hotels," especially those with a variety of nesting substrates can promote bee nesting for tunnel-nesting species (Fortel et al., 2016). These tube nest boxes need frequent monitoring and maintenance, however, to keep out parasites and predators. Nest tube liners, such as paper straws, can be used to reduce mites and other pests, but need to be replaced annually (Wilkaniec and Giejdasz, 2003; Joshi et al., 2020). Many of these tunnel-nesting bees also use mud, leaf pulp, or resin in their nest construction, and need those materials available close to their nest boxes (Torchio, 1989). Most bee species, however, are ground nesting, preferring to dig tunnels into soil. The preferences of bees, as far as soil compaction, texture, alkalinity, can vary greatly by species (Cane, 1991). Providing safe areas for these bees can involve leaving patches of untilled and exposed ground within wildflower gardens. One study in France found that many ground nesting bee species were willing to nest in more artificial nests, as well such as wood frame boxes filled with soil (Fortel et al., 2016). Many studies have shown that diverse floral resources can improve pollinator abundance and species richness, but safe nesting sites near these flower planting can also greatly benefit pollinator populations (Bortolotti et al., 2016).

4 Conclusions

Anthropogenic habitats can offer the potential to aid in pollinator conservation, as long as the land use requirements of both the humans and insect pollinators are considered. For humans, the safety, effectiveness, and perception of the land are important. Any conversion of managed land into pollinator habitat cannot be so drastic as to lose the original function of the land, and collaborations between ecologist and other stakeholders such as landscape architects could strengthen conservation efforts to maximize biodiversity in urban areas (Kiers et al., 2022). For pollinators, both generalist and specialist feeders can benefit from a diverse selection of flowering plants, with staggered bloom times throughout the bee foraging seasons (Aronson et al., 2017), as well as undisturbed nesting sites. Low frequency mowing and reduced pesticide usage can also greatly benefit pollinator populations (Blaydes et al., 2021; Russo et al., 2021). As a result of different conservation efforts, it is likely that the benefits to pollinator populations will be greatest in areas with more intensive agriculture and urbanization, which may have declines in their pollinator communities. Additionally, increased pollinator populations in urban, suburban, and industrial areas have the potential to spill over into agricultural and even natural lands (Blitzer et al., 2012). Most of the research in this field has been done in Europe, and to a lesser extent North America, and so more information is needed globally to better plan pollinator conservation schemes effectively. Effective pollinator conservation schemes rely on the coordination of research entomologists, landowners, and other stakeholders (Stout and Dicks, 2022), but they have great potential to mitigate some of the recent pollinator population declines and aid in enhancing pollinator populations in these developed areas.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

OK: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. NJ: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Comparing species richness and abundance of bumble bees between urban and natural areas using a photographic survey approach

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Bumble bees are essential pollinators that provide critical ecosystem services yet, studies are documenting global species declines while recognizing those declines may be understated due to insufficient baseline data. This study investigates bumble bee species richness and abundance across urban and natural sites in Prince Edward Island, Canada, focusing on Charlottetown (urban) and Prince Edward Island National Park (natural). We conducted fieldwork in August and September 2019 using a non-invasive photographic survey technique. We used published keys and sought feedback from citizen science platforms like iNaturalist and Bumble Bee Watch to verify species identification. Our results revealed nine bumble bee species, with *Bombus impatiens* being the most abundant and *Bombus perplexus* the rarest. Species richness was higher in natural sites, while urban sites demonstrated moderate levels of bumble bee diversity. Additionally, our findings suggest that sites containing a mix of natural and human-cultivated plant types, predominantly found in our urban study sites, may support higher diversity and evenness levels than those of homogenized plant types (natural or human-cultivated). This research illustrates the practicality of photographic surveys to document the species richness and diversity of bumble bees while avoiding disturbance to populations in urban and natural habitats of Prince Edward Island.

KEYWORDS

bumble bees, urbanization, photographic surveys, pollinators, species richness, conservation, baseline data

1 Introduction

Urbanization is recognized as a major cause of pollinator habitat loss, mainly promoted by the rapid growth and concentration of human populations in urban centers. From the ecological point of view, urban areas are a unique mosaic of residential, commercial, and industrial habitats ameliorated by green spaces (Breuste et al., 2008). Researchers frequently document urbanization's negative impacts on species diversity and abundance of a broad range of taxa. Yet, with effective conservation measures, pollinators, including bumble bees, can successfully use urban habitats (Blackmore and Goulson, 2014) and may prefer urban spaces to agriculturally dominated spaces (Samuelson et al., 2018).

Bumble bees (genus *Bombus*) are a major group of bees comprising approximately 260 species globally (Fisher et al., 2022). They pollinate a wide range of flora, including species vital to agriculture (Milanoa et al., 2019; Samuelson et al., 2018), species of conservation concern (Baldock, 2020; Potts et al., 2016), and those that support global food security (Fauser-Misslin et al., 2013; Marshman et al., 2019). *Bombus* species possess several physiological (e.g., Heinrich, 1975; Heinrich and Kammer, 1973; Masson et al., 2017), morphological (e.g., variable tongue phenology; Arbulo et al., 2015; Grixti et al., 2009) and ecological (e.g., buzz pollination; Nunes-Silva et al., 2013) characteristics that contribute to their success as pollinators (Bond, 1994; Sheffield et al., 2003). Not only have bumble bees earned the label of keystone species within urban habitats (Goulson et al., 2011; Parrey et al. 2021), their nests can host parasitic and commensal species (Cameron et al., 2007), demonstrating their further value in providing ecosystem services (Winfree et al., 2007). The queens of parasitic species within the *Bombus* genus, also called cuckoo bumble bees (subgenus *Psithyrus*), locate established nests and kill or dominate the resident queen of a preferred *Bombus* host species (Lhomme and Hines, 2018). The dominant queen will then use the resident queen's workers to rear her reproductive offspring (Lhomme and Hines, 2018); therefore, *Psithyrus* subgenus species lack worker castes.

