RESEARCH ARTICLE

Landscape-level honey bee hive density, instead of field-level hive density, enhances honey bee visitation in blueberry

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Abstract

Context To date, managing honey bees and wild bees within crop fields remains challenging. Landscape structure is often overlooked when studying the pollination contribution of honey bees. Increasing our understanding on how to predict honey bee visitation in crops is crucial for sustainable management of agroecosystems.

Objectives With this study we investigated which landscape and field-level variables determine honey bee and wild bee visitation, and whether honey bee or wild bee visitation influence crop pollination.

Methods Sixteen highbush blueberry fields were surveyed for honey bees, wild bees, and crop pollination in Washington, USA. Additionally, within a radius of 1000 m around each field all honey bee hives were located and the surrounding landscape was characterized.

Results Honey bee hive numbers in the landscape positively correlate with the proportion of blueberry in the landscape. Honey bee visitation was best predicted by landscape-level hive density within a radius of 1000 m, whereas semi-natural habitat and field-level hive density did not impact honey bee visitation. The amount of semi-natural habitat and blueberry within a radius of 1000 m had a positive and negative impact, respectively, on wild bee visitation. Honey bee visitation had a positive effect on blueberry seed set.

Conclusion We conclude that honey bee visitation is determined by the number of honey bee hives in the surrounding landscape. Hence, field-level hive density recommendations miss contributions from other hives in the landscape. Furthermore, semi-natural habitat did not impact honey bee visitation and contributes to diversifying pollinator diets and provides wild bee habitat.

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Introduction

Insect-mediated pollination is crucial for the reproduction ca. 80% of angiosperm species (Ollerton et al. 2011; Rodger et al. 2021) and contributes to global food production as more than 75% of all crops depend on insect pollination (Klein et al. 2007). In addition, from 1981 to 2016, the global area of land dedicated to pollinator-dependent crops increased faster (+137%) than the increase in area of all crops (+41%; Aizen et al. 2019). This results in an increased dependence on insect pollinators in agriculture. For most pollinator-dependent crops, the pollination contribution of wild pollinators is at least as important or even more important than that of domesticated honey bees (*Apis mellifera*) (Dainese et al. 2019; Reilly et al. 2020; Pisman et al. 2022). However, crop pollination management is mainly focused on the application of honey bees (Osterman et al. 2021a, b).

Crop pollination is dependent on many factors such as landscape structure, weather conditions during crop flowering, and the abundance and efficiency of the present pollinator taxa. Indeed, certain wild pollinators have been shown to have a higher pollination efficiency in multiple crops compared to honey bees (Eeraerts et al. 2020a; Foldesi et al. 2021). Regarding blueberry and similar *Vaccinium* species, the ability of bumble bees (*Bombus* spp.) and certain solitary bees to sonicate flowers enables them to pollinate blueberry efficiently (i.e., buzz pollination; Rogers et al. 2013; Sun et al. 2021). Therefore, honey bees must visit a blueberry flower multiple times to deposit adequate pollen and facilitate full pollination (Hoffman et al. 2018; Kendall et al. 2022). Honey bee foraging activity is also susceptible to suboptimal weather conditions, whereas most wild bees can forage within a wider range of conditions (Tuell and Isaacs 2010; Rogers et al. 2013). Despite being a less efficient pollinator, honey bees have the advantage of attaining high abundances through deployment of honey bee hives in fields during crop flowering (Isaacs and Kirk 2010; Mallinger et al. 2021).

The composition and configuration of agricultural landscapes affects wild bee communities visiting crops (Tscharntke et al. 2005; Dainese et al. 2019). The diversity of wild pollinators is associated with semi-natural habitat (SNH), which provides a variety of foraging and nesting habitat (Timberlake et al. 2019; Eeraerts et al. 2021a). In addition, increasing landscape heterogeneity can improve pollinator diversity and pollination services to crops (Martin et al. 2019). Mass flowering crops (MFC) are a land use type that can be beneficial for wild pollinators as they provide abundant floral resources during crop flowering (Mallinger et al. 2016). However, after crop flowering, they provide scarce floral resources (Mallinger et al. 2016; Eeraerts et al. 2021a). Indeed, as the proportion of MFC increases, landscapes become more homogenized, which negatively affects wild pollinator diversity (Holzschuh et al. 2016), reproduction (Proesmans et al. 2019; Eeraerts et al. 2021b) and their corresponding pollination services (Eeraerts et al. 2017).

