

Season and landscape composition affect pollen foraging distances and habitat use of honey bees

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Abstract. Honey bees (*Apis mellifera* L.) show a large variation in foraging distances and use a broad range of plant species as pollen resources, even in regions with intensive agriculture. However, it is unknown how increasing areas of mass-flowering crops like oilseed rape (*Brassica napus*; OSR) or a decrease of seminatural habitats (SNH) change the temporal and spatial availability of pollen resources for honey bee colonies, and thus foraging distances and frequency in different habitat types. We studied pollen foraging of honey bee colonies in 16 agricultural landscapes with independent gradients of OSR and SNH area within 2 km and used waggle dances and digital geographic maps with major land cover types to reveal the distance and visited habitat type on a landscape level. Mean pollen foraging distance of 1347 decoded bee dances was 1015 m (± 26 m; SEM). In spring, increasing area of flowering OSR within 2 km reduced mean pollen foraging distances from 1324 m to only 435 m. In summer, increasing cover of SNH areas close to the colonies (within 200 m radius) reduced mean pollen foraging distances from 846 to 469 m. Frequency of pollen foragers per habitat type, measured as the number of dances per hour and hectare, was equally high for SNH, grassland, and OSR fields, but lower for other crops and forests. In landscapes with a small proportion of SNH a significantly higher density of pollen foragers on SNH was observed, indicating that pollen resources in such simple agricultural landscapes are more limited. Overall, we conclude that SNH and mass-flowering crops can reduce foraging distances of honey bee colonies at different scales and seasons with possible benefits for the performance of honey bee colonies. Further, mixed agricultural landscapes with a high proportion of SNH reduce foraging densities of honey bees in SNH and thus possible competition for pollen resources.

Key words: *Apis mellifera* L.; *Brassica napus*; Land use intensification; oilseed rape; pollination; resource competition; seminatural habitat.

INTRODUCTION

The honey bee, *Apis mellifera* L., has been managed for centuries in agricultural landscapes and provides substantial pollination for many crops and wild plant species (Klein et al. 2007). Today pollinators are globally under decline, which is associated with agricultural intensification (Potts et al. 2010a). The resulting loss of seminatural habitats (SNH) providing nesting sites is considered a major threat for wild pollinators (Brown and Paxton 2009). Other effects like lack of floral resources or increased pesticide use concern both wild pollinators and managed honey bees. Potential drivers of honey bee colony losses in particular can be grouped into pests and pathogens, environmental stressors, and lack of genetic diversity and vitality (Neumann and Carreck 2010, Potts et al. 2010b). Environmental stressors, e.g., malnutrition or exposure to agrochemicals, are linked to agricultural intensification and reduced landscape heterogeneity. Increasing areas of

mass-flowering crops like oilseed rape (*Brassica napus*; OSR) and a decrease of SNH as multifloral resource change the temporal and spatial availability, quality, and diversity of food resources for honey bee colonies in fragmented agricultural landscapes. However, the consequences for pollen foraging of honey bees in these fragmented landscapes, the influence of landscape composition, and the relevance of specific habitat types are mainly unknown.

Pollen is the only protein source for honey bees and essential for colony growth and development (Haydak 1970). Its quality and diversity has been identified as an important factor for honey bee health (Alaux et al. 2010, Di Pasquale et al. 2013). In contrast to nectar, it is stored in only small amounts within the hive (Seeley 1995). To secure pollen supply during breeding, a continuous availability of resources, presumably ascertained by SNH or weeds in arable landscapes is required (Requier et al. 2015).

In intensive farming systems crops can contribute significantly to pollen harvest of honey bee colonies (Odoux et al. 2012). The influence of mass-flowering crops like OSR on pollen foraging of honey bees is not

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well known, though. Honey bees are thought to be tightly associated with mass-flowering crops like OSR (Rollin et al. 2013). They collect huge amounts of OSR nectar and are important pollinators for winter OSR (Stanley et al. 2013). However, the probability of pollen collection on OSR seems to be low (Odoux et al. 2012, Woodcock et al. 2013, Garbuzov et al. 2015, Requier et al. 2015), but has never been systematically analyzed while taking account of the influence of landscape composition. In general honey bees are attracted by mass-flowering crops but little is known about the use of SNH relative to OSR (Rollin et al. 2013).

