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# Estimating genus-specific effects of non-native honey bees and urbanization on wild bee communities: A case study in Maryland, United States



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#### HIGHLIGHTS

# G R A P H I C A L A B S T R A C T

- Honey bees, a broadly-distributed, managed species, may negatively affect wild bees.
- Joint species distribution models assess apiary density effects on wild bee genera.
- Six of 33 genera show >90 % probability of negative effect of urban land/ beekeeping.
- Bees imperiled by urban beekeeping are mostly late season, ground nesting, specialist.
- Genera detection differed by sampling method (hand net, pan trap, vane trap).

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# ABSTRACT

Non-native species have the potential to detrimentally affect native species through resource competition, disease transmission, and other forms of antagonism. The western honey bee (Apis mellifera) is one such species that has been widely introduced beyond its native range for hundreds of years. There are strong concerns in the United States, and other countries, about the strain that high-density, managed honey bee populations could pose to already imperiled wild bee communities. While there is some experimental evidence of honey bees competing with wild bees for resources, few studies have connected landscape-scale honey bee apiary density with downstream consequences for wild bee communities. Here, using a dataset from Maryland, US and joint species distribution models, we provide the largest scale, most phylogenetically resolved assessment of non-native honey bee density effects on wild bee abundance to date. As beekeeping in Maryland primarily consists of urban beekeeping, we also assessed the relative impact of developed land on wild bee communities. Six of the 33 wild bee genera we assessed showed a high probability (> 90 %) of a negative association with apiary density and/or developed land. These bees were primarily late-season, specialist genera (several long-horned genera represented) or small, ground nesting, season-long foragers (including several sweat bee genera). Conversely, developed land was associated with an increase in relative abundance for some genera including invasive Anthidium and other urban garden-associated genera. We discuss several avenues to ameliorate potentially detrimental effects of beekeeping and urbanization on the most imperiled wild bee groups. We additionally offer methodological insights based on sampling efficiency of different methods (hand netting, pan trapping, vane

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Received 26 March 2024; Received in revised form 22 August 2024; Accepted 23 August 2024 Available online 2 September 2024 0048-9697/© 2024 Elsevier B.V. All rights are reserved, including those for text and data mining, AI training, and similar technologies. trapping), highlighting large variation in effect sizes across genera. The magnitude of sampling effect was very high, relative to the observed ecological effects, demonstrating the importance of integrated sampling, particularly for multi-species or community level assessments.

# 1. Introduction

For most of history, humans have aided in the introduction and dispersal of species into novel environments (Buckley and Catford, 2016). These non-native species have shaped ecosystems, a trend which has only accelerated since the Industrial Revolution, with more rapid and longer distance human-mediated introductions accelerating the rate of global change (Ellis et al., 2010; Buckley and Catford, 2016). While some argue that non-native versus native is a flawed or even harmful paradigm, particularly in the Anthropocene (Hill and Hadly, 2018; Warren, 2021), a biodiversity metanalysis found that species extinction records cite non-native species more often than native species as a driver of extinction (Blackburn et al., 2019), suggesting provenance may indeed be a useful trait for informing conservation decisions.

One of the most widely introduced species across the terrestrial world is the western or European honey bee (*Apis mellifera*, henceforth referred to as honey bee) (vanEngelsdorp and Meixner, 2010; Requier et al., 2019). Honey bees, originally native to Asia, migrated into Europe and Africa (Dogantzis et al., 2021). Evidence of beekeeping is found as early as 2450 BCE in Egypt, and by 1500 BCE, beekeeping was widespread in the Mediterranean region and flourished throughout Europe in the Middle Ages (Kritsky, 2017). Early European settlers brought honey bees with them to North America for honey and wax production (Ransome, 2004). Today, honey bees are found across every continent except Antarctica (vanEngelsdorp and Meixner, 2010) and in some cases are managed in the thousands of colonies (each containing tens of thousands of individual bees) for pollination services for crops (Jabr, 2013; Degrandi-Hoffman et al., 2019) and honey production (Otto et al., 2016).

Recent estimates value insect pollination services to various sectors of the US economy at \$31-36 billion USD (Jordan et al., 2021), a value which relies heavily on honey bee pollination (Calderone, 2012; Jordan et al., 2021). Many agricultural systems have high demand for honey bee pollination (Aizen and Harder, 2009), with growers often paying a premium to rent these colonies for the bloom period of the crop (Goodrich, 2023). In addition to honey bees, there are approximately 20,000 described species of bees worldwide (Michener, 2007), with over 4000 species of wild bees that are native to the US (Michener, 2007). In some cropping systems, these native, wild bees are the primary crop visitors (Winfree et al., 2008), and can increase crop yields, regardless of the presence of honey bees (Garibaldi et al., 2013; Reilly et al., 2024). These bees represent a huge biodiversity of species traits and life histories across the solitary to social spectrum and range in body size from the width of a grain of rice (< 2 mm long) to the size of a chicken egg (39 mm long, with a wingspan of 63.5 mm) (Michener, 2007; Buchmann and Nabhan, 2012; Vereecken, 2018). The diversity and specific traits of wild pollinators can make them more efficient pollinators than honey bees on a per-flower basis for certain crops (Parker et al., 1987; Hoehn et al., 2008; Mallinger and Gratton, 2015; Winfree et al., 2018). However, most wild bee pollination services in agricultural crops are provided by a core set of common species (Kleijn et al., 2015), and honey bees remain the most economically important insect pollinator across much of the world (Klein et al., 2007; Jordan et al., 2021), contributing equally to crop pollination as all other insect pollinators, combined (Reilly et al., 2024).

There is widespread recognition that insect pollinators, both managed (vanEngelsdorp and Meixner, 2010; Bruckner et al., 2023) and unmanaged (Colla and Packer, 2008; Potts et al., 2016; Cameron and Sadd, 2020; Kammerer et al., 2021) have experienced physiological stress, population declines, and elevated loss rates in recent decades.

These declines imperil pollination services (Aizen and Harder, 2009) and threaten ecosystem integrity (Senapathi et al., 2015; Winfree et al., 2018). For both groups, the primary causes of these declines are floral resource limitation (which bees rely on for food i.e., pollen and nectar), pests, pathogens, parasites, pesticides, and climate change (Winfree et al., 2009; Potts et al., 2010, 2016; Kennedy et al., 2013; Goulson et al., 2015; Koh et al., 2016; Settele et al., 2016). There is also concern that non-native, managed pollinators may be exacerbating these effects for native bees by competing for limited floral resources and by introducing and/or spreading diseases (reviewed: Russo, 2016; Mallinger et al., 2017; Wojcik et al., 2018; Iwasaki and Hogendoorn, 2022).

Honey bees' versatility, efficiency, and sheer abundance, which makes colonies prized for pollination services and honey production, are also traits that increase their potential negative effects on wild bees (Russo et al., 2021). As a generalist forager, honey bees are a versatile pollinator for a wide breadth of crops (Aizen and Harder, 2009), but as generalists they also share resources with many wild pollinators (Rohr et al., 2014). This niche overlap creates the opportunity for disease transmission (Figueroa et al., 2019) as well as floral resource competition (Elliott et al., 2021). As a social species, honey bees maintain large numbers of individuals in a colony throughout the warm season in temperate climates, with colonies consisting of up to 50,000 bees. Large colony sizes can increase pollination services but also require large volumes of floral resources to sustain these populations (Cane and Tepedino, 2017). Resource competition may be further exacerbated by honey bees' tendency to hoard large volumes of nectar, in excess of their biological needs, in the form of honey, potentially limiting nectar availability for wild bees (Dupont et al., 2004; Henry and Rodet, 2018; Page and Williams, 2023). Furthermore, because honey bees are managed by beekeepers, who provide nesting habitat and supplemental feed during low-resource periods, honey bee populations may be buffered from natural ecological limits. Finally, honey bees are strong dispersers and have a unique ability to scout for, and recruit nestmates to high quality resources in the landscape (Seeley, 1986). This behavior makes them extremely efficient pollinators but also very efficient at finding and exploiting resources over a wide foraging range (up to 6 km from their nest) (Couvillon et al., 2014), compared to wild bees, whose ranges are typically much smaller (< 1 km) (Greenleaf et al., 2007).