Aside from collection reviews, scientists typically survey bumble bees using traps or bowls (Armistead, 2023; Bell et al., 2023), which are passive techniques involving lethal capture. Lethal capture techniques vastly reduce time and labor commitments (e.g., Brooks and Nocera, 2020; Montero-Castaño et al., 2022) but involve a certain level of disturbance in populations and ecological communities surveyed. Conducting surveys while limiting population disturbance is particularly important when studying rare or at-risk species (Montero-Castaño et al., 2022; Bell et al., 2023). A more labor-intensive yet still effective approach is netting to capture individuals for collections or subsequent analysis and release (Bell et al., 2023; Dominey, 2021). A non-lethal, non-invasive approach that may be used to survey pollinators, such as bumble bees, is the photographic survey. In this method, the researcher collects photos of individual animals and identifies them via their color patterns and physical characteristics (Williams et al., 2014). While requiring more labor than lethal capture, photographic surveys are very cost-effective. The studies that have used photographic surveys to document the presence or abundance of bumble bees have shown that this method of surveying can effectively quantify and distinguish bumble bee species provided the researchers possess expertise in bumble bee taxonomy (e.g., MacPhail et al., 2020). In addition, digital cameras are not required to take high-quality images of most bumble bee species. Most smartphones possess cameras that can provide excellent photos of bumble bees hovering around and on flowering plants. Citizen science platforms like iNaturalist and Bumble Bee Watch rely on photographic submissions and have become a popular approach to documenting bumble bee abundance and distribution (Falk et al. 2019; MacPhail et al., 2020; Suzuki-Ohno et al., 2017). Typically, experts take time to review submissions on citizen science platforms that improve accurate species identification. Yet, it is important to distinguish that some platforms allow any user to suggest identification. For example, Bumble Bee Watch submissions are verified by experts, whereas iNaturalist allows any user to suggest an identification that may falsely become considered "Research Grade."

Within the urban context, green spaces may include human-made gardens, parks, playgrounds, trails, cemeteries, and enclaves of natural and semi-natural plant communities (Daniels et al., 2020; Wood et al. 2018). Some researchers studying bumble bees in urban areas have documented lower flower visitation rates, lower species richness, loss of rare species, and homogenization of species pools (Deguines et al., 2016; Harrison et al., 2019; Hernandez et al., 2009), while others are documenting that many large-bodied, social, and generalist pollinator species can thrive in urban environments (Liang et al., 2023). Some have found bumble bee diversity to be relatively higher in urban areas because of the assortment of flora that characterizes urban green spaces (Baldock et al. 2015; Theodorou et al., 2021), particularly individual and community gardens (Baldock, 2020). Studies have shown that bumble bees can colonize urban areas with a relatively small cover of green space (e.g., Hernandez et al., 2009; Matteson et al., 2008; Matteson and Langellotto, 2010; Tommasi et al., 2004), provided the green space offers favorable and beneficial characteristics (Nunes et al. 2024). Urban spaces may offset the negative impacts that surrounding agricultural (e.g., lower reproductive rates, smaller peak sizes) and rural areas (e.g., less variation of floral resources) may pose on bumble bee populations (Nunes et al. 2024; Samuelson et al., 2018). It is important to note that habitat requirements vary between bumble bee species, which also helps explain how studies focusing on specific bumble bee species can produce contrasting results (Liczner and Colla, 2020).

Prince Edward Island (PEI) is the smallest Canadian province with only 600,000 hectares of land (Kolinjivadi et al., 2020), situated in the Gulf of St. Lawrence on the eastern coast of Canada. Since European colonization, roughly three centuries ago, anthropogenic activities such as forestry, agriculture, and urbanization have altered the natural habitats of PEI. Some active research has been conducted on bumble bees in Eastern Canada (e.g., Brown, 2022; Dominey, 2021). However, only one study (Laverty and Harder, 1988) has supplied precise information about bumble bees in PEI. Laverty and Harder used museum and private collections and recorded nine bumble bee species in the natural areas of PEI: *Bombus borealis*, *Bombus citrinus*, *Bombus fervidus*, *Bombus* *insularis*, *Bombus rufocinctus*, *Bombus sandersoni*, *Bombus ternarius*, *Bombus terricola*, and *Bombus vagans* (1988). Unfortunately, they did not offer any details pertaining to bumble bee species in urban PEI.

Specifically, the objectives of this study were (1) to provide baseline data on species richness, diversity, and relative abundance of bumble bees occurring in urban and natural areas of PEI (2) to assess the usefulness of photographic surveys for monitoring bumble bee populations; and (3) to compare the diversity and composition of bumble bee communities between urban and natural areas of PEI. Based on studies conducted in other regions of North America, we predicted that the natural areas of Prince Edward Island would support a more diverse bumblebee community compared to urban areas. This is because of the availability of preferred native flora (Carvell et al. 2017) and less anthropogenic disturbance. We also expected higher bumble bee abundance levels in sites dominated by natural flora compared to human-cultivated flora (i.e., ornamental plants). Although Laverty and Harder did not document *Bombus impatiens* in PEI (1988), we expected to find this species in both urban and natural sites. This prediction was based on *B. impatiens* being a generalist species that is widely distributed in Eastern North America (e.g., Matteson and Langellotto, 2009) and their range has artificially expanded because of their usefulness in commercial crop pollination (Palmier and Sheffield, 2019; Velthuis and Doorn, 2005).

2 Materials and methods

2.1 Study sites

PEI is Canada's smallest Atlantic province, located in the Gulf of St. Lawrence (Silva et al., 2005). The largest urban area of PEI is its capital, the city of Charlottetown (50 km^2 area), which has a population of roughly 44,000 individuals (Statistics Canada, 2018) (Figure 1).

