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MANAGED HONEYBEES AFFECT THE FORAGING BEHAVIOUR OF BUMBLEBEES IN *GERANIUM SYLVATICUM*

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Abstract—Due to shared evolutionary history, native pollinator diversity and coexistence is promoted by niche partitioning and behavioural differences between species. Introduced insect species, however, have potential to compete with wild pollinators and negatively affect native insect populations. Honeybee (*Apis mellifera*) is an introduced pollinator species in northern Europe and may affect native pollinator populations negatively. Diversity in plant communities also promotes variation in the associated pollinator communities. Diversity of a community encompasses not only species diversity but includes within species variation as well. Within species, genetic diversity could promote insect coexistence and affect competitive interactions between pollinator insects.
In this study, we measured floral visitation rates in female and hermaphrodite *Geranium sylvaticum* genotypes in the presence and absence of a beehive (*Apis mellifera*) in an experimental field located in Central Finland. We show that competition with honeybees reduced visitation rates by bumblebees, but not by other native pollinator groups. Furthermore, bumblebees preferred some plant genotypes in the absence of the honeybees, but not in the presence of honeybees. Overall, bumblebees preferred females over hermaphrodite plants, but honeybees showed no such preference. Our study links the native pollinators and genetically diverse plant populations, and sheds light on the competition between pollinator insects.

Keywords—*Apis mellifera*, floral resource competition, genetic variation, sexual dimorphism.

INTRODUCTION

Most of the competition between pollinator insects is usually indirect competition for floral resources (Henry & Rodet 2018; Taggar et al. 2021), although competition for overwintering and nesting sites may also affect the populations (Thomson & Page 2020). A recently visited flower is left unrewarding for the next visitor. Day-active flowers are usually filled with nectar during the night, and the number of visited flowers and the timing of active period benefit a given pollinator species (Real 1981). If a pollinator is active early during the day or during colder weather, it may be more efficient in emptying resources than those active later or requiring warmer weather (Real 1981). The more intensive the competition, the less resources a certain pollinator species may gather per unit of time spent and energy expended during its foraging bout (Real 1981; Henry & Rodet 2018; Thomson & Page 2020; Taggar et al. 2021).

Competition for shared resources may select for partitioning of the resource (MacArthur 1958) and pollinators can show remarkable behavioural plasticity. In addition to niche partitioning in time of day and foraging temperature (Mizunaga & Kudo 2017; Zaragosa-Trello et al. 2023), pollinators may also shift the focal foraged plant species (Roubik et al. 1986). Morphology of an insect determines which flowers it can access, and bumblebee species can be classified according to the tongue length and their ability to access different flowers (Brian 1957; Heinrich 1976; Ranta & Lundberg 1980; Harder 1985). As a result, the pollinator community consists of a range of species which forage on different plant species. Furthermore, as the pollinator species have different traits, their foraging phenology differs short-term within daytime and long-term in foraging intensity over the growth season (Mizunaga & Kudo 2017; Zaragosa-Trello et al. 2023). For example, Mizunaga & Kudo (2017) noted that hoverfly activity depended mainly on temperature whereas bumblebee visitations were tied to temporal abundance variation caused by the annual life cycle of bumblebees. These results emphasize that several variables affect floral visitation rates.

Native pollinator communities partition resources as well as compete for them and, as a by-product, provide efficient pollination for plant communities. However, invasive pollinator species may disturb the local communities (Fürst et al. 2014; Morales et al. 2017). For example, according to Nishikawa & Shimamura (2016) a non-native bumblebee did not partition resources with the native bumblebee species and was a strong competitor. Honeybees (*Apis mellifera* L.) are commercially farmed in Europe. There are approximately 70 000 managed beehives in Finland (Suomen Mehiläishoitajain Liitto 2023), each hive containing up to 65 000 bees (Beekman & Ratnieks 2000). Honeybee is an introduced species in northern Europe and has the potential to affect native pollinators in many ways (Goulson & Sparrow 2009; Mallinger et al. 2017; Nanetti et al. 2021). Honeybees visit more than 40 000 different species of plants, which makes them potential competitors in various habitats (Crane 1999). Effects of honeybees are likely to be shaped by the characteristics of the study system. Thomson (2004) found that the proximity of introduced honeybee hives reduced the reproductive fitness and foraging success of a native social bee which was an important pollinator. Another study investigated the size of workers in four bumblebee species and found that the proximity of honeybee hives significantly reduced the sizes of bumblebee workers (Goulson & Sparrow 2009). Several other studies also show that honeybees successfully compete over resources with native pollinators (Goulson 2003; Cappellari et al. 2022; Page & Williams 2023; Pascual Tudanca et al. 2024) and may transmit pathogens (Nanetti et al. 2021) and other microbes to them (Hietaranta et al. 2023). A minority of studies, however, find no competitive effect by honeybees highlighting that the research results are not applicable to all ecosystems. For example, a monitoring study lasting 17 years in Panama failed to record negative effects of the introduction of Africanized *Apis mellifera* on native pollinators (Roubik & Wolda 2001). Moreover, the review article by Paini (2004) concluded that some of the studies investigating honeybee and native pollinator competition have also methodological and interpretational problems and assessing the exact influences of honeybees is difficult. There is clearly a need to investigate the competition between honeybees and native pollinators in various contexts, environments and means of interaction.