While the potential for honey bees to negatively impact populations of wild bees is theoretically supported, demonstrating these negative effects is difficult and an ongoing area of research (Iwasaki and Hogendoorn, 2022). In the last two decades, there has been a proliferation of studies on the effects of managed pollinators on wild pollinators, with several reviews on the topic (Goulson, 2003; Paini, 2004; Mallinger et al., 2017; Wojcik et al., 2018; Iwasaki and Hogendoorn, 2022). Some of the best evidence for negative effects, particularly in recent years, has been on pathogen transmission. Most of these studies (81 %) cite negative effects, defined by novel pathogen detection/pathogen spillover from honey bees to wild bees (Iwasaki and Hogendoorn, 2022). However, we are aware of only three studies that investigate pathogen replication and fitness effects on the wild-bee host, and these studies found negligible or no effect (Dolezal et al., 2016; Müller et al., 2019; Tehel et al., 2020). Furthermore, recent work suggests that pathogen transmission may be impeded by temporal mismatch in disease dynamics between bee groups (Martínez-López et al., 2023). Studies on competition for floral resources are among the most common overall (Iwasaki and Hogendoorn, 2022), and while most authors conclude negative relationships, results are mixed (Mallinger et al., 2017: 55 % reporting negative effects, 33 % no effects, and 11 % mixed effects; Iwasaki and Hogendoorn, 2022: 66 % reporting negative effects).

Furthermore, the majority of studies on floral competition between honey bees and wild bees focus on niche overlap and changes in foraging behaviors (shifts in floral visitation patterns) (Mallinger et al., 2017; Iwasaki and Hogendoorn, 2022). But because wild bees may be able to shift to other resources without appreciable consequences for fecundity, niche overlap and behavioral change are only the first step in demonstrating competition (Mallinger et al., 2017; Worthy et al., 2023). A recent review of the wild bee-honey bee competition literature found only 8 % of studies have examined down-stream population-level effects of floral competition, with 6 of these 7 studies reporting negative consequences (Iwasaki and Hogendoorn, 2022). In light of their review, Mallinger et al. (2017) called for studies that assess effects of colony density on wild bees at the population level (i.e., abundance, diversity, or fecundity).

Here, our goal was to address some of these shortcomings by modeling abundance of 33 wild bee genera as a function of honey bee apiary density across the diverse landscape of Maryland, US. To do so, we leveraged a wild bee monitoring dataset, curated by USGS and USFWS (Droege and Maffei, 2023) and the Maryland State Apiary Program registration database (as a measure of honey bee abundance) to fit abundance-based Bayesian joint species distribution models (JSDMs; Ovaskainen et al., 2010; Warton et al., 2015). JSDMs are a flexible approach to model the distributions and/or abundance patterns of multiple genera simultaneously within a multivariate framework, which generally provides more precise and accurate estimates compared to fitting separate models for each genus (Clark et al., 2014; Warton et al., 2015). This approach also improves our ability to estimate relationships for rare genera with minimal sample sizes (e.g., Dorazio and Royle (2005)) and increases precision of estimated relationships in comparison to single-species models (e.g., Zipkin et al. (2010)). Thus, our resulting genus-level estimates can help inform specific, data-driven conservation measures - even for rare genera. We hypothesized that honey bee apiary density is negatively correlated with the abundance of most genera, but that the magnitude of effect differs across genera. Understanding the impact of the introduced honey bee is not only significant for management, policy, and conservation, but provides a lens through which to understand the impact of non-native species introduction on native species biodiversity loss and ecosystem structure and function, a fundamental question in ecology (Sutherland et al., 2013; Buckley and Catford, 2016).

### 2. Methods

### 2.1. Honey bee apiary data

Locations of nearly 4000 registered apiaries were obtained from the Maryland State Apiary Program for 2017 and 2018. To ensure privacy of beekeepers, in our project repository we shared the aggregated apiary density surface (see below) rather than specific locations of apiaries. The Maryland State Apiary Program recorded apiary locations as addresses of registered apiaries. We utilized the Google Geocoding API (https ://developers.google.com/maps/documentation/geocoding/overview) via the ggmap R package (Kahle and Wickham, 2013) to translate apiary addresses into GPS coordinates. For registrations that indicated apiaries were located at private residences (e.g. apiary address was 'backyard'), we geocoded the listed mailing address. Approximately 6 % of apiary addresses included only road name (no specific house or building number) or the listed house number was invalid. For these addresses, we utilized the latitude and longitude of the centroid of the listed road. To evaluate accuracy of geocoding, we manually checked 20 % of the 3967 addresses of registered apiaries in the state. We excluded 48 apiaries whose addresses were incomplete or in a non-standard format and could not be translated to coordinates. This left 3840 geocoded apiaries for further use.

We created a surface of expected honey bee forager density around apiary locations using an exponential decay function. Our approach ensured that the majority (~67 %) of weight (i.e., forager density) was contained within 2 km of each apiary, while still allowing for the possibility that foragers could fly up to 6 km (maximum foraging distance) (Couvillon et al., 2014) (Fig. S1). First, each apiary location was buffered by 6 km. We then generated a metric of forager density across a 100  $\times$  100 m grid of the buffered apiary location using the inverse exponential half-distance (i.e., 1/exp.(0.5 \* distance)) of each pixel from the apiary location. Overlapping, weighted apiary buffers were then summed to create the final apiary density surface (Fig. 1A).

We chose to use apiary density instead of honey bee forager abundance in our analysis because our goal was to evaluate long-term and population scale impacts of honey bee density on wild bee populations, which is better captured by apiary density. Trapping captures coforaging bee populations, which could answer questions related to direct resource competition, rather than population-level effects. Previous studies, explicitly aimed at describing the relationship between honey bee forager densities and distance to apiary, find a negative correlation between forager density and distance to apiary (Steffan-Dewenter and Tscharntke, 2000; Otto et al., 2021), consistent with our mathematical model. However, based on the bee occurrence dataset that we used (Droege and Maffei, 2023; see next section), we found no evidence for a correlation between the relative abundance of honey bees and our apiary density metric (Mean: -0.10, 95 % CI [-0.50, 0.31]). This is likely because collecting honey bees is often beyond the scope of wild bee sampling efforts. Indeed, there were only 296 records of Apis mellifera (i.e., honey bee). Given that there were thousands of known apiaries across the state, each with one or more colonies, each containing tens of thousands of honey bees, this number is low. For context, bumble bees (Bombus), another common, eusocial bee, with typical colony sizes in the hundreds, had more than five times the number of records (n =1529). Still, we cannot discount the possibility that other biological factors/foraging behaviors could have confounded the relationship between apiary density and honey bee forager abundance, such as honey bees' broad foraging range and tendency to forage on mass blooming crops (St. Clair et al., 2020).

