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RESEARCH ARTICLE

Land-use change alters specialist bee diet and drives body size declines

Sarah E. Anderson · Philip Hahn · Gabriela Gonzalez · Rachel E. Mallinger

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Abstract

Context Land-use change can cause decreases in plant abundance and richness and the replacement of wild plants with domesticated plants. Changes in plant community composition disrupt mutualistic plant-pollinator interactions with ecological consequences for plants and pollinators, and especially for specialists that rely on certain plants.

Objectives We assessed the effects of land-use change and subsequent shifts in plant communities on resource collection and body size for a bee pollinator, *Habropoda laboriosa*, a purported specialist of blueberries and related Ericaceae plants.

Methods We collected *Habropoda laboriosa* across a gradient of land use in north-central Florida including agricultural, natural, and urban habitats. We assessed landcover and floral community composition at each site and related these to bee body size (intertegular distance) and resource use (proportion host plant pollen and pollen diversity collected).

Results Host plant pollen collection and bee body size generally responded similarly to the landscape, both increasing with habitats containing host plants (blueberry farms and natural habitat) but decreasing with urban development. However, host pollen collection and bee body size responded in opposite ways to overall cropland in the landscape, with cropland negatively affecting body size despite positively affecting host pollen collection, indicating other factors associated with cropland might drive declines in bee body size.

Conclusions Land-use change can adversely affect bee diet and body size, and changes in diet likely contribute to changes in body size over time. Specialists are particularly at risk for negative impacts of land-use change due to their inability to shift plant hosts.

Keywords Land-use change · Urbanization · Agricultural intensification · Specialist · Pollinator · Bee

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Introduction

Anthropogenic changes to habitat composition and quality threaten biodiversity and heighten the risk of species extinctions globally (Brooks et al. 2002; Newbold et al. 2015; Powers and Jetz 2019; Sánchez-Bayo and Wyckhuys 2019). In particular, land-use change causes both animal and plant species loss and community shifts both in the areas directly affected by land-use change and in the surrounding regions (Giam et al. 2010; Laliberté et al. 2010; Lee et al. 2012; Hahn and Orrock 2015; Skultety and Matthews 2018; Fourcade et al. 2019; Sales et al. 2020; Ohler et al. 2023). Such shifts often include decreases in plant species richness and abundance, losses in plant functional diversity, and replacement of wild plants with domesticated plants (José-María et al. 2010; Clough et al. 2014). Changes in plant community composition can impact a wide range of interspecies interactions including mutualistic relationships (Scheper et al. 2014; Welti et al. 2017; Cutter et al. 2021). Of particular concern are interactions between plants and bees that are critical for maintaining ecosystem functioning in both natural and agricultural systems (Kremen et al. 2007; Singer and Parmesan 2010; Potts et al. 2016). Bees rely almost exclusively on flowering plants for both protein and carbohydrate resources (Vaudo et al. 2015), and habitat loss and associated changes in plant communities can have impacts on bee population declines (Biesmeijer et al. 2006; Winfree et al. 2009; Kiers et al. 2010; Potts et al. 2010; Powney et al. 2019; Ropars et al. 2020). In turn, flowering plants that rely on bee pollination can suffer reproductive declines when isolated from bees, and reproductive strategies can shift to increasing levels of autonomous self-fertility (Eckert et al. 2010).

Even when overall plant species richness and abundance are not reduced by land-use change, shifts in plant community composition can reduce bee fitness. Wildlands converted to urban habitats have an increased abundance of ornamental plants bred for attractive appearance, including both non-native and native species. Agricultural habitats in the United States are dominated by crop plants that are typically non-native. Furthermore, even native crops such as blueberries or squash are domesticated and differ in many ways from their wild relatives. For example, domesticated ornamental and crop plants often have lower concentrations of nectar sugar and pollen protein than their wild counterparts (Roulston and Cane 2002; Egan et al. 2018; Roger et al. 2017; Lawson et al. 2021). Additionally, some domesticated plants may not be recognized by bees as suitable floral resources if they display domestication syndromes including altered size and appearance, and changes in nectar chemistry, pollen protein content, and pollen amino acid profile, all of which can impact pollinator recruitment (Pickersgill 2007; Egan et al. 2018; Pacheco-Huh et al. 2021).

Changes in floral resource availability and quality resulting from land-use change can cause declines in adult bee body size that have negative implications for both bee populations and pollination services. Bee body size is a highly plastic trait that is largely dependent on environmental variables and has been shown to vary with land-use change (Persson and Smith 2011; Renauld et al. 2016; Garlin et al. 2022). Specifically in bees, the pollen type that bee larvae are reared on significantly affects larval growth, size, and survival to adulthood (Standifer 1967; Schmidt et al. 1987; Génissel et al. 2002; Roulston and Cane 2002; Tasei and Aupinel 2008; Burkle and Irwin 2009; Filipiak 2019). For instance, bees reared on pollen with lower protein concentrations achieve smaller adult body size and reduced fecundity as compared to bees foraging on floral resources with high concentrations of pollen protein (Roulston and Cane 2002). As domesticated plants often differ from wild plants in their pollen chemistry (Egan et al. 2018), the replacement of wild plants with domesticated ones in human-managed landscapes could have significant consequences for bee body size.

Bee body size declines are in turn related to reductions in bee fitness as well as declines in pollination services within the broader ecosystem. Insect fecundity generally decreases with declines in body size (Honek 1993; Preziosi et al. 1996; Calvo and Molina 2005; O'Neill et al. 2014). Additionally, within a species, smaller adult bees showed reduced access to flowers and collected lower quality nectar and pollen for nest provisioning than larger-bodied conspecifics (Roulston and Cane 2002; Peterson and Roitberg 2006; Burkle and Irwin 2009; Baron et al. 2014). Smaller bees are also less competitive in nest provisioning than larger bees because of their limited foraging range and can suffer greater exposure to pesticides than larger bees because they ingest more

pollen and nectar per unit body mass than larger bees (Bosch and Vicens 2006; Neff 2008; Sgolastra et al. 2019; Goulson and Nicholls 2022). In addition to negative impacts on bee fitness, reduced bee body size is also associated with lower pollination efficacy and can have consequences for pollination services in both agricultural and natural systems (Willmer and Finlayson 2014; Jauker et al. 2016).