Geranium sylvaticum L. is a long-lived Eurasian perennial herb which is common throughout Finland. Phenotypically diverse, the gynodioecious *Geranium sylvaticum* is known for female and hermaphrodite sexes. The nectar sugar content is affected by flower sex and phase (Varga et al. 2013). The flower colours range from pale whitish to deep purple and pink (Asikainen & Mutikainen 2005; Varga & Kytöviita 2010). The flowers are mainly pollinated by bumblebees and are a source of nectar and pollen to various hoverflies, solitary bees, wasps and other insects (Varga & Kytöviita 2010; Soininen & Kytöviita 2022). The flowers are also readily visited by honeybees (*Apis mellifera).*

Most pronounced differences between plants are found between different plant species and higher taxonomic orders, and the importance of genotype and the intraspecific variation has gained limited interest previously (Hughes et al. 2008; Burkle et al. 2013). Therefore, a potentially important component of plant-pollinator interactions has been left largely unexplored: the effect of genetic diversity within plant species (but see Little et al. 2005; Hajjar et al. 2008). Nevertheless, different plant genotypes may support different pollinator communities due to within species differences in resources provided by the individuals. For example, a study by Burkle et al. (2013) noted that the differences in floral phenology between genotypes of *Solidago altissima* shaped the pollinator community visiting the plants. Due to limited research effort, the significance of within species diversity on pollinator behaviour is largely unknown.

Furthermore, it is unknown whether within species diversity could allow for further niche partitioning in addition to plant species diversity, or adaptive foraging to alleviate the competition between native and introduced pollinator species. To fill this knowledge gap, we studied pollinator behaviour in *Geranium sylvaticum* clones under field conditions over two seasons. Pollinator visitation rates and behaviour when visiting flowers were observed in the presence and absence of non-native honeybees. We predicted that:

I) Honeybees compete with native pollinators for floral resources in *Geranium sylvaticum*, which results in reduced visitation rates by native pollinator taxa, and

II) in response to presence of honeybees, the native pollinators shift their preferences over *Geranium sylvaticum* genotypes to avoid competition.

MATERIALS AND METHODS

STUDY SITE

The study site is a former agricultural field in Konnevesi Central Finland (Coordinates: 62°35′N 26°14′E) where cultivated *Geranium sylvaticum* plants have been growing since 2008. The study site is described in Appendix 1. The plant material consists of 14 genotypes which were repeated on average 8 ± 1.1 times (mean ± SE) resulting in 119 plants included in the present study. Of the genotypes, 6 were females and 8 hermaphrodites. The plants were grown in rows and the distance between each plant was approximately 0.8 m. The genotypes were randomly located within the 10 m x 40 m study site.

METHODS

The experiment consisted of two treatments, the control when no honeybees were present (hive absent) and treatment when the honeybees were present (hive present). The hive present-treatment was achieved by placing one honeybee hive (*Apis mellifera italica*) with two Langstroth compartments to the study site for two days. The hive absent-treatment was achieved by transferring the hive 20 km away from the site for two days. There were no honeybees present in the study site in the absence of the honeybee hive. Because there was only one study site, the treatments were replicated in time on alternate days over the flowering period of *Geranium sylvaticum* between 12.6.-24.6.2021 and 9.6.-29.6.2022. This resulted in 30 observation days with 1-2 observers and 18 days of observations in the absence of the hive and 12 days of observations in the presence of the hive, and altogether 11 transitions between the hive treatments. The beehive was placed close to the study site, so that its distance was approximately 20 meters from the centre of the study site, and the flight board was directed towards the study site. During the experiment, naturally occurring *Geranium sylvaticum* bloomed coincidentally with the study plants, making *Geranium sylvaticum* the most numerous and visible flower in the area.

During the active daytime hours of the pollinators (8:00-20:00), all insects visiting the study plants were recorded in approximately twenty-minute observation periods. The length of the observation period was subject to slight variation depending on pollinator activity (during low activity a longer period was observed (max 40 min) and during high activity shortened period was observed (min 10 min)). During June in the field site, the sun sets at approximately 11 pm, and the long observation period was aimed to gather as exhaustive data as possible over the foraging period of the insects. The observed plants were chosen randomly from the set of concurrently flowering plants, so that there were several repeated measures for each plant during different stages of flowering and times of the day. Altogether 290 hours of observation- during which 13 822 insect visits were recorded - were gathered over the two flowering seasons 2021 and 2022. The total number of visits to the observed plant, the number of flowers visited within one visiting bout, and the length of each flower visit were recorded. A single visiting bout was classified so that it started when the insect made contact with the first flower and continued until the moment the insect left the last visited flower. A flower visit was defined when part of the insect made contact with the inner corolla or reproductive structures of the flower. Thus, an insect sitting on the outer surface of the flower or corolla or inspecting the flower by hovering in front of it was not counted as a flower visit. The species of a visitor was identified to the lowest feasible taxonomic level under field conditions, but in a manner that all species identification was carried out unintrusive to the insects, i.e., keeping a sufficient distance and not capturing the insect for identification. Weather variables were acquired from the Finnish meteorological institute (see Appendix 1), and all observations were conducted under good weather conditions. Weather prerequisites for the observations were determined as follows: no rain, temperature is at least 15°C and wind speed less than 7 meters per second. Cloudiness was not considered a limiting factor given otherwise favourable weather.

