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Effects of competition and climate on a crop pollinator community

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A B S T R A C T

Plant-pollinator interactions are ubiquitous in nature where both wild and domesticated pollinators interact with wild plant communities and entomophilous crops. Honeybees are important pollinators in many crop systems, but recent declines in honeybee stocks in Europe and the US have caused concern about the sustainability of crop systems solely depending on honeybees. In addition, several studies have shown that honeybees might negatively affect native pollinator populations, bumblebees in particular. Here we have studied flower visitation to two raspberry farms and surrounding wildflower communities in SE Norway. Bumblebees were excluded from the raspberry field by means of exploitative competition from honeybees (> 97% of flower visits in the raspberry fields were conducted by honeybees). More than 55% of the visits recorded in wild plant communities surrounding the farms were conducted by bumblebees, showing that bumblebees were present in the system. Pollinator taxa were affected differently by temperature; honeybee visits showed a unimodal relationship with maximum flower visitation activity at a temperature of 24.1 °C, while flower visits by bumblebees showed a positive, linear relationship with temperature. The effect of temperature was much weaker for bumblebees than for honeybees (~2.2% of the variation was explained by temperature, compared to ~46% for honeybees). Farming practice affected flower visitation, as flowers within growing tunnels received fewer visits. However, the number of flower visits, also within the growing tunnels, was far above what other studies have shown to be sufficient for optimal pollination in raspberry. We conclude that the raspberry fields were sufficiently pollinated by honeybees but that the system should be considered vulnerable as it is solely dependent on this particular pollinator species. The honeybees were sensitive to ambient temperature suggesting that they might suffer more from future climate change than bumblebees.

1. Introduction

Plant-pollinator interactions are ubiquitous in nature where both wild and domesticated pollinators interact with wild plant communities and entomophilous crops. Of the total number of crops used for human consumption 70% benefit from pollination (Klein et al., 2007), and 84% of the crops cultivated in Europe depend (at least to some extent) on pollinators, of which bees are most important (Williams, 1994). The value of the ecosystem service that pollinators provide to global agriculture is substantial, with estimates ranging from €153 billion (~167 billion USD) (Gallai et al., 2009) to 235–577 billion USD (~€213–€522 billion) (IPBES, 2016; Potts et al., 2016) every year. Furthermore, a recent estimate suggests that 87.5% of all angiosperms are pollinated by animals (Ollerton et al., 2011), illustrating the importance of pollinators also for maintaining the structure and diversity in wild plant communities (Potts et al., 2010a).

Managed honeybees (*Apis mellifera* L.) are considered the most important pollinator for crops (Carreck and Williams, 1998), although

their superiority in delivering crop pollination services has been questioned (Breeze et al., 2011; Ollerton et al., 2012; Rader et al., 2016). Recent declines in colony numbers in Europe and USA (Johnson, 2010; Potts et al., 2010b) have caused concern about the sustainability of crop production solely depending on honeybees. In temperate regions, bumblebees (*Bombus* spp.) are important pollinators in both wild plant communities (Memmott et al., 2004; Fontaine et al., 2006) and crops (Cameron et al., 2011; Button and Elle, 2014). Several studies have shown that bumblebees can be more efficient pollinators than honeybees as they are better adapted to their local climate, can work longer hours, carry more pollen and are active earlier in spring (Willmer et al., 1994; Stubbs and Drummond, 2001). Garibaldi et al. (2013) showed that an increase in wild insect visitation enhanced fruit set by twice as much as an equivalent increase in honeybee visitation in 41 crop systems worldwide. They suggested that pollination by honeybees is a supplement rather than a substitute for wild insect pollination. Managed honeybees occur in large numbers and there has been an increased emphasis on the potential competition for floral resources between

managed honeybees and wild pollinators, including bumblebees. Forup and Memmot (2005) found a negative association between honeybee and bumblebee abundances in lowland heaths in southern England. They also showed that where honeybees were present, the diet width of bumblebees was narrower and skewed towards other plant species than the ones preferred by honeybees. They conclude that honeybee presence most likely is not responsible for recent bumblebee declines, but state that "competition between the two species cannot be ruled out". Several studies have however, shown a negative association between honeybees and wild bees and ascribed this pattern to competition for floral resources (Thomson, 2004; Nielsen et al., 2012; Herbertsson et al., 2016; Torné-Noguera et al., 2016). In a study from coastal California, Thomson (2016) also found a negative relationship between honeybee and bumblebee densities. In addition, she found a negative effect on bumblebee densities of diminishing floral resources due to drought. She concluded that both adverse climatic conditions, i.e. drought causing a reduction in available floral resources, and competition from honeybees might have negative impact on bumblebee populations. Xie et al. (2016), on the other hand, found that flower visits to squash by bumblebees delayed the time before a honeybee visited the same flower. They also showed that the number of bumblebees visiting flowers was negatively correlated with number of honeybee visits. They suggest that this negative effect of bumblebees on honeybees was due to the bumblebees' ability to deplete the flowers for nectar, making them unattractive to honeybees. These studies show that competitive interactions between honeybees and bumblebees can be difficult to detect, that they are context and climate dependent and that honeybees are not always the competitively superior species.