Contrary to wild pollinators, landscape structure is an often-overlooked factor when studying and managing pollination services of honey bees. Previous studies conclude a positive (Petersen and Nault 2014; Eeraerts et al. 2017) or no relationship (Pisman et al. 2022) between honey bee visitation and the proportion of MFC. The relationship between SNH and honey bee visitation is variable as well (no effect: Holzschuh et al. 2012; Klein et al. 2012; Alomar et al. 2018; Mallinger et al. 2021; positive effect: Gibbs et al. 2016; negative effect: Gibbs et al. 2016; Eeraerts et al. 2019). Interestingly, Holzschuh et al. (2016) detected increasing honey bee densities in SNH with increasing proportion of MFC, suggesting a redistribution of honey bees to SNH. Both land use types, SNH and MFC, are hypothesized as important concerning honey bee visitation. The amount of SNH is expected to have a negative effect on honey bee visitation due to providing additional floral resources, which draws honey bees away from the crop (Pettis et al. 2013; Danner et al. 2017). On the other hand, the amount of MFC may contribute positively to honey bee visitation as it provides additional honey bee hives in the landscape during crop flowering. Yet, to date the latter has not been investigated.

Another critical component is the field-level management of honey bee hive densities. To date, the relationship between field-level hive densities

and honey bee visitation is not clear (Benjamin and Winfree 2014; Gibbs et al. 2016; Arrington and DeVetter 2018; Mallinger et al. 2021). The strength of honey bee hives can be variable (Geslin et al. 2017; Grant et al. 2021) and this aspect is rarely considered in hive density recommendations to date. However, some studies that considered hive strength detected a positive relationship between field-level hive density and crop visitation by honey bees (Geslin et al. 2017; Grant et al. 2021; Mallinger et al. 2021). In addition, using long term data on cranberry (*Vaccinium macrocarpon*) yield and field-level hive density, Gaines-Day and Gratton (2016) found that hive density had a positive effect on cranberry yield, but only in landscapes with low amounts of SNH. Yet, few studies have considered how managed honey bees interact with variation in the landscapes. Improving our understanding of both landscape structure and hive densities and their relationship with honey bee visitation in crops is essential for sustainable crop pollination management.

The objective of this study is to extend the knowledge and research on which variables influence honey bee and wild bee visitation in cultivated northern highbush blueberry (*Vaccinium corymbosum*, hereafter "blueberry"). We also explore how bee visitation affects the pollination success. To do so, 16 blueberry fields in Washington State (USA) were surveyed for honey bees and wild bees. Honey bee hives within the fields and the surrounding landscape were also located and mapped and crop pollination was measured. With this information we aimed to study the following research questions:

1. How does the proportion of blueberry predict the number of honey bee hives present in the landscape?
2. Which landscape- and field-level variables best predict both honey bee and wild bee visitation in blueberry and at what landscape scales?
3. Does increasing honey bee or wild bee visitation influence blueberry pollination?

Materials and methods

Site selection and landscape set up

The study was performed in 2021 in Skagit and Whatcom counties in Washington State, USA (Fig. S1). In total, we selected 16 blueberry fields as study sites, of which 15 were conventionally managed, monoculture 'Duke' fields and one was an organically managed, mixed field with 'Chandler', 'Reka' and 'Bluecrop'. Field size of the study sites ranged from 3.6 ha to 10.2 ha (6.8 ± 0.5, mean ± standard error), and the distance between sites ranged from 1.9 to 69.9 km. The geographical center of each field was determined on maps and in this center, we constructed four, fixed transects of 100 m along the berry rows for data collection (see below).

To test our research questions, we selected fields with a sufficient gradient in the amount of area in blueberry fields and SNH within a radius of 1000 m from the center of each field, with these gradients being uncorrelated. We only mapped blueberry fields as crop fields because this is the only MFC that contained honey bee hives during blueberry bloom in our study area. Land use was mapped and quantified using QGIS software (Madeira version 3.4.13), using the National Land Cover Database and Cropland Data Layer maps (NLCD and CDL) as reference land use maps (Dewitz 2019; USDA 2020). We quantified the amount of SNH (NLCD) and blueberry (CDL) in a 1000 m buffer zone around the central point of each field. Land use types that were considered as SNH were: shrubland, extensive grassland, woody and herbaceous wetlands, and forest. The amount of blueberry fields and SNH in the surrounding landscape ranged from 6.8 to 38.0% and 0.0% ± 32.9%, respectively (19.4% ± 2.4% and 12.2% ± 2.7%, respectively). Other land use types in the surrounding landscapes within 1000 m were arable crops (52.7% ± 5.6%), pastures (27.2% ± 4.4%), and other areas (e.g., water bodies, urban areas; 7.9% ± 1.5%). For analyses, the percentages of SNH and blueberry within a buffer zone of 250 m, 500 and 750 m around the center of fields were determined for each study field. The gradients of SNH and blueberry around the center of fields and their correlations for the different landscape scales are given in Tables S1 and S2.

Pollinator surveys

Honey bees and wild bees were sampled in all study sites between April 24 and May 15, 2021 (mid-bloom of 'Duke'), via transect walks performed for 30 min per transect (four transects = 120 min per field). Transect walks were performed once per site between 11:00 and 17:30 with temperatures ranging from 14 to 20 °C to ensure optimal pollinator activity. Using insect nets, we sampled all honey bees and wild bees foraging on blooming blueberry flowers. All sampled bee specimens were kept in individual conical tubes, and for each specimen it was noted whether it was foraging for pollen or not. All honey bees were released after each pollinator survey. Wild bees were identified to genus, subgenus, species and morphospecies.