Specialist bees may be particularly vulnerable to changes in plant community composition resulting from land-use change as they rely on a narrower group of plants and have less flexible diets. Specialist bees foraging on cultivated crops may experience greater exposure to pesticide residues in pollen and nectar than generalists that may spread their foraging effort across cultivated and non-cultivated crops. Most herbivorous insects are thought to be dietary specialists, feeding on one plant family or smaller taxonomic plant unit, and fewer than 10% of herbivorous insects feed on three or more plant families (Bernays 1998; Danforth et al. 2019). Amongst bees, specialization may be less common but still prevalent in particular habitat types; up to 66% of bee species specialize in the collection of pollen from one single plant family, genus, or narrow group of species in certain habitats such as North American deserts (Moldenke 1979; Cane and Sipes 2006; Danforth et al. 2019). However, estimates of specialization will depend on definitions of specialization, which have varied over time. While specialists were originally defined as those species restricting the pollen diet to one single plant family (Robertson 1899), more recently bee researchers have used floral visitation and pollen load compositions of 90% or greater from a single plant family as evidence for bee specialization (Cane and Sipes 2006). Subsequent work on bee dietary specialists has shown that in certain contexts, specialists will practice flexible foraging and collect pollen from non-host plants (Michener and Rettenmeyer 1956; Cruden 1972; Nelson and Griswold 2015). This work suggests that specialist bee diets may be hierarchical, wherein specialists will accept non-primary host pollen if primary host pollen is not available (Danforth et al. 2019). Thus, understanding how the diet and fitness of specialist bees are influenced by land-use change and subsequent shifts in plant community composition is important because the ability of these bees to use alternative resources will determine their ability to persist in altered habitats.

In this study, we assessed the effects of land-use change on the pollen collection and body size of a purported specialist bee, *Habropoda laboriosa.* This bee is thought to specialize on *Vaccinium* spp. including wild and domesticated blueberries and closely related plants in the family Ericaceae (Cane 1994) but has been observed on non-Ericaceous plants as well as on highly domesticated plants such as ornamental Azalea (*Rhododendron* spp.) (Pascarella 2007). Wild *Vaccinium* spp. grow abundantly in native landscapes in the southeastern United States, while cultivated *Vaccinium* spp. are grown abundantly on blueberry farms in the same region and closely related plants in the family Ericaceae (e.g., azaleas) are grown abundantly in suburban and urban landscapes. Furthermore, there are documented records of *H. laboriosa* across multiple habitat types in the southeastern United States, likely due to the widespread distribution of wild and domesticated plants in the family Ericaceae. This wide distribution is somewhat atypical for specialist bees that are often found only in habitats associated with host plants (Fowler 2016; Davis et al. 2020). Because of its widespread distribution, *H. laboriosa* is an ideal organism for examining the impacts of land-use change and associated shifts in plant community composition, including the replacement of wild plants with domesticated plants, on pollen collection and body size.

To assess changes in pollen collection and body size resulting from land-use change and plant domestication, we collected 371 female *H. laboriosa* across a gradient of land use in 29 sites categorized as agricultural (cropland), natural (forested), and urban (developed) habitats. In this study system, natural habitats are dominated by wild plants while urban habitats are dominated by highly domesticated plants, and agricultural habitats are dominated by more recently domesticated plants. We measured the diversity of pollen as well as the proportion of host plant pollen collected from plants in the family Ericaceae in each bee's pollen load and measured the intertegular distance (ITD) of bees as an indicator of body size (Cane 1987). We hypothesized that specialist bee body size and pollen collection would vary over gradients of land use. Specifically, we predicted that the adult body size of *H. laboriosa* would be highest in highly forested landscapes where wild *Vaccinium* are abundant and would be lower in areas dominated by cropland and urban development where wild plants

have been replaced with domesticated crop and ornamental plants. Similarly, we predicted that the proportion of host plant pollen collected would be highest in highly forested areas and would be lowest in areas dominated by cropland and urban development.

Methods

Site selection

Sites were selected during the year prior to starting the study to represent three habitat types: agricultural, natural, and urban. Sites also spanned a land-use gradient of proportion cropland, proportion forest, proportion cultivated blueberry farmland, and proportion urban development in the surrounding landscape. We sampled seven sites in each habitat category during 2020 and seven sites in each habitat category in 2021; thus, 21 sites were sampled each year. Agricultural sites were conventional or organic blueberry farms with abundant cultivated southern highbush blueberry *Vaccinium corymbosum* x *darrowii*. Natural sites included state forests, conservation areas, or nature centers with abundant native, wild blueberry *Vaccinium myrsinites*. Urban sites were public and private gardens with abundant flowering ornamental plants, including plants related to blueberries in the Ericaceae family such as azalea, *Rhododendron* spp. Study sites were replaced during the second year of the study due to business closures, changes in accessibility resulting from the COVID-19 pandemic, and prescribed burns, but still maintaining seven sites per habitat category. Over two years, a total of 29 sites were sampled including 13 sites that were sampled in both years, eight sites that were only sampled in 2020, and eight sites that were only sampled in 2021. Sites within a sampling year were separated by a minimum distance of 2 km to ensure independent bee and plant communities (Fig. 1; Gathmann and Tscharntke 2002; Zurbuchen et al. 2010). We selected a 2-ha sampling area within each site and established two