Climate change is an important driver affecting pollinators and plant-pollinator interactions (Memmott et al., 2007; Hegland et al., 2009; Kjøhl et al., 2011; Bartomeus et al., 2013; Papanikolaou et al., 2016; Thomson, 2016). Increasing temperatures, droughts and more frequent extreme events are all suggested to affect plant-pollinator interactions (Kjøhl et al., 2011). Increasing temperature has been suggested to affect both pollinator species distributions (Kerr et al., 2015) and phenology (Hegland et al., 2009; Bartomeus et al., 2013), and temperature induced changes in diurnal activity patterns and search behaviour have been shown to change and weaken pollinator services (Corbet et al., 1993; Willmer and Stone, 1997).

Schweiger et al. (2010) discussed how the outcome of competitive interactions between native and alien pollinators might change under future climate change. They conclude that social bees, such as bumblebees and honeybees, would be the species least affected, due to their relatively generalist behaviour, climate tolerance and ability to buffer periods of food shortage through storage within the hive. Furthermore, this study reveals that our understanding of the interaction among environmental drivers is limited, but that there is reason to believe that numerous drivers acting in concert might indeed result in complex effects (Gonzalez-Varo et al., 2013).

While honeybees are approaching their northern limit in southeast Norway (Pritchard, 2006), bumblebees are common pollinators in alpine and arctic ecosystems even further north (Kerr et al., 2015). Their large and hairy bodies coupled with their ability to heat their body by use of their flight muscles make them less affected by adverse weather conditions (Heinrich, 1979). Consequently, bumblebees can forage and conduct pollination in poorer weather conditions than honeybees (Tuell and Isaacs, 2010).

Here we study the relationship between managed honeybees and bumblebees on a farm scale. We observed flower visits to domestic raspberry (*Rubus idaeus* L. var. Glen Ample), a crop that has previously been shown to be visited mainly by honeybees and bumblebees (Willmer et al., 1994; Saez et al., 2014). We also observed flower visits in wild vegetation surrounding the farm. To assess whether the activity of flower visitors was affected by weather conditions and whether this might give implications for effects of future climate change, we used temperature, wind speed and air humidity measures on different spatial scales.

In particular, we ask, (1): Is there competition between honeybees and bumblebees for a local floral resource hotspot (a raspberry field)? (2): Can weather variables (e.g. temperature, wind speed and air humidity), recorded at different spatial scales, explain variations in flower visitation by honeybees and bumblebees?

2. Material and methods

2.1. Study system and farming practice

The fieldwork was conducted at two farms in Vestfold County (SE Norway); Moskvil (59°24′32.39″N, 10°22′1.40″E) and Aarsland (59°13′45.54″N, 10°26′20.56″E). The distance between the two farms is approximately 20 km and although they vary slightly with respect to distance to the coast and elevation, the climate conditions they experience is relatively similar. Both farms grow most of their raspberry (*Rubus idaeus* var. Glen Ample) inside growing tunnels made of (semi) transparent tarp, but still have some rows grown in the open. The Aarsland farm had in total 24 000 m² of raspberry fields, while Moskvil had 15 000 m². There was substantial difference in stocking density of honeybees between the two farms. Both farms had honeybee hives (8 at Aarsland and 17 at the Moskvil), placed less than 100 m from the focal raspberry fields.

2.2. Study species

Raspberry belongs to the rose family (Rosaceae) and has simple generalist flowers, with five small white petals, and many stigmas and stamens. The nectar is freely exposed and 10–50 μl are often present and can stay liquid even on warm days (Willmer et al., 1994). The fruit (the "raspberry") is an aggregate fruit of numerous drupelets developed from the many free pistils in the flower. Flowering in raspberry is continuous and consecutive, where only some buds flower at the same time. A single flower is open for about three days. Raspberry can self-pollinate, but selfing results in asymmetric fruits with fewer drupelets, and it has been shown that insect pollinated flowers can produce 50% greater fruit weight (Willmer et al., 1994). Raspberry of the variety Glen Ample is a Scottish cultivar well suited to the cool Norwegian climate. The plants are perennial with biennial stems; the currently reproducing parts of the plant die after each season, while new shoots produced from suckers (root sprouts) are developing for flowering the next year (Heide and Sonsteby, 2011). The Glen Ample raspberry plants are themselves sensitive to temperature and have a threshold of about 28 °C, above which the plants show heat-stress symptoms (Nina Heiberg *pers comm*). Fruit weight has also been shown to decrease significantly for higher, more unfavourable temperatures post flowering (Remberg et al., 2010).