Honey bee hive mapping

Together with information provided by farmers, beekeepers, extension agents, and personal expertise, we mapped the location of all honey bee hives within a radius of 1000 m of the transects of our study sites. Farmers rent honey bees annually for blueberry and raspberry, which are the two main pollinator-dependent crops in Skagit and Whatcom counties. Additional honey bee hives beyond these two crops are very scarce in the study area. In order to map the location of the honey bee hives, we made landscape maps of all blueberry and raspberry fields with QGIS and the CDL map. Each field that was indicated as blueberry was also verified with Google Earth, and all other adjacent land parcels were checked with Google Earth to make sure we did not miss any blueberry fields (Google Earth Version 9.159.0.0). In case of uncertainty, we indicated doubtful fields, and these were verified via field visits as well. During mid-bloom of 'Duke' (between April 24 and May 15, 2021), all blueberry fields within the 1000 m radii were visited and inspected for honey bee hives within and around fields, which were then located and mapped. All blueberry fields were checked, including other blueberry cultivar fields. For each hive we noted its position on printed hardcopies of the maps. All the observed hives were Langstroth hives with one brood chamber and one or two supers. Only rarely did we encounter hives with only a brood chamber or with three supers. In 2021, there was no overlap between 'Duke' blueberry bloom and raspberry bloom, so at the time of pollinator sampling and honey bee hive mapping, the raspberry fields were not yet stocked with honey bee hives.

Pollination measurements

Blueberry pollination was measured on 20 bushes per study site. To this end, five representative blueberry bushes were selected in each of the four 100 m transect per site. From each bush, three one-year old branches at mid-canopy height were selected and randomly assigned one of the following treatments: (1) open (exposed to pollinator visitation), (2) bagged (excluded from pollinator visitation by placement of fine-mesh pollinator exclusion bags over inflorescences at pre-bloom), and (3) hand pollination (flowers left open and provided with supplemental pollen). For supplemental hand pollination, pollen was collected from adjacent bushes of the same cultivar and applied the same day it was collected using a fine paintbrush that deposited pollen to the stigma of each open flower. All flowers from each branch were counted for fruit set estimates. Both hand pollination and counting the flowers was performed twice during the bloom period. All pollination measurements were conducted between April 24 and May 15, 2021.

After bloom, all branches were covered with a mesh bag to prevent premature harvest or depredation by birds. When approximately 60% of the fruits were ripe, fruits were hand harvested at the branch level, and transported back to the lab (July 6–21). Fruits were harvested a second time 10–14 days after the first harvest to sample all remaining fruits (July 26–August 4). For each branch, total berry number and berry weight were determined, and these data were pooled for the two harvest rounds. Berry number was used to calculate percent fruit set (based on the maximum flower number of counting rounds 1 and 2) and average berry weight (calculated with blue, ripe berries only; g/berry). Three berries per branch were then randomly selected from the pooled berry sample per branch. One by one, these berries were macerated in a clear plastic bag, and seeds were extracted and counted to determine viable seed number. Only melanized, plump, and dark seeds were counted to ensure viable seed number was measured (Dogterom et al. 2000; Strik and Vance 2019).

Statistical analyses

Honey bee hives and bee visitation

Spearman rank correlations between the proportion of blueberry fields in the surrounding landscape and the landscape-level honey bee hive densities were calculated for the different landscape scales (250 m, 500 m, 750 m, and 1000 m).

Bee data from the different transects were pooled for every site to obtain honey bee visitation and wild bee visitation as response variables. Generalized linear models (GLM, function *glmmTMB*, R package *glmmTMB*) were used to determine the influence of field-level honey bee hive density, landscape-level honey bee hive density, and proportion of SNH on honey bee visitation. Due to the high correlations between the proportion of blueberry and landscape-level hive densities, we opted to use the landscape-level hive density, instead of the proportion of blueberry, as the explanatory variable in this analysis. Regarding wild bee visitation, we tested the model with proportion of blueberry, proportion of SNH, and their interaction as fixed factors. Before analyses, all fixed factors were scaled and centered to a mean of 0 and a standard deviation of 1. Honey bee and wild bee visitation were both modelled with a Conway-Maxwell Poisson distribution. For both honey bee and wild bee visitation, we tested the full model for each landscape scale and selected the scale for which the full model was the most informative (lowest AIC_C). Based on the full model of the best predicting landscape scale, the best model was selected by means of an automated model selection program that calculates all possible models based on a set of explanatory variables and then ranks these models based on their AIC_C (function *dredge*, R package *MuMIn*). Subsequently, the best model was selected ($\Delta AIC_C > 2$).