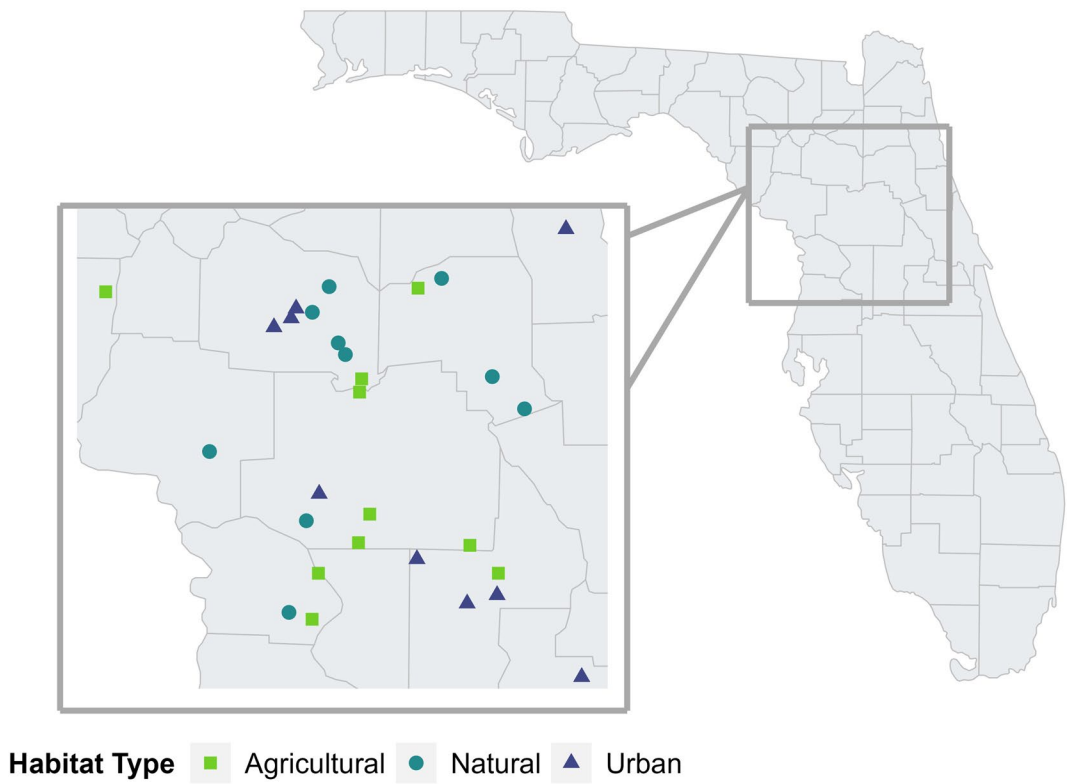


Fig. 1 Site map including all 29 sites sampled and their assigned habitat category. All sites sampled within a year are a minimum of 2 km apart

roughly perpendicular 50×2 m sampling transects. Transects were not randomly placed but rather established where the floral abundance within the 2-ha sampling area was apparently greatest, including the abundance of flowering Ericaceous plants, to maximize captures of bees and bee activity.

Bee visitation rates and collection

We collected *H. laboriosa* and floral data from January 13 – March 26 in both 2020 and 2021. These weeks cover most of the adult foraging period of *H. laboriosa*, which like many specialist bees, is only a few weeks long (Cane 1994). During each site visit, we recorded *H. laboriosa* visitation rates to flowering plants in both sampling transects by walking each transect and maintaining a steady walking pace over the length of the transect for a period of approximately five minutes. Visits were defined as *H. laboriosa* making contact with any part of the flower. After recording visitation rates to flowering plants in the transects, we hand netted up to ten *H. laboriosa* females with pollen loads throughout the 2-ha study area at each site during each site visit. Collected bees were euthanized in the field in individual containers to maintain specimen independence and later stored at -18 °C until pollen removal and body size measurement. All sites were sampled a minimum of six times in 2020 and a minimum of five times in 2021. Sites were only sampled on days when the temperature was a minimum of 10 °C, and all sampling took place between the hours of 9 am—4 pm.

Flower density and richness

During each site visit, we also recorded the density and richness of flowering plants within both sampling transects. In agricultural sites, transects were placed between blueberry rows and included both cultivated blueberry plants (on one side of the transect) as well as the interrow space with flowering weeds (on the other side of the transect). In urban sites, transects were placed to include ornamental plants and flowering weeds and sometimes included dirt walking paths, areas of lawn or mulch, and portions of sidewalks. Transects in natural sites included leaf litter, understory plants, and bare soil. To estimate the density of individual flowering plant species, we counted the total number of open inflorescences of each flowering species occurring at low densities within the transects. For densely flowering plant species, where counting each open inflorescence was infeasible, we counted the number of open inflorescences in five 1×2 m quadrats at evenly spaced intervals along the transect and multiplied the mean number of open inflorescences within the 1-m long quadrats by 50, or the total length of the transect in meters. Within quadrats, we only counted inflorescences for flowering plants occurring densely throughout the transect but did not count inflorescences of low-density flowering plants as these were counted precisely and separately, as described above. On blueberry farms, we estimated the density of cultivated blueberry flowers (a densely blooming plant species) per transect by counting the number of blueberry flowers on five bushes at evenly spaced intervals along the transect and multiplying the mean number of flowers per bush by the total number of bushes in the transect. Weeds and other flowering plants within blueberry farms were precisely counted per transect (when occurring infrequently) or estimated using quadrats (when occurring frequently) as described above. These combined methods yielded both an estimate of flowering density for each flowering plant species as well as the total flowering density within transects. For plants with compound flowers, we counted the number of open flower heads as the number of open inflorescences. Most flowering plants were identified to species, but in some cases, plants were only identified to genus. During each site visit, we also completed a 15-min meandering walk throughout the 2-ha sampling area to record additional flowering plant species presence for plant species not represented in the two transects. Flowering plant species presence was included in site-level flowering plant richness estimates as described below in the statistical analysis section.

Pollen load composition

We removed the pollen load from the scopa of each collected female bee and vortexed each individual pollen load in 500 µL of Alexander's stain (a solution of acid fuchsin and malachite green in water) to completely homogenize the sample (Alexander 1969). We added 50 µL of the homogenized pollen solution to a clean microscope slide prepped with glycerin, placed a 0.5 micron slide cover over the sample, and sealed

the slide using clear nail polish. To ensure that pollen samples were thoroughly stained, we allowed slides to cure for at least 24 h before identifying individual pollen grains.

We visualized pollen grains at 400×magnification under a Nikon Eclipse E800 compound microscope. We categorized the first 100 grains of pollen observed along a perpendicular transect of the slide into 13 morpho types; pollen in the family Ericaceae, including *Vaccinium* spp. represented one of these 13 pollen morpho types. Pollen morpho types were photographed and used for reference so that morphotype identification remained consistent across all slides.

Bee body size

The distance between the wing bases of a bee, i.e., intertegular distance (ITD), is allometrically related to overall body size and has been used as a proxy for body size in numerous studies (Williams et al. 2010; Greenleaf et al. 2007; Grab et al. 2019). We took one measurement of the ITD of each female *H. laboriosa* after removing any thoracic hair obstructing the view of the tegula and using a Swift MCX3 stereo microscope and Moticam photo-measuring software. For each measurement, specimens were placed in a dish of small glass beads so the specimen could be easily adjusted such that both tegula were on the same plain and precisely in focus under the microscope. The microscope calibration and stage height as well as the dish and volume of glass beads were held constant across all measurements.

Land cover quantification across sites

As described above, sites were selected to represent three broad habitat categories: agricultural, natural, and urban. For each of the sites included in the study, we also assessed the proportion of blueberry, other cropland, forest, and urban development within a 500 m radius surrounding each site using the 2020 CropScape land cover data provided for USGS (Han et al. 2014) and QGIS software (Quantum GIS Development Team). We used a 500 m radius of landcover data surrounding each site because solitary bee maximum foraging distance is reported to be between 150-600 m depending on body size, and *H. laboriosa* is a larger-bodied solitary bee (Gathmann and Tscharntke 2002). We specifically quantified four landcover categories to measure the proportion of potential focal habitat (including *Vaccinium* spp. and related Ericaceae plants) surrounding each site and including the site itself. The category blueberry included cultivated blueberry farms, including the selected study farms. The category other cropland included all fruit, vegetable, nut, seed, and row crops, but excluded pasture and fallow fields. This category thus includes mixed farms that may have cultivated blueberry present but not represented in the landcover map. The category forest included the studied forest sites and the sum of evergreen forest, mixed forest, and shrubland surrounding the site at 500 m (habitats likely containing wild *Vaccinium* spp.). Finally, the category urban development included the proportions of developed open space, low intensity urbanization, medium intensity urbanization, and high intensity urbanization and represented the urban development within and surrounding the site that may contain ornamental Ericaceae plants (Table S1.1).