In order to compare the diversity and composition of bumble bee communities in urban and natural areas of PEI, a total of 20 sites were surveyed in PEINP and another 20 sites in Charlottetown (Figure 1). Charlottetown sites (20/20) included walking trails, parks, public gardens, and open green spaces, in locations that could represent the interior and boundaries of the city. Sites typically consisted of native and non-native naturally occurring species (e.g., aster spp., autumn hawkbit, clover spp., dandelion spp., goldenrod spp., and thyme spp.) and/or human cultivated species (e.g., begonia spp., chrysanthemum spp., cinquefoil spp., phacelia spp., and sedum spp.). PEINP sites consisted mainly of open green spaces with native and non-native wildflowers (aster spp., clover spp., common eyebright, goldenrod spp., knapweed spp., wild rose, and tufted vetch). PEINP contains 27 km^2 of protected natural habitats but it is important to note that it also includes human infrastructures (e.g., campgrounds, visitor and

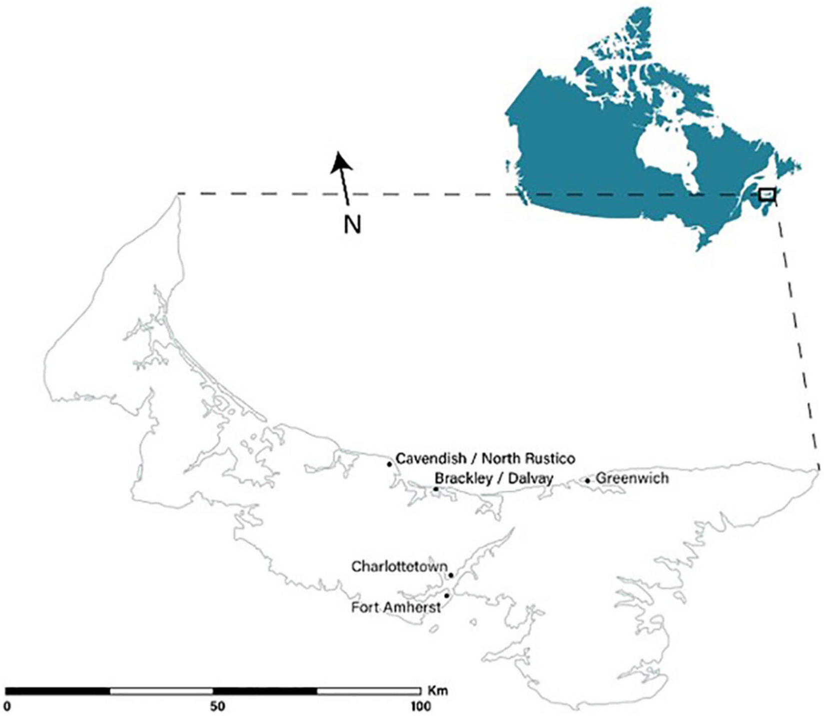

FIGURE 1
General location of bumble bee photographic surveys conducted in August and September 2019 between urban (Charlottetown, Prince Edward Island) and natural sites (Prince Edward Island National Park).

interpretation centers) that are used predominantly during the summer. Given the substantial level of anthropogenic disturbance in Charlottetown, three major areas within PEINP were selected to encompass a broad spectrum, ranging from moderate anthropogenic disturbance to predominantly natural environments. The Cavendish/North Rustico sites (9/20) display moderate disturbance and the least natural characteristics. This area was selected for this study because of its similarity with Charlottetown, as it sustains a higher level of anthropogenic activities and human infrastructure while encompassing the least abundant amounts of green space compared to other PEINP locations. Disturbance is especially obvious during the summer when tourists visit PEINP and the town of Cavendish. In contrast, the Brackley/Dalvay sites (5/20) exhibit a moderate level of disturbance along with moderate instances of human infrastructure. Finally, the Greenwich/Fort Amherst sites (6/20), while geographically separated, demonstrate the least amount of infrastructure and rates of visitation, while displaying the highest influx of natural characteristics (forested areas, wetlands, and uncultivated fields), that could represent natural areas of PEI. In this study, we categorized the vegetation at all surveyed sites into three main groups: natural (including native and non-native plants), human-cultivated (such as ornamental plants), and mixed (a combination of natural and human-cultivated) based on the dominant plants present at each site. We used the provincial vegetation classification standards (e.g., Government of Prince Edward Island, 1977; Pollinator Partnership Canada, 2017) for this classification.

2.2 Photographic survey of bumble bees

For this study, we opted for a non-lethal, non-invasive photographic survey method at the request of Parks Canada. This decision was made to avoid capturing live animals within PEINP and to minimize disturbance to bumble bee populations. We chose photographic surveys because we believe photographs are a reliable survey instrument, especially when complimented via citizen science platforms utilized or managed by field experts that verify identification. We conducted a literature review to identify the specific characteristics of species expected to occur in PEI and used the identification key published by Williams et al. (2014). In addition, we also consulted local and regional experts to ensure that our list of characteristics was accurate and exhaustive. Experts from the citizen science platforms were consulted for species that exhibited similar physical characteristics or if we were unsure of an individual species identification.

2.3 Survey protocol

We surveyed each study site in August and September 2019, between 1000 and 1600, when the ambient temperature was at least 12°C, and no prolonged rain periods or strong winds during the survey time (*sensu* Pacific Northwest Bumble Bee Atlas, 2019). Even though bumble bees can fly in less suitable weather conditions relative to other bees, maintaining optimal weather conditions allows for high-quality photos of bumble bees, as strong winds can make selective focusing extremely challenging, and low light periods can greatly reduce photo quality. Two sites in Charlottetown and one in PEINP could not be re-surveyed in September for reasons out of our control. We opted not to use pre-determined transect lines to avoid the unintended exclusion of flora in bloom within the selected site (Nielsen et al. 2011). Therefore, transect lines varied slightly from August to September, as required, if the location of blooming floral resources had alternated. To reduce the possibility of double counting the same individual bumble bee, each survey was conducted for 10 minutes and involved continuously walking in a direction (e.g., meandering East to West) and only changing directions sharply if required (e.g., urban park site with flora positioned in a bordering L shape). Timers were paused if an individual bumble bee displayed uncharacteristic color patterns requiring significant photographs to further aid in accurate identification (e.g., individuals with lost hair, unusual pigmentation, and morphologically similar species).