# 2.2. Wild bee data

Wild bee count data were obtained from the USGS Insect Species Occurrence Data from Multiple Projects Worldwide with Focus on Bees and Wasps in North America (Droege and Maffei, 2023). These data are globally distributed, with an emphasis on the eastern US, and span 1990–2019 in temporal extent. This dataset aggregates USGS collections across various projects, and detailed information on sampling date, location, method (i.e., hand netting and pan, malaise, and vane trapping), and effort (e.g., sampling duration, trap number) are included for these records. Additional information and associated metadata for this dataset can be found in the GBIF data repository (Droege and Maffei, 2023; doi.org/10.15468/6autvb).

To match the spatial and temporal extent of our apiary data, we filtered insect records to Maryland, US for 2017 and 2018. We only used data points that fell outside a 6 km buffer of the state boundary to ensure estimated relationships between apiary density and wild bee abundance were not underestimated due to unrecorded apiaries in neighboring states. We included records that resulted from pan trapping (n = 3761; 38 % of records), vane traps (n = 3649; 37 %), and hand netting (2570; 26 %). Collections that used malaise traps (n = 3) or that involved convenience sampling (n = 5) were excluded. We filtered to include only genera with >10 occurrence records, which resulted in 33 common bee genera. The genus *Apis*, which consisted entirely of *Apis mellifera* (i.e., honey bee) was excluded (n = 296; see previous section for explanation). Wild bee genera were sampled across 141 locations which spanned >99 % of the distribution of apiary density values across the state (Fig. S2A).



Fig. 1. Study system maps, showing wild bee sampling locations (A), modeled apiary density (B), and land use/landcover (C) across Maryland, United States. The NA category includes water and background/undefined classes.

# 2.3. Honey bee apiary density correlation with land use

Because beekeepers may choose to locate their apiaries based on land access and surrounding land use quality (Otto et al., 2016) (resulting in

non-random apiary locations), we accounted for the potentially confounding effects of land use in the relationship between apiary density and wild bee abundance. More specifically, we assessed the correlation between apiary colony density and four broad land use categories (crop, grassy/herbaceous, forest, and developed) within 0.5 km of each wild bee collection location (Greenleaf et al., 2007). Land use was determined using the 2018 cropland data layer (CDL) for Maryland and the surrounding area (US Department of Agriculture National Agricultural Statistics Service, 2018) (accessed: 10/24/23). Raster reclassification, buffering, and extraction was completed with the raster (Hijmans et al., 2020), exactextractr (Baston et al., 2021), and sf (Pebesma, 2018; Pebesma and Bivand, 2023) packages. Details on binning for each of these categories can be found in associated code. Wild bee sampling locations were representative of the gradient of developed land across the state (Fig. S2B).

#### 2.4. Joint species distribution model

Bayesian joint species distribution models (JSDMs; Ovaskainen et al. (2010); Warton et al. (2015)) were used to quantify genus-specific relationships between apiary density and wild bee relative abundance. Let  $y_{i,j,t}$  denote the number of observed individuals of genus *i* at site *j* in year *t*. We modeled  $y_{i,j,t}$  according to

 $y_{i,j,t} \sim \text{Negative Binomial}(\mu_{i,j,t}, \kappa_i),$ 

where  $\mu_{ij,t}$  is the mean relative abundance of genus *i* at site *j* during year *t*, and  $\kappa_i$  is a genus-specific dispersion parameter to account for overdispersion in observed counts. We modeled  $\mu_{ij,t}$  as a function of apiary density, developed land, sampling variables (to account for differences in detection probability of the 33 genera across different sampling methods), and multiple random effects to account for additional spatial and/or temporal variation in wild bee relative abundance. More specifically, we have

$$log(\mu_{i,j,t}) = \beta_{0,i,PROTOCOL_{j,t}} + \beta_{1,i,YEAR_t} + \beta_{2,i} \cdot APIARY_j + \beta_{3,i} \cdot DEVEL_j$$
$$+ \beta_{4,i,PROTOCOL_{j,t}} \cdot EFFORT_{j,t} + \beta^*_{i,DAY_{j,t}} + \mathbf{w}^*_{i,j},$$

where  $\beta_{2,i}$  and  $\beta_{3,i}$  are the parameters of main interest and represent the genus-specific linear relationships between apiary density and developed land, respectively, on relative abundance for genus *i*. The parameters  $\beta_{0,i,PROTOCOL_{i,t}}$  and  $\beta_{4,i,PROTOCOL_{i,t}}$  account for genus-specific differences in detection probability across the three sampling methods, where  $\beta_{0,i,PROTOCOL_{j,t}}$  is a genus-specific and protocol-specific intercept and  $\beta_{4,i,PROTOCOL_{j,t}}$  is a genus-specific and protocol-specific effect of sampling effort (EFFORT<sub>it</sub>). Sampling effort was defined as sampling duration for hand netting and vane traps, and sampling duration multiplied by the number of traps for pan traps, at a given sampling location.  $\beta_{1,i,YEAR_t}$  is a genus-specific and year-specific intercept to account for variation in relative abundance across the two years, while  $\beta_{i,DAY_{it}}^{*}$  is a species-specific random effect of survey day to account for variation in wild bee activity and detection rates as a result of differences in weather, sampling variability, and other non-accounted for variation over time. Finally,  $w_{i,i}^*$  is a genus-specific site-level random effect that accounts for additional spatial variation in wild bee abundance, which may arise from additional abiotic variables not included as covariates in the model (e.g., nesting habitat) or true biotic interactions across genera. We estimated  $w_{i,i}^*$  using a factor modeling approach (Hui et al., 2015; Warton et al., 2015; Doser et al., 2023), which decomposes  $w_{i,i}^{*}$  into a set of q latent variables (i.e., factors) and their associated genus-specific regression coefficients (i.e., factor loadings). In particular, we have

 $\mathbf{w}_{i,i}^* = \lambda_i^\top \mathbf{w}_j$ 

where  $\lambda_i^{\top}$  is the i<sup>th</sup> row of factor loadings from an  $N \times q$  loadings matrix  $\Lambda$ , and  $w_j$  is a vector of length q of independent factors at site j. The latent

factors were assumed to arise from independent standard normal distributions. This approach inherently accounts for residual correlations across genera via their genus-specific responses to the q latent factors (Warton et al., 2015).

Genus-specific regression coefficients (e.g.,  $\beta_{2,i}$ , the effect of apiary density on relative abundance) were estimated as random effects arising from a common, community-level normal distribution. For example, the genus-specific effect of apiary density on relative wild be abundance  $\beta_{2,i}$  was modeled according to

$$\beta_{2,i} \sim \operatorname{Normal}\left(\mu_{\beta_2}, \tau_{\beta_2}^2\right)$$

where  $\mu_{\beta_2}$  is the average effect of a piary density across all genera, and  $\tau_{\beta_2}^2$  is the variation in the effect across genera.