Statistical analysis

Site selection

All analyses were completed in R Version 4.2.2. All sites sampled were included in the analyses, but to ensure empirically that the site selection method described above yielded sites with varying floral communities and surrounding landcover, we compared floral diversity, proportion of Ericaceae inflorescences, and landcover (i.e. cultivated blueberry, other cropland, forest, and urban development) in the 500 m radius surrounding sites across the three habitat categories (natural, urban, and agricultural) used in site selection. We calculated floral diversity within the 200 m^2 focal area of each site using the Shannon Diversity Index and calculated the proportion of Ericaceae inflorescences as the total number of Ericaceae inflorescences counted within the 200 m^2 focal area of each site divided by the total number of inflorescences counted in the focal area. We also compared *H. laboriosa* visitation rates across habitat types and calculated visitation rate as the number of *H. laboriosa* visits observed within the 200 m^2 focal area per site per day.

We used a linear mixed effects model to assess the response of floral diversity, a generalized mixed effects model with a beta distribution to compare the

proportion of Ericaceae inflorescences across habitat types, and a generalized mixed effects model with a negative binomial distribution to assess the response of *H. laboriosa* visitation rates to habitat type. All linear mixed effects models were built in the *lmer4* R package, and all generalized mixed effects models were built in the *glmmtmb* R package. We used beta distributions in generalized mixed effects models because they are appropriate for assessing response variables with values between zero and one, such as proportions (Ferrari and Cribari-Neto 2004; Douma and Weedon 2019). Because beta distributions cannot handle values equal to zero and one, we performed a data transformation by adding 0.00001 to all proportions equal to zero and subtracting 0.00001 from all proportions equal to one (Douma and Weedon 2019). We used a generalized mixed effects model with a negative binomial distribution to assess the response of *H. laboriosa* visitation rates to habitat type. Negative binomial distributions are appropriate for assessing count data with many zeros and are often used to assess visitation data (Hardin and Hilbe 2007). Each above-described model included the fixed effect of habitat type and two random effects of site and collection week nested within year. Finally, we used linear models to compare the continuous measures of landcover (other cropland, cultivated blueberry, forest, and urban development) across habitat types. No random effects were included in these models, as each landcover variable was only assessed once for each site. We assessed model significance for all models using a type II Anova and conducted a priori comparisons of means for all variables assessed across habitat types using Tukey's HSD test.

Pollen collection

We assessed the response of *H. laboriosa* pollen collection to land-use change by examining both the diversity of pollen and the proportion of Ericaceae pollen collected in pollen loads. Pollen diversity for each pollen load was calculated using the Shannon Diversity Index after pollen was visually categorized into 13 morphotypes as described above. The proportion of Ericaceae pollen was calculated as the number of Ericaceae grains divided by 100 grains, i.e., the total number of grains identified in each pollen load (plus/minus 0.00001 as described above). We related pollen collection to the following predictor variables: floral diversity per site per collection day (as an indicator of the dominance of host plant pollen and the prevalence and diversity of non-host plant pollen), cultivated blueberry, other cropland, forest, and urban development in the 500 m radius surrounding the site (as an indicator of primarily wild versus primarily domesticated host plants within the bee's foraging radius). We did not include the proportion of Ericaceae inflorescences per site per collection day in the model because this variable was highly negatively correlated to floral diversity per site per collection day (-0.93). Between the two highly correlated variables, we chose to include floral diversity because it captures information about the entire flowering plant community and indirectly but significantly and strongly indicates the dominance of Ericaceae flowers in the landscape. While proportion Ericaceae flowers also indicates dominance of the host plant, it does not include information about the rest of the flower community, which could affect even specialist bee foraging behavior (Guzman et al. 2019).

We used model selection to determine which fixed effects included in the initial models influenced response variables. For each response variable, all combinations of fixed effects and the null model (i.e., intercept only) were compared using Akaike's Information Criterion (AIC). Models within four ΔAIC of the model with the lowest AIC score were then averaged to obtain estimates and standard errors of each fixed effect included in the averaged model (Tredennick et al. 2021). For pollen diversity, models were linear mixed effects models, while models for the proportion of Ericaceae pollen collected were generalized mixed effects models with a beta distribution. All possible models included the same two random effects of site and collection week nested within year, and the reported estimates and standard errors are taken from the conditional model average including random effects. Model selection was not used to select random effects structures as data clustering geographically and temporally was inherent to the study design (Gelman and Hill 2007).

Additionally, we assessed the relationship between the proportion of Ericaceae pollen collected and habitat type as a categorical variable (urban, agricultural, and natural). To assess this relationship, we used a generalized mixed effects model with a beta distribution that included the proportion of Ericaceae pollen as a response

variable, habitat type as a fixed effect, and site and collection week nested with year as random effects. We assessed significance of this model using a type II ANOVA and conducted a priori comparisons of means across habitat types using Tukey's HSD test.

Body size

To assess the response of *H. laboriosa* body size to land-use change, we created a full model including the same predictor variables described above (floral diversity per site per collection day, cultivated blueberry, other cropland, forest, and urban development in the 500 m radius surrounding the site). We then used the above-described model selection procedure to determine which of these fixed effects influenced body size. The candidate models and averaged model were linear mixed effects models that included the two random effects of site and collection week nested within year.

Finally, we assessed the relationship between the proportion of Ericaceae pollen collected and bee body size because previous work has shown that larger bees are more competitive in pollen collection compared to smaller conspecifics (Roulston and Cane 2002; Peterson and Roitberg 2006; Burkle and Irwin 2009; Baron et al. 2014). We tested this relationship using a generalized mixed effects model with a beta distribution that included the proportion of Ericaceae pollen collected as the response variable, body size as a fixed effect, and site and collection week within year as random effects.

All models for both pollen collection and body size were checked for multicollinearity using the *car* R package. Predictors in all full models were found to have variance inflation factors (VIF) between 1.046 – 3.008. We report the relative variable importance (RVI) as the sum of Akaike weights (SW) per predictor variable for all models included in the averaged model (Anderson and Burnham 2002). RVI ranges from zero to one, where zero indicates that the predictor variable is not found in any models included in the averaged model (Anderson and Burnham 2002; Giam and Olden 2016). We also report the number of models within the average model that include each predictor variable.