Photographs were taken with a smartphone (Samsung S8 generation; 2268 x 4032 pixels) to provide an optimal view of the abdomen, face, and thorax of bumble bees (Figure 2). An initial attempt was made to distinguish each bumble bee at the species level during the photographing process in the field. Confirmation of

FIGURE 2
Example of photographic procedure for each individual bumble bee so that multiple angles of the specimen are recorded to ensure accurate species identification **(A–D)**. Photos taken by Janelle MacLeod of *B. bimaculatus* on August 17, 2019.

the identification was made by examining the photographs on a laptop and noting distinct morphological features (e.g., abdomen/tail color, facial hair, and the number/pattern of bands) (*sensu* Laverty and Harder, 1988). We could confidently recognize most species in our study sites by assessing morphological traits. Field observations and photographs did not permit us to distinguish confidently between *B. vagans* and *B. sandersoni* (two species expected to occur in PEI), therefore we grouped all potential observations of individuals from these two species into one group for data analyses (*B. sandersoni/B. vagans*). The photographs depicting bumble bees with un-characteristic color patterns were posted on iNaturalist (iNaturalist, 2020) and/or Bumble Bee Watch (The Xerces Society et al., 2020) as well as individuals from each species with typical patterns to confirm surveyor validation.

2.4 Data analysis

To assess community structure at each site in Charlottetown and PEINP, we computed species richness and Simpson's index of diversity. We used evenness as a measure of relative abundance. Evenness values were calculated as the inverse of the Simpson's index for each study site in both August and September (Krebs, 1989). Evenness reflects the relative abundance of species, indicating whether a community is dominated by a few species or if species are more evenly distributed. For example, if a community has high evenness, species are in similar abundance. Conversely, low evenness indicates that a few species are much more abundant than others. All community measurements, including species richness, species diversity, and evenness, were computed using Stata. Log transformation was applied to variables as needed to meet the assumptions of parametric statistical analyses. Multiple regression analyses were employed to investigate the influence of vegetation types and surveyed months on species diversity and evenness, while Poisson regression analysis was utilized to explore their effects on species richness.

3 Results

Overall, we observed 1,414 individual bumble bees in the 40 sites surveyed in this study (Table 1). Approximately the same number of bumble bees were photographed for Charlottetown (n = 705) and PEINP (n = 709). The most frequently observed species was *B. impatiens* representing ~79% of the observed bumble bees in Charlottetown sites and 58% in PEINP sites. *B. perplexus* and *B. bimaculatus* were only photographed in the Charlottetown sites (Figures 3–6). The average species richness in Charlottetown sites was 2.47 ± 1.33 (Table 2) and 3.56 ± 1.17 in PEINP (Table 3). Charlottetown displayed relatively lower species diversity, averaging 1.58 ± 0.67 compared to 2.13 ± 0.79 within PEINP. For evenness, the average in Charlottetown was 0.73 ± 0.23, while in PEINP, it was 0.62 ± 0.19.

Of the total individuals photographed in this study, 7.3% were submitted to either iNaturalist or Bumble Bee Watch platforms to attempt to ascertain the accuracy of our initial species identification. Identifications via iNaturalist were predominantly confirmed by expert John Ascher (curator for the platform and Assistant Professor at the National University of Singapore). Identifications via Bumble Bee Watch were confirmed by expert Victoria MacPhail (Environment and Climate Change Canada). Photographs of bumble bees identified as *B.vagans/sandersoni* were posted on iNaturalist and Bumble Bee Watch platforms but generally only confirmed to *Pyrobombus*. Based on all the responses from the experts on these platforms, only 3% of our preliminary identifications were inaccurately identified.

For the statistical analysis, month and site were significant for species richness (p-value = 0.0314). Species diversity was higher in all PEINP sites than Charlottetown in August and September (p-value = 0.0006). Cavendish/North Rustico sites displayed a 30% higher diversity index than Charlottetown. Plant type was the only significant predictor of evenness (p-value = 0.0184). Evenness index was lower in anthropogenic settings than natural, yet mixed settings

TABLE 1 Total bumble bee abundances based on photographic surveys conducted in August and September 2019 in Charlottetown, Prince Edward Island and Prince Edward Island National Park.

Charlottetown			Prince Edward Island National Park		
Species	August	September	August	September	
B. bimaculatus	12	0	0	0	
B. borealis	2	0	16	5	
B. fervidus	1	0	3	0	
B. impatiens	249	309	138	274	
B. perplexus	1	0	0	0	
B. rufocinctus	72	32	88	25	
B. ternarius	3	4	40	45	
B. terricola	9	1	7	0	
B. vagans/sandersoni	6	4	36	32	
Totals	355	350	328	381	**1414**