Other recorded factors were the number of open flowers in the plant, the phase of flowering, the colour of the petals, and the proportion of receptive stigma in the plant during the observation period. The phase of flowering was defined as early phase = more flower buds than open flowers or fruits, middle phase = more open flowers than buds and fruits, late phase = more fruits than buds or open flowers. Stigma receptiveness ratio in the plant was counted from a minimum of 30 open flowers in the plant (number of receptive flowers/total number of counted flowers). One flower lasts about 30–48 hours depending on weather conditions, and the opening flowers present first only pollen as the first whorl of 5 anthers matures, then the second whorl of 5 anthers matures a few hours later adjoined with the opening of the receptive stigma (Varga et al. 2013). Therefore, the proportion of receptive stigmas in open flowers is an index of the age of the presented flowers, the more receptive flowers among all flowers, the older the presented flowers are. Petal colour was determined with the Royal Horticultural Society colour chart. In the end of the season, number of floral shoots from all the observed plants were counted and then collected, and the total number of fruits and withered flowers (brown, stigma not elongated) were counted. Each fruit produces up to 5 seeds that leave a seed scar, which allows counting the number of seeds in each fruit. Average seed success rate was calculated as (the number of fruits that produced at least one seed)/(number of withered flowers + all fruits).

STATISTICAL ANALYSES

All visitation data that were used as response variables in the statistical models were recorded in the format of visits per flower per minute in a plant (hereafter the term FPM will be used for simplicity). This standardization allows accounting for the differences in observation period length and number of open flowers. In the statistical analyses, the main response variable was the FPM by the individual insect groups (hereafter referred to as visitor group bumblebees, honeybees, solitary Hymenoptera, true flies (excluding hoverflies), hoverflies, and all insects). The group bumblebees were further split into the individual species of bumblebees; *Bombus lapidarius, Bombus soroeensis, Bombus lucorum* group, *Bombus hypnorum, Bombus pratorum* and *Bombus pascuorum*.

The negative binomial distribution was used to fit the data due to overdispersion. The statistical models were built using the negative binomial generalized linear model (function: glm.nb) from the R (ver. 4.2.1. x64) package "MASS" (Venables & Ripley 2002). The predictor value of the hive treatment (Factorial; 2 levels: hive absent and hive present) was incorporated in all models. The foundation of the model consisted of visitor groups as response and beehive treatment as the predictor variable. Other predictor variables were incorporated to the models according to the relevance for the hypotheses and their interaction with the response and/or predictor variables. The tested predictor values were the following: genotype of the plant (Factorial; 14 levels), stigma receptiveness ratio (proportional), temperature (continuous), cloudiness (factorial; 3 levels: cloudy, half-cloudy, clear), sex of the plant (factorial; 2 levels: female, hermaphrodite), number of open flowers (count), flowering stage (factorial; 3 levels: early, middle, late phase), air humidity (proportional), wind (factorial; 4 levels: calm, weak, moderate, strong; see Appendix 1.) and the year of observation as well as the time of the day. Predictor variables and their interaction with the response were tested individually and with the context of each other. The final model was built according to the smallest AIC value, highest relevance to the hypothesis and the independence of the used predictor values.

The effect of the genotype on the visitation rate was assessed using Kruskal-Wallis test in base R. In the model, the FPM value for given insect groups was set as the response variable, and genotype as the predictor (group). Each genotype was furthermore tested separately using negative binomial generalized linear model to determine whether the hive present/absent had an effect on the visitation rates in specific genotypes. In the model, genotypes were split, and the model consisted of visitor group FPM as the response, and hive absent/present as the predictor. When testing the effects of visitor preferences by different insect groups (bumblebees, hoverflies, solitary Hymenoptera, honeybees) on seed production per plant and the ratio of developed to undeveloped fruits and withered flowers (seed success rate), the mean seed production per fruit and seed success rate were used as response variables and the visitation rates were used as predictors in a negative binomial generalized linear model in the package MASS in R (Venables & Ripley 2002).

In all models, the test statistics Akaike Information Criteria (AIC, used as a tool for model comparison), degrees of freedom (df), probability (p), model estimates, and F-, z-, or Chi squared values are reported according to output of the model in R.

RESULTS

COMPETITION BETWEEN HONEYBEES AND WILD POLLINATORS

Hive presence reduced bumblebee visitations by 29 % (AIC = 1525, df = 682, estimate = -0.29, *P* = 0.006) (Fig. 1). Furthermore, when honeybee FPM were accounted for, bumblebee FPM were predicted to decrease by 0.34 by the addition of each further honeybee FPM (AIC = 1520, df = 682, estimate = 0.34, z = -3.30, *P* = 0.001). Hive presence did not affect the FPM of other common native pollinator groups: solitary Hymenoptera (AIC = 339, df = 682, estimate = -0.23, z = -0.73, *P* = 0.46), hoverflies (AIC = 389, df = 682, estimate = -0.03, z = -0.0105, *P* = 0.92) or other true flies (AIC = 287, df = 682, estimate = 0.02, z = 0.059, *P* = 0.95).