#### 2.5. Hierarchical partitioning

Given that honey bee apiary density was correlated with developed land (Pearson's r = 0.73; see results below), hierarchical partitioning was used to determine the relative contribution of apiary density versus developed land to the explained variation in our data (Chevan and Sutherland, 1991). Hierarchical partitioning is useful in cases with correlated predictor variables because it offers a variable importance score (i.e., relative contribution of each predictor variable to estimating the outcome of interest). It does so by independently and jointly assessing explained variation for each predictor variable, and then calculating variable importance based on the change in model fit (Nally, 1996). For our hierarchical partitioning approach, we first fit four alternative JSDMs following our previous description, with the four models differing only in whether they included apiary density and/or developed land as covariates in the model. More specifically, our four candidate models were: 1) an apiary density + developed land model, 2) apiary density model, 3) developed land model, and 4) a null model that did not include either apiary density or developed land. We then calculated the improvement in log likelihood for each genus associated with the presence or absence of each variable in this list of nested models and used these changes to calculate variable importance as in (Zylstra et al., 2021; Ouinlan et al., 2023). We interpreted the effects of apiarv density from the apiary density model (i.e., model without developed land) and the effects of developed land from the developed land model (i.e., model without apiary density), and used the variable importance estimates from the hierarchical partitioning to determine the most supported relationship for each genus.

#### 2.6. Model implementation and assessment

All models were fit in a Bayesian framework using Markov chain Monte Carlo (MCMC) via the spAbundance R package (Doser et al., 2024). We specified vague Gaussian priors with a mean of 0 and variance of 100 for all community-level mean parameters and vague inverse-Gamma priors with shape and scale parameters equal to 0.1 for all variance parameters. We used standard normal priors for the lowertriangular elements of the factor loadings matrix and set the upper triangular elements to 0 and diagonal elements to 1 to ensure identifiability of the factor loadings (see Doser et al. (2023) for additional details). All models were run using three MCMC chains, each with 125,000 iterations, a burn-in period of 65,000 samples, and a thinning rate of 20 for a total of 9000 samples from the posterior distribution. Convergence was assessed using visual assessment of traceplots and ensuring the potential scale reduction factor (Rhat; Brooks and Gelman (1998)) was <1.1. Goodness-of-fit was assessed using a posterior predictive check with a Freeman-Tukey fit statistic. Posterior predictive checks were summarized visually and by using Bayesian p-values calculated for each genus, ensuring that each Bayesian p-value fell between 0.1 and 0.9 (Hobbs and Hooten, 2015).

### 3. Results

#### 3.1. Correlation between honey bee apiary density and developed land

Locations of registered apiaries in Maryland in 2017 and 2018 were obtained from the Maryland State Apiary Program. In total, 3840 apiaries passed quality controls and were used in this analysis. Our study system of Maryland represents a variety of land use conditions, with forests dominating to the west and south of the state, soy/corn/small grain cropland interspersed with fields of grasses and herbaceous plants (termed "grassy-herbaceous" in the binned land use categories) dominating to the east and north-center, and developed land associated with the greater Washington DC, Annapolis, and Baltimore metropolitan areas in the center of the state (Fig. 1B). Honey bee apiary density was positively correlated with developed land (r = 0.73; Fig. 1). Apiary density did not show a strong correlation with any other land use category (crop: r = -0.17, grassy/herbaceous: r = -0.18, forest: r = -0.39).

# 3.2. Association between wild bee genera abundance, apiary density, and developed land

We used data on wild bee abundance at 141 sites across the state of Maryland, US, obtained from the USGS Insect Species Occurrence Data from Multiple Projects Worldwide with Focus on Bees and Wasps in North America (Droege and Maffei, 2023). We used these data to examine the association between the abundance of 33 wild bee genera and apiary density (Figs. 2A and 3) as well as developed land (Fig. 2B). Because apiary density and developed land were positively correlated (more beekeepers are in suburban and urban areas), we examined the relative importance of each factor to describing wild bee genus abundance using hierarchical partitioning (Fig. 4). In descending order of abundance our focal genera were *Lasioglossum* (total individuals observed = 2112), *Bombus* (1529), *Ptilothrix* (1411), *Melissodes* (882), *Ceratina* (668), *Andrena* (516), *Augochlorella* (466), *Halictus* (385), *Augochlora* (335), *Agapostemon* (325), *Megachile* (297), *Hylaeus* (118), *Osmia* (115), *Xylocopa* (97), *Panurginus* (82), *Calliopsis* (81), *Svastra* (76), *Nomada* (74), *Peponapis* (59), *Florilegus* (41), *Anthidium* (40), *Anthophora* (37), *Perdita* (35), *Eucera* (32), *Dieunomia* (27), *Coelioxys* (25), *Colletes* (25), *Melitoma* (20), *Triepeolus* (17), *Hoplitis* (14), *Anthidiellum* (14), *Heriades* (13), *Augochloropsis* (12).

Of these 33 genera, we found strong support (Probability >95 %) of apiary density and/or developed land for 5 genera (2 showing a negative effect, 3 showing a positive effect). A negative effect was observed for relative abundance of *Melissodes* and *Lasioglossum*, which was primarily attributable to developed land (Fig. 4). We also observed strong support for a positive effect on relative abundance of *Ptilothrix, Anthidium*, and *Hylaeus*. These positive effects were similarly primarily related to effects of developed land, except for *Ptilothrix*, which showed a mixed role of apiary density and developed land (Fig. 4).

At Probability >90 %, an additional 4 genera (6 total) showed evidence of a negative correlation with apiary density and/or developed land, and at Probability >80 %, 15 total genera (11 negative, 4 positive) showed support for an effect of apiary density and/or developed land. Additional details for these genera are shown in Table 1 (genera showing a negative correlation) and Table 2 (genera showing a positive correlation). In these tables, genera are ordered according to the importance of apiary density versus developed land to describing variation. Morphological, behavioral and natural history traits of these genera are included, as well as the bee common name group (long-horned, sweat, etc.).



Fig. 2. Caterpillar plot of genus-level effects (on the log scale) of apiary density (A) and developed land (B). Median effect sizes are shown as points (colored by probability of effect <0), with 50 % (thick line) and 95 % (thin line) Bayesian credible intervals.



**Fig. 3.** Change in relative abundance for four genera (*Svastra* (A), *Melitoma* (B), *Triepeolus* (C), and *Augochloropsis* (D)) with substantial support for a negative effect of apiary density, from the highest to lowest values of apiary density across the observed locations. Relative abundance values correspond to the average number of individuals observed during a single survey at average sampling effort for the best sampling method for the given genus. The lowest apiary density corresponds to 0 apiaries within a 6 km radius of the sampling location, while the highest apiary density corresponds to 79 apiaries within a 6 km radius of the sampling location, with an average distance of 4.15 km to each apiary. Median effect sizes are shown as points, with 50 % (thick line) and 95 % (thin line) Bayesian credible intervals.

# 3.3. Genera with substantial evidence of a negative correlation with apiary density and/or developed land

There was substantial support for a negative effect of apiary density (100 % variable importance relative to developed land) on bees in the genera Svastra (92 % probability of a negative effect of apiary density; median effect = -0.46 [-1.28-0.18 95 % credible interval]), *Melitoma* (*M. taurea*) (P = 86 %; effect = -0.36 [-1.19-0.27]), *Triepeolus* (P = 86%; effect = -0.38 [-1.28-0.29]), and Augochloropsis (P = 74 %; effect = -0.21 [-0.98-0.42]) (Table 1, Fig. 2). Estimated changes in relative abundance for these genera across the range of observed apiary densities in Maryland are shown in Fig. 3 (see Fig. S3 for effects across all genera). Relative abundance values correspond to the average number of individuals that would be observed during a single survey at average sampling effort for the best sampling method for the given genus. The lowest apiary density corresponds to 0 apiaries within a 6 km radius of the sampling location, while the highest apiary density corresponds to 79 apiaries within a 6 km radius of the sampling location, with an average distance of 4.15 km to each apiary (Fig. S2 A). Median estimates suggest that across this range, relative abundance of Svastra is estimated to decrease from 0.031 to 0.003 (-89.9 %), Melitoma (M. taurea) 0.026-0.004 (-83.5 %), Triepeolus 0.005-0.0007 (-85.5 %) and Augochloropsis 0.010-0.003 (-66.4 %) (see Table S1 for estimate for all species). However, there is large, overlapping uncertainty in these estimates as highlighted by the credible intervals in Fig. 3 (see Table S1 and Fig. S3 for estimate for all species). These genera are late-season (summer, fall) foragers, have more specialized diet niches and habitat preferences, and nest in the ground (Table 1). Triepeolus, interestingly, is a cuckoo bee, parasitizing Eucerine (i.e., long-horned bee) nests, such as that of Svastra (the genus with the highest probability of a negative effect of apiary density).