The highly rewarding and open flowers of raspberry are well suited for generalist pollinators such as honeybees. Bumblebees can handle more complex flowers than honeybees, but other studies have shown that bumblebees can be important pollinators for the open raspberry flowers (Willmer et al., 1994; Saez et al., 2014) and other crops (Garibaldi et al., 2013).

2.3. Pollinator surveys in raspberry

Plot observations are the best method to assess flower visitation frequencies, as one can have full control of the number of flowers over which visits are counted (Reitan and Nielsen, 2016). At each farm we selected raspberry plants within and outside the growing tunnels. In both years we used five plants growing in the open and plants growing in five different tunnels. In 2014, in each tunnel, we selected one plant in the tunnel opening, one 20 m inside the tunnel and one in the middle of the tunnel (~40 m inside); 20 plants in total on each farm. On each plant, we selected and permanently marked one branch and observed

flower visits to all open flowers on this particular branch only. We undertook observations on non-consecutive days throughout the peak flowering period of June (June 3rd, 11th and 19th at Aarsland, June 4th, 12th and 20th at Moskvil). Not all focal plants had open flowers all days of observation, resulting in 77 observation periods (43 from Aarsland and 34 from Moskvil) in 2014. In 2015, we selected plants in the same rows in the open and the same tunnels as in 2014, but for logistic reasons we only selected plants in the tunnel opening and in the middle of the tunnels. In the statistical analyses, we defined each plant as growing inside a tunnel, in a tunnel opening or in the open. Due to the small number of open flowers found on each branch in 2014, we selected and permanently marked four branches in 2015. We undertook observations on 17 non-consecutive days throughout the peak flowering period of June (June 6th to June 24th), in total 463 observation periods; 70 at Moskvil and 393 at Aarsland. In both years, an observation period involved counting flower visits to all open flowers on the focal branch(es) for 10 min. On the final day of flower visitation observations (June 24th 2015), we increased the sampling effort substantially. On this particular day, we focused on raspberry plants grown in the open and used four field workers observing in parallel, i.e. at the exact same time. Flower visitors were identified to species when possible (honeybees and most bumblebees), while other groups were assigned to the lowest possible taxonomic level. Observations were conducted between 8am and 8pm. Six observations were done after 7pm while for the rest of the day the number of observations per hour of the day varied from 14 (between 3pm and 4pm and between 5pm and 6pm) to 32 (between 4pm and 5pm). The order of which the sampling plots were observed was randomized within each day. Since several field workers were involved in the observations we included "Observer ID" as a potential random effect when deciding on the best model describing flower visitation. This to account for any observer related bias due to contrasting skills in bee identification and ability to record flower visits (Westphal et al., 2008; Nielsen et al., 2011). Observations were done in fair weather only, i.e. not when raining or at temperatures below 12 °C.

2.4. Pollinator surveys in the wild plant communities

To assess flower visitations in the vegetation surrounding the raspberry fields, we conducted 203 transect walks at the Aarsland farm in 2015. The transect walks were conducted in 2015 only, on the same days, during the same hours and with the same weather requirements as the surveys in the raspberry field (between June 6th and June 24th, between 8am to 8pm, no rain and temperatures above 12 °C). Transect walks cover a larger area and is a method that has been shown to be well suited for estimating plant-pollinator interactions (Westphal et al., 2008; Nielsen et al., 2011). Due to the scattered distribution of floral resources in the vegetation surrounding the raspberry field, we considered plot observations were not the best sampling method. However, visitation frequencies (numbers of visits per flower per time) obtained from transect walks will be biased (under estimated), as the observer will not be able to have an overview of the entire transect at any given time. This underestimation bias must be considered in the interpretation of the results. To assess flower visitation to the wild plant communities surrounding the raspberry farms, we selected and permanently marked ten, 10 m long and 2 m wide transects. Five transects were situated close to the raspberry field (< 5 m) and five further away (> 100 m). Before each transect walk all plant species within the transect were identified and the number of open flowers in each species were counted. (See Supplementary material Table S1 for list of all plant species observed). Each transect walk lasted 10 min with the observer walking back and forth along the transect, counting all insects visiting flowers (spending approximately 1 min covering the full length of the transect). We assigned each flower visit to a particular plant species.

