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Do Buzz-Pollinating Bumble Bees Facilitate Honey Bee Pollination in Southern Highbush Blueberry Through Increasing Pollen Release?

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ABSTRACT

Facilitation between species in diverse communities can enhance ecosystem services like pollination, a crucial service for southern highbush blueberry (SHB). SHB growers rely heavily on managed honey bees, but often experience insufficient pollination, possibly because blueberries require buzz pollination for optimal pollen release, which honey bees are incapable of providing. Buzz-pollinating bumble bees could help to facilitate pollination services provided by honey bees through increasing pollen release, though this has never been explicitly tested. To test whether bumble bees facilitate pollination by honey bees, we caged SHB bushes with only honey bees (HB only) and with honey bees plus bumble bees (HB + BB). Across treatments, we assessed foraging honey bee pollen loads on their bodies to see if this increased when buzz-pollinating bumble bees were present; as well as bee visitation rates, direct interactions between bees that could enhance cross pollination, and berry weight. We found no evidence that pollen loads (incidental or corbiculate) on honey bees were higher when bumble bees were present. Instead, we found that honey bees could release and collect blueberry pollen under the constraint of a caged environment with no alternative forage, even when buzz pollinators were absent. We did find evidence for other forms of facilitation and complementarity such as three-fold more direct interactions in the HB + BB treatment and differential foraging across temperatures by honey bees and bumble bees. Finally, berry weight did not vary between treatments likely due to the high pollinator density in both treatments. Our experiment provides clear evidence that honey bees can collect blueberry pollen despite the inability to buzz pollinate; alternatively, it did not support our hypothesis that bumble bees would facilitate pollen release and transfer by honey bees. However, we found evidence that bumble bees and honey bees complement and facilitate each other in additional ways, suggesting that using both could improve pollination.

1 | Introduction

Ecological services are crucial to functioning ecosystems, with insects playing a key role in important services such as pollination, biological control, and soil regulation, among others (Schowalter et al. 2018). These services are especially important in agroecosystems where producers are often reliant upon them to ensure a profitable harvest. In many specialty crops including fruits, seeds, and nuts, pollination services are a priority, and there is a heavy reliance on managed honey bees (Delaplane and Mayer 2000; Klein et al. 2012; Campbell et al. 2018; Mallinger et al. 2021). However, honey bees are often insufficient on their own to achieve optimal pollination success due to low attraction to focal crops, ineffective foraging behaviors, and variable activity rates across the bloom period and environmental conditions (Brittain et al. 2013; Sapir et al. 2017; Miñarro and García 2021;

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Mallinger et al. 2021; Osterman et al. 2021). Diversifying the use of managed pollinators alongside native wild pollinators could improve yields through numerous mechanisms including complementarity, insurance, and facilitation. For example, in almond and apple production, facilitation between pollinator species occurred when non-*Apis* bee species enhanced the movement of honey bees across rows and increased overall cross-pollination rates (Brittain et al. 2013; Sapir et al. 2017). Additional studies have shown complementarity among species, including foraging across different weather conditions, time, or areas of the crop plant and field (Chagnon et al. 1993; Blüthgen and Klein 2011; Miñarro and García 2021; Fijen et al. 2023).

Certain pollinator species may also be able to facilitate pollination by other species through increasing pollen release in crop flowers. In crops with poricidal anthers, a vibration is needed to induce the release of pollen (Desjardins and De Oliveira 2006; Morgan et al. 2016; Sun et al. 2021). Buzz pollinators apply this vibration when visiting flowers by contracting their thoracic muscles. This behavior makes them valuable pollinators as they can effectively release and therefore actively collect pollen. Indeed, bees that are foraging for pollen have been shown to be more effective pollinators than those foraging for nectar, even when compared intraspecifically (Rogers et al. 2013; Benjamin and Winfree 2014), and buzz pollinators have been shown to be more efficacious on a per visit basis than non-buzz pollinators (Desjardins and De Oliveira 2006; Morgan et al. 2016; Sun et al. 2021; Cortés-Rivas et al. 2023). Without buzz pollinators, flowers with poricidal anthers express restricted pollen release, which may reduce cross- and self-pollination rates in crop fields (De Luca and Vallejo-Marín 2013; De Luca et al. 2013; Cooley and Vallejo-Marín 2021). At least one study in a plant system with poricidal anthers indicated that non-buzz-pollinating bees were able to gather previously released pollen from floral surfaces such as the stigma (Renner 1983). Thus, the presence of buzz pollinators causing increased release of pollen may facilitate pollen collection and transfer by non-buzz pollinators.