Results

The site selection procedure yielded 29 sites that varied in floral density, floral diversity, and the proportion of host plant inflorescences (Table S2.1; Fig. S2.1), as well as represented a gradient of surrounding land use including cultivated blueberry, other cropland, forest, and urban development (Table S2.1; Fig. S2.2). *Habropoda laboriosa* were recorded visiting flowering plants in all sites, and *H. laboriosa* visitation rates did not vary across habitat types (Table S2.1; Fig. S2.1C). This study included 371 female *H. laboriosa* specimens with 269 pollen loads (as some collected females did not have pollen loads). It also included 272 assessments of floral diversity and *H. laboriosa* visitation rates across 29 sites and two years.

Agricultural sites were blueberry farms where the most common flowering plant was cultivated southern highbush blueberry, *Vaccinium darrowii x corymbosum*, but flowering agricultural weeds, such as *Hydrocotyle* spp., were also abundantly present (Table S1.2). In natural habitats, two of the most common plants were *Vaccinium* spp., *Vaccinium myrsinites*, and *Vaccinium darrowii,* while another plant in the family Ericaceae, *Gaylussacia nana,* was also very common (Table S1.2). The most common flowering plants in urban habitats were *Pentas* spp., and though *Vaccinium* spp. were not common, other Ericaceae plants including *Rhododendron* spp. were relatively abundant (Table S1.2).

Pollen collection

The proportion of Ericaceae pollen collected by *H. laboriosa* varied significantly with habitat type ($\chi 2 = 13.934$, $p = 0.001$). The proportion of Ericaceae pollen collected by *H. laboriosa* was significantly lower in urban habitats (estimate = 0.18) than in natural habitats (estimate = 0.45) or agricultural habitats (estimate = 0.37). Other cropland, cultivated blueberry, forest, and urban development in a 500 m radius were all included in the averaged models predicting both the diversity of pollen loads and the proportion of host plant (Ericaceae) pollen collected by *H. laboriosa* females (Table 1). The most important predictor variables in the averaged model assessing both the diversity of pollen

Table 1 Estimates and standard errors for averaged models assessing the response of pollen diversity collected, proportion host plant pollen collected, and bee body size to five fixed effects. The relative variable importance (RVI) of each predictor variable and the number of models (N) that each predictor variable was included in is also provided. Fixed effects included proportion blueberry, other cropland, forest, and urban development in a 500 m radius, and local floral diversity, and random effects included site and collection week nested within year. NAs indicate variables that were not included in the averaged model for the given response variable

Fixed Effects	Pollen Diversity			Proportion Host Plant Pollen			Body Size		
	Slope ± Std Error	RVI	N Models	Slope ± Std Error	RVI	N Models	Slope ± Std Error	RVI	N Models
Prop. Cropland	-1.992 ± 1.010	0.90	3	3.570 ± 4.874	0.88	5	-0.155 ± 0.151	0.13	2
Prop. Blueberries	-1.790 ± 2.389	0.79	3	5.332 ± 7.954	1.00	7	0.410 ± 0.249	0.45	4
Prop. Forest	-0.472 ± 0.168	1.00	4	1.210 ± 0.875	0.72	5	0.049 ± 0.020	0.17	2
Prop. Urban Development	-0.041 ± 0.268	0.13	1	-1.102 ± 0.926	0.69	5	-0.047 ± 0.021	0.12	2
Floral Diversity	NA	NA	0	0.115 ± 0.174	0.10	2	NA	NA	0

loads and the proportion host plant (Ericaceae) pollen collected were forest (RVI = 1.00, 0.72, respectively), other cropland (RVI = 0.90, 0.88, respectively), and cultivated blueberries (RVI = 0.79, 1.00, respectively). The diversity of pollen in pollen loads increased as all focal landcover categories decreased in the 500 m radius (Table 1; Fig. 2), while the proportion of host plant (Ericaceae) pollen in pollen loads increased with increasing amounts of cultivated blueberry,

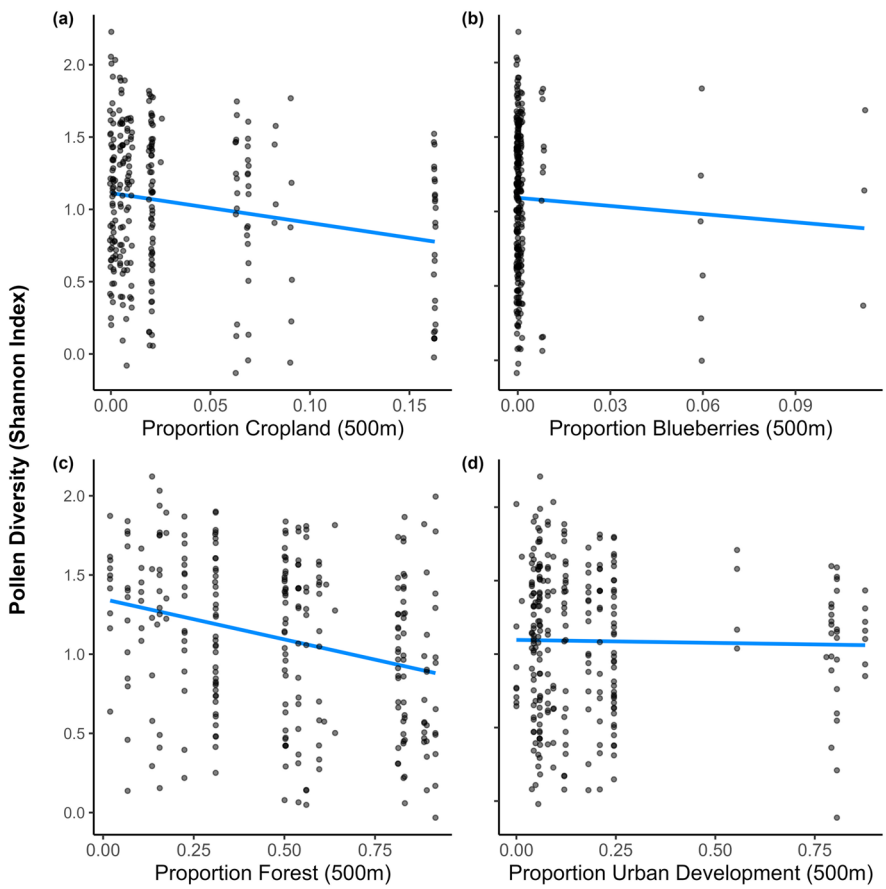


Fig. 2 Response of collected pollen diversity to each variable included in the averaged model. Displayed are estimates and model residuals for the response of pollen diversity to the proportions of **a**) cropland, **b**) blueberries, **c**) forest, and **d**) urban development in a 500 m radius surrounding each site. Site and collection week nested within year were included as random effects in the averaged model. Points are slightly transparent such that darker points indicate overlapping values

cropland, and forest in the landscape, but decreased with increasing amounts of urban development (Table 1; Fig. 3). Floral diversity was also included in the averaged model predicting the proportion of host plant (Ericaceae) pollen collected but not in the model predicting the diversity of pollen collected (Table 1). The proportion of host plant pollen collected increased with increasing floral diversity (Table 1; Fig. 3). The null model was not included in the averaged models assessing either pollen diversity collected or host pollen collection.