Two genera (*Florilegus* and *Melissodes*) likewise showed a high probability of a negative correlation with apiary density and/or developed land (Table 1, Fig. 2), but based on variable importance the negative effects for these genera were more associated with developed

land than apiary density. Both genera were ground-nesting late-season, specialist, long-horned bees (Table 1), and both showed high probability (P > 90 %) of a negative effect of developed land (*Florilegus*: developed Variable Importance (VI) = 100 %, P = 94 %, effect = -0.63 [-1.74–0.16] and *Melissodes*: developed VI = 76 %, P = 100 %, effect = -0.62 [-1.08 to -0.18]).

Genera with moderately high probability of a negative effect (P > 80%), but with a mixed role of developed land and apiary density included primarily green bees: *Agapostemon* (VI apiary = 78 %; VI developed = 22 %), *Augochlorella* (VI apiary = 59 %; VI developed = 41 %), *Augochlora* (*A. pura*) (VI apiary = 43 %; VI developed = 57 %), as well as a cellophane bee genus (*Colletes*; VI apiary = 64 %; VI developed = 36 %) and a sweat bee genus (*Lasioglossum*; VI apiary = 32 %; VI developed = 68 %) (Table 1, Fig. 2). Most of these genera that showed a contribution of both apiary density and developed land were small, ground nesting, generalists, and had long flight periods, foraging throughout the season, or in the case of *Colletes*, have both a spring-foraging and fall-foraging group (Table 1).

# 3.4. Genera with substantial evidence of a positive correlation with apiary density and/or developed land

Very few genera showed strong evidence of a positive correlation with either apiary density (Fig. 2A; Table 2) and/or the proportion of developed land in the surrounding area (Fig. 2B; Table 2). Only three genera (*Ptilothrix, Hylaeus, Anthidium*) of the 33 assessed genera showed substantial support (P > 95 % probability) for a positive effect of either factor. There was also moderate support for a positive effect of apiary density on *Megachile* (P = 83 %). Based on our hierarchical partitioning results (Fig. 4), most of the explained variation for *Anthidium* (99 %), and *Hylaeus* (91 %) can be attributed to developed land, while apiary density accounted for the majority of variation for *Megachile* (100 %) as well as a marginal majority for *Ptilothrix* (54 %).



**Fig. 4.** Hierarchical partitioning results showing the importance of honey bee apiary densities (HB Density) relative to developed landcover area in describing genusspecific abundance across Maryland, United States. Bars are shaded by the amount of support for a positive or negative effect of each variable from either model (Positive = P(positive effect) > 0.8; Negative = P(negative effect) > 0.8); No Support = P(positive effect) < 0.8 and P (negative effect) < 0.8). *Bombus, Perdita,* and *Eucera* were excluded from this figure because the null model was better than either apiary density and/or developed land area in describing genus abundance. It should be noted that this figure shows the importance of each variable relative only to the other. Shaded bars do not necessarily imply high probability of an effect. Rather, they show the proportion of explained variance attributable to either variable (even if the total explained variance is small).

#### 3.5. Wild bee sampling method bias

Detection of genera varied by collection method (Fig. 5), and the magnitude of effect of sampling method was far greater than the effect of either apiary density or developed land (Figs. 2 and 5). When comparing hand netting versus pan trapping, *Bombus, Xylocopa, Colletes*, and *Andrena* were collected more often by hand netting (P > 95 %), while *Agapostemon, Calliopsis, Peponapis, Lasioglossum, Augochlorella, Melissodes, Ceratina,* and *Halictus* (P = 100 %), as well as *Melitoma, Hylaeus, Ptilothrix,* and *Augochlora* (P > 95 %) were more often collected with pan traps than hand netting (Fig. 5A). Vane trapping detected relatively more *Ptilothrix, Melissodes, Florilegus, Augochlora, Bombus, Peponapsis, Ceratina, Melitoma, Lasioglossum, Agaposteomon, Eucera, Hylaeus,* and *Augochlorella* (P > 95 %) than hand netting (Fig. 5B). These detection probability values are drawn from our apiary density model, although findings were consistent across the different models.

#### 4. Discussion

Very few studies to date have connected landscape-level honey bee apiary density, apiary distance, or forager density with wild bee community data and none have done so at the spatial or phylogenetic scale of our study. In this study we were able to estimate the effect of apiary density on genus-specific abundance – even for rare genera – using a joint species distribution model. Our genus-specific findings help to address the current bias in the literature for *Bombus*-specific studies (Wojcik et al., 2018) and those that only account for total wild bee abundance and/or richness. We examined these trends across Maryland ( $\sim$ 32,000 km<sup>2</sup>, about the size of Belgium), a state that represents a diversity of land use. Given the prevalence of urban beekeepers, we further parsed the effect of developed land from that of apiary density. Of the 33 genera examined, 6 showed negative associations with apiary density and/or developed land with probability >90 %, corresponding to 18 % of assessed bee genera.

The absence of a negative response to apiary density for the majority (~80 %) of genera at the landscape-scale is consistent with previous findings at the local, field scale that describe weak or no effect of honey bee presence/abundance on total wild bee abundance and/or richness (Steffan-Dewenter and Tscharntke, 2000; Hudewenz and Klein, 2013; Otto et al., 2021; Prendergast et al., 2021; St. Clair et al., 2022; Kilpinen et al., 2022). We highlight in particular work by McCune et al. (2020), who similarly accounted for variation in detection probability when modeling wild bee abundance within the Montreal metropolitan area, and found no evidence of honey bee-wild bee competition. Though see also, MacInnis et al. (2023) who worked in the same urban system and found substantial evidence for a decrease in wild bee richness following a massive (>12×) increase in honey bee colony density over <10 years.

There has been a proliferation of urban beekeeping in recent years (Lorenz and Stark, 2015) and concern around the effects this could have on wild bee communities (Lorenz and Stark, 2015; McCune et al., 2020;

#### Table 1

Genera with fairly substantial support (Probability >80 %) of a negative effect of either honey bee apiary density and/or developed landcover area. Genera are shown with the probability of a positive effect, such that values <0.10 indicate >90 % probability of a negative effect ('\*') and values <0.05 indicate >95 % probability of a negative effect ('\*'). Variable importance of apiary density ('Apiary') and developed landcover area ('Devel') based on hierarchical partitioning is shown for each genus, and rows are ordered by apiary density importance. Genera (*Perdita* and *Eucera*) for which the null model was better than either the apiary model or developed land model were excluded. We provide estimates of percent change in median relative abundance for each genus under the lowest apiary density and highest apiary density, represented by sampled locations across the state of Maryland (See Fig. 3 and Table S1). Functional traits for each genus are provided based on North American Native Bee Collaborative (2017), including bee group, body size (relative to honey bees), nesting, seasonal flight period, habitat (*Lasioglossum* is a speciose genus that is abundant across many different environments), and diet (with host plant given for more specialist genera).