Cultivated blueberry is highly dependent upon insect pollination for profitable harvest, with fruit set and berry weight both decreasing dramatically in the absence of pollinators (MacKenzie 1997; Klein et al. 2007; Martin et al. 2021; Eeraerts et al. 2023). This high pollinator dependence is due in part to their poricidal anthers and to early-acting inbreeding depression that results in only partial self-fertility (Krebs and Hancock 1990; Cardinal et al. 2018; Cooley and Vallejo-Marín 2021; DeVetter et al. 2022). Due to this, the abundance, behaviors, and efficacy of pollinator species are closely tied to successful blueberry production. In North America, wild pollinator visitation rates to cultivated blueberry vary greatly across production regions (Isaacs and Kirk 2010; Nicholson et al. 2017; Benjamin and Winfree 2014; Gibbs et al. 2016; Campbell et al. 2018). As a result of this and the predictability of stocking, managed honey bees (*Apis mellifera* L.) are the dominant pollinators in the system, making up over 85% of flower visits in some cases (Benjamin and Winfree 2014; Gibbs et al. 2016; Campbell et al. 2018). Despite the ubiquity of honey bees, pollination is still a limiting factor for blueberry yields, leading many producers to deploy managed common eastern bumble bees (*Bombus impatiens* Cresson) alongside honey bees to improve pollination (Rogers et al. 2013; Campbell et al. 2018; Reilly et al. 2020; Mallinger et al. 2021). While some studies have examined the use of managed bumble bees alongside managed honey bees for blueberry pollination, there is little research on whether bumble bees could facilitate pollination provided by honey bees.

In addition to an inability to buzz pollinate, honey bees may be less effective pollinators in blueberry crops due to infrequent foraging in inclement weather conditions (Tuell and Isaacs 2010; Mallinger et al. 2021) and to their trap-lining foraging behaviors. Crop rows are commonly planted in a single cultivar, causing the linear foraging down crop rows of honey bees to limit cross-pollination between cultivars, while other bee species display this behavior less consistently (Greenleaf and Kremen 2006b; Brittain et al. 2013; Buatois and Lihoreau 2016; Taber and Olmstead 2016). Despite their limitations, honey bees have been shown to deposit pollen when visiting blueberry flowers (Rogers et al. 2013; Benjamin and Winfree 2014) and are often present in high densities that can compensate for reduced efficacy (Campbell et al. 2018). Alternatively, buzz-pollinating bumble bees are more effective pollen collectors and deposit more pollen per visit (Sun et al. 2021) while also foraging across more inclement weather conditions as compared to honey bees (Tuell and Isaacs 2010), but are typically present in lower densities in blueberry systems. Finally, bumble bees have also shown increased movement between blueberry rows (Miñarro and García 2021), potentially leading to increased cross-pollination, and possibly increased direct interactions that increase honey bee movement between bushes and rows (Brittain et al. 2013; Sapir et al. 2017).

The objective of this study was to examine whether bumble bees facilitate honey bee pollination in southern highbush blueberry (*Vaccinium corymbosum* L. and hybrids) (SHB) and to identify specific mechanisms of facilitation as well as complementarity. To do this, we examined pollen loads carried by honey bees in the presence and absence of common eastern bumble bees as a proxy for individual pollination potential and pollinator facilitation. We hypothesized that honey bees would carry and collect more pollen in the presence of bumble bees due to greater pollen release achieved by buzz pollinators leading to increased contact with leftover pollen from these visits. We additionally assessed complementarity between honey bees and bumble bees when used together, hypothesizing that bumble bees would be the dominant pollinator on cool days and honey bees on warm days. Finally, we assessed whether the combined use of honey bees and bumble bees would lead to increased direct interactions, which have the potential to increase bee movement across cultivars, and thus increased potential for cross-pollination. Support for these hypotheses would highlight the value of diversifying managed and wild pollinators in blueberry crops.