Foraging is an energy-consuming effort for the honey bee and it can be assumed that shorter flight distances are of advantage for colony health and development. Foraging distances vary depending on landscape structure, resource availability, and season (Visscher and Seeley 1982, Steffan-Dewenter and Kuhn 2003), but few studies analyzed pollen foraging distances in particular (Waddington et al. 1994, Steffan-Dewenter and Kuhn 2003, Danner et al. 2014, Couvillon et al. 2015). Foraging distances might be reduced and therefore colony fitness increased in landscapes with a high amount of floral resources, provided by SNH or mass-flowering crops (Requier et al. 2015). Further pollen supply in the landscape depends on season and landscape structure (Steffan-Dewenter and Kuhn 2003). Intensively managed landscapes with mass-flowering crops and little or no SNH often provide only pollen for short time periods, but see Requier et al. (2015). Larger foraging distances as a result of resource scarcity might arise to meet the pollen demand of honey bee colonies. The development of honey bee colonies follows seasonal stages showing a strong growth in spring with a high demand for pollen, which turns regressive in summer when the swarming period ends (Seeley 1995). With the seasonal changes in pollen supply and demand there might be temporal differences in the influence of landscape composition on honey bee habitat preferences and foraging distances.

In this study, we took the perspective of honey bee colonies by decoding waggle dances to test (1) the influence of the amount of OSR and SNH in a landscape on pollen foraging distances and (2) the frequency of pollen foraging on OSR compared with SNH and other land use types. Successful foragers communicate about the location of most rewarding food resources to their nest mates using the waggle dance (von Frisch 1965, Seeley 1995). Distance and direction are encoded in the duration of the waggle run and in the angle of the run relative to the vertical, respectively. There is variation in these signals (Schürch et al. 2013), but decoding a large number of dances and combining them with digitalized geographical maps is a unique tool to study the landscape ecology of honey bees (Steffan-Dewenter and Kuhn 2003, Couvillon et al. 2014a, Danner et al. 2014, Härtel and Steffan-Dewenter 2014, Garbuzov et al. 2015).

In this study we aimed to quantify pollen foraging of honey bee colonies in relation to landscape context. We

selected 16 landscapes with independent gradients in the percent cover of OSR fields and SNH to answer the following questions: (1) Do pollen foraging distances depend on the amount of OSR and SNH within the main flight range? (2) Are there seasonal differences in the influence of landscape composition on pollen foraging distances? (3) Do honey bee pollen foragers prefer mass-flowering OSR compared to mixed floral resources in SNH? (4) How does landscape composition influence pollen foraging frequency of honey bees in different habitat types?

MATERIALS AND METHODS

Study region and sites

The study region is situated in a 40 km radius around Würzburg, Germany. The landscape is dominated by agriculture with cultivation of wheat and barley (together ~50% of agricultural land). Cultivation of mass-flowering OSR accounts for ~8% of agricultural land. Intensive wine-growing is established on sun-exposed hills next to the river Main. SNH are present at varying extent and typically represented by flower rich calcareous grassland, extensive meadows, and hedges. We selected 16 circular landscapes with 2 km radius and a minimum distance between landscape centers (observation hive position) of 4 km (Fig. 1). Landscape selection aimed to maximize an OSR area gradient and an independent SNH area gradient over all landscapes (Pearson's product-moment correlation; $r = -0.16$, $n = 16$, $P = 0.55$). OSR and SNH area gradients reached from 0% to 13% and 0% to 14% of total landscape area, respectively (Table 1). The distance of OSR/SNH from the honey bee colony could also influence foraging on the respective food source. We assured that the distance to the nearest OSR field/SNH from the landscape center was correlated with OSR and SNH area within 2 km, respectively (Pearson's product-moment correlation; OSR, $r = -0.59$, $n = 16$, $P = 0.016$; SNH, $r = -0.50$, $n = 16$, $P = 0.048$). Distance to the nearest field ranged from 52 to 1752 m for OSR and 0 to 1126 m for SNH. The calculation of areas and landscape selection was based on individual mapping in combination with digital land use maps (provided by Bayerische Landesvermessungsverwaltung) and processing in ArcGIS 10 (ESRI 2011).