Body size

Like the models assessing pollen collection, all land-cover variables in the 500 m radius were included in the averaged model assessing female bee body size, but floral diversity was not included (Table 1; Fig. 4). Female bee body size was negatively related to the amount of urban development and other cropland in the landscape but was positively related to the abundance of cultivated blueberries and forest in the landscape (Table 1; Fig. 4). The most important predictor

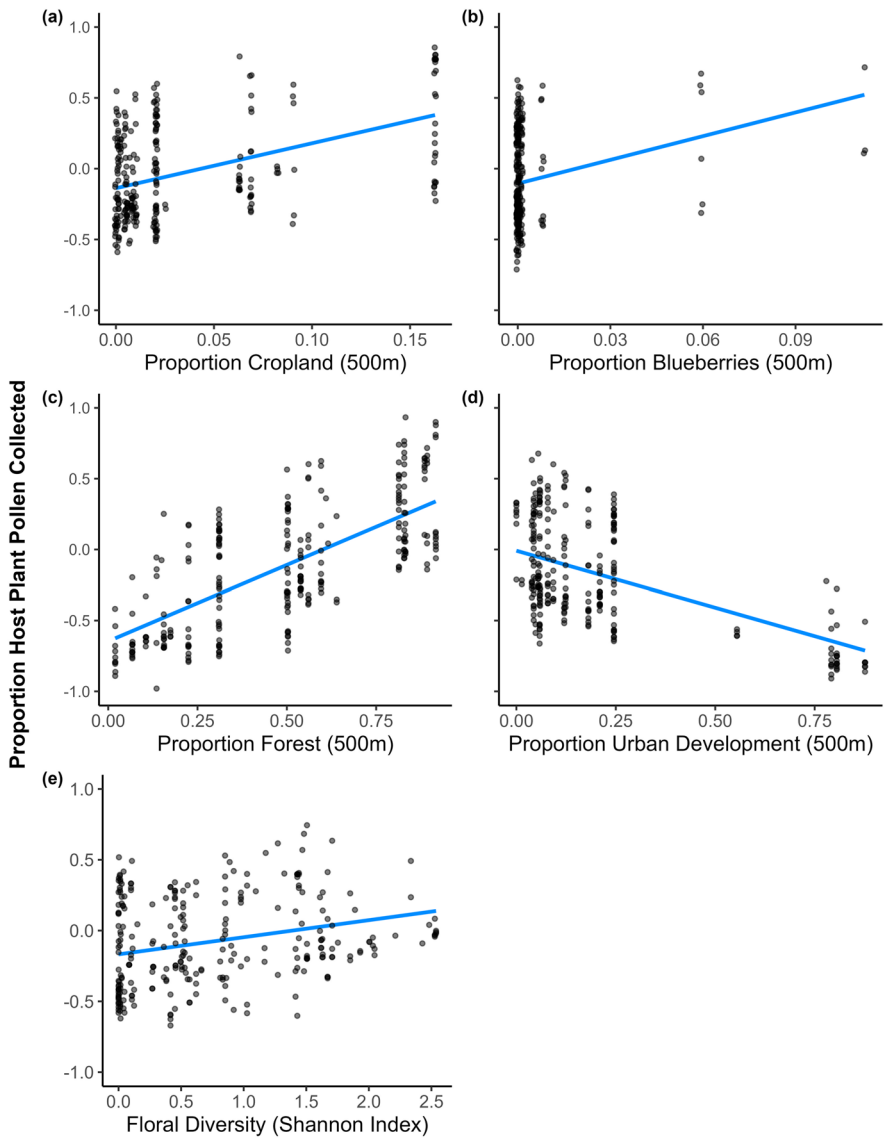


Fig. 3 Response of proportion host plant pollen (i.e., Ericaceae pollen) collected to all variables included in the averaged model. Displayed are estimates and model residuals for the response of proportion host plant pollen collected to the proportions of **a**) cropland, **b**) blueberries, **c**) forest, and **d**) urban development in a 500 m radius surrounding the site, and **e**) local floral diversity. Site and collection week nested within year were included as random effects in the averaged model. Points are slightly transparent such that darker points indicate overlapping values