2 | Materials and Methods

2.1 | Experimental Design

This study was carried out at a commercial blueberry farm in Waldo, FL, USA in a high tunnel production system with potted blueberry bushes. The experiment was repeated over 2 years in 2022 and 2023. A total of 10 large field cages (15 × 2.5 m), each representing an experimental unit and containing 60 mature commercial southern highbush blueberry bushes, were used. Each cage consisted of three unnamed breeding genotypes and the Chickadee and Vireo cultivars, with each unique genotype and cultivar represented by 12 bushes per cage. The 10 cages were split between two treatments for a total of five cages per treatment each year. The honey bee only (HB only) treatment contained two small honey bee hives, consisting of a single deep brood box prepared for blueberry pollination sourced from a local commercial beekeeper. The honey bee plus bumble bee (HB + BB) treatment contained one small honey bee hive sourced from the same beekeeper and two production-sized managed colonies of the common eastern bumble bee (Koppert Biological Systems, Howell, MI), containing a queen and approximately 250 workers per colony. We attempted to vary bee diversity while keeping the density of foraging bees consistent through replacing a single honey bee hive with two bumble bee colonies in the HB + BB treatment, as bumble bee colonies have significantly fewer workers with higher per bee pollination efficiency than honey bee colonies. We did not include a treatment of only bumble bees as (1) using only managed bumble bees for blueberry pollination is not feasible due to the cost and limited availability of bumble bees, and (2) we were interested in testing hypothesized mechanisms wherein bumble bees facilitate honey bee pollination rather than potential honey bee facilitation of bumble bee pollination.

2.2 | Pollinator Foraging Activity and Direct Interactions

To evaluate pollinator foraging activity and direct interactions between treatments, we assessed pollinator visitation rates to blueberry flowers within experimental cages and recorded direct interactions between bees. Three pollinator foraging observations on individual bushes were conducted in each cage on each observation date. Each observation focused on a densely blooming blueberry bush for 2 min with the genotype and a flower count estimate of the focal bush, and weather conditions being recorded. During each observation, the identity of floral visitors was recorded as well as any direct interactions between pollinators that occurred on focal flowers. A direct interaction was classified as any contact that occurred between any two pollinators at a flower. These interactions typically occurred when one bee was making a visit to a focal flower and another bee attempted to visit the same flower leading to physical contact. Direct interactions could take place between any combination of pollinators present in experimental cages. As a result of this, direct interactions account for both inter- and intra-specific interactions in HB + BB cages but only intra-specific interactions in HB only cages. Direct interactions frequently led to one or both pollinators flying away from the flower where the interaction occurred. A total of 798 2-min observations on individual bushes occurred across the 2022 and 2023 seasons.

2.3 | Honey Bee Pollen Loads

Honey bees were collected throughout the experiment to examine the quantity of pollen tetrads present on their bodies in the presence and absence of bumble bees. Collections took place over four dates per year for a total of eight times across the 2022 and 2023 seasons. Collections occurred between January 9 and February 1, 2022, and between January 12 and February 1, 2023. A total of 196 honey bees were collected with 118 collected from HB only cages and 78 from HB + BB cages. Honey bees were collected directly from blueberry flowers with clean microcentrifuge tubes to reduce loss of pollen present on honey bee bodies that could occur from hand netting. Within each of the 10 cages and on each collection date, collections occurred until five honey bees were collected or 15 min of collecting time had elapsed per cage. Collected bees were stored on ice prior to being transferred to a −18°C freezer where they remained until processing occurred. The quantity of blueberry pollen tetrads present on honey bee corbiculae and the quantity of incidental pollen (i.e., pollen on the rest of their body) were recorded separately for each bee and will hereafter be referred to as corbiculate pollen and incidental pollen. Corbiculate pollen samples were isolated by removing the hind legs of honey bees and processing them separately from the rest of the honey bee body. Samples were subsequently washed, vortexed, diluted, stained, and plated on slides to allow for quantification via microscopy. A more detailed description of this methodology can be found in the Supporting Information.

2.4 | Berry Weight

Berries were collected in each cage on 10 focal branches of the 09-311 genotype, which was selected because it was the most densely flowering genotype with the longest bloom period in both years. Focal branches were left open to pollinators throughout the bloom period before being individually bagged to ensure that fruit were not lost prior to harvest. Harvest of fruit occurred every 7–12 days from March 8—April 21 in 2022 and from March 2—April 18 in 2023 for a total of five harvests per year. Harvested fruit were subsequently weighed to assess their size, which is related to pollination success. The average weight of ripe berries harvested during each harvest date from each branch was subsequently analyzed.

2.5 | Statistical Analyses

All statistical analyses were conducted using R version 4.3.1 and the ‘lme4’, ‘stats’, and ‘car’ packages (Bates et al. 2015; R Core Team 2023; Fox and Weisberg 2018). Model diagnostics were performed to assess for heteroscedasticity and overdispersion, with appropriate distributions and transformations applied. ANOVA tests were run on all models to determine the significance of fixed effects with type II sum of squares utilizing Anova in the ‘car’ package. Figures were generated using the ‘ggplot2’ package (Wickham 2016).