Pollination treatment and pollinator contribution

To test the influence of pollination treatment (i.e., bagged, open, and hand) on blueberry fruit set and berry weight, linear mixed-effects models were used (LME, function *lme*, R package *nlme*). Generalized linear mixed-effect models were used to test the influence of pollination treatment on seed number per blueberry (GLMM, function *glmmTMB*, R package *glmmTMB*). Seed number was modelled with a Conway-Maxwell Poisson distribution. For all three response variables, the tested model consisted of pollination treatment as a fixed factor, and bush ID nested in site ID as random factors. Tukey's Honest Significant Difference test was used to calculate adjusted p-values for multiple comparisons between the different pollination treatments (function *contrast*, R package *emmeans*).

The effect of honey bee and wild bee visitation on blueberry fruit set, berry weight, and seed number per blueberry of the open pollination treatment was also evaluated. For blueberry fruit set and berry weight, LME were used and for seed number per blueberry GLMM were used, modelling seed number with a Conway-Maxwell Poisson distribution. For all three response variables, the full model consisted of honey bee visitation, wild bee visitation, and their interaction as a fixed factor, with site ID included as random factor. Based on the full model, the best model was selected by means of an automated model selection program ($\Delta AIC_C > 2$).

All analyses were performed with R version 4.0.3 (R Development Core Team 2020). For the bee visitation and pollination contribution analyses, we checked collinearity between explanatory variables before data analyses by means of variance inflation factor (VIF) analyses, and all variables had a VIF lower than 2. Model fit of the LME model was evaluated visually by checking the normality of the model residuals (QQ-plot and plot of the residuals versus the fitted values) and with the Lilliefors test. Model fit of the GLM(M)s was evaluated with the residual diagnostics and goodness-of-fit tests from the *DHARMa* R package.

Results

General

In total we located and mapped 6340 honey bee hives in the landscapes around our study sites, with the landscape-level hive density within a radius of 1000 m ranging from 16 to 920 hives per landscape (396.3 ± 15.8, mean $\pm$ standard error; Table S3). At all landscape scales, the landscape-level hive density expressed as hives per landscape was positively correlated with the landscape-level hive density expressed as hives per ha blueberry in the landscape

(Table S4). Field-level hive density ranged from 3.5 to 25.3 hives per ha (12.2 ± 1.5; Table S3). The field-level hive density was not correlated with the size of the field (Spearman rank correlation coefficient $= 0.27$, $p = 0.32$). Honey bees were the dominant pollinator with 1155 individuals caught in total and 54 wild bees caught on blueberry blossoms. Across fields, honey bee visitation ranged from 44 to 114 (73.5 ± 5.0) and wild bee visitation ranged from 0 to 14 (3.4 ± 1.0, Table S5). A low percentage of honey bees foraged for blueberry pollen, ranging from 0.0 to 18.5% ($2.9\% \pm 1.3\%$).

Honey bee hives and bee visitation

At the 500 m, 750 m, and 1000 m landscape scale, the landscape-level hive density was positively correlated with the proportion of blueberry, whereas this correlation was not significant at the 250 m scale (Figs. 1A, S2; Table 1).

Fig. 1 Scatterplot visualizing the relationship between the proportion of blueberry fields and the number of honey bee hives in the surrounding landscape within a radius of 1000 m around our study sites (**A**). Relationship between the number of honey bee hives in the surrounding landscape within a radius of 1000 m and honey bees visiting blueberry blossoms (**B**). Relationship between the proportion of semi-natural habitat (**C**, SNH) and the proportion of blueberry fields (**D**) within a radius of 1000 m around our study sites and the wild bees visiting blueberry blossoms. The solid lines indicates significant relationships, grey shaded areas indicate 95% confidence intervals and black points show raw data
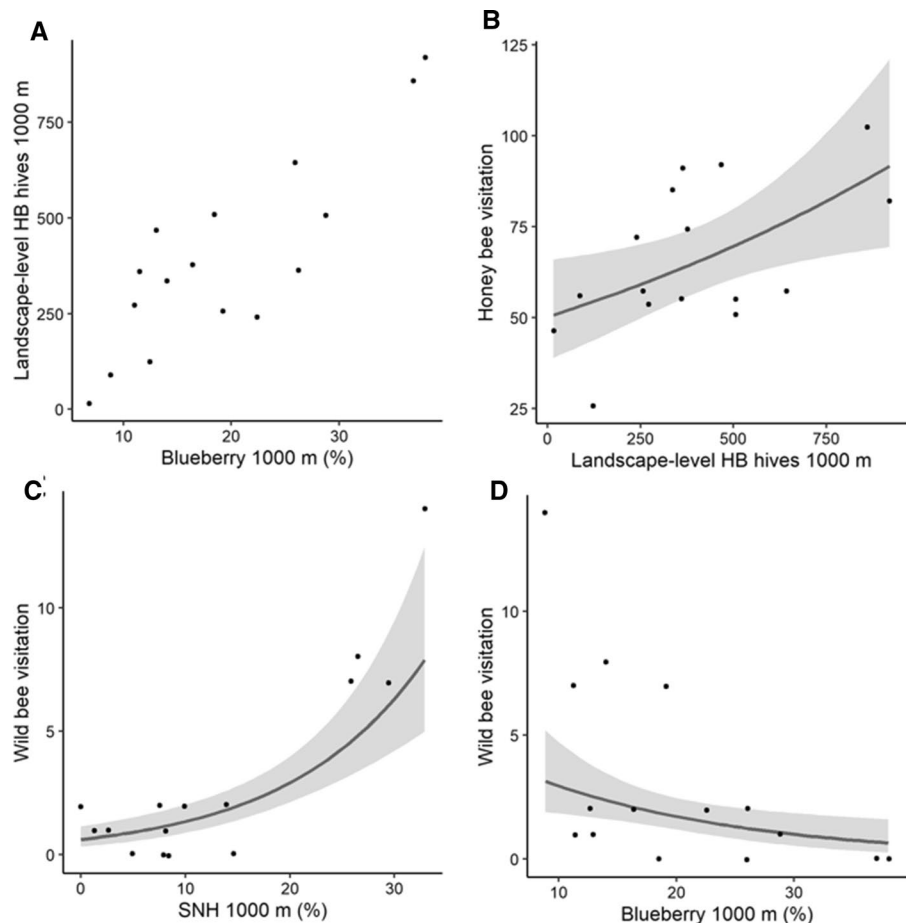