Landscape variables

Oilseed rape fields were individually mapped within the study region in winter/early spring 2012 and digitalized into vector data. SNH vector data were obtained from the Bavarian mapping of biotopes provided by the Bavarian State Office for the Environment. For our purpose SNH included calcareous grasslands, species rich extensive meadows, natural hedges, initial shrubs, grassland fallows and orchards. OSR and SNH area were each calculated on five spatial scales; 200, 500, 900, 1400,

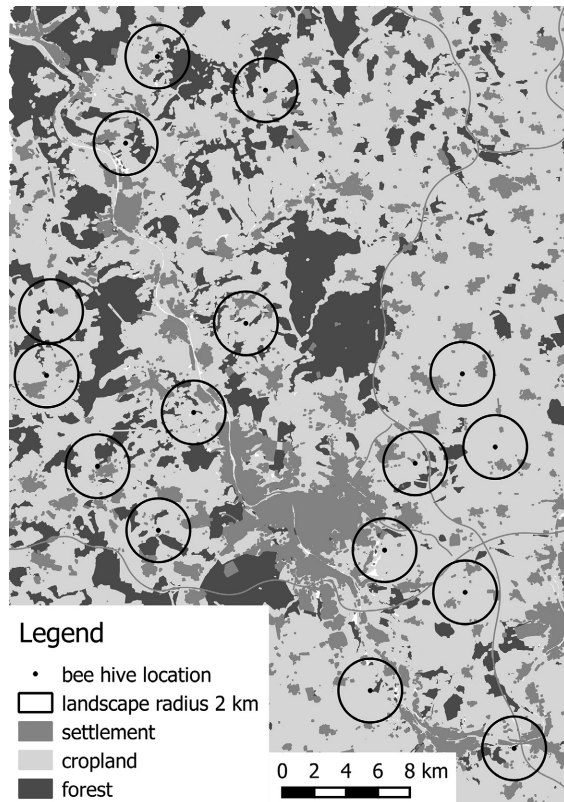


FIG. 1. Geographical distribution of 16 study sites (landscapes, 2 km radius each) around Würzburg, Germany.

TABLE 1. Land-use characteristics for 16 landscapes in a 2000 m radius around observation hives.

Habitat type	Mean \pm SE	Range (%)
Oilseed rape	5.6 \pm 1.0	0.2–12.6
Seminatural habitat	4.6 \pm 1.2	0.2–14.3
Crop total	66.2 \pm 4.0	37.8–93.3
Forest	16.7 \pm 3.0	0.1–33.6
Settlement	7.1 \pm 0.8	2.3–13.8

Notes: Means are shown \pm standard error (SE). Crop total includes oilseed rape.

and 2000 m radii around the landscape centers. The choice of maximum radius was based on a previous study by Danner et al. (2014), where over 96% of dances indicated foraging locations within 2000 m. In our case, almost 90% of foraging locations were within the mapped landscape radius of 2000 m, proving that it is a suitable scale for landscape analysis of honey bee foraging. The correlation between variables on all scales (within and between scales) was always $r < 0.5$ (Pearson's product-moment correlation). For the analysis of foraging frequency on different land use types vector data for other cropland (excluding OSR), grassland, forest, and settlement within the study region was obtained from Bayerisches Landesvermessungsamt.