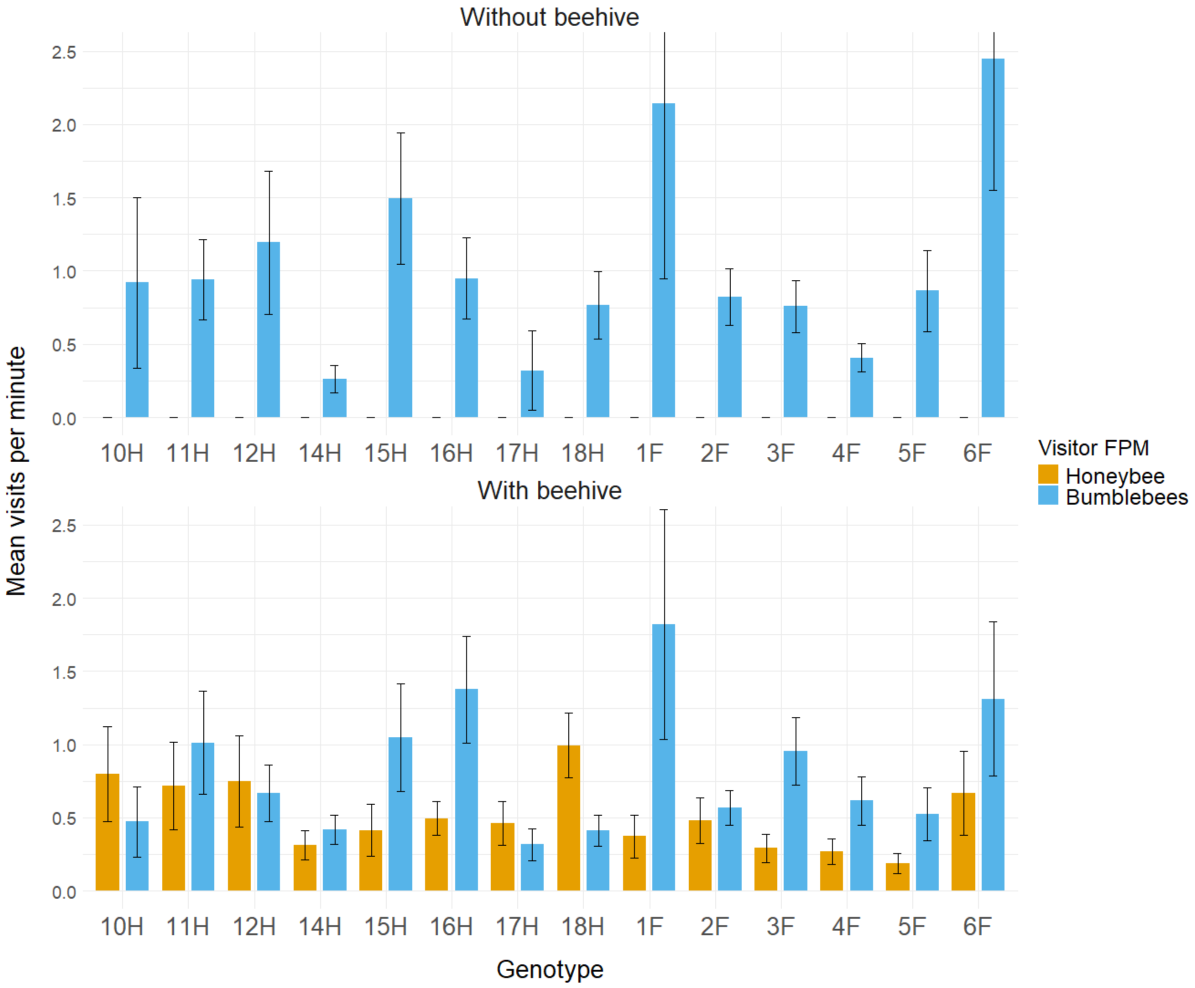

Figure 1. Mean ±SE visitation rates (FPM, flowers visited per minute in a plant) by the insect groups (Y-axis) in the *Geranium sylvaticum* genotypes. Data from both observation years are pooled and FPM in the absence of hive (top) and FPM in the presence of hive (bottom) are shown.

Table 1. Relative change in flower visitation frequencies per minute in a plant (average floral visits per minute) in each *Geranium sylvaticum* genotype. Genotype columns denote the change between hive absent and hive present in each bumblebee species. The table expresses the change from the hive absent to hive present treatment. When the value is negative, the FPM decreases when the hive is present in relation to when hive is absent. * Denotes statistically marginally significant ($P < 0.1 > 0.05$) change and ** statistically significant ($P < 0.05$) change with the predicted effect size. NA means the species did not visit the clone in question. The abbreviations from left to right stand for *Bombus lapidarius*, *B. soroeensis*, *B. lucorum* group, *B. hypnorum*, *B. pascuorum*, and *B. pratorum*.

Genotype	All Bombus	Lapid.	Soro.	Luco.	Hypno.	Pasc.	Prato.
H10	-89%	NA				NA	
H11	-53%						
H12	-79%			NA			
H14	-22%						
H15	-29%						
H16	+34%						
H17	+49%					NA	
H18	-69% **						
F1	-70%	NA					
F2	-71% **						
F3	+16%						
F4	+1%						
F5	-51%	NA					
F6	-54%				-108% *		
All	-38% **				-28% *	-188% *	

Although reducing bumblebee FPM and not affecting the other insect groups, hive presence increased the total FPM received by the plant by 24% (AIC = 1902, df = 682, estimate = 0.24, z = 3.16, *P* = 0.002, Fig. 1) due to honeybee visits.