Table 1 Results of Spearman correlation tests between the landscape-level honey bee hive density and the proportion of blueberry at each landscape scale

	Corr. Coef.	p
Landscape-level HB hives 250 m – Blueberry 250 m	0.36	0.17
Landscape-level HB hives 500 m – Blueberry 500 m	0.67	< 0.01
Landscape-level HB hives 750 m – Blueberry 750 m	0.74	< 0.01
Landscape-level HB hives 1000 m – Blueberry 1000 m	0.75	< 0.001

For both honey bee and wild bee visitation the most informative landscape scale was the 1000 m landscape scale (Tables S6, S7). Consequently, the best model on this scale showed that honey bee visitation was positively influenced by landscape-level hive density (Tables 2, S8; Fig. 1B). For wild bee visitation, the best model showed a positive effect of SNH and a negative effect of the proportion of blueberry (Tables 2, S9; Fig. 1C, D).

Pollination treatment and pollinator contribution

The pollination treatments had a significant effect on fruit set, berry weight, and seed set (Table 3). Post hoc tests showed that the bagged pollination treatment had lower fruit set and berry weight compared to the open and hand pollination treatments (Fig. 2A, B; Table S10). Regarding seed set, we found that the bagged treatment had a lower seed number per berry compared to the open and hand pollination treatments and that the open treatment had a lower seed number per berry compared to the hand pollination treatment (Fig. 2C; Table S11).

Regarding fruit set and berry weight, we did not detect an effect of honey bee or wild bee visitation as the null models were selected as best models (Table 4). Honey bee visitation on the other hand did have a positive effect on seed set (Table 4; Fig. 3).

Discussion

This study provides further evidence on how landscape structure and farming practices influence visitation of honey bees and wild bees in agricultural fields. We found that landscape-level hive densities best explain variations in honey bee visitation. Although this is a fairly simple and intuitive result,

Table 3 Generalized linear mixed-effects models assessing the effect of pollination treatment on blueberry fruit set, berry weight and seed set. Model statistics are given (X^2 and p-value)

Response	X^2-value	p
Fruit set	360.7	< 0.001
Berry weight	194.3	< 0.001
Seed set	891.3	< 0.001

this is the first study to our knowledge that investigates this relationship in detail through systematically mapping both the composition of the landscape as well as locating and mapping honey bee hives at relevant landscape-level scales. In addition, we conclude that wild bees are supported by SNH in the surrounding landscapes, yet these wild bees get diluted in landscapes containing a high proportion of fields with mass-flowering blueberry. These findings provide clear evidence that can be used to further optimize insect-mediated crop pollination as well as pollination research.

Our study further confirms the general, driving role of the wider landscape on ecosystem functioning and biodiversity conservation. This accounts for pollination services (see Dainese et al. 2019), but also for other ecosystems services such as biological control and species persistence in different types of landscapes (Tscharntke et al. 2005; Martin et al. 2016). Our results emphasize that considering the species' traits is recommended to evaluate the species-landscape relationships and according to relevant landscape scales (Jackson and Fahrig 2015).