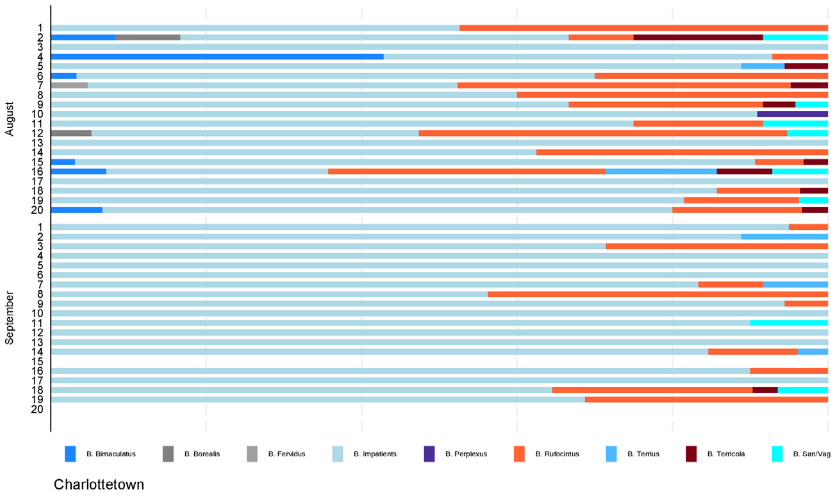

FIGURE 3
Distribution of bumble bees by site. Proportions of identified species by sampling month and location from photographic surveys conducted in Charlottetown, Prince Edward Island in August and September 2019. Site number is indicated on the y-axis which accounts for all sites within the study area. Sites were surveyed in August and re-surveyed in September; sites with no data in September indicate sites that could not be re-surveyed due to reasons out of our control.

displayed a higher index than natural by 24%. The results of all models are presented in Table 4.

4 Discussion

4.1 Baseline data for Charlottetown, PEI and PEINP

In our study sites, we observed nine bumble bee species, six of which were also recorded by Laverty and Harder in 1988. Two expected species, *B. vagans* and *B. sandersoni*, are difficult to differentiate without close inspection. Therefore, we only confirmed the subgenus *Pyrobombus* as representing one species, but both species may be present, which would account for seven of the nine species expected. In addition, we found two species, *B. perplexus*, and *B. bimaculatus*, only in Charlottetown sites, which had not previously been reported in PEI. This is an important finding suggesting that *B. bimaculatus* may be expanding its range into Atlantic Canada, confirming observations made by Dominey (2021) in the neighboring province of Nova Scotia. Furthermore, based on "Research

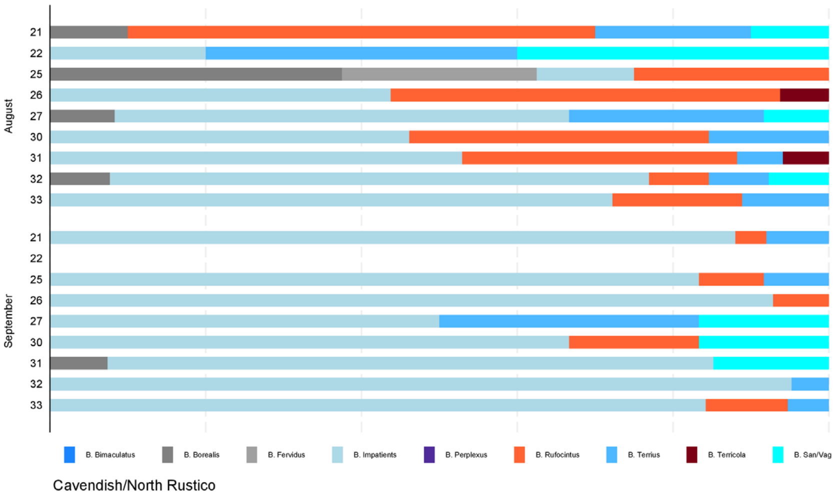

FIGURE 4
Distribution of bumble bees by site. Proportions of identified species by sampling month and location from photographic surveys conducted in the locations within Cavendish and North Rustico of Prince Edward Island National Park in August and September 2019. Site number is indicated on the y-axis which accounts for 9 of the 20 sites in the study area. Sites were surveyed in August and re-surveyed in September; sites with no data in September indicate sites that could not be re-surveyed due to reasons out of our control.

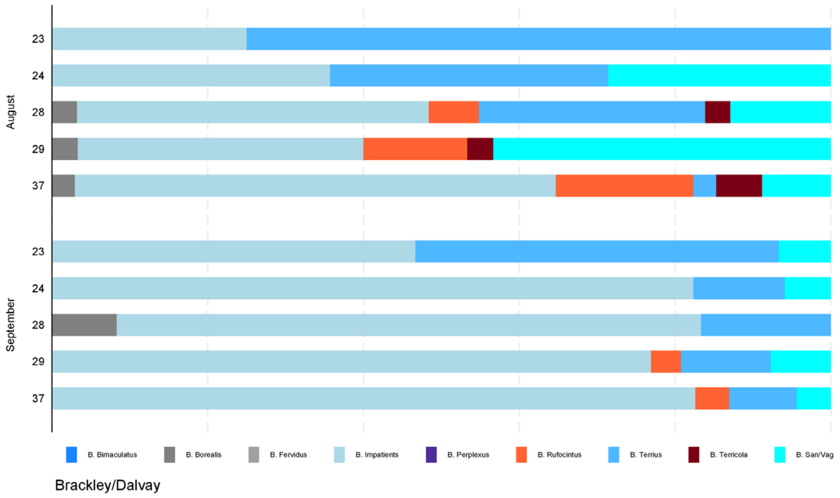

FIGURE 5
Distribution of bumble bees by site. Proportions of identified species by sampling month and location from photographic surveys conducted in the locations within Brackley and Dalvay of Prince Edward Island National Park in August and September 2019. Site number is indicated on the y-axis, accounting for 5 sites of the 20 sites in the study area. Sites were surveyed in August and re-surveyed in September.

Grade" iNaturalist records, *B. bimaculatus* is most abundant between July and early September. This may explain why all 12 individuals we observed from this species were photographed only in August.

We only observed one individual of *B. perplexus*, documented in urban site (Site 10) on the southern border of the survey area and on an ornamental plant (chrysanthemum sp.). While listed as secure for the research location (NatureServe, 2024), limited documentation is not completely surprising given with the restricted survey period. Yet, we observed relatively higher abundances of *B. terricola*; while *B. terricola* is considered a common species (NatureServe, 2024), they are listed as Species of Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2015). Although the seasonal activity of *B. perplexus* typically reaches peak abundance slightly earlier than *B. terricola*, our observations showed overlap. The higher number of *B. terricola* (n=10) compared to *B. perplexus* (n=1) suggests that *B. perplexus* may be experiencing declines. However, additional studies are necessary to confirm this trend throughout the species' active life cycle in PEI.