PREFERENCE OF GENOTYPE AND SEX

Genotypes

Genotype identities affected the mean FPM rates over all of the visitors (X^2 = 40.71, df = 13, *P* = 0.0001) and bumblebees (X^2 = 39.31, df = 13, *P* = 0.0001), but not in terms of honeybee FPM (X^2 = 17.1, df = 13, *P* = 0.20) or hoverfly FPM (X^2 = 11.67, df = 13, *P* = 0.55). The mean bumblebee visitation rates in the genotypes ranged from 0.25 to 2.25, and honeybees (although not statistically significant) from 0.25 to 0.85 FPM in the presence of the hive. The hive presence affected the bumblebee FPM by increasing visitation rates to some genotypes while decreasing the rates to others (Table 1.). Furthermore, honeybees affected the visitation rates of individual bumblebee species differently (Table 1). The resulting species and genotype interactions are illustrated in Fig. 2. The insects visited the different genotypes relatively equally in the absence of the beehive. *Bombus hypnorum,* however, preferred two genotypes over others in the absence but not in the presence of the beehive (Fig. 2)

Proportion of receptive flowers, total number of open flowers, the phase of flowering (early, middle, late), temperature and other weather variables as well as the time of the day were evaluated and did not interact with the FPM rates.

Sex

Hermaphrodites had statistically marginally significantly larger floral display (W = 22202, *P* = 0.06) and hermaphrodite plants had 48±2.42 flowers simultaneously open whereas females had 40±2.39. The pooled visitation FPM of all insects received by the plant was predicted by the sex of the plant so, that total FPM was lower in the hermaphrodite (1.11±0.06 FPM) vs female (1.26±0.09) plants (AIC = 1811, df = 753, estimate = -0.28, z = -3.16, *P* = 0.002). Overall, bumblebees favoured female over the hermaphrodite plants (AIC = 1450, df = 653, estimate = -0.50, z = -4.22, *P* < 0.0001). Honeybees in turn showed no such preference (AIC = 601, df = 327, estimate = 0.47, z = 1.04, *P* = 0.30) (Fig. 3). Hive presence reduced the