Honey bee visitation

The number of honey bee hives was highly correlated to the amount of blueberry fields in the surrounding

Table 2 Generalized linear models assessing the effect of landscape-level honey bee hive density on honey bee visitation. Generalized linear models assessing the effect of the proportion of blueberry and semi-natural habitat (SNH) in the landscape on wild bee visitation. The most explanatory landscape scale and model statistics are provided (model estimate, standard error (SE), z-value, p-value and ∆AICc (difference between the AICc of the two best models)
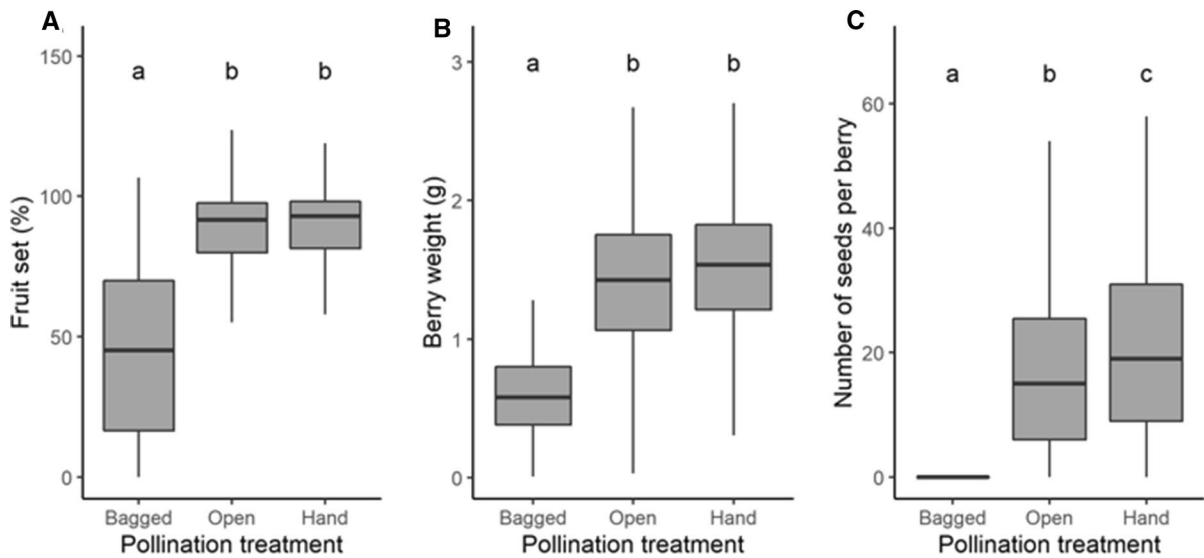
Response	Landscape scale	∆AICc	Model parameter	Estimate	SE	Z-value	p
Honey bee visitation	1000 m	2.2	Landscape-level HB hives	0.00066	0.00024	2.7	< 0.01
Wild bee visitation	1000 m	4.5	Blueberry	− 0.055	0.019	− 2.85	< 0.01
			SNH	0.077	0.012	6.38	< 0.001

Fig. 2 Blueberry fruit set (**A**), average berry weight (**B**) and seed set (**C**) as a function of different pollination treatments. The different letters indicate significant differences from pairwise comparisons (Tukey contrasts, alpha = 0.05)
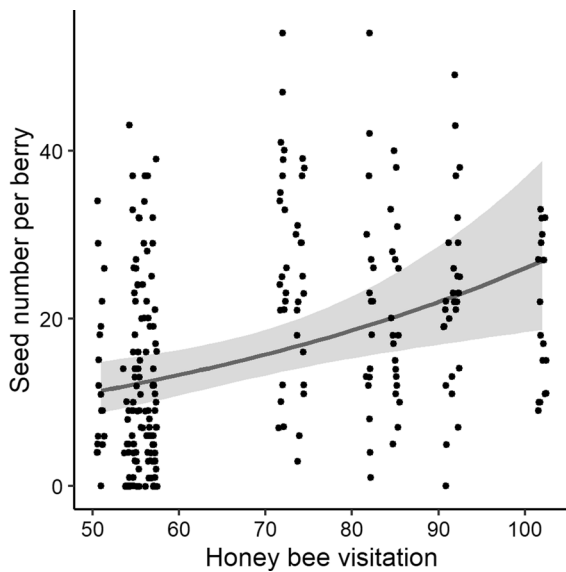
landscapes (landscape scale 500 m, 750 and 1000 m; Fig. 1A). The lack of a positive correlation at the 250 m scale is probably explained by the variability of field-level hive densities and the effect this can have on the landscape-level densities on this small, more local landscape scale (Table S3). As honey bee hives are placed in blueberry fields, and MFC fields in general, during bloom, these positive correlations are expected as they reflect the hive densities in the fields. Our study also concludes that honey bee visitation to blueberry flowers was best explained by the number of honey bee hives within the landscape radius of 1000 m around our study sites. Studies to date have only focused on mapping honey bee hive numbers on a field-level scale and their effect on honey bee visitation and crop pollination, and the findings of these studies are variable and landscape-dependent (Benjamin and Winfree 2014; Gaines-Day and Gratton 2016; Geslin et al. 2017; Mallinger et al. 2021). Benjamin and Winfree (2014), however, did show that mapping the honey bee hives themselves to obtain the field-level hive density provided a better explanation for the observed variation in honey bee visitation compared to grower reported field-level densities. Honey bees can forage in a radius of several kilometers around their hive, yet a radius of approximately 1000 m is known to be their optimal foraging radius (Zurbuchen et al. 2010; Hagler et al. 2011;