2.5.1 | Pollinator Foraging Activity and Direct Interactions

To test whether overall bee foraging activity and the number of direct interactions varied between treatments, the visitation rates of all pollinators (total number of honey and/or bumble bee visits per cage per period), visitation rates of honey bees

TABLE 1 | Test statistics from analysis of variance run on GLMMs testing for the effect of treatment (HB only and HB + BB) on the number of honey bee visits adjusted for the number of hives, all pollinator visits, and direct interactions between bees across study cages.

Response variable	Predictor	Test statistic	*p*
Honey bee visits per hive per cage	Treatment	62.599	< 0.001***
All pollinator visits per cage	Treatment	238.720	< 0.001***
Direct interactions between bees per cage	Treatment	59.502	< 0.001***

Note: Statistical evidence of significant treatment effects is indicated by asterisks with *** indicating significance at $p < 0.001$.

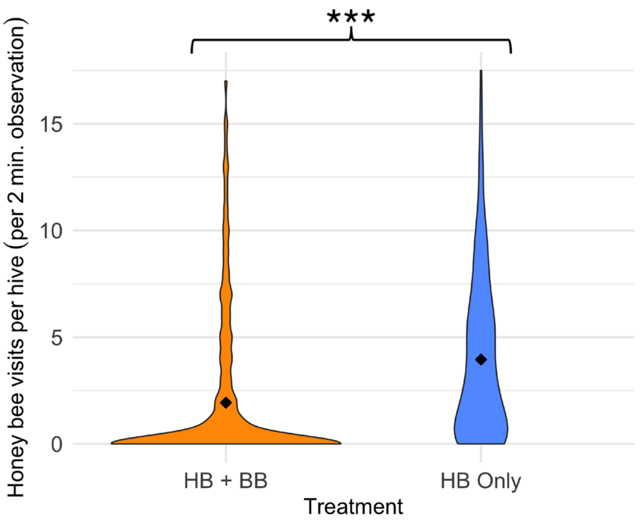

FIGURE 1 | Honey bee visits per hive to a single SHB bush for a 2-min period. Observations were completed on three focal bushes within each cage on each day of observation. The black diamond on each violin represents the mean. Statistical evidence of significant treatment effects is indicated by asterisks with *** indicating significance at $p < 0.001$.

standardized on a per hive basis (total number of honey bee visits per cage per period/number of hives per cage), and the number of direct interactions between bees were compared between treatments. Each response variable (honey bee visits per hive, all pollinator visits, and direct interactions) was analyzed with a generalized linear mixed model (GLMM) and a negative binomial distribution appropriate for over-dispersed count data. All models included treatment as a fixed effect with cage treated as a random effect. To test complementarity in response to temperature, the ratio of honey bee visits to bumble bee visits in the HB + BB treatment was compared across observation periods using a GLMM and a binomial distribution appropriate for proportions. This model included temperature as a fixed effect and cage as a random effect with total pollinator visits (honey bees and bumble bees) included in the model as a weight to account for the total number of bees associated with each ratio (Zuur et al. 2009).

2.5.2 | Honey Bee Pollen Loads

Incidental and corbiculate pollen were analyzed in relation to each other and as a function of treatment. To determine the effects of treatment on the quantity of both corbiculate and incidental pollen carried by honey bees, LMMs were run with treatment as the fixed effect and cage as a random effect. Both corbiculate and incidental pollen loads were square root transformed for analysis and analyzed separately. Additionally, to determine whether honey bees actively collecting pollen had more incidental pollen on their bodies, a linear mixed-effects model (LMM) was run with sqrt-transformed incidental pollen as the response variable and sqrt-transformed corbiculate pollen as a fixed effect with cage as a random effect.

2.5.3 | Berry Weight

The average weight of ripe berries harvested on each branch for each harvest date was analyzed using a linear mixed-effects model (LMM) with treatment as a fixed effect and year and cage as random effects. Initial models assessed an interaction between treatment and harvest round (1–5) but found no interaction between them. As a result, harvest date and its interaction with treatment were removed from the final model.

3 | Results

3.1 | Pollinator Foraging Activity and Direct Interactions

Honey bee visits per hive were significantly higher in honey bee only (HB only) cages than in honey bee plus bumble bee (HB + BB) cages ($z = 7.912$, $p < 0.001$) (Table 1; Figure 1). The mean number of honey bee visits per hive per 2-min observation was 3.95 ± 3.81 in HB only cages compared to 1.91 ± 3.56 in HB + BB cages. However, when examining total visits made by all pollinators, HB + BB cages had significantly more total visits than did the HB only cages ($z = 15.450$, $p < 0.001$) (Table 1; Figure 2). The mean visit count of all pollinators was 20.07 ± 13.97 visits per observation in the HB + BB cages, more than double that of the mean visit count in HB only cages (7.9 ± 7.62 visits per observation) (Figure 2). In the HB + BB combined treatment, bumble bees made up most of the pollinator visits, though this varied significantly with temperature. The proportion of total pollinator visits made by honey bees in HB + BB cages significantly increased as temperature increased ($z = 6.781$, $p < 0.001$). At cool temperatures below 18°C, honey bees made up 29.12% of all pollinator visits. At temperatures exceeding 18°C, the proportion of honey bees increased, accounting for 42.51% of all pollinator visits (Figure S1).