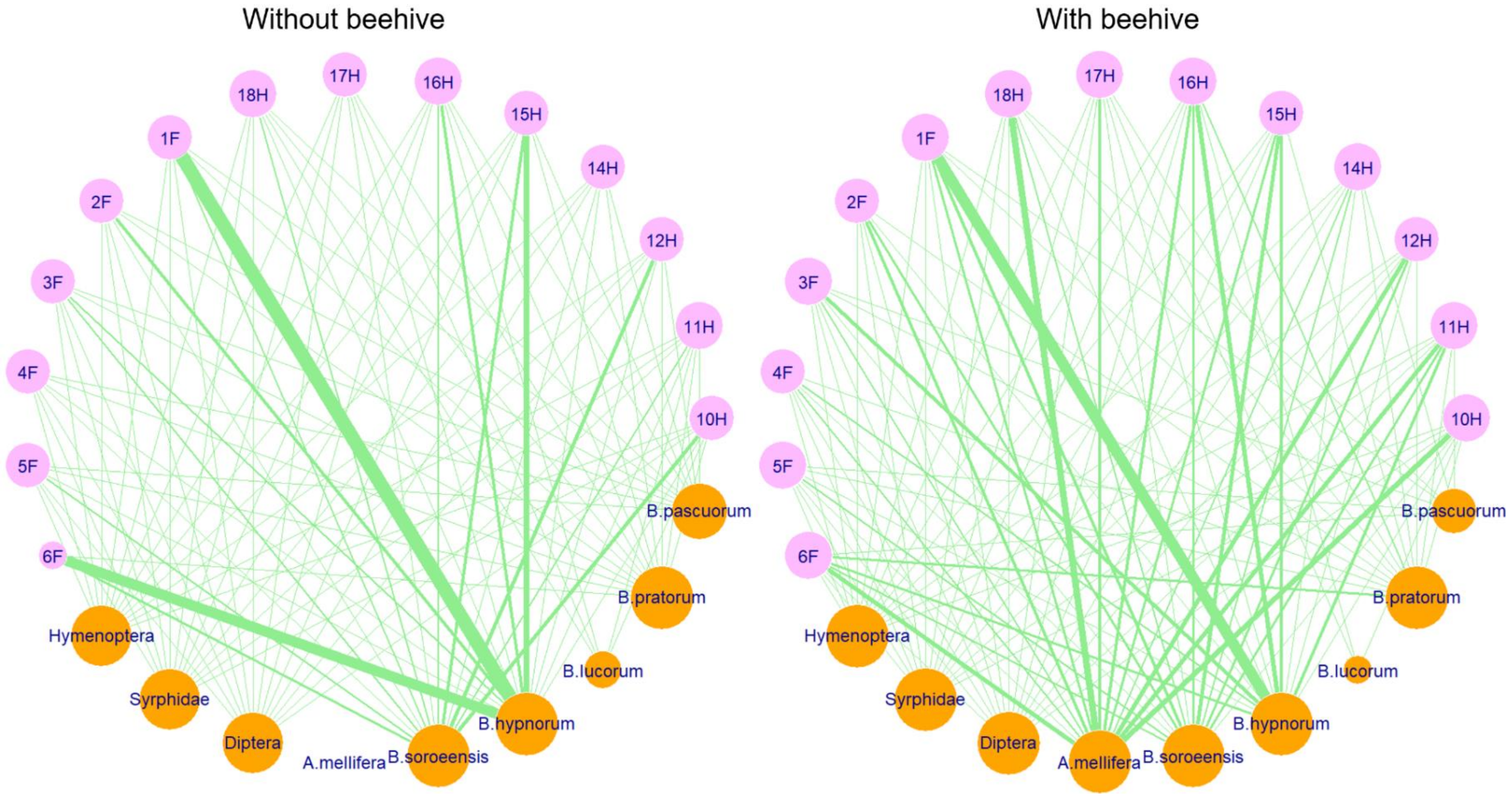

Figure 2. Visitation frequencies of different pollinator groups (Orange: Solitary Hymenoptera, hoverflies (Syrphidae), other true flies (Diptera), honeybees and the main bumblebee species) to different *Geranium sylvaticum* genotypes (Pink). Letters F stand for female and H for hermaphrodite. Line width reflects the intensity of frequency of visitations and the node size relative total number of visits by visitor group. Data consists of the 8623 visits recorded during the study year 2022.

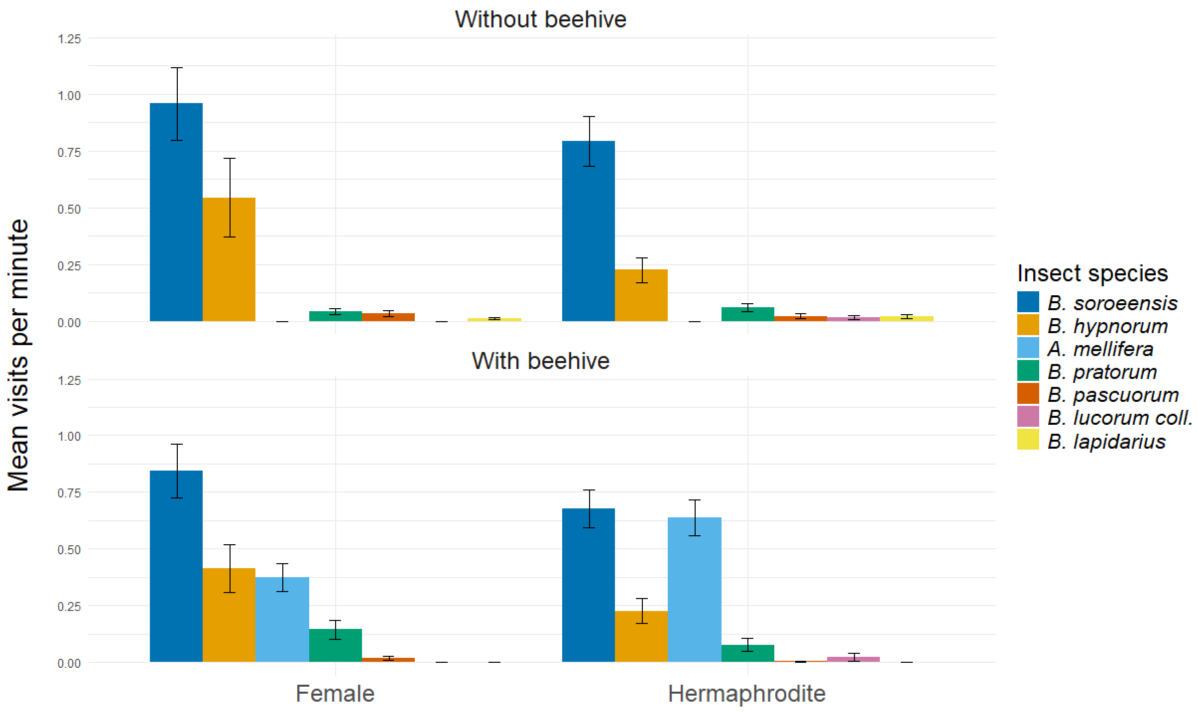

Figure 3. Mean ±SE visitation rate (FPM, flowers visited per minute in a plant) by honeybees and native bumblebee species in female and hermaphrodite *Geranium sylvaticum* in the absence of hive (top) and in the presence of hive (bottom).

FPM in both sexes (AIC = 1717, df = 778, estimate = -0.36, z = -3.33, *P* < 0.001). Bumblebee visitation rates in hermaphrodite/female plants in absence of the hive were, respectively, 0.72/1.05 FPM and in presence of the hive 0.50/0.71 FPM.

Effect of visitations on seed production

Only plant sex predicted mean seed production and hermaphrodites produced fewer seeds per flower (3.16±0.05) than females (3.77±0.03) (df = 233, estimate = -0.17, z = -2.44, *P* = 0.015). Visitation rates by bumblebees in the hive presence treatment (df = 208, estimate = 0.01, z = 0.28, *P* = 0.78) or absence treatment (df = 208, estimate = 0.007, z = 0.29, *P* = 0.87) did not affect mean seed production per fruit. The same was true in terms of hoverfly preference in the hive presence (df = 208, estimate = -0.002, z = -0.006, *P* = 0.99) and absence treatments (df = 233, estimate = 0.05, z = 0.12, *P* = 0.90) as well as in the case of solitary Hymenoptera in the hive presence (df = 208, estimate = -0.03, z = -0.14, *P* = 0.88) and hive absence (df = 233, estimate = -0.08, z = 0.74, *P* = 0.74) treatments. Honeybee FPM in the hive presence treatment did not affect mean seed production (df = 208, estimate = -0.02, z = -0.42, *P* = 0.68).