2.5. Environmental variables

We obtained weather variables on different spatial scales to assess how weather conditions affected flower visitation by honeybees and bumblebees. On the per observation scale, we recorded temperature, relative air humidity and wind speed with a hand held weather recorder (WeatherHawk: SM-28 Skymaster) prior to each observation (raspberry plot and transect walk). On the farm scale, we recorded temperature and relative air humidity every hour throughout the entire season by use of four weather loggers (iButton − Hydrochron from Maxime Integrated). The loggers were mounted on wooden poles approximately 30 cm above ground and covered by tinfoil top to protect them from rain and direct sunlight and placed at different locations throughout the two farms (one in the middle of one of the growing tunnels, one outside in a row of raspberry, one close to the honeybee hives and one in the wildflower transects adjacent to the raspberry field). To obtain measures of temperature and humidity for each observation from these data, we used linear interpolation between the two recordings closest in time to the start time of the observation. In our statistical models we used the nearest logger, i.e. the logger inside a tunnel for inside tunnel observations, the logger in the open raspberry field for observations done in the open and the logger situated in the wildflower transects for the transect walks. In addition, we averaged the recordings over all four loggers to get average, on farm measurements, of temperature and humidity. The weather loggers were not available in 2014, so we used the measurements from the hand held weather recorders also on the farm scale for the 2014 observations. To obtain measures of temperature, relative air humidity, wind speed and air pressure on a regional scale, we used observations from the nearest weather station (Stokke) operated by the Norwegian Meteorological Institute, retrieved through the web service http://www.xgeo.no. We used the same linear interpolation technique as for the weather loggers to get estimates for each flower visitation observation. In addition, we used estimates representing daily mean temperature for each day of observations. Finally we included a modelled temperature measure representing daily mean temperature for each day of observation at each farm, retrieved through the web service http://www.xgeo.no. The mean values, and span, for temperature and relative air humidity associated with all flower visitation observations for the three spatial scales are listed in Supplementary material Table S2.

2.6. Data analyses

To examine if honeybees and bumblebees had preference for particular plant species, we included "plant species visited" as a fixed factor in our models. In the case of bumblebees, we also included the honeybee preference for each plant species as an offset variable in the model. This was to get an estimate of bumblebee preference relative to honeybee preference and in order to statistically test whether there really are differences in flower preference between honeybees and bumblebees. Farmed and wild raspberry were treated the same, but we included a variable discriminating between flowers observed in the wildflower transects (including raspberry) and flowers on the farm (raspberry only). To assess the variation in flower visits related to farming practice we included a variable (plot type) discriminating between observations within growing tunnels, in tunnel openings, in the raspberry field in the open and wildflower transects. To assess whether wildflower transects received contrasting visitation frequency depending on whether they were located close to or further away from the raspberry field, we also included a variable discriminating between the raspberry field, nearby transects (< 5 m) and more distant transects (> 100m).

To test whether honeybee visits affect bumblebee visits on a per observation basis, we added the observed honeybee visits as a fixed effect to the model best explaining bumblebee visits. In addition, we generated two new variables based on predictive models of honeybee

Table 1

An overview of total number of visits and visitation rate (visits per flower per 10 min) to the four most visited plant species from all insects and for bumblebees and honeybees separately. Numbers given for raspberry (Rubus idaeus) are divided into those observed on the farm and those observed in wild plant communities surrounding the farm. "On farm" include both farms in both years and "Wild" all observations outside the field (in the wildflower transects) at Aarsland farm in 2015. Numbers given for the remaining plant species are from wildflower transects at Aarsland farm in 2015.

Plant species	Number of flowers	Total visits	Bumblebee visits	Honeybees visits
Rubus idaeus (On farm)	3209	3321 (1.035)	97 (0.0302)	3194 (0.995)
Rubus idaeus (Wild)	7608	893 (0.117)	272 (0.0358)	618 (0.0812)
Silene dioica	21892	198 (0.009)	185 (0.0085)	5 (0.0002)
Trifolium repens	5094	187 (0.037)	160 (0.0314)	25 (0.0049)
Rosa canina	510	154 (0.302)	150 (0.2941)	4 (0.0078)

Table 2

Model output of the best model listing the fixed effects explaining the flower visits of honeybees at Moskvil and Aarsland farms in 2014 and 2015. The temperature measure (as a quadratic term, giving a unimodal relationship between temperature and flowering visitation) included in the best model was the average over four temperature loggers placed throughout the farm. The different plot types variable shows the estimated flower visitation frequency of observation plots in the raspberry field grown in the open (Open), in the middle of the tunnels (Middle) and in the wildflower transects (Transects) and are tested against observation plots situated in the tunnel opening. The three plant species listed are tested against *Trifolium repens*.