There were significantly more direct interactions between bees occurring in HB + BB cages ($z = 7.714$, $p < 0.001$) in comparison to HB only cages (Table 1). The mean number of direct

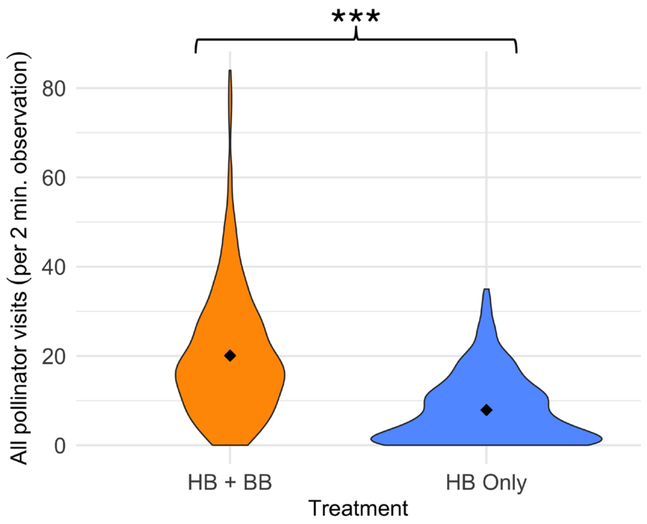

FIGURE 2 | All pollinator visits to focal flowers on a SHB bush for a 2-min observation period. Observations were completed on three focal bushes within each cage on each day of observation. The black diamond on each violin represents the mean. Statistical evidence of significant treatment effects is indicated by asterisks with *** indicating significance at $p < 0.001$.

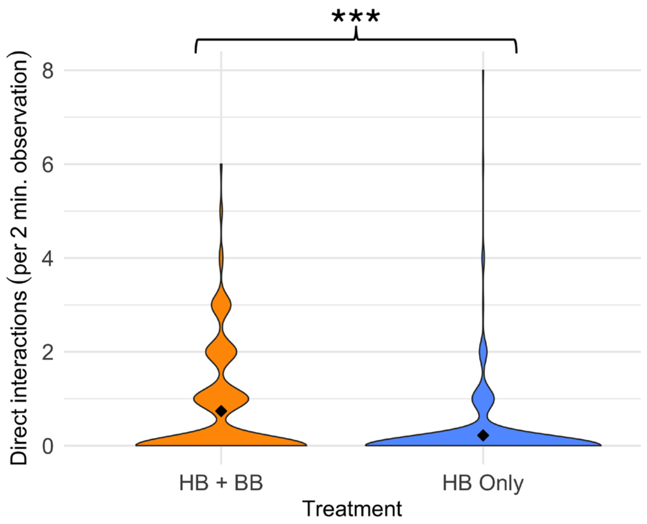

FIGURE 3 | Direct interactions between pollinators occurring on flowers on observed SHB bushes for a 2-min period. Direct interactions occur when any two individual pollinators have an interaction at a flower. The black diamond on each violin represents the mean. Statistical evidence of significant treatment effects is indicated by asterisks with *** indicating significance at $p < 0.001$.

interactions observed in HB + BB cages (0.74 direct interactions per observation) was over three times higher than in HB only cages (0.22 direct interactions per observation) (Figure 3).

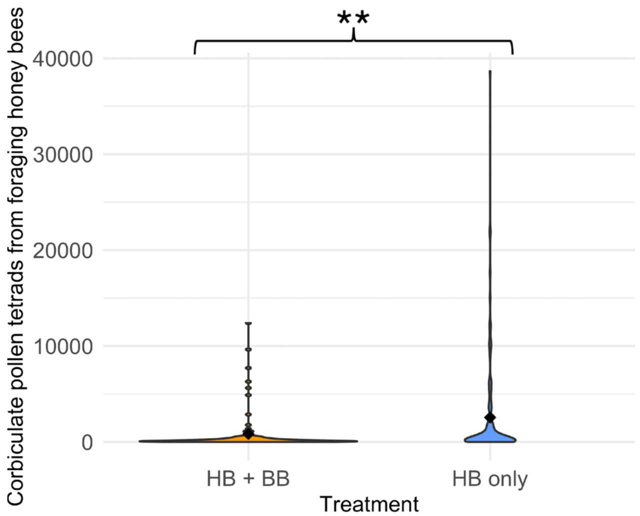

FIGURE 4 | Pollen tetrads present in the corbiculae of foraging honey bees collected from treatment cages. The black diamond on each violin represents the mean. Statistical evidence of significant treatment effects is indicated by asterisks with ** indicating significance at $0.01 > p > 0.001$.