The overall seed success rate was 0.82±0.01, (hermaphrodites 0.77±0.01, females 0.88±0.01). Visitation rates by bumblebees in the hive presence (AIC = 407, df = 208, estimate = 0.02, z = 0.26, *P* = 0.80) or hive absent treatment (AIC = 449, df = 233, estimate = 0.009, z = 0.18, *P* = 0.85) did not predict seed success rate. The same was true in case of hoverfly FPM in the presence (AIC = 407, df = 208, estimate = 0.01, z = 0.02, *P* = 0.98) and absence of hive (AIC = 449, df = 233, estimate = 0.08, z = 0.10, *P* = 0.92) as well as in case of solitary Hymenoptera in the presence (AIC = 407, df = 208, estimate = 0.04, z = 0.08, *P* = 0.93) and absence (AIC = 449, df = 233, estimate = -0.02, z = -0.05, *P* = 0.96) of the hive. Honeybee FPM in the presence of the hive did not affect the seed success rate (AIC = 407, df = 208, estimate = 0.006, z = 0.60, *P* = 0.95). All focal results are summarized in Table S1.

DISCUSSION

COMPETITION BETWEEN HONEYBEES AND NATIVE POLLINATORS

Honeybees share many similarities with native eusocial bees, and therefore niche overlap is likely (Goulson & Darvil 2004, Elliott et al. 2021). Our results support the notion that honeybees and bumblebees compete for floral resources. We show further that bumblebees shift foraging preferences in the presence of honeybees. This could result from pre-emptied floral resources by honeybees (Goulson 2003, Cappellari et al. 2022), although we did not measure nectar or pollen foraging in this study. There could also be evolutionarily promoted tendencies to avoid pests and parasites by not visiting the same plants (Koupilová et al. 2022). Some studies indicate that pollinator species partition resources in respect to temperature and time (Scriven et al. 2016, Jeavons et al. 2020). The measured flower visitation rates per minute remained relatively constant during the day, and despite different temperature ranges measured, we conclude that no evidence for niche partitioning was evident between honeybees and bumblebees in terms of temperature and time of the day. We did not find evidence of competition between honeybees and the pollinators other than bumblebees. However, other studies have identified such effects in various groups of pollinators (Lindström et al. 2016, Requier et al. 2024). Jeavons et al. (2020) note that honeybees and hoverflies differ temporally in their foraging behaviour, and overall true flies and solitary Hymenoptera are expected to share less similarity and niche overlap with honeybees than bumblebees do. These results support the previous findings of the importance of competition between the most important bee pollinators the honeybee and bumblebees (Requier et al. 2024).

INTERACTIONS BETWEEN PLANT GENOTYPE AND NATIVE AND INTRODUCED POLLINATORS

The closer the resemblance between the functional characteristics and resource use of two groups of insects, the higher the degree of niche overlap and competition (Feinsinger et al. 1981; Montero-Castaño & Vila 2016). This is especially true for closely related species such as bumblebees which share many traits in common. In the absence of honeybees, different species of bumblebees intrinsically favour different genotypes of *Geranium sylvaticum*. Pollinators can prefer certain plant morphologies (Cooley et al. 2008) or genotypes (Burkle et al. 2013). The preferences themselves are generally related to specific nutrient or energetic needs (Petanidou et al. 2006, Ruedenauer et al. 2019), and the general economics of visiting a flower (Woodward & Laverty 1992, Alcorn et al. 2012). In this study, pollinators did not respond to the measured characteristics in the genotypes (flower colour, number of open flowers, phase of flowering, age of open flowers), so we can only speculate the reasons for preferences. However, competition with other pollinators through pre-emption of flowers (Henry & Rodet 2018) may affect foraging behaviour. In the presence of competition, pollinators with overlapping niches tend to shift their foraging behaviour to alleviate the negative effects of competition (Roubik et al. 1986, Scriven et al. 2016, Jeavons et al. 2020). It has been shown, for example, that bumblebees forage in a more generalist manner in different plant species when competition for floral resources increased (Fontaine et al. 2008). In return, competition with native pollinators also affects honeybee foraging behaviour (Greenleaf & Kremen 2006). Most studies address niche partitioning in terms of shifting foraging preferences (Valdovinos 2016, Wei et al. 2021) or spatio-temporal variation (Jeavons et al. 2020). Our study contributes to the knowledge on pollinator behaviour by documenting behavioural shift between pollinator insects in relation to plant genotype.