	Importance		Probability >0		Median Pct Chg	Traits					
Genus	Apiary	Devel	Apiary	Devel		Bee Group	Size	Nesting	Flight	Habitat	Diet
Svastra	100	0	0.08*	0.06*	-89.86	Long- horned	large	ground	summer- fall	high quality meadows	composites
Melitoma (taurea)	100	0	0.14	0.15	-83.54	Round- headed	same	ground	summer	rural/urban	morning glories
Triepeolus	100	0	0.14	0.14	-85.54	Cuckoo	small	ground (parasite)	summer- fall	parasite of Eucerines	pollen parasite
Augochloropsis	100	0	0.26	0.10	-66.38	Green	small	ground	throughout	open gardens/ fields	generalist
Agapostemon	78	22	0.08*	0.73	-80.90	Green	small	ground	throughout	field	generalist
Colletes	64	36	0.20	0.30	-69.37	Ce <u>l</u> lophane	small	ground	spring/fall	ground (spring: aggregate)	spring: tree/shrub; fall: specialists
Augochlorella	59	41	0.50	0.13	2.28	Green	small	ground	throughout	gardens/fields	generalist
Augochlora (pura)	43	57	0.14	0.09*	-72.51	Green	small	rotting logs	throughout	woodlands	generalist
Lasioglossum	32	68	0.08*	0.02**	-60.10	Sweat	small	ground, rotting logs	throughout	many	generalist
Melissodes	24	76	0.08*	0.00**	-78.57	Long- horned	large	ground	summer- fall	flowering composites	composites
Florilegus	0	100	0.14	0.06*	-85.80	Long- horned	same	ground	summer	coastal plain	pickerelweed

#### Table 2

Genera with fairly substantial support (Probability >80 %) of a positive effect of either honey bee apiary density and/or developed landcover area. Genera with a >95 % probability of a negative effect (\*\*\*) are highlighted. Variable importance of apiary density ('Apiary') and developed landcover area ('Devel') based on hierarchical partitioning is shown for each genus, and rows are ordered by apiary density importance. Genera (*Bombus*) for which the null model was better than either the apiary model or developed land model were excluded. We provide estimates of percent change in median relative abundance for each genus under the lowest apiary density and highest apiary density, represented by sampled locations across the state of Maryland (See Table S1 for estimate for all genera). Functional traits for each genus are provided based on (North American Native Bee Collaborative, 2017), including bee group, body size (relative to honey bees), nesting, seasonal flight period, habitat, and diet (with host plant given for more specialist genera). *Megachile* and *Hylaeus* can be found across many habitat types, with some species favoring different habitats (e.g., urban/disturbed, coastal, wetland) (Maryland Biodiversity Project, 2024).

	Importance		Probability >0		Median Pct Chg	Traits					
Genus	Apiary	Devel	Apiary	Devel		Bee Group	Size	Nesting	Flight	Habitat	Diet
Megachile	100	0	0.83	0.50	140.84	Leaf cutting	same	cavity (wood or ground)	summer- fall	many	wide range; many specialists
Ptilothrix (bombiformis)	54	46	0.97**	0.97**	1031.73	Round- headed	large	ground	summer	wetlands and urban	Mallow family (esp. Hibiscus)
Hylaeus	9	91	0.79	0.99**	176.81	Masked	small	pithy stems and wood	summer	many	flat-topped flowers
Anthidium	1	99	1.00**	1.00**	5479.70	Yellow block	small	cavity	summer	gardens, weedy fields	many; mints and pea family

MacInnis et al., 2023). Indeed, in our study system we found evidence for high density of managed honey bee colonies in developed areas. Developed landscapes present several unique challenges to native, wild species including negative interactions (i.e., competition, antagonism) with non-native species, resource limitation, habitat fragmentation, urban heat island effects, increased exposure to pollution and pesticides, and human conflict (Forman, 2014). Due to these concerns, there has been particular emphasis in recent years on the effects of urban habitats on wild bee communities (reviewed in Wenzel et al. (2020)). Our study, by leveraging the extensive wild bee sampling data and distribution of apiaries across the state, explores not only the effects of developed land on wild bee communities, but is able to parse these effects from that of honey bee densities. 4.1. Genera negatively associated with apiary density and/or developed land

The genera in our study that were most negatively associated with apiary density and/or developed land have specific aspects of their foraging and habitat needs that could be taken into consideration to support these groups. Consistent with our genus-specific findings, previous studies have found variable responses to increased honey bee density among bees with different functional traits (i.e., different body size, nesting preference, and species identities) (Hudewenz and Klein, 2013; Herbertsson et al., 2016; Ropars et al., 2019; McCune et al., 2020; Prendergast et al., 2021). We found that many of the affected genera were late-season, specialist bees (i.e., long-horned bees and their nest parasites and fall cellophane bees) or small, season-long, ground nesting



Fig. 5. Caterpillar plot of genus-level effects (on the log scale) of pan trapping (A) and vane trapping (B) compared to hand netting. Median effect sizes are shown as points (colored by probability of effect <0), with 50 % (thick line) and 95 % (thin line) Bayesian credible intervals.

bees (i.e., sweat bees, particularly green bees). However, we also note that many other genera that fit these descriptions, including *Dieunomia* and *Calliopsis*, respectively, showed no effect. Indeed, most wild bee species are small ground nesters, so there may be other aspects of these bees' biology that makes them especially vulnerable.

#### 4.2. Late-season, specialist genera

We found late-season specialist bees represented among those genera most negatively associated with apiary density/developed land. These bees' vulnerability likely stems from resource limitation and/or competition. Late summer and early fall is a time of resource dearth in the Mid-Atlantic US, falling between the summer (brambles, holly, white clover, poplar, locust, basswood, and sourwood) and fall (thistle, goldenrod, asters) plant communities' bloom periods (Avers and Harman, 1992; Sponsler et al., 2020). Honey bee colonies are at their peak population size during this time (Chabert et al., 2021), creating a greater demand for resources on a per-colony basis. During this time, honey bee colonies are also collecting and storing large volumes of nectar to sustain themselves throughout the winter months (Seeley and Visscher, 1985; Harbo, 1986). Honey bee foragers can become so desperate for resources in fall that they rob nectar and honey from other, surrounding colonies (Rittschof and Nieh, 2021). Thus, honey bees' elevated demand for resources, the depressed environmental supply, and temporal niche overlap with late-season foragers may set the stage for resource competition. Late-season at-risk bee genera were generally also larger in body size than honey bees (particularly Svastra, which had the greatest probability of a negative effect of apiary density and is ~1.5 times bigger than a honey bee, approaching the size of a carpenter bee (North American Native Bee Collaborative, 2017)). Larger bodied bees require

more resources on a per-bee basis, potentially exacerbating the effects of resource limitation (Cane and Tepedino, 2017).

Many of these at-risk genera also have narrower diet breadth than honey bees. For example, long-horned bees primarily forage on Asteraceae, with some species specializing on sunflowers, thistle, ironweed (*Melissodes*), evening primrose (*Svastra*), and pickerelweed (*Florilegus*, *Melissodes*) and various late-season cellophane bees specialize on specific perennial forbs (North American Native Bee Collaborative, 2017). Therefore, if they are displaced by honey bees while foraging, as has been suggested in experimental studies (Hudewenz and Klein, 2013; Ropars et al., 2019; Page and Williams, 2023), they may not be able to easily switch to a different resource.