TABLE 2 | Test statistics from analysis of variance run on LMMs testing for the effect of treatment (HB only and HB + BB) on square root transformed corbiculate pollen tetrads and incidental pollen tetrads on foraging honey bee bodies.

Response variable	Predictor	Test statistic	*p*-value
Corbiculate pollen tetrads (sqrt-transformed)	Treatment	9.623	0.002**
Incidental pollen tetrads (sqrt-transformed)	Treatment	0.280	0.597^{ns}

Note: Statistical evidence of significant treatment effects is indicated by asterisks with ** indicating significance at $0.01 > p > 0.001$ and ns indicating no significance.
Abbreviation: ns, nonsignificant.

3.2 | Honey Bee Pollen Loads

Corbiculate pollen loads were found on honey bees foraging in both treatments (HB only and HB + BB) indicating that honey bees were capable of effectively accessing and foraging for pollen in the absence of buzz pollinators (Figure 4). Honey bees collected in HB only cages were found to have significantly more corbiculate pollen than those collected in HB + BB cages ($t = 3.102$, $p = 0.002$) (Table 2; Figure 4). Alternatively, there was no significant difference in the amount of incidental pollen carried by honey bees between treatments ($t = 0.529$, $p = 0.597$) (Table 2; Figure 5). In other words, the amount of pollen available for pollination did not significantly differ between honey bees in the presence or absence of bumble bees. Finally, there was no relationship between the number of pollen tetrads present in honey bee corbiculae and the number of tetrads present as incidental pollen on the rest of the honey bee body ($t = 1.403$, $p = 0.162$) (Figure S2).

3.3 | Berry Weight

The average ripe berry weight showed no significant difference between treatments ($t = 0.919$, $p = 0.359$) (Figure S3).

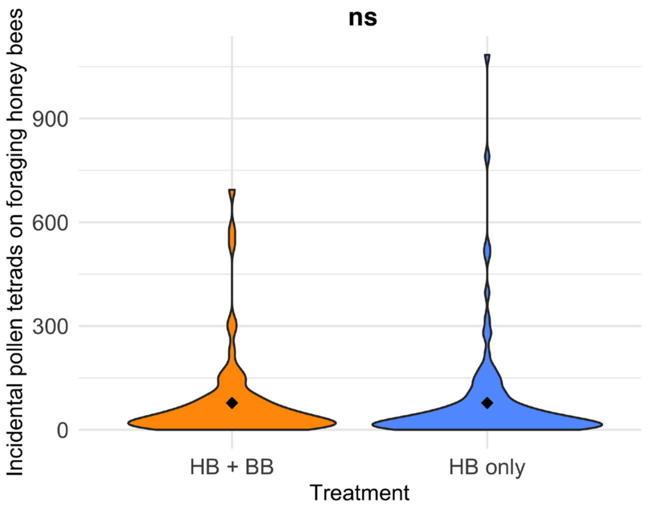

FIGURE 5 | Incidental pollen tetrads present on the bodies of foraging honey bees collected from treatment cages. The black diamond on each violin represents the mean. Statistical evidence of significant treatment effects is indicated by asterisks with ns representing no statistical significance at $p > 0.05$.

4 | Discussion

Currently, much of our understanding of crop pollination is limited to the effect of individual pollinators rather than the ways in which species facilitate or complement each other. However, the evidence we do have suggests that when placed alongside honey bees that alternative managed pollinators improve crop productivity when compared to honey bees alone (Hünicken et al. 2022). This study set out to assess the hypothesis that using buzz pollinators (i.e., bumble bees) in tandem with honey bees would improve honey bee pollinator efficacy and overall pollination. We predicted this could occur via two mechanisms of facilitation: (1) increased pollen release and transfer by honey bees in the presence of buzz pollinators, and (2) increased movement by honey bees across bushes and cultivars resulting from direct interactions on flowers with other bees in a more diverse pollinator community. Additionally, we hypothesized that bumble bees and honey bees would show complementarity by foraging under different weather conditions. Among the proposed mechanisms, we found strong support that direct interactions between bees increase when bumble bees and honey bees are used in tandem, which can lead to greater bee movement between bushes and cultivars, and support for complementarity across different weather conditions. However, we did not find that foraging honey bees carried more pollen in the presence of bumble bees. Alternatively, the quantity of pollen found on honey bees (both corbiculate and incidental) in the absence of all buzz pollinators suggests that blueberry plants may not strictly require buzz pollination for pollen release.