No specimens of *B. citrinus* or *B. insularis* were observed at any of our urban or natural sites. The most likely explanation for the absence of these two species is that they are parasitic species without worker castes, making them difficult to observe. According to both iNaturalist and Bumble Bee Watch, there are sufficient "Research Grade" sightings of individuals from both *B. insularis* and *B.*

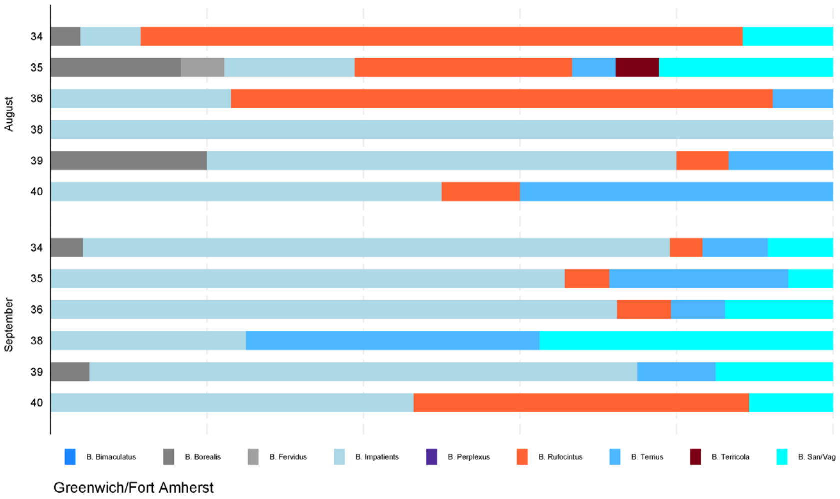

FIGURE 6
Distribution of bumble bees by site. Proportions of identified species by sampling month and location from photographic surveys conducted in the locations within Greenwich and Fort Amherst of Prince Edward Island National Park in August and September 2019. Site number is indicated on the y-axis, accounting for 6 of the 20 sites in the study area. Sites were surveyed in August and re-surveyed in September.

TABLE 2 Measurements of species richness, species diversity, and evenness for all photographic bumble bee survey locations in Charlottetown, Prince Edward Island, surveyed in August and September 2019.

Area	Site Number	Latitude	Longitude	August 2019			September 2019		
				Species Richness	Diversity	Evenness	Species Richness	Diversity	Evenness
Charlottetown	1	N 46.240921	W −63.114520	2	1.994	0.997	2	1.105	0.552
	2	N 46.232382	W −63.120434	6	3.273	0.545	2	1.246	0.623
	3	N 46.238311	W −63.124696	1	1.000	1.000	2	1.690	0.845
	4	N 46.248434	W −63.127440	3	2.279	0.760	1	1.000	1.000
	5	N 46.254488	W −63.134771	3	1.256	0.419	1	1.000	1.000
	6	N 46.229486	W −63.136883	3	1.867	0.622	1	1.000	1.000
	7	N 46.248482	W −63.153200	4	2.410	0.602	3	1.412	0.471
	8	N 46.262694	W −63.149789	2	1.923	0.962	2	1.969	0.985
	9	N 46.229310	W −63.128495	4	1.959	0.490	2	1.117	0.559
	10	N 46.233774	W −63.132065	2	1.198	0.599	1	1.000	1.000
	11	N 46.257847	W −63.147050	3	1.674	0.558	2	1.220	0.610
	12	N 46.258091	W −63.147240	4	2.456	0.614	1	1.000	1.000
	13	N 46.256281	W −63.140350	1	1.000	1.000	1	1.000	1.000
	14	N 46.265843	W −63.142116	2	1.882	0.941	3	1.368	0.456
	15	N 46.253660	W −63.130671	4	1.296	0.324	–	–	–
	16	N 46.253285	W −63.101355	6	4.083	0.681	2	1.220	0.610
	17	N 46.259564	W −63.172319	1	1.000	1.000	1	1.000	1.000
	18	N 46.276650	W −63.157093	3	1.338	0.446	4	2.049	0.512
	19	N 46.247083	W −63.133652	3	1.455	0.485	2	1.753	0.877
	20	N 46.250015	W −63.132995	4	1.751	0.438	–	–	–

– indicates sites that could not be re-surveyed.

citrinus in early and mid-summer to confirm that these two species occur on PEI (iNaturalist, 2020; The Xerces Society et al., 2020). As our photographic surveys were conducted in August and September, it is evident that potential opportunities to capture images of these two species at our study sites may have been missed. To mitigate this issue, it is recommended that future studies incorporate surveys that encompass the entire seasonal activity of *Bombus*, preferably spanning from May to October. The acquisition of a more comprehensive dataset would enable scientists and conservationists to effectively gauge the focal areas for their endeavors and identify species warranting a conservation management program.

One species not previously recorded in PEI but expected to be present was *B. impatiens*, given its presence in nearby Canadian provinces and American states (Matteson and Langellotto, 2009). Our study revealed the species' presence in urban (n=558) and natural sites (n=412). *B. impatiens* dominated most survey areas irrespective of month and site, indicating its adaptability to various conditions. These findings are consistent with those of Dominey (2021), indicating that while *B. impatiens* was not historically recorded in the study area, it is now firmly established within the region. Contrary to other species, *B. impatiens* populations typically reach peak abundance in September and continue their colony cycle into the fall (Colla and Dumesh, 2010), explaining its prevalence in our study sites during that period. The fact that Laverty and Harder (1988) did not document the presence of this species in PEI may be attributed to their study's reliance on museum specimens rather than field surveys. Alternatively, the species may have expanded its distribution since their research, approximately 36 years ago. Future studies should explore other areas of PEI to assess the potential widespread distribution of this species throughout the province.