Observation hives and colonies

Sixteen glass-sided observation hives, each with two Zander brood frames were used for observations. Sixteen colonies were built using artificial swarms with young, mated queens (*Apis mellifera carnica*). All queens derived from a single mother and were mated at the same queen-mating station (Gehlberg, Germany) to assure minimal genetic differences between colonies. Brood frames with similar amounts of brood cells, honey, and pollen stocks were transferred to each observation hive along with a queen and ~4000 worker bees. Returning foragers were restricted to perform their dances on one side of the comb by a diagonal wooden block in the passage at the bottom of the observation hive. A tent of lightproof cloth prevented light-induced confusion of bees during observations (Danner et al. 2014).

Sampling design

One observation hive was placed during spring and summer 2012 in the center of each of the 16 landscapes (Fig. 1). In total we performed seven observation rounds, divided into a block of four rounds during OSR bloom (season spring, 18 April 2012–24 May 2012), and a second block of three rounds after bloom of OSR (season summer, 16 July 2012–20 August 2012). SNH provided flower resources in both seasons and allowed us to analyze its effect in interaction with a mass-flowering crop (OSR) in spring and in the absence of it in summer, respectively. During one observation round lasting several days, pollen waggle dances of each colony were observed for 90 min (based on previous studies; Steffan-Dewenter and Kuhn 2003, Danner et al. 2014). After finishing one round, all hives were moved overnight to five landscape centers further following a fixed order that was determined by the optimal connection through paved roads. This rotation scheme ensured that bees would not find their way back to the previous landscape since distances were ~10 km minimum, and allowed data collection from seven independent colonies in each landscape (Steffan-Dewenter and Kuhn 2003).

Observation and decoding of bee dances

Over the whole study period, observation units per landscape were relatively equally distributed over the day. For each waggle dance, we monitored the duration of a series of circuits, the correspondent number of circuits, and the average angle of the waggle runs relative to the vertical and the time of day. We decoded only dances of pollen-carrying foragers with a minimum of five consecutive circuits (Couvillon et al. 2012). The sun azimuth relative to the north was added to the waggle run angle to determine the direction of the pollen foraging site indicated by each dance. Flight distance (y) was calculated via the mean duration of a single dance circuit (x) according to a third-order polynomial fit ($y = 92.137 - 346.659 \times x + 228.454 \times x^2 - 10.963 \times x^3$)

based on data presented by von Frisch (1965), previously used by Steffan-Dewenter and Kuhn (2003), Waddington et al. (1994), Beekman et al. (2004), and Beekman and Ratnieks (2000). The locations of pollen foraging sites were plotted into land use maps using the software ArcGIS 10 (ESRI 2011). Dance frequency for different land use types was calculated as number of dances per hour observation time and per hectare of the corresponding land use area (Danner et al. 2014). Therefore foraging locations within 2000 m around the hives were assigned to the six land use types they directly intersected with in ArcGIS maps (OSR, other cropland, SNH, grassland, forest, settlement). A new approach, developed by Schürch et al. (2013), is based on spatial probability distributions of the resource locations advertised by dances and was recently applied for determining foraging preferences in the landscape (Couvillon et al. 2014b). In our study region, landscapes were characterized by small patches of focal habitats like OSR or SNH (on average 1.7 and 0.4 ha, respectively) in contrast to a relatively large mean patch area of 130 ha in Couvillon et al. (2014b). Therefore, we based the analysis on original foraging locations, also matching with OSR and SNH patches, which helped to avoid a possible bias of estimated foraging locations.