Bänsch et al. 2020). Hence, our results are consistent with this radius. This finding is novel and provides new knowledge to optimize deployment of honey bees in agricultural landscapes, which is important as honey bees are the main managed pollinator for multiple crops (Osterman et al. 2021a, b). The absence of an effect of field-level hive density corresponds with previous studies (Gibbs et al. 2016; Mallinger et al. 2021). Our results provide a mechanistic explanation for this lack of effect because the foraging range of honey bees is a lot greater than the area of crop fields and, therefore, honey bee visitation depends on the number of honey bees hives within the wider landscape.

The proportion of SNH did not have a negative effect on honey bee visitation, a result consistent with previous studies (Holzschuh et al. 2012; Klein et al. 2012; Alomar et al. 2018; Mallinger et al. 2021). However, some studies do detect a negative effect of SNH on honey bee visitation (Gibbs et al. 2016; Eeraerts et al. 2019). This would mean that honey bees are drawn away from the crop by alternative, preferred forage in SNH elements. Another explanation might be that farmers place less honey bee hives in landscapes with a higher proportion of SNH, as these landscapes can provide more wild pollinators which can be very effective crop pollinators (Gaines-Day and Gratton 2016; Dainese et al. 2019; Pisman

Table 4 Generalized linear mixed-effects models assessing the effect of honey bee and wild bee visitation on blueberry fruit set, berry weight and seed set. Model statistics are given (model estimate, standard error (SE), z-value, p-value and ΔAICc).

Response	ΔAICc	Model parameter	Estimate	SE	Z-value	p
Fruit set	1.6	Null model				
Berry weight	7.7	Null model				
Seed set	2.1	Honey bee visitation	0.28	0.089	3.22	<0.01

Fig. 3 Relationship between honey bee visitation and blueberry seed set. The solid line indicates the significant relationship, the grey shaded area indicates the 95% confidence interval and the black points show the raw data

honey bee hives during flowering, and this simplified mapping given there were no other MFC with overlapping blooms. It would be useful for further research to undertake this approach of hive mapping in more heterogeneous landscapes that contain other co-flowering crops that use honey bee hives for pollination at the same time (e.g., apple, pear and cherry). If similar relationships were to emerge, this would provide clear insights into the importance of landscape structure and farming practices in determining honey bee visitation in pollinator-dependent crops. In addition, previous studies have shown that when considering the strength of honey bee hives, instead of number of hives, the relationship between field-level honey bee hives and honey bee visitation becomes positive (Geslin et al. 2017; Mallinger et al. 2021). Incorporating this hive strength parameter in similar studies that include landscape-wide hive mapping is likely to further improve our understanding between landscape-level as well as field-level hive densities and their effect on honey bee visitation to crops. Development of decision aid tools that provide data on hive densities within landscapes could be used to guide stocking densities at the individual farm level and at different spatial scales (Fedoriak et al. 2021; DeVetter et al. 2022). This will require beekeepers and/or growers to share information about hive placement on their farms so adjacent farms could benefit. Research on the effects of landscape-level honey bee hive densities on resource competition between wild bees should be conducted in parallel to understand how optimal honey bee visitation can be achieved while safeguarding wild bees and other wild pollinators (see Mallinger et al. 2017).

et al. 2022). The latter remains to be investigated, but farmers are becoming increasingly aware of the contribution of wild pollinators for crop pollination (Eeraerts et al. 2020b; Osterman et al. 2021b). However, our study is one of the first to simultaneously test the trade-offs between the number of honey bee colonies and the proportion of SNH in the landscape, and we clearly find that the number of hives in the landscape strongly determines the visitation of honey bees in the crop. Overall, honey bees are generalist pollinators, and the colonies benefit from a diverse diet, hence, foraging outside crop fields is inevitable (Pettis et al. 2013; Danner et al. 2017).