Direct interactions between bees typically cause both pollinators to fly away from the site of the interaction and begin foraging on another flower or bush altogether. This response may result in increased cross pollination that improves fruit set and yield in blueberry. In sunflower, apple, and almond production, where increased direct interactions were also observed when bee communities were more diverse, researchers were able to link these direct interactions with increased movement across rows to improved cross pollination and yield outcomes (Greenleaf and Kremen 2006a; Brittain et al. 2013; Sapir et al. 2017). However, we were unable to link the increase in direct interactions between bees to increased movement across bushes/cultivars by honey bees, or to increased berry size, due to limitations of using cages. Specifically, the high density of bees in a confined space made it challenging to track individual bees after a direct interaction occurred and likely contributed to a lack of pollen limitation in both treatments (i.e., maximum pollination and berry size across all cages). As shown in other studies, pollination in open field settings is likely more of a limiting factor for blueberry yields (Benjamin and Winfree 2014; Gibbs et al. 2016; Campbell et al. 2018). Since blueberries experience early-acting inbreeding depression that results in reduced fruit quantity and quality under self-pollination, cross-pollination is known to reduce pollen limitation and increase fruit set, yields, and fruit quality (Krebs and Hancock 1990; Lang and Danka 2019; Taber and Olmstead 2016; Martin et al. 2019). Greater bee movement between bushes, specifically of different cultivars, can increase cross-pollination and thereby yields. For example, in plantings wherein bumble bees and honey bees frequently moved from one cultivar to another during a foraging trip, yields were higher (Mallinger et al. 2024). Our results indicate that direct interaction between bees occur more frequently in diverse bee communities, which previous studies have found to increase movement, cross pollination, and yield. Future research should assess whether the increase in direct interactions leads to greater cross-pollination and yields in production blueberry fields.

Our study is the first to test the prediction that honey bees would carry increased pollen on their bodies in the presence of buzz pollinators due to increased pollen release from blueberry flowers. We found no support for this prediction, as there was no difference in incidental pollen present on honey bees between treatments. In fact, nearly all honey bees, regardless of treatment, were found to be carrying some incidental pollen. The majority of collected individuals were found to be carrying over 100 pollen tetrads, with some exceeding 900 tetrads. These findings support previous research in blueberry field settings that found foraging honey bees carrying incidental pollen on nearly all parts of their body, with some individuals carrying nearly 1000 pollen tetrads (Hoffman et al. 2018). However, in past research, buzz pollinators were present in the field and may have facilitated pollen release to some degree. Interestingly, honey bees were found to carry more pollen in their corbiculae in the absence of bumble bees. These findings indicate that honey bees can release and collect pollen from blueberry flowers even when buzz pollinators are absent and may, in fact, be more effective at doing so due to reduced competition for pollen in the absence of bumble bees. Importantly, our study took place in cage environments that excluded alternative floral resources and had high densities of honey bees. These constraints mean that honey bees had to forage for blueberry pollen and were capable of doing so successfully. Herein, we found strong evidence that honey bees can accumulate incidental pollen and collect pollen in their corbiculae in environments that are devoid of buzz pollinators. This indicates that buzz pollinators are not strictly necessary to induce blueberry pollen release. It also supports past findings that honey bees act as effective pollinators of blueberry despite not being buzz pollinators (Benjamin and Winfree 2014; Campbell et al. 2018; Mallinger et al. 2021).

The frequency and abundance with which honey bees carried pollen in their corbiculae was an interesting finding. Combined with previous studies that show very little blueberry pollen collection by honey bees, our findings suggest that honey bees are capable of collecting blueberry pollen but do so infrequently where alternative forage is available (Bobiwash et al. 2018; Graham et al. 2023). Hoffman et al. (2018) found that in an open blueberry field only nine of the 90 honey bees collected were carrying any pollen in their corbiculae. In our cage design, which only included blueberry flowers, honey bees were forced to collect blueberry pollen frequently due to a lack of alternative forage. These findings suggest that the efficacy of honey bees as blueberry pollinators could be increased when alternative forage is not available as they would be more likely to collect blueberry pollen, and past studies have found bees collecting pollen to be more effective pollinators than those collecting nectar (Rogers et al. 2013; Benjamin and Winfree 2014). To better understand when honey bees collect blueberry pollen in the field, future research should continue to assess the role of competing forage and its effects on honey bee foraging behavior.