	Estimate	Std. Error	z value	P-value
Intercept	−6.9829	0.9799	−7.126	< 0.001
Open	0.5814	0.2713	2.143	< 0.05
Middle	−0.2501	0.1062	−2.355	< 0.05
Transect	−2.2115	0.3757	−5.885	< 0.01
Temperature	0.1599	0.0353	4.522	< 0.001
Temperature^2	−0.0407	0.0061	6.710	< 0.001
Silene dioica	−2.9698	0.7139	−4.160	< 0.001
Rosea canina	0.6592	0.8962	0.736	ns
Rubus ideaus	2.8854	0.5335	5.408	< 0.001

visits. One variable was based on the full model explaining honeybee visits and one strictly spatiotemporal model containing only the random effects from the best model explaining honeybee visits.

Due to the relatively low number of recordings of individual bumblebee species, we treated bumblebees as a single group in the statistical analyses. We analysed honeybees and bumblebees separately.

We analysed our data on flower visits as counts where number of visits were used as response variable and the number of flowers over which visits were observed was included as an offset variable, i.e. defining the exposure (following Reitan and Nielsen, 2016). We used a Poisson error distribution as this fits well the nature of flower visitation data (Reitan and Nielsen, 2016). This approach enabled us to include data from both seasons despite the four-fold increase in exposure in 2015 (flowers on four branches in 2015 as compared to flowers on one branch in 2014). Before the analyses we excluded the least visited plant species observed in the wildflower transects. The excluded plant species represent < 0.5% of the total number of visits recorded in the wildflower transects. The remaining flower visits were observed in only four plant species that were retained in the analysis (Table 1). To explain the variation in flower visits, we used a Generalized Linear Mixed Model (GLMM) approach. All fixed and random effects tested in search for the best model are listed in Supplementary material Table S3. To assess whether weather variables had contrasting effects on different locations and on different points in time, we included in the model selection procedure interactions between the weather variables (temperature and humidity on different spatial scales) and the large-scale spatial (farm, plot-type [wildflower transect, raspberry growing inside tunnel, in tunnel opening or outside] and temporal (year, day, time of day) random factors. In addition, we included interactions between time of day and large scale spatial (farm) and temporal (year, day of season [as random factor]) variables to assess whether diurnal patterns of flower visitation varied among farms, years and days throughout the season. The best model was selected based on the Bayesian Information Criterion (BIC). The model selection procedure was conducted on the two pollinator groups (honeybees and bumblebees) separately.

All statistical analyses were conducted in R, version 3.3.0 for Windows 10 (R Core Team, 2014). The R package "lme4" (version 1.1.10) (Bates et al., 2015) was used to generate the GLMMs.

3. Results

In total we conducted 540, 10 min observations of flower visitors to raspberry flowers on the two farms over two years. In the raspberry fields we found that out of the total number of flower visits recorded (3270), 3194 (97.8%) were conducted by honeybees, illustrating clearly that honeybees are the main pollinators in our focal fields.

However, from the observations conducted in the wildflower transects, we recorded 779 (52.5%) visits conducted by bumblebees and 660 (44.5%) by honeybees, indicating that honeybees were not the only pollinators inhabiting the area. Of the bumblebees observed in the wildflower transects, seven species were identified. In addition, 44 visits were conducted by flies, butterflies, solitary bees and beetles but due to the low numbers they were excluded from further analyses.

3.1. Honeybee visits

The best model explaining honeybee visits to domestic raspberry contained the fixed effects "temperature" (averaged over four temperature loggers as a quadratic term with an overall optimum at 24.1 °C), "plot type" (less visits were observed in the tunnels compared to the raspberry fields in the open and even lower in the wildflower transects, suggesting that farming practice affected flower visitation) and "plant species" (showing that honeybees preferred *Rubus idaeus* over *Rosa canina* over *Trifolium repens* over *Silene dioica*) (Table 2). In addition, it contained the random effects "day of season" (day as factor, indicating that certain days had higher or lower number of flower visits than expected, e.g. due to differences in solar radiation), an interaction between "day of season" and the linear term of temperature (suggesting that the optimal temperature varied between days), and an interaction between "section of the farm" (each tunnel, including the middle and opening, each row outside tunnels and each wildflower transect was assigned to a "section of the farm") and plant species. This interaction suggests that there was higher, or lower, flower visitation rate than expected to certain plant species in certain sections of the farm. More than 46% of the variation in flower visitation was explained by temperature (when including both temperature as fixed effect and the interaction between day of season and temperature [random effect]), suggesting that the honeybee activity was strongly affected by ambient weather (Table 3).