In our study, most of the *Geranium sylvaticum* genotypes received fewer visits by bumblebees in the presence of honeybees. Some genotypes, however, received increased bumblebee visitation rates in the presence of the honeybees, which indicates that the bumblebees shifted their preference over the genotypes. Overall, honeybees visited different *Geranium sylvaticum* genotypes more indiscriminately than bumblebees in our study. Discrimination of genotypes can be translated to higher floral constancy to certain genotypes by bumblebees. Bumblebees are credited as highly constant among pollinators (Osborne et al. 1999) and there are studies that regard honeybees as more generalist than wild pollinators in reference to plant species (Steffan-Dewenter & Tscharntke 1999; Leonhardt & Blüthgen 2011). In our study, the bumblebee floral constancy detailed in literature extended to the level of plant genotype. Generalism and flower constancy in bees are dependent on optimal foraging, i.e. the availability of energy in the flowers and the distance to the nest (Ranta & Lundberg 1980). As the honeybee hive was next to the study field while the location of the bumblebee nests was unknown, it is possible that the distance to the nest affected genotype preferences in bumblebees more than in honeybees. In our data, some genotypes were favoured by the bumblebees even on a year-to-year basis, and these preferences persisted despite honeybee presence. Although the competition with honeybees affected bumblebee visits in *Geranium sylvaticum* genotypes differently, the trend, however, was an overall decrease in bumblebee visitations in presence of honeybees.

Honeybee presence had a pronounced effect on the foraging behaviour of different bumblebee species. This potentially affects the selective pressures to certain genotypes of *Geranium sylvaticum* since bumblebees are the principal pollinators in this species. Native species of bumblebees have differential flower preferences for example due to their tongue lengths (Heinrich 1976, Ranta & Lundberg 1980). As the tongue length intrinsically creates preferences and resource allocation between species of bumblebees, and the honeybee is relatively short tongued (Balfour et al. 2013), honeybees can be expected to compete more with short tongued species of bumblebees. Indeed, we noticed that in response to honeybee presence, most notable decrease over the *Geranium sylvaticum* genotypes (-26%) was among the long tongued *Bombus pascuorum*, which can move to other species with deeper flowers that are inaccessible by honeybees. These results highlight the importance of identifying pollinator and plant traits when determining the effect of non-native pollinator to native pollinator community.

EFFECT OF PLANT SEX AND HONEYBEES ON FLORAL VISITS BY NATIVE POLLINATORS

Due to behavioural and structural reasons, honeybees are not effective pollinators of *Geranium sylvaticum* (Soininen & Kytöviita 2022). Consequently, the presence or absence of honeybees did not affect seed success and seed production in this study. Honeybees visited the sexes equally and reduced bumblebee visitation rates in both sexes. Bumblebees on the other hand maintained their preference of females irrespective of honeybee presence. Bumblebees have been shown to be the primary pollinators of *Geranium sylvaticum* (Soininen & Kytöviita 2022). Consequently, seed success was higher in females as has been shown previously (Varga & Kytöviita 2010). The preference of females by bumblebees is surprising as the females have no pollen, have smaller floral display (this study), smaller flowers (Asikainen & Mutikainen 2005; Varga & Kytöviita 2010) and produce less nectar (Varga et al. 2013). In this study we could not identify any factor that could be responsible for the bumblebee preference of females. However, it is possible that the nectar produced by females is preferred by bumblebees because it has more favourable vitamin or amino acid contents than that produced by hermaphrodite plants. Male plants have been shown to be visited more frequently in dioecious species (Carlsson-Granér et al. 1998; Bond & Maze 1999; Van Etten & Chang 2014; Ramadoss et al. 2023). The difference in floral rewards and visual cues between female and hermaphrodite *Geranium sylvaticum* should be studied in more detail before concluding on the reasons for pollinator behaviour.

CONCLUSIONS

Honeybees reduced bumblebee foraging rates in the *Geranium sylvaticum* plants, despite having no effect on other groups of pollinators. We tested pollinator interactions using a single species of plant and a single experimental site with its unique surrounding flora and care must be taken when generalizing these results. In general, replacement of native bumblebee visits by honeybees can have dramatic effects on plant pollination as honeybees are not as effective pollinators as bumblebees (Westerkamp 1991). Honeybees do not compensate for the loss of bumblebee visits as honeybees are much less likely to pollinate *Geranium sylvaticum* flowers than bumblebees are (Soininen & Kytöviita 2022). In the world of declining native pollinator abundances (Hallmann et al. 2017; Sánchez-Bayo & Wyckhuys 2019), managed honeybees do not seem to be the remedy to conserve wild plant diversity.

Honeybees are indiscriminate in regard to plant genotype. We therefore expect that their presence in numbers selects for lower genetic diversity in *Geranium sylvaticum*. Our study further highlights the susceptibility of bumblebees to competition with honeybees. This is alarming since many studies note that pollinator diversity rather than abundance increases pollination efficiency (Klein et al. 2003), and lower pollinator diversity begets lower plant diversity (Ramos-Jiliberto et al. 2020).

Our study calls attention to the importance of plant genetic diversity for the maintenance of diverse pollinator communities, and conversely, the importance of native pollinators for genetically diverse plant populations in the future.

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AUTHOR CONTRIBUTION

Concept and design MMK, JS & JP, data collection JS & MMK, data analysis JS, writing JS, MMK & JP, edits and approval for publication MMK, JP & JS.

DISCLOSURE STATEMENT

Authors of the manuscript declare no potential conflicts of interest.

DATA AVAILABILITY STATEMENT

Data will be made available upon request.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix 1. Description of the field site and weather parameters.

Table S1. Summary of the focal results.

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