Resource dearth and/or competition between honey bees for late season, specialist bees may be heightened in urban settings. While some developed areas can provide season-long resources to support pollinators, abundant late season forage (goldenrod/asters) is often more associated with old fields rather than disturbed urban habitats (Sponsler et al., 2020). Moreover, many of these specialists' host plants are primarily found in high quality meadows, herbaceous wetlands, and/or grassy/herbaceous fields (North American Native Bee Collaborative, 2017). This likely explains, for example, the major role of developed land on *Florilegus condignus*, a pickerelweed (wetland) specialist. Each of these bees are also ground nesting, which previous research has shown are less likely to succeed in developed areas, likely due to extensive hardscaping (Wenzel et al., 2020).

Compellingly, we also observed a negative association between apiary density and *Triepeolus*, a nest parasite of Eucerine bees (i.e., longhorned bees). These late-season, kleptoparasitic cuckoo bees do not collect pollen themselves, but rather lay eggs on pollen provisions collected by long-horned bees (Michener, 2007). Their reliance on longhorned bee populations makes them an apex member of the community and highly susceptible to disturbance. As such, kleptoparasitic bees have been suggested as an indicator of bee community health (Sheffield et al., 2013), making it notable that we observed a negative correlation with honey bee apiary densities. These genus-specific findings highlight the strength of our joint modeling approach for elucidating genus-specific effects, particularly for rare genera (such as these cuckoo bees) (Zipkin et al., 2010). Still, other nest parasites including *Coelioxys* and *Nomada* were not similarly affected. For *Coelioxys*, this may relate to the relative abundance of their host genera, *Megachile*, which were one of the few genera positively correlated with apiary density. This explanation does not hold for *Nomada*, however, which parasitizes nests of *Andrena* and *Agapostemon*, both of which each were negatively associated with urban beekeeping (North American Native Bee Collaborative, 2017).

#### 4.3. Small, ground-nesting, season-long foraging genera

In our study, we found that many sweat bee genera, particularly the green bee group, as well as Lasioglossum, were negatively correlated with developed land and apiary density. Each of these genera are small, generalist foragers with flight periods that span the growing season, and are mostly ground-nesting (except Augochlora pura and some Lasioglossum species) (North American Native Bee Collaborative, 2017). Season-long foraging may make these bees particularly vulnerable to resource limitation, as they require continuous access to flowering plants throughout the year. Their season-long flight period may also help explain the mixed role of developed land and apiary density. That is, developed land and apiary density may affect these bees at different times of the season depending upon bloom phenology, colony growth, and their additive effects. As previously mentioned, ground nesting bees tend to do less well in urban environments than cavity nesters (Cane et al., 2006; Threlfall et al., 2015; Wenzel et al., 2020; Ayers and Rehan, 2021), in line with our findings. Contrary to our findings, some studies find that small-bodied bees thrive in urban environments (likely due to their lower resource requirements) (Banaszak-Cibicka and Żmihorski, 2012; Ayers and Rehan, 2021). Other studies suggest larger bodied bees (which may more easily transverse the urban matrix to find habitat patches) are more suited to urban environments (Gunnarsson and Federsel, 2014; Guimarães Alves and Gaglianone, 2021), and still others find no effect of body size (Cane et al., 2006). Our findings therefore contribute valuable data to the body of literature and may offer a more nuanced understanding of urbanization effects on bee communities.

# 4.4. Genera positively associated with apiary density and/or developed land

Three genera in our study – Anthidium, Hylaeus, and Ptilothrix – had a positive association with developed land. Previous studies suggest that developed land can be a refuge for a diversity of bee genera, as it provides year-round resources via urban parks, gardens, and other green spaces (Matteson and Langellotto, 2010; Tonietto et al., 2011; Threlfall et al., 2015; Turo et al., 2020). However, we did not find strong evidence for developed land supporting many different genera (only 3 of 33 genera), consistent with a recent European metanalysis, which found limited evidence of urban land affecting various pollinator taxa (Bottero et al., 2023). Furthermore, Anthidium (i.e., A. manicatum and A. oblongatum), are non-native wool carder bees that were introduced to the Mid-Atlantic in the last century (Gibbs and Sheffield, 2009; Maier, 2009; Russo, 2016) and there is some concern about the effect these bees could have on the wild bee community (Gibbs and Sheffield, 2009; Strange et al., 2011; Graham et al., 2019). As cavity nesters and collectors of plant material from garden species (e.g., ornamental mints such as lamb's-ear) for their nests (North American Native Bee Collaborative, 2017) these bees, like other non-native bees (Kammerer et al., 2021), are known associates of urban environments (Strange et al.,

2011; Miller et al., 2018). *Hylaeus* is likewise a cavity nester, which are known to benefit from the novel nesting opportunities presented by urban environments (Cane et al., 2006; Wenzel et al., 2020). *Hylaeus* forage on easily accessible, flat-top flowers (e.g., daisy-like flowers and umbellifers) (North American Native Bee Collaborative, 2017), which may be found as weeds in disturbed environments or grown as part of gardens/landscaping. *Ptilothrix* likewise benefits from home gardens. *Ptilothrix* is a specialist on mallow flowers, particularly rosemallow (*Hibiscus* sp.), a wetland native, often planted in home gardens along with other non-native Hibiscus flowers (North American Native Bee Collaborative, 2017).

Interestingly, there was some evidence that apiary density may positively correlate with *Ptilothrix* and *Megachile* abundance. One possible explanation for this is that urban beekeepers may be more active in home gardening and/or engage in practices that support wild bees (e.g., providing wild bee nesting resources such as bee hotels) (Smith et al., 2021). In this way, honey bees may act as an effective flagship species, capable of raising support and attention for pollinator conservation. Thus, interest in supporting honey bees could be leveraged to encourage the design of gardens that can support a broader bee community (Cruz and Grozinger, 2023).

# 4.5. Wild bee sampling method bias

Beyond the ecological findings that can be gained from these data, our approach also provides important methodological insights. By integrating data from different sampling methods, we demonstrate that different methods introduce systematic bias, and that integrated approaches are preferable (Zipkin et al., 2023). Our findings were consistent with what is known in the literature about sampling bias. Relative to hand netting, in pan traps we found an overrepresentation of Halictus (Rhoades et al., 2017; Portman et al., 2020) and Lasioglossum (Giles and Ascher, 2006; Wilson et al., 2008; Grundel et al., 2011; Larsen et al., 2014; Joshi et al., 2015) and an underrepresentation of Colletes (Giles and Ascher, 2006). Among blue vane traps, we documented more Lasioglossum, Ptilothrix, Melissodes (Acharya et al., 2022) and Agapostemon (Rhoades et al., 2017; Acharya et al., 2022), and more Andrena in net collections relative to pan traps (Rhoades et al., 2017). Overall, bees collected more often by hand netting tended to be larger-bodied (e.g., Xylocopa, Bombus and Andrena), while bees collected more often with pan traps were smaller-bodied (e.g., Agapostemon, Calliopsis, Lasioglossum, Augochlorella, Ceratina, Halictus, Hylaeus) (North American Native Bee Collaborative, 2017). This is likely due to poor detection of small-bodied bees by human collectors due to size as well as differences in foraging height (North American Native Bee Collaborative, 2017). Some medium-bodied, ground-nesting bees (e.g., Ptilothrix, Melitoma, Melissodes, Peponapis) were more often collected by pan trap than hand netting. Many of these genera will often be found resting inside flowers with deep corollas (e.g., Ptilothrix in Hibiscus flowers, Melitoma in Convolvulus flowers, and Peponapis in Cucurbita flowers), and therefore may be difficult to detect while hand netting, unless specifically targeting their host plants (Cane et al., 2000; Rhoades et al., 2017). Many of the genera that were more effectively sampled with vane traps were on the social spectrum (Bombus and various Lasioglossum), or communal nesters (e.g., Agapostemon) which may help explain greater probability of catch with passive methods (Selfridge et al., 2017) than active hand netting. By accounting for sampling method in our modeling approach, we are able to obtain more accurate and precise estimates for our primary variables of interest (i.e., apiary density and developed land use) on wild bee population estimates (Zipkin et al., 2023).