Statistical analyses

Statistical analysis was performed using the open source statistical software R (R Development Core Team 2015). Separate linear mixed models (R package lme4; Bates et al. 2015) were applied per season to analyze foraging distances in the spring season with OSR and SNH area as continuous explanatory variables and in the summer season with SNH area only (questions 1 and 2). To determine the most relevant spatial scale for each variable (OSR and SNH area) in spring, we performed single models for each scale and variable first and then combined both variables at their most predictive scale in one model to test their significance (Graf et al. 2005). In detail, one model per scale was performed with OSR area as explanatory variable on the five scales 200, 500, 900, 1400, and 2000 m radii, resulting in five models. The scale of the model with the lowest Akaike information criterion (AIC) value was chosen to enter the final analysis. This procedure was repeated with SNH as explanatory variable. All single scale models contained landscape and colony as random factors. We did not include random slopes for OSR and SNH at this point since they would be scale-dependent and hinder the comparison of fixed effects (the different scales) only. In the final analysis, the random structures were tested with the full models considering colony and landscape as random factors and OSR and SNH area on their respective scale as possible random slopes for each factor. The random structures resulting in the lowest AIC values of the models were chosen: colony as random intercept with random slopes for OSR and SNH, and landscape as random intercept.

Further model simplification was done by stepwise reduction of fixed effects and likelihood ratio tests. Foraging distance data were log-transformed in order to achieve normal distribution and homogeneity of variance of the model residues. Interaction between the predictors was tested. Chi-square and *P* values (significance level 0.05) were calculated by likelihood ratio tests. The difference of the slope from zero was tested post hoc. The whole procedure of scale determination and modeling was repeated for summer, considering only SNH as explanatory variable. The final random structure contained colony as random intercept with random slope for SNH, and landscape as random intercept.

Linear mixed models were performed to analyze log transformed dance frequency in each season (questions 3 and 4). Explanatory variables were land use type, SNH area, OSR area, and the one-way interaction with SNH and OSR area in spring. Land use type, SNH area, and the interaction between both entered the model for summer season. Post hoc comparisons after Tukey and “BH” corrections (Benjamini and Yekutieli 2001) were applied. Both models contained landscape and colony as random factors. In all cases, model diagnostic plots were checked for validity of the full model.

RESULTS

Pollen foraging distances

Pollen foraging distances of 1347 observed and decoded bee dances ranged between 35 and 9510 m with a mean of 1015 m (± 26 m; standard error of the mean; SEM). Ninety percent of all dances were within 2193 m and 75% were within 1355 m around the hives (Fig. 2). The influence of OSR and SNH area on pollen foraging distances was analyzed on the five scales 200, 500, 900, 1400, and 2000 m. The most predictive scales (chosen via comparing AIC values of single scale models, see Table S1) of explanatory variables were 200 m for SNH and 2000 m for OSR in spring and 200 m for SNH in summer. Differences of models between scales were in general small ($\Delta\text{AIC} \leq 2$), indicating the absence of a strong scale effect. In spring ($n = 940$ dances) the OSR area within 2000 m influenced overall pollen foraging distances most significantly (Fig. 3A; for statistics see Table 2), whereas the area of SNH had no effect. Distances decreased with increasing OSR area from 1324 to 435 m (post hoc test for slope: $P = 0.045$). There was no interaction between SNH and OSR. In summer ($n = 407$ dances) SNH area within 200 m around the hive reduced mean pollen foraging distances from 846 to 469 m (Fig. 3B; post hoc test for slope: $P = 0.024$).

Pollen foraging frequency in different habitat types

We assessed the value of different habitat types as pollen resources for honey bee colonies by pollen foraging frequency measured as number of dances per hour