4.2 Photographic survey approach

The study used photographic surveys to examine bumble bee populations in urban and natural habitats and sought expert opinion via citizen science platforms to aid accurate identification. The effectiveness and cost-efficiency of this approach were successfully demonstrated, indicating its potential for application in areas where different species can be distinguished based on physical characteristics. However, our findings also revealed that

TABLE 3 Measurements of species richness, species diversity, and evenness for all photographic bumble bee survey locations in Prince Edward Island National Park, surveyed in August and September 2019.

Area	Site Number	Latitude	Longitude	August 2019			September 2019		
				Species Richness	Diversity	Evenness	Species Richness	Diversity	Evenness
Prince Edward Island National Park	21	N 46.489467	W −63.393249	4	2.381	0.595	3	1.278	0.426
	22	N 46.482217	W −63.422326	3	2.778	0.926	–	–	–
	23	N 46.416146	W −63.075894	2	1.600	0.800	3	2.273	0.758
	24	N 46.415941	W −63.073833	3	2.970	0.990	3	1.438	0.479
	25	N 46.497804	W −63.390387	4	3.556	0.889	3	1.412	0.471
	26	N 46.497856	W −63.392159	3	2.246	0.749	2	1.153	0.576
	27	N 46.486723	W −63.377581	4	2.400	0.600	3	2.571	0.857
	28	N 46.436710	W −63.244517	6	3.214	0.536	3	1.674	0.558
	29	N 46.426735	W −63.190583	5	2.922	0.584	4	1.633	0.408
	30	N 46.488100	W −63.313388	3	2.600	0.867	3	2.000	0.667
	31	N 46.492950	W −63.390828	4	2.429	0.607	3	1.581	0.527
	32	N 46.465465	W −63.302113	5	1.988	0.398	2	1.100	0.550
	33	N 46.464648	W −63.309831	3	1.780	0.593	3	1.383	0.461
	34	N 46.443535	W −62.695950	4	1.633	0.408	5	1.725	0.345
	35	N 46.443380	W −62.700279	7	5.226	0.747	4	2.038	0.510
	36	N 46.444748	W −62.681104	3	1.857	0.619	4	1.809	0.452
	37	N 46.426876	W −63.192517	6	2.350	0.392	4	1.441	0.360
	38	N 46.196300	W −63.135466	1	1.000	1.000	3	2.909	0.970
	39	N 46.194887	W −63.131359	4	2.368	0.592	4	1.905	0.476
	40	N 46.192351	W −63.141995	3	2.381	0.794	3	2.435	0.812

– indicates sites that could not be re-surveyed.

photographic surveys of bumble bees had limitations when two or more species showed morphological resemblances, such as in the example of *B. vagans* and *B. sandersoni*. Individuals from these two species were indistinguishable based on photographs because of their similar morphological traits. Other photographic surveys have also found that with two or more morphologically similar species, only 94-98% of sightings could be identified to the species level (Armistead, 2023; Flaminio et al. 2021). To enhance taxonomic identification, we suggest researchers consider integrating netting to temporarily capture individuals, especially morphologically similar species. This would more effectively enable the differentiation between species that share similar morphological characteristics. Yet, in some cases, identification may be impossible without lethal capture (microscopic inspection and/or genetic analysis), for example, differentiating *B. vagans* and the subspecies *B. vagans bolsteri*. While more labor intensive than passive capture, this combination of surveys ensures minimal disturbance to populations. With the advancements posed by artificial intelligence, it is perceivable that future citizen science platforms may not require humans to dedicate time to confirm species identification (Montero-Castaño et al., 2022; Suzuki-Ohno et al., 2017).

Like any other citizen science approach, species identification based on photographs of bumble bees requires a certain level of taxonomic knowledge or expertise from the part of the surveyor. To verify surveyor expertise in accurately identifying bumble bee species, one should refer to published keys to test abilities before conducting field surveys (MacPhail et al., 2020; Montero-Castaño et al., 2022). However, the effectiveness of this approach also largely depends on what *Bombus* species are present. If the temporal region includes multiple species that are not easily distinguishable from field surveys, another approach may be deemed more appropriate. Limitations will still be present when conducting photographic surveys. Aside from morphologically similar species, some temporal regions support higher volumes of expected species, which can further complicate accurate identification in the field. When considering other pollinator species, such as solitary bee species, it can be impossible to differentiate without lethal capture and genetic analyses. Nonetheless, it is noteworthy that photographic surveys of bumble bees continue to offer high-quality data for preliminary assessments or to acquire informative diversity and richness indexes without necessitating permits or intrusive techniques. We suggest considering all possible

TABLE 4 Results of the Poisson and Linear regression models (log-transformed).

Survey area	Coefficient	95% C.I.	P-value
Species Richness Intercept (Poisson)	1.038	0.811; 1.266	<0.001
Habitat*			0.031
Cavendish/ North Rustico	0.267	−0.065; 0.600	
Brackley/Dalvay	0.463	0.090; 0.837	
Greenwich/ Fort Amherst	0.424	0.069; 0.780	
Month September+	−0.303	−0.565; −0.042	0.023
Species Diversity Intercept (Adj-R^2=0.31)	0.542	0.418; 0.667	<0.001
Habitat*			<0.001
Cavendish/ North Rustico	0.267		
Brackley/Dalvay	0.339		
Greenwich/ Fort Amherst	0.363		
Evenness Intercept (Adj-R^2=0.08)	−0.471	−0.554; −0.389	<0.001
Plant Type$^{@}$			0.018
Anthro	−0.176	−0.442; 0.090	
Mixed	0.221	0.036; 0.407	

Reference category: *Charlottetown, +August; @Natural.
Only significant predictors are shown on this table (n=77).

limitations given the expected species for the region, and comparing the photographic survey approach to other capture methods (Armistead, 2023) to properly facilitate research objectives.