3.2. Bumblebee visits

The best model explaining bumblebee visits contained the fixed effects 'temperature' (modelled mean values for each farm each day of observation as a positive linear effect), "wild flowers" (higher visitation frequencies in the wildflower transects) and "plant species" (showing that bumblebees preferred *Rosa canina* over *Silene dioica* over *Trifolium repens* over *Rubus idaeus*, relative to honeybees) (Table 4). Temperature explained only 2.2% of the variation in bumblebee visits for any given plant species, suggesting that bumblebee activity was mainly affected by other factors (Table 3). None of the random effects tested were included in the best model.

Table 3

Variation explained by the different variables included in the models best explaining the variation in flower visits by honeybees and bumblebees. Note that the variation explained is related to visits to any given plant species so that a lot of the unexplained variation is explained by variation in plant species preference. For honeybees "Temperature" is included as both a linear and quadratic term and the "Temperature:Day" interaction is based on the linear term suggesting a change in optimal temperature among days. Plot type refers to whether the flower visit was recorded in the wildflower transects, in raspberries grown in the open, in tunnel openings or within growing tunnels. For bumblebees "Temperature" is included as a linear, positive effect, while "Wild vs farm" refers to whether the flower visit was observed on the raspberry farm or in wildflower transects surrounding it.

Variable	Honeybees	Bumblebees
Temperature	35.78%	2.22%
Temperature:Day of season	9.84%	
Day of season	10.05%	
Plot type	21.78%	
Wild vs farm		9.36%
Unexplained variation	22.55%	88.42%

Table 4

Model output from the best model explaining bumblebee visits to flowers at Aarsland and Moskvil farms in 2014 and 2015. Bumblebees preferred wild flowers and their visitation frequency increased with increasing daily temperature (included as a modelled value for each farm, each day of observation). Note that the bumblebees' preference for particular plant species are relative to the preference of honeybees and is given on a log scale, meaning that i.e. the preference for *Rosea canina* is ~1.6 times higher for bumblebees than for honeybees.

	Estimate	Std. Error	z value	P-value
Intercept	−4.0591	1.3086	−3.102	< 0.01
Wild vs farm	1.6941	0.4325	3.917	< 0.001
Temperature	0.2029	0.0764	2.656	< 0.01
Trifolium repens	−0.3071	0.3480	−0.883	0.38
Silene dioica	0.5198	0.3524	1.475	0.14
Rosa canina	1.6327	0.4737	3.446	< 0.001
Rubus idaeus	−1.8454	0.3363	−5.487	< 0.001

None of the variables describing honeybee presence were included in the best model explaining flower visitation by bumblebees. To illustrate the difference in plant species preference between honeybees and bumblebees, we included honeybee preference as an offset variable in the model explaining bumblebee visits. Estimates of the relative bumblebee preference for particular plant species compared to honeybee preference are given in Table 4.

4. Discussion

4.1. Interactions between honeybees and bumblebees

Honeybees were the most frequent flower visitors in the raspberry fields included in this study, while bumblebees were surprisingly rare. At the same time, we observed that 54.1% of the flower visits in the vegetation surrounding the field were conducted by bumblebees, showing that bumblebees were present in the area. Although bumblebees frequently visited several plant species, they also conducted 30.6% of the visits to raspberry outside the field. This is in line with previous studies showing that bumblebees can be important pollinators of raspberry (Willmer et al., 1994; Saez et al., 2014). When excluding visits to raspberry, 92.3% of visits to wildflowers were conducted by bumblebees. This suggests that honeybees show high fidelity to raspberry also outside the field, and do not contribute substantially to the pollination of other wild plant species. We ascribe the observed pattern to a combination of floral constancy within honeybees and exploitative competition between honeybees and bumblebees. Floral constancy has long been recognized as a common phenomenon in plant-pollinator interactions (Darwin, 1876; Grant, 1950; Free, 1963; Waser, 1986; Chittka et al., 1999; Goulson, 2000). The tendency for particular

pollinators to stick to flowers of a particular plant species increases the probability of plants receiving conspecific pollen, reduces flower handling times and increases foraging efficiency for the pollinators. In our system honeybees seemed to show high constancy, focusing on raspberry, as only 107 out of 3836 visits were recorded to flowers of other species than raspberry. This is not surprising given their ability to recruit fellow workers to floral resource hotspots, i.e. the raspberry field.