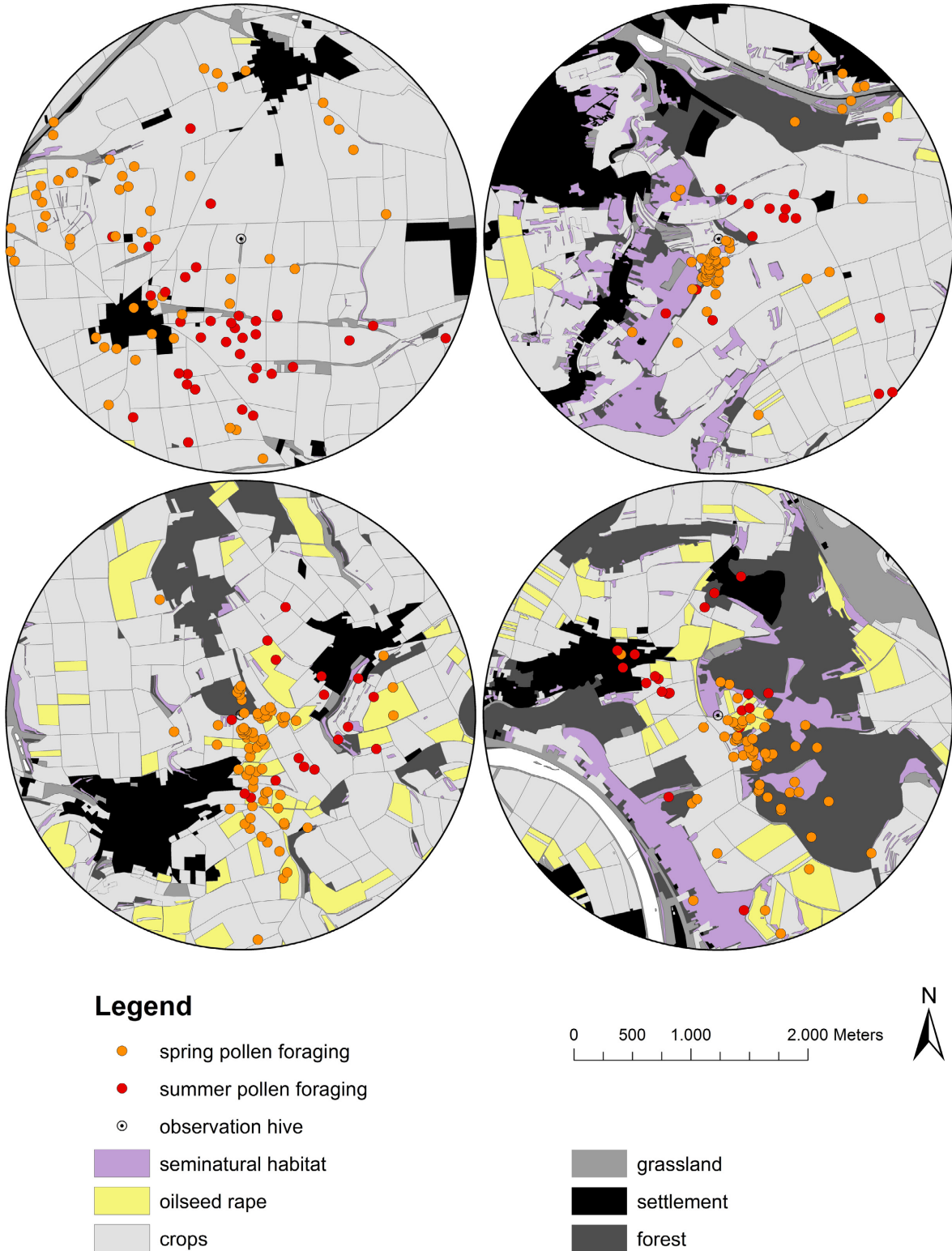


FIG. 2. Pollen foraging locations in four exemplary landscapes out of 16, representing the independent gradients of oilseed rape (*Brassica napus*) and seminatural habitat area. Foraging locations derive from decoded waggle dances that were observed in observation hive colonies placed in the landscape centers.