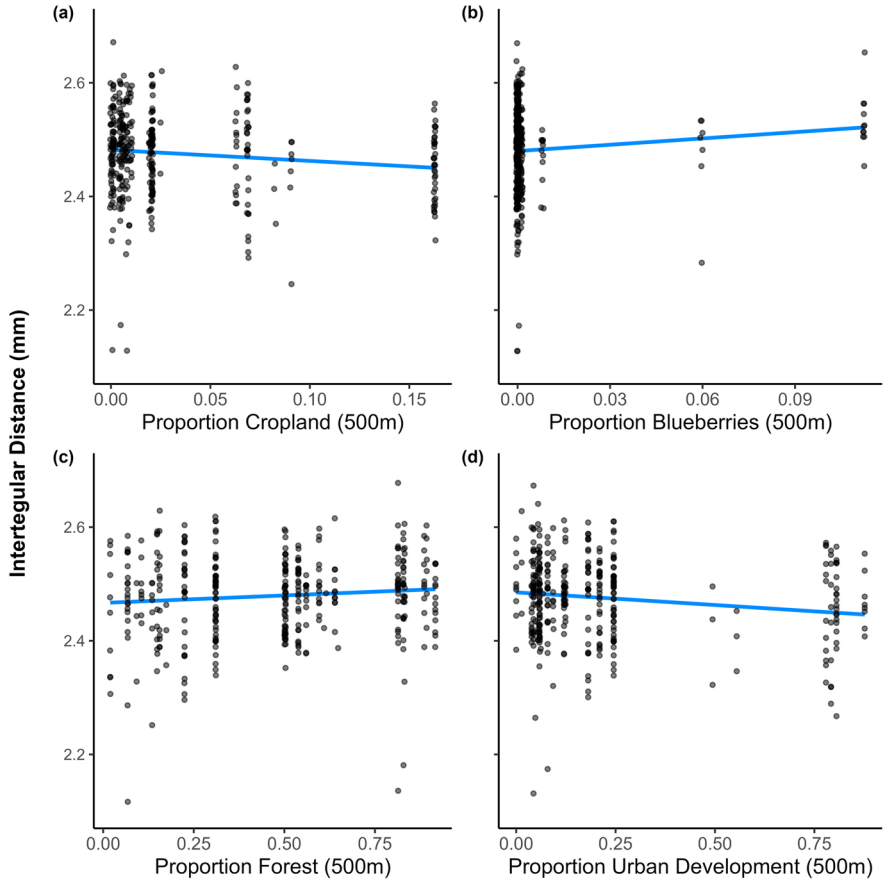


Fig. 4 Response of female body size as intertegular distance (ITD) to all variables included in the averaged model. Displayed are estimates and model residuals for the response of ITD to the proportions of **a**) cropland, **b**) blueberries, **c**) forest, and **d**) urban development in a 500 m radius surrounding each site. Site and collection week nested within year were included as random effects in the averaged model. Points are slightly transparent such that darker points indicate overlapping values

included in the averaged model assessing body size was the amount of cultivated blueberries (RVI = 0.45) followed by forest (RVI = 0.17), other cropland (RVI = 0.13), and urban development (RVI = 0.12). The null model was included in the average model as well. Finally, we found that larger bees collected higher proportions of Ericaceae pollen than smaller bees (Fig. S3.1).

Discussion

Land-use change and subsequent changes in plant community composition can alter plant-bee interactions and cause changes in bee diet and performance (Biesmeijer et al. 2006; Winfree et al. 2009; Powney et al. 2019; Garlin et al. 2022). Even though specialists may be more sensitive to these changes than generalists, little previous work has been done to assess the impacts of land-use change on specialist bee resource collection and body size. Using a specialist bee that is widely distributed across natural and human-managed systems, we found that pollen collection and body size were both impacted by land-use change. Host plant pollen collection by specialist bees and specialist bee body size generally responded to landcover variables in the same way, i.e., both decreasing with urbanization, suggesting that changes in bee body size are mediated by changes in host plant pollen availability and quality across human-managed habitats. Our study importantly demonstrates that specialist bees are at risk for negative impacts of land-use change and subsequent changes in plant community composition.

Compared to other specialist bees, *H. laboriosa* collected relatively less host plant pollen than might be expected, and the amount of host plant pollen collected varied significantly across habitat types. In natural habitats with abundant, wild Ericaceae plants, *H. laboriosa* collected the greatest proportion of host plant pollen. Alternatively, in urban habitats containing relatively lower abundances of highly

domesticated Ericaceae plants, *H. laboriosa* collected the lowest proportion of host plant pollen. This finding suggests that *H. laboriosa* may practice flexible foraging with a hierarchical preference for Ericaceae pollen when wild plants are abundant. However, *H. laboriosa* may have a lower preference for pollen of highly domesticated Ericaceae plants and/or collect less Ericaceae pollen when those plants are relatively less abundant.

Additionally, we found that *H. laboriosa* collected relatively more host plant pollen at sites surrounded by higher amounts of forest where wild *Vaccinium* spp. dominate the longleaf pine understory and at sites surrounded by more cultivated blueberry farms. However, *H. laboriosa* collected less host plant pollen with increasing urban development, further supporting our conclusion that they practice flexible foraging and collect less host plant pollen from highly domesticated, ornamental plants. In blueberry farms where host plant pollen collection was high, cultivated southern highbush blueberry, *Vaccinium corymbosym x darrowii* (the species of cultivated blueberry found in Florida), have a relatively short history of cultivation. The first southern highbush blueberry cultivars were released in 1976, and southern highbush blueberries share the same floral shape, color, and flower clustering pattern as the wild *Vaccinium* spp. commonly observed in longleaf pine forests. Alternatively, in urban habitats where host plant pollen collection was comparably low, floral surveys showed that ornamental *Rhododendron* spp., rather than *Vaccinium* spp., were the available Ericaceae floral resource. Ornamental *Rhododendron* spp. varieties have been cultivated for over 400 years and are native to Asia (Phillips et al. 2022; De Riek et al. 2018). If *H. laboriosa* preferentially forages on *Vaccinium* spp. with a lesser preference for other Ericaceae plants, then host plant pollen may make up a smaller proportion of their diet in urban habitats dominated by *Rhododendron* spp. as compared to those dominated by the preferred *Vaccinium* spp. *Habropoda laboriosa* may also collect less Ericaceae pollen in urban habitats if non-native, ornamental *Rhododendron* spp. are not as readily recognized by this native bee as a suitable floral resource as compared to the native *Vaccinium* spp. present in natural and agricultural habitats.

Habropoda laboriosa also collected relatively more host plant pollen as the amount of other cropland in the landscape increased. This finding is less intuitive and may reflect a common limitation of landcover data. Cultivated blueberry is often grown on a small scale, especially in Florida where the average size of blueberry farms is 10.7 acres (Garbach and Morgan 2016) and is thus not always represented in the landcover data. In fact, the landcover data only showed the presence of cultivated blueberries at half of the studied blueberry farms. Additional cultivated blueberry is likely embedded within the summed other cropland variable but not distinguishable in the landcover data, especially if grown on mixed crop farms. The presence of cultivated blueberry within other cropland could thus explain the positive relationship between host plant pollen collection and other cropland. Future studies that involve specialty crops commonly grown at relatively small scales should consider the potential limitations of landcover data in reliably distinguishing those focal crops from other agricultural landcover.

Although host plant pollen collection was most strongly related to landcover variables, it was also weakly and positively associated with floral diversity, but this predictor had very low importance and was only included in two of the seven models used in the average model. We propose that the weak relationship between these variables is likely due to other factors associated with floral diversity that were not measured in this study. Specifically, we did not directly assess the amount of Ericaceae pollen in the landscape. It is feasible that after accounting for land cover variables in the average model, sites with higher floral diversity also had more available Ericaceae pollen. This could occur if sites with higher floral diversity also had more Ericaceae plants in the landscape that were not accounted for in our floral surveys, or if sites with higher floral diversity had healthier Ericaceae plants with flowers that produced more pollen. Additionally, this positive relationship could reflect a decrease in competition for Ericaceae pollen between *H. laboriosa* and generalist pollinators. We regularly observed generalists (specifically, *Apis mellifera, Xylocopa micans, Xylocopa virginica,* and *Bombus* spp.) visiting Ericaceae plants alongside *H. laboriosa*. As floral diversity increased, these pollen generalists may have collected more pollen from non-Ericaceae plants, increasing access to host pollen for *H. laboriosa*. Although we did not measure the amount of Ericaceae pollen available or competition

for Ericaceae pollen in the landscape, we posit that one or both factors could explain the positive relationship between host plant pollen collection and floral diversity.