Mapping of honey bee hives was feasible in our study area because of available qualitative baseline maps to start with. Additionally, the study region and time period only had blueberry fields stocked with

Wild bee visitation

Wild bee visitation was best explained by the amount of SNH, as well as the amount of blueberry fields within a 1000 m radius of the surrounding

landscape. Most wild bees in this study were bumble bees (77.8%), which are known to have greater foraging ranges compared to solitary bees (Zurbuchen et al. 2010). This explains why we detected that the 1000 m scale was the best explanatory landscape scale for wild bee visitation. This finding is consistent with previous studies that conclude that bigger, social bees are affected by landscapes at greater spatial scales compared to smaller, solitary bee species (Greenleaf et al. 2007; Benjamin et al. 2014). Similarly, other studies have found that pollinators with different functional traits are influenced by agricultural practices and landscape structure (Beyer et al. 2020; Roquer-Beni et al. 2021). Both the positive effect of SNH, as well as the diluting effect of MFC on wild bee visitation and their pollination contribution are well known in the literature (Garibaldi et al. 2011; Holzschuh et al. 2016; Eeraerts et al. 2017, 2019; Alomar et al. 2018; Dainese et al. 2019; Shaw et al. 2020). Yet, pollination studies in blueberry have only reported the positive effect of SNH (Gibbs et al. 2016; Nicholson et al. 2017; Mallinger et al. 2021). The dilution effect of wild pollinators in mass-flowering blueberry fields is a new finding and has implications for efforts to promote wild pollinators in this crop (but see Eeraerts et al. 2017; Shaw et al. 2020). Detecting a positive effect of SNH, as well as a negative effect of blueberry at the same time in our study, is likely explained by the fact that we designed our study to include an independent gradient of both variables. Likewise, the low abundances of wild bees in multiple sites in our study are probably explained by including many study sites with high amounts of blueberry fields in the surrounding landscape.

Regarding wild pollinator management, the next step is to investigate how to conserve and support these species in large scale, intensively managed agricultural landscapes like our study. Establishing pollinator-friendly habitat in and around farms can be realized through herbaceous and/or woody floral plantings (Morandin and Kremen 2013; Blaauw and Isaacs 2014). When it comes to herbaceous floral plantings, recent research has found that these are not always effective at promoting key crop pollinators of blueberry (Wood et al. 2018). Indeed, key crop pollinators of spring-flowering crops like blueberry mainly forage on spring-flowering, woody plants (e.g., *Salix* spp., *Prunus* spp.; Wood et al. 2018; Eeraerts et al. 2021b). To this end woody

linear habitat elements take up less area relative to the amount of floral resources they provide, and they also provide nesting habitat for wild bees (Donkersley 2019: Eeraerts et al. 2021a). These measures can be combined with provision of trap nests to increase local populations of above-ground nesting solitary bees that are known to forage on blueberry (Osterman et al. 2021a; Eeraerts et al. 2022).

Pollination contribution

Despite the dominance and variation in honey bee visitation in our sampled fields, we only detected a positive effect on blueberry seed set. In addition, no effects of wild bee visitation on blueberry pollination were found. Overall, these results are contrary to previous studies that conclude a positive effect of wild pollinators (Dainese et al. 2019; Mallinger et al. 2021; Pisman et al. 2022) or honey bees on crop pollination (Geslin et al. 2017; Arrington and DeVetter 2018; Mallinger et al. 2021). The lack of any positive relationship between bee visitation and fruit set and berry weight in this study is probably because there was no difference between the hand and open pollination treatments. This implies that, for both fruit set and berry weight, full pollination had been achieved in the study fields. As highbush blueberry has a high degree of self-fertility, it is relatively easy to reach full pollination for certain cultivars (Kendall et al. 2020; DeVetter et al. 2022). Indeed, multiple studies report very high pollination rates in 'Duke', the cultivar used in our study (Arrington and DeVetter 2018; Grant et al. 2021) and this has been attributed in part to floral morphology and its compatibility with the anatomy of the honey bee (Courcelles et al. 2013). Even though honey bees cannot buzz-pollinate and therefore rarely collect pollen from blueberry flowers, they can still transfer pollen via different body parts on blueberry flowers and pollinate this crop, which explains how high pollination success was reached in our study (see Hoffman et al. 2018).

Berry weight is an important economic characteristic of blueberry and is often positively correlated with seed set (Dogterom et al. 2000; Isaacs and Kirk 2010). Given seed set in our study indicated full pollination was not achieved, it would be interesting to study if farming practices could be optimized to further increase berry weight. Indeed, irrigation, fertilization, pest management, and soil fertility are known

to interact positively with pollination to improve yield of multiple crops (Melathopoulos et al. 2014; Tamburini et al. 2019). Pruning severity is another cultural practice that can vary across farms and influence yield and berry size (Strik et al. 2003).

Conclusion

The proportion of mass-flowering blueberry was positively correlated with the number of honey bee hives in the landscape, and honey bee visitation was best predicted by the landscape-level hive density within a radius of 1000 m. Crop pollination management should consider the contributions of honey bee hives in the surrounding landscape. This strategy should help overcome the shortcomings of field-level hive density recommendations that risk missing the contributions of other honey bees in the landscape. This will require communication and coordination among beekeepers, growers, and crop consultants, but the net result should avoid the financial repercussions of over- or under-stocking fields across crops. Appropriately stocked fields and landscapes may also benefit honey bees and other pollinators by reducing competition for floral resources that may otherwise arise. Semi-natural habitat should also be conserved or created to support wild pollinators that can supplement honey bee pollination.

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