Several studies have showed that bumblebees compete with honeybees for floral resources (Forup and Memmott, 2005; Thomson, 2006, 2016; Walther-Hellwig et al., 2006; Goulson and Sparrow, 2009; Herbertsson et al., 2016; Torné-Noguera et al., 2016). These studies have focused on either population measures, effects on individual bees or have used a landscape scale. Forup and Memmott (2005) found that increased honeybee abundance reduced bumblebee abundance in lowland heaths in southern England while Thomson (2006) showed that the number of bumblebee foragers observed increased significantly with greater distance from introduced honeybee colonies. Goulson and Sparrow (2009) found that bumblebee workers were smaller in areas where honeybees were present while Herbertsson et al. (2016) showed that introducing honeybee hives to homogenous landscapes reduced bumblebee abundance by 81% due to niche-overlap, but that this effect disappeared in heterogeneous landscapes. Here we have studied the relationship between honeybees and bumblebees on a farm scale, focusing on pollinator activity (flower visits) rather than pollinator populations or individuals. Our focus is on floral resource use and pollination service, not on pollinator population dynamics. Our analyses of bumblebee visits could not reveal any effect of honeybees suggesting that honeybee presence on the particular flowers observed did not affect bumblebee visitation. Although our experimental setup did not include any manipulation of honeybee densities, our results support the hypothesis of exploitative competition for a floral resource hotspot, i.e. that honeybees monopolize the resource pool (here the raspberry field). Exploitative competition can alter flower visitation patterns among co-occurring pollinators in subtle ways. Torné-Noguera et al. (2016) showed that high honeybee densities reduced visitation to thyme and rosemary flowers by other pollinators, bumblebees in particular. On the contrary, Balfour et al. (2015) showed that bumblebees effectively excluded honeybees from lavender flowers due to the bumblebees superior ability to handle lavender flowers. Walther-Hellwig et al. (2006) showed that introduced honeybees made certain bumblebee species switch between plant species, i.e. presumably avoiding flowers of particular plant species the honeybees preferred. Lye et al. (2011) found no effect of introduced *Bombus terrestris* hives on flower visitation to raspberry conducted by other bees (including honeybees). They suggested that the introduced bumblebees might affect wild bumblebees from the *B. lucorum* complex, but their sampling protocol did not enable them to assess this. Here we have shown high density of honeybees within the raspberry field and we suggest that honeybees excluded the bumblebees from this apparent floral resource hotspot. Bumblebees have, due to their larger bodies, greater energetic demand than honeybees (Heinrich, 1975; Torné-Noguera et al., 2016). The raspberry flowers are open, easy accessible and contain abundant nectar and pollen (Willmer et al., 1994) and other studies have shown that bumblebees can be important pollinators in raspberry fields (Willmer et al., 1994; Saez et al., 2014). Although we did not measure nectar or pollen content in flowers, we suggest that the flowers were quickly depleted by the more energy effective honeybees occurring in high numbers. Consequently, foraging in the raspberry field became too costly for the bumblebees as the potential reward was too small on a per flower basis. The flowers were still attractive to honeybees, on an individual basis, as these pollinators need less nectar to meet their energetic demands (Torne-Noguera et al., 2016). The bumblebees were therefore forced to search for other resources, ultimately foraging in the patchy distributed and far less abundant wildflower community surrounding the fields.

4.2. Climate effects on pollinator activity

Different pollinators respond in contrasting ways to environmental conditions (Bluthgen and Klein, 2011). We have shown that flower visits by bumblebees increased slightly with temperature, while visits by honeybees displayed a bell-shaped relationship i.e. included as a quadratic term in the model. The bell-shaped pattern has also been shown for honeybees in other studies (e.g. Rader et al., 2013). The variation explained by temperature was however, substantially lower for bumblebees (~2%) than for honeybees (~46%) suggesting that honeybees respond more strongly to ambient conditions. Through our model selection procedure, we found that temperature variables representing *in situ* recordings (hand held weather recorders) were outperformed by temperature variables recorded at coarser spatial and temporal scales. For bumblebees the best temperature measure was the modelled daily average temperature for each farm, suggesting that the temperature conditions experienced throughout the particular day was the main driver of bumblebee activity. In the case of honeybees, the average temperature over four weather loggers was identified as the best measure. Corbet et al. (1993) suggested that for honeybees the temperature at the hive is more important than the temperature at the flower patch observed. We did not find this particular pattern (i.e. none of the single weather loggers performed best), but a closer look at the temperature recordings showed that the temperature loggers recorded some significant outliers, probably due to unintended sun exposure. Averaging over four loggers dampened these extremes, making the inclusion of several loggers a better measure of temperature at the farm scale. Hand held weather recorders can also be prone to measurement error as they are susceptible to sun exposure and effects of the person conducting the measurements. We can therefore not rule out the effect of temperature at the hive or at the flowers observed as explanatory factor for flower visits by honeybees. We will however, recommend using more precise recording techniques, such as weather loggers properly covered from sun exposure, or recordings obtained from weather recording stations such as those run by the Norwegian Meteorological Institute (in line with Corbet et al., 1993). With respect to temperature we have shown that even under Norwegian climate conditions, honeybees experience temperatures above their optimum (24.1 °C), causing reduced pollination activity (Supplementary material Table S2). For bumblebees we were not able to detect an optimal temperature. In addition, the low percentage of variation explained suggests that bumblebees are less affected by temperature than honeybees, as has been shown in other studies (e.g. Stubbs and Drummond, 2001; Tuell and Isaacs, 2010).