Host plant pollen availability can shape bee body size and fitness over multiple generations and may explain why *H. laboriosa* body size responded to landcover variables in similar ways to host plant pollen availability and collection. That is, there was a positive relationship between bee body size and the landcover variables associated with abundant availability of host plants (i.e., cultivated blueberry and forest) but a negative relationship with urban development. These relationships mirror those between the same landcover variables and the amount of host plant pollen collected, suggesting that the availability of host plant pollen influences specialist bee body size. However, because the null model was included in the average model assessing body size variation, other variables that were not accounted for in this study may also be important drivers of bee body size. For example, previous work has shown that agrochemical use can negatively impact bee body size (Bernauer et al. 2015). Further supporting that idea, bee body size responded negatively to other cropland despite a positive relationship between host plant pollen and other cropland. Previous work has shown that agricultural intensification can drive declines in bee body size, but that body size declines can be mitigated by establishing habitat enhancements (Renauld et al. 2016; Grab et al. 2019; Garlin et al. 2022). This is consistent with our finding that bee body size is negatively related to other cropland, which is generally intensively managed, but positively related to cultivated blueberry, which may act similarly to a habitat enhancement with very high availability of host plants. Furthermore, unlike other crops grown in the region, cultivated blueberry is a highly pollinator-dependent crop and is thus often managed to protect pollinators, thereby limiting the negative effects of agricultural intensification (Mallinger and Phillips 2022). However, other cropland excluding blueberry is not necessarily managed for bee pollinators, and the application of agrochemicals within these crops may mitigate resource value these habitats have for bees. Thus, the negative relationship between other cropland and bee body size could be driven by exposure to agrochemicals in other cropland that is not managed for pollinator protection.

Urban development in the landscape was also associated with smaller bee body size, which may be due to the lower amounts of available host plant pollen, lower quality pollen resources provided by non-native, domesticated ornamental plants, and/or agrochemical use. Pollen chemistry, including protein content and amino acid composition, can change with plant domestication, and reduced protein content of nest provisions can cause declines in bee body size (Roulston and Cane 2002; Somme et al. 2015; Roger et al. 2017; Egan et al. 2018; Lawson et al. 2021). Although cultivated *Vaccinium* spp. may also have differing pollen and nectar quality than wild *Vaccinium* spp., the sheer abundance of cultivated *Vaccinium* spp. on blueberry farms may compensate for any reduction in floral resource quality while in urban habitats, ornamental *Rhododendron* spp. were present but comparatively much less abundant. Thus, in urban habitats, the reduced quality of resources offered by ornamental plants may be compounded by a lack of host plant availability. Additionally, cultivated *Vaccinium corymbosym x darrowii* have a much shorter history of cultivation than ornamental *Rhododendron* spp. (Phillips et al. 2022; De Riek et al. 2018). Thus, the degree of domestication and subsequent changes in pollen and nectar chemistry may be lesser for cultivated *Vaccinium* spp. than observed *Rhododendron* spp. in studied habitats.

In addition to assessing host plant pollen collection, we also found that the diversity of pollen collected by *H. laboriosa* females was negatively related to all landcover variables that represent focal habitat in the surrounding landscape, including other cropland, cultivated blueberry, forest, and urban development, though it was most strongly related to cropland and forest. Thus, as the amount of focal habitat potentially containing host plants decreases, bees are forced to forage on other non-Ericaceae plants, thereby increasing pollen diversity in the diet. Cropland and forest have the highest dominance of *Vaccinium* spp. plants of all habitat types in the region, thus their presence in the landscape most strongly predicts the diets of this specialist bee. Specialist bees may be negatively impacted by the collection of non-host pollen as specialist bee larvae may fail to develop on non-host pollen and/or will be smaller in size than bees reared on host pollen (Praz et al. 2008; Haider et al. 2013). Thus, in this study system, a higher diversity of pollen is likely not beneficial, and

diverse pollen provisions could negatively impact *H. laboriosa* larval survival to adulthood and body size.

Taken together, the similarities in the relationships between pollen collection and landcover variables and the relationships between body size and landcover variables suggest that *H. laboriosa* pollen collection likely impacts body size over time. Because we did not have pollen provisions from the first year of the study matched with known offspring reared on those provisions, we were unable to directly assess how pollen collection impacts bee body size. However, we were able to directly assess how body size of individual bees impacts pollen collection within the same year. This is important because previous work has shown that within a species, larger-bodied bees are more competitive in nest provisioning (Roulston and Cane 2002; Peterson and Roitberg 2006; Burkle and Irwin 2009; Baron et al. 2014). We found that larger bees collected higher proportions of host plant pollen than smaller bees, indicating that larger *H. laboriosa* are more competitive in pollen foraging. Thus, our results both indirectly suggest that pollen collection influences body size over time and directly show that body size impacts pollen collection with potential impacts on nest provisioning and offspring success.

This large dataset (371 female *H. laboriosa* and 269 scopal pollen loads) allowed us to investigate the impacts of land-use change on intraspecific variation in specialist bee pollen collection and body size. Our results show that land-use change can adversely affect specialist bee diet and body size, and changes in diet significantly contribute to changes in body size. Specifically, both the amount of host plant pollen collected and body size increased with the presence of cultivated blueberry and forest but decreased with urban development. However, host pollen collected and body size responded in opposite ways to other intensively-managed cropland, with intensively-managed cropland negatively affecting body size despite apparently providing host plant resources. This suggests that other factors, such as pesticide exposure, may also drive changes in bee body size. Our findings are consistent with previous work indicating that pollen collection behaviors vary with plant community composition and as a result of land-use change, and bee body size declines with agricultural intensification (Renauld et al. 2016; Grab et al. 2019; Pardee et al. 2023). Taken as a whole, these results suggest that urban development may negatively impact specialist bee diet and body size, but that access to abundant host plants on blueberry farms likely benefits this bee species.

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Author contributions Anderson and Mallinger designed the study. Anderson and Gonzalez collected data. Anderson wrote the first manuscript draft with contributions from Gonzalez. Hahn provided significant guidance on analyses. Hahn and Mallinger revised the manuscript.

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Data availability Data generated and analyzed for this study will be made available in the Dryad data repository.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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