4.3 Bumble bee community comparison: urban *vs*. other sites

Our study found that PEINP sites exhibited the highest levels of species richness, relative abundance, and diversity compared to Charlottetown urban sites. The highest species richness observed in a single survey was within a Greenwich site (n=7). This site documented the presence of seven of the nine total species observed. Cavendish/North Rustico, while experiencing increased levels of anthropogenic activity, is predominantly surrounded by agriculture. This survey area would benefit from a comparative analysis to assess how exactly bumble bees use and adapt to each landscape use. A monthly analysis revealed a decrease in both species richness and abundance across all study sites in September. These findings are consistent with previous studies that have documented seasonal variations in the abundance of bumble bees, including some of the species found in PEI (e.g., Novotny et al., 2021). A plausible explanation for this decline is that most bumble bee species may have concluded their colony cycles by late August.

Interestingly, sites characterized by a mix of natural and human-cultivated (ornamental) vegetation—largely, sites within urban Charlottetown—showed greater bumble bee species diversity and abundance when compared to sites with solely natural vegetation or human-cultivated. Supporting this, other studies (Baldock et al. 2015; Kaluza et al. 2016; Marín et al. 2020; Nakamura and Kudo 2019; Sirohi et al., 2015) propose that urban green spaces with varied land use and moderate human activity promote species diversity by enhancing habitat and foraging diversity. For bumble bees, the mix of natural and human-cultivated vegetation offers a continuous and diverse supply of floral resources throughout the growing season, able to support a wider range of species with different foraging preferences and needs (Nakamura and Kudo 2019; Sikora et al., 2020). Furthermore, moderate disturbances like occasional mowing, planting, or construction in urban sites may prevent any single species from dominating the ecosystem. It is also possible that while ornamental plants may be visited, naturally occurring species (e.g., aster, clover, goldenrod) are the drivers for visitation within the area. To further this finding, studies should be conducted to encapsulate the entire active life cycle of bumble bees, as well as documenting floral preferences and visitation rates among each species.

5 Conclusion

Our study significantly contributes to the conservation of bumble bee species by demonstrating that photographic surveys offer a practical and cost-effective method for obtaining baseline data in urban sites and other areas where traditional or more invasive sampling methods may not be easily feasible. Citizen science platforms, when utilized by field experts, also create an opportunity to ensure the accuracy of surveyor identifications. Yet, they should not replace verification using taxonomic keys or expert consultation. Knowledge of the species in a given habitat is essential for practical conservation efforts. Considering the fragmentation caused by urbanization and agricultural activities on PEI, our findings suggest that urban green spaces, including, but not limited to, human-made gardens, parks, playgrounds, trails, cemeteries (Daniels et al., 2020; Wood et al. 2018), may serve as refuges for certain bumble bee species, aligning with the observations of Samuelson et al. (2018). Specifically, urban areas that incorporate a variety of native floral resources can play a crucial role in preserving bumble bee diversity, as observed in similar studies (Boone et al., 2022; Conflitti et al. 2022; Liang et al., 2023), especially when surrounded by habitats such as monoculture cropping (Deguines et al., 2016). Although human-introduced vegetation is sometimes undervalued and often removed from urban green spaces, we suggest further investigation into the role of these flora species in supporting urban fauna, including pollinators, before deciding on their removal.

In situations where several morphologically similar species are expected, we recommend adopting a survey methodology that integrates photography with temporary capture (netting) to facilitate the scrutiny of critical attributes and the accurate identification of these species (Armistead, 2023; Bell et al., 2023; Montero-Castaño et al., 2022). Accumulating additional data will inform and enhance conservation measures, especially for rare and specialized species; what benefits a generalist species may prove harmful to a rare species in peril (Liczner and Colla, 2020). Furthermore, it will help visualize which local species are stable and which are struggling beyond those officially listed by COSEWIC. Constructing a more comprehensive dataset combined with in-depth pollinator-plant interaction analyses will allow for additional advantages, such as informing local municipalities in targeted green space planning. It will also provide valuable insights to PEINP on enhancing their natural environments and constructing vital habitat corridors.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because there was no handling of any animals in this study (photographic only).

Author contributions

JM: Conceptualization, Data curation, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing. MS-O: Conceptualization, Formal Analysis, Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing. JS: Formal Analysis, Supervision, Validation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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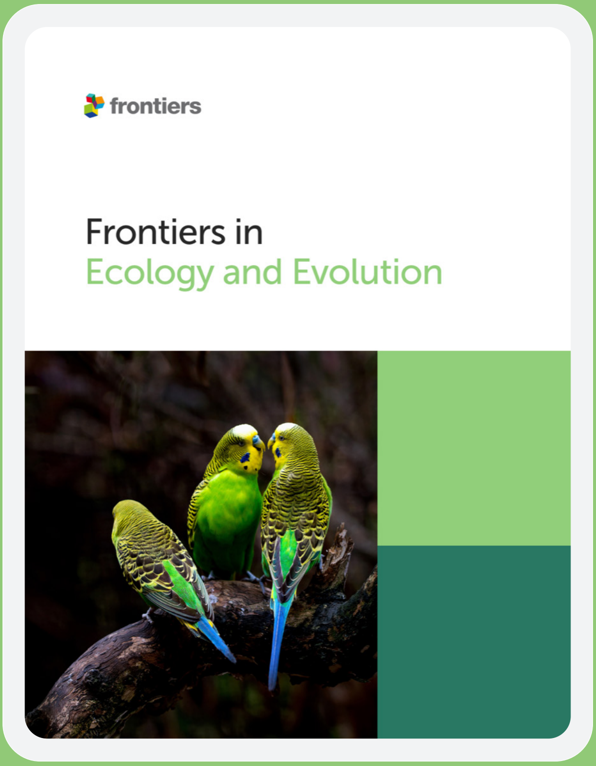

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