4.3. Implications for pollination in commercial raspberry and the wider floral community

Saez et al. (2014) showed that in their focal raspberry fields in Argentina, four flower visits per day were sufficient to maximize fruit size. We observed, on average, ~ one flower visit per flower per 10 min observation. We therefore conclude that the raspberry fields included in this study did not suffer from pollinator limitation. The random factor "farm" did not appear in the best models explaining flower visits by honeybees, neither alone nor in interaction with any of the weather variables. This suggest that the substantial difference in honeybee stocking density between the farms did not affect flower visitation. We found lower visitation frequencies within the growing tunnels, suggesting that the honeybees are affected by the apparent barrier the tunnels represent. The effect of "plot type" was however, mainly driven by the substantially lower visitation frequencies observed in the wildflower transects. This is not surprising due to the honeybees' high numbers and strong fidelity for raspberry. In addition, the visitation frequencies recorded in the wildflower transects are most likely underestimated due to the limitations of the sampling method (increased probability of missing flower visits due to the large area covered by the

transects) and this result should therefore be interpreted with caution. This would not however, affect the comparison between flower visits conducted by honeybees and bumblebees in the wildflower transects. On average each raspberry flower in the fields received more than one visit per 10 min, resulting in ~62 visits per flower per day, assuming 10 h of pollinator activity per day, following the definitions of Saez et al. (2014). For comparison, Saez et al. (2014) did not find pollen limitation in raspberries visited ~4 times per day, suggesting that in our system even within the tunnels all flowers received sufficient pollination. Saez et al. (2014) did find a negative effect on berry size related to too many visits due to pistil damage caused by the insects, but this effect was only seen for visitation frequencies far beyond what was experienced in our system (above ~140 visits per day). Even though the visitation frequency provided by bumblebees was low within the raspberry fields, they still provided ~1.8 visits per flower per day, suggesting that they could still play a role in the absence of honeybees. If honeybees were removed from the system, the exploitative competition experienced by the bumblebees would cease, making the raspberry field a more attractive pollen and nectar source for the bumblebees. Furthermore, previous studies have shown that bumblebees are better pollinators of raspberries suggesting that an even lower number of bumblebee visits is needed for sufficient pollination (Willmer et al., 1994; Garibaldi et al., 2013). A pollinator community based solely on honeybees should be considered highly vulnerable (Winfree, 2008; Potts et al., 2010a). In particular, the apparent climate sensitivity of honeybees as compared to bumblebees should cause concern regarding the sustainability of raspberry production based on honeybees only, under future climate change.

In the wild plant community surrounding the raspberry fields, bumblebees comprised the major part of the pollinator community (> 92% of visits when excluding "wild" raspberry). We did not assess seed set in the wild plant community, but since the bumblebees did not visit the raspberry fields to any extent, we suggest that the farm did not compete with the wild plant community for pollinators. Our results show that the raspberry fields monopolized the honeybees, while the wild plant community appeared most attractive to the bumblebees. This makes the two floral communities distinct entities with respect to their pollinator community, despite being localized only a few meters apart.

5. Conclusion

Honeybees were the main pollinator to the focal raspberry fields while bumblebees were common in the wild plant community surrounding the fields. The lack of bumblebees in the raspberry fields we attribute to flower constancy in both honeybees and bumblebees, and to exploitative competition from the honeybees. We suggest that the raspberry fields were sufficiently pollinated by honeybees but that the system should be considered vulnerable, as it is solely dependent on this particular pollinator species. Honeybees are managed animals and beekeepers can mitigate climate change effects through hive management options. However, individual behaviour during a foraging bout is hard to manipulate and will affect the honeybees' ability to conduct pollination. We found that the foraging activity of honeybees were more sensitive to ambient temperature than the foraging activity of bumblebees. We therefore suggest that the pollination service the honeybees provide to crop production might suffer more from future climate change than pollination from bumblebees.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.06.006.

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