We predicted that bees with high corbiculate pollen loads would carry more incidental pollen due to increased contact with anthers and pollen resulting from active pollen collection. An alternative hypothesis is that these pollen loads would be negatively correlated due to more frequent pollen grooming behaviors in honey bees actively collecting pollen, resulting in incidental pollen being groomed into the corbiculae (Jander 1976; Thorp 1979). We found no support for either of these hypotheses, possibly due to variable degrees of grooming found across honey bees while collecting pollen (Marcelo et al. 2022). Past models on honey bee grooming behaviors combined with our findings indicate that individual variation in honey bee foraging and grooming behaviors makes the relationship between incidental and corbiculate pollen loads nonuniform and challenging to predict.

In addition to some support for facilitation via direct interactions, we also found support for pollinator complementarity between honey bees and bumble bees across temperature gradients. Bumble bees made up most of the pollinator visits (70.88%) at cool temperatures (below 18°C). Once temperatures exceeded 18°C, the proportion of visits made by honey bees and bumble bees became more even, illustrating increased foraging frequency by honey bees and relatively stable foraging frequency by bumble bees across temperatures. These findings are widely supported, with bumble bees repeatedly being shown to forage more in cooler temperatures than honey bees (Gibbs et al. 2016; Tuell and Isaacs 2010). While this finding is not new, it does offer further evidence for pollinator complementarity in blueberry production. These differences in foraging frequency could result in significant improvements in pollination outcomes on farms using both bumble bees and honey bees during seasons with fluctuating temperatures.

Previous research has also supported the value of bumble bees on blueberry farms to improve pollination outcomes, but the mechanisms responsible for increased pollination and yields when bumble bees are used with honey bees were not clear (Campbell et al. 2018; Mallinger et al. 2021). Managed bumble bee adoption could prove especially valuable for growers who had previously exceeded recommended honey bee stocking densities without receiving a benefit from these additional honey bee hives (Mallinger et al. 2021). In these cases, it may be more valuable for growers to purchase managed bumble bees in place of more honey bee hives. Additional practices such as pollinator plantings and preserving nesting habitat on farms could also be implemented to promote wild pollinators (*Bombus* spp. and *Habropoda laboriosa*). This strategy has been implemented successfully in northern highbush blueberry and other pollinator dependent crops, where significant increases in wild pollinator visitation and improved fruit set were observed (Blaauw and Isaacs 2014; Williams et al. 2015; Rundlöf et al. 2022). Our study provides support that diversifying managed pollinators, along with or in place of diversifying through wild pollinators, could improve blueberry pollination. Although the magnitude of pollination improvements in open field settings should be further evaluated.

5 | Conclusions

This study provides evidence for the important role of bumble bees in facilitating and complementing honey bee pollination in a system dominated by managed honey bees. Bumble bees may ensure pollination during cool and cloudy bloom periods and could increase cross-pollination rates through their interactions with foraging honey bees. However, we also found new support for the role of honey bees in blueberry pollination. Despite an inability to buzz pollinate, honey bees were capable of releasing and collecting blueberry pollen in relatively large quantities in the absence of all other bee pollinators including bumble bees. We also show that they will readily collect blueberry pollen when alternative forage is not available. Overall, this study provides new evidence for the value of a diverse pollinator community in commercial crop production and the value of honey bees as pollinators in the system regardless of the presence of other pollinators.

Author Contributions

John J. Ternest: conceptualization (equal), data curation (lead), formal analysis (lead), funding acquisition (equal), investigation (lead), methodology (equal), project administration (equal), validation (equal), visualization (lead), writing – original draft (lead), writing – review and editing (equal). **Patricio R. Muñoz:** conceptualization (equal), funding acquisition (equal), project administration (equal), resources (equal), supervision (equal), writing – review and editing (equal). **Rachel E. Mallinger:** conceptualization (equal), data curation (supporting), formal analysis (supporting), funding acquisition (equal), methodology (equal), project administration (equal), resources (equal), supervision (equal), visualization (supporting), writing – original draft (supporting), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the required data are uploaded as Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** ece373208-sup-0001-Figures.pdf. **Figure S2:** ece373208-sup-0001-Figures.pdf. **Figure S3:** ece373208-sup-0001-Figures.pdf.