# 4.6. Study limitations

There are limitations of this study that may affect the broad applicability of our results. Firstly, our study system is limited to Maryland because of the unique availability of both beekeeper and wild bee data within this state. While Maryland is a valuable study system in that it offers a unique range of land use, it may not be representative of other, more agriculturally intensive states in either its cropping systems or apicultural practices. In many pollinator-dependent cropping systems, growers will rent honey bee colonies for pollination services on their farms (Delaplane and Mayer, 2000). Beekeepers may also preferentially locate apiaries near cropland to capitalize on mass-blooming melliferous crops and on-farm conservation land for honey production (Otto et al., 2016). Maryland agriculture is dominated by corn, soy, and small grains (US Department of Agriculture National Agricultural Statistics Service, 2018), which are not typically considered beneficial forage for honey bees, nor do they benefit greatly from insect pollination (Free, 1993). This likely explains the low density of apiaries in the agricultural regions of the state.

Furthermore, apicultural practices in Maryland may not reflect those in more apicultural intensive states. For example, the Dakotas, perhaps the most apicultural intensive states in the country, host  $\sim 1$  million colonies each summer (40 % of US registered stocks) (Otto et al., 2016). While the overall apiary densities are similar between the two regions  $(\sim 3 \text{ apiaries/km}^2)$ , apiaries in the Dakotas are primarily managed by commercial beekeepers, who typically keep large numbers of colonies at each apiary (e.g., 50 colonies/apiary), while apiaries in Maryland are likely managed by hobbyist beekeepers (given the location of apiaries and agriculture of Maryland) who typically manage fewer colonies per apiary (e.g., 2-5). Our inability to account for colony densities within apiaries is a limitation of this study, but because Maryland is not a destination for commercial beekeepers (Jabr, 2013), we assume that densities are relatively consistent and low. We also assume in this approach that the apiary records are representative of honey bee populations. This potentially ignores effects such as feral honey bee colonies and systematic bias in beekeeper reporting (e.g., beekeepers in more rural or urban areas are more/less likely to report). Feral colonies are assumed to be rare in the landscape, due to low survival rates brought on by lack of beekeeper management for Varroa destructor mites (Korpela et al., 1992; Tarpy et al., 2015), however, there are reports of persistent populations (Seeley, 2007). We additionally feel that because apiary registration is required by Maryland Law (COMAR 15.07.01.02), demographic biases in reporting are minimized in this dataset.

An additional limitation of this study is that the available data only spanned two years. Previous studies found strong inter-annual variation in wild bee communities' response to honey bees (Prendergast et al., 2021; Bommarco et al., 2021). Given that most beekeepers (especially hobbyists) establish apiary locations that they use for many years (and sometimes pass down through families) it seems likely that the wild bee patterns we observed reflect long-term associations with apiary densities. As additional data becomes available, our modeling framework could be used to understand the broad-scale effects of honey bee densities within different contexts.

Similarly, the short time scale and modest number of wild bee sampling locations (n = 141) resulted in a limited number of detections for many of the rare genera (e.g., *Hoplitis* [14 observations]). This could result in low power to detect relationships with apiary density and/or developed landcover for these groups. However, our joint modeling approach improves the precision of estimates for rare genera by sharing information across genera (e.g., Zipkin et al. (2010)), and our use of probability to assess the amount of statistical support for an effect as opposed to a strict reliance on significance (e.g. whether the 95 % credible overlaps 0) minimizes our potential for Type II errors.

Finally, by assessing wild bee relative abundance at the genus level, there is the possibility of introducing taxonomic bias. For example, while most genera were represented by one to a few species, other genera are extremely speciose (e.g., *Andrena, Lasioglossum, Nomada, Megachile*). This taxonomic diversity may introduce the potential for a confounding effect, known as Simpson's paradox. That is, species with different natural histories/traits, within the same genus, could respond differently to apiary density and or develop land, thereby masking

effects at the genus level. While ours is the most taxonomically resolved assessment of wild bee responses to honey bee density to date, future efforts to further parse species-specific and trait-specific responses would be valuable.

#### 4.7. Conservation implications and recommendations

Based on our findings, we suggest that urban areas could focus on planting abundant, late-season forage, particularly host plants for known oligolectic (specialist) bee species, such as Asteraceae species for long-horned bees and specific perennial forbs for fall cellophane bees. Indeed, our results suggest that urban gardening is effective means of promoting certain specialist genera (such as Ptilothrix). Generally, previous research has demonstrated that floral abundance is a key determinant of whether cities are beneficial or detrimental to pollinators (Wenzel et al., 2020) and that garden ornamentals can support pollinators throughout the year in developed areas (Sponsler et al., 2020; Erickson et al., 2020, 2021). Other gardening practices (e.g., leaving bare ground) could help support ground-nesting bees, which are typically at odds with developed land (Wenzel et al., 2020). Targeting groups with special interest in pollinators, such as beekeepersgardeners, for these initiatives may be particularly effective (Smith et al., 2021). Outreach could also communicate to beekeepers the potential for competition with wild bee communities and encourage beekeeping practices that help to alleviate this competition, such as offering supplemental feed during periods of dearth.

### 5. Conclusions

Many studies indirectly assess honey bee-wild bee competition by assessing changes to resource abundance and/or plant-pollinator network structure (Wojcik et al., 2018). While these studies offer important mechanistic understanding of how honey bees could alter the foraging landscape and wild bee foraging behavior, our study examines the downstream consequences on wild bee communities. We found evidence for genus-specific responses to both apiary density and developed land that highlight several areas for conservation intervention. These findings reflect fundamental ecological principals and offer an interesting case study through which to understand effects of non-native species on biodiversity, as well as effects of anthropogenic land use on non-native species persistence and environmental filtering. Since the early 20th century, most land use is now characterized by anthropogenic factors, which has caused massive changes for ecosystem structure and function (Ellis et al., 2010). Studies such as ours that elucidate the consequences of this shift are important to understanding the effects of human-altered landscapes and to building resiliency in the face of anthropogenic change.

#### CRediT authorship contribution statement

Gabriela M. Quinlan: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. Jeffrey W. Doser: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis. Melanie A. Kammerer: Writing – review & editing, Validation, Data curation. Christina M. Grozinger: Writing – review & editing, Validation, Supervision, Resources, Funding acquisition.

# Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Gabriela Quinlan reports financial support was provided by National Science Foundation. Christina Grozinger reports financial support was provided by National Institute of Food and Agriculture. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

#### Data availability

Code and data required to fit all models is available on GitHub (https://github.com/doserjef/Quinlan\_et\_al\_2024\_STOTEN) and Zenodo (https://doi.org/10.5281/zenodo.13695107).

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175783.

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#### G.M. Quinlan et al.

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