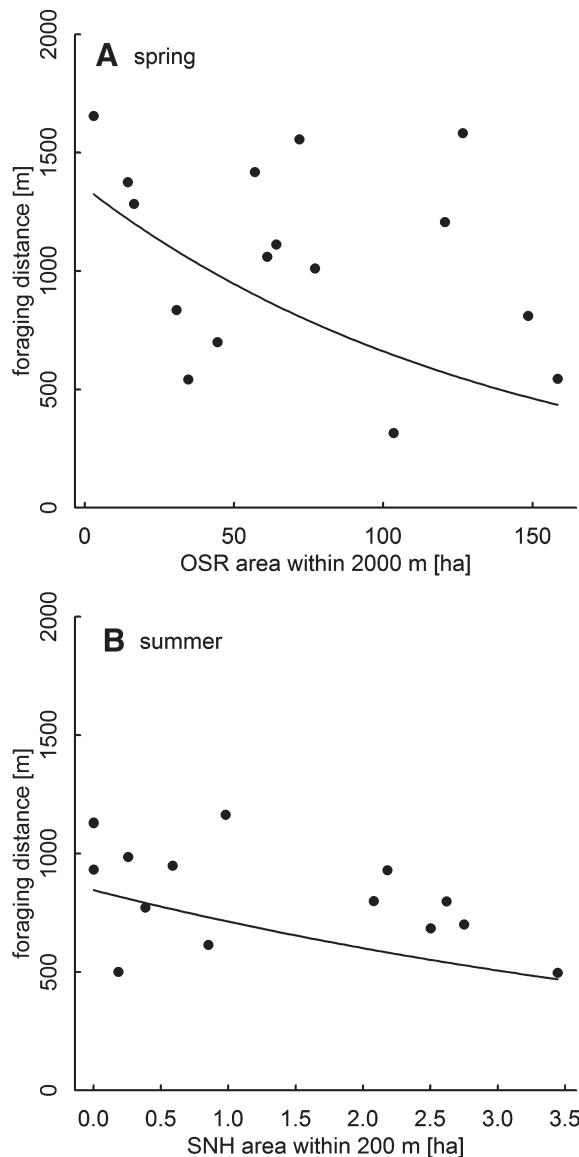


FIG. 3. Pollen foraging distances in relation to oilseed rape and seminatural habitats area in 16 landscapes in (A) spring and (B) summer. Points show distance means per landscape while fitted lines derive from analysis of original data ($n = 940$ dances and $n = 407$ dances in spring and summer, respectively), back-transformed for plotting.

and hectare (Danner et al. 2014). There were significant differences between land use types within seasons (Fig. 4; for statistics see Table 2). In spring OSR was as frequently foraged as other pollen sources like SNH and grassland. In summer the number of dances per observation unit decreased in general. Settlement was as frequently foraged as SNH and grassland. Other crops and forest played a subordinate role in both seasons regarding number of dances per hour and hectare. We found a significant interaction between habitat type and SNH and OSR area within 2000 m (Fig. 4). Post hoc multiple

TABLE 2. Seasonal effects of OSR area, SNH area, and land use type on foraging distances and frequencies.

Explanatory variable, by response and season	χ^2	df	<i>P</i>
Foraging distance			
Spring			
OSR area	4.04	1	0.044
SNH area	0.16	1	0.69
Summer			
SNH area	4.86	1	0.027
Foraging frequency			
Spring			
Land use type	106	5	<0.001
Land use type \times OSR area	13.61	5	0.018
Land use type \times SNH area	19.61	5	0.001
Summer			
Land use type	41.27	4	<0.001
Land use type \times SNH area	15.22	4	0.004

Note: Results from likelihood ratio tests between mixed effects models with and without the respective explanatory variable or interaction (stepwise backward testing) are shown.

comparisons of slopes revealed that foraging frequency on SNH significantly increased with decreasing SNH area in both seasons (spring: $P < 0.001$; summer: $P = 0.002$). For example, decreasing SNH area from 100 to 10 ha would increase dance frequency in spring by 2.5 times and in summer by almost four times. Further, with increasing OSR area in spring, foraging frequency on forest increased ($P = 0.027$).

DISCUSSION

Our results show that a mass-flowering crop (OSR) and SNH influence pollen foraging distances on different scales and depending on season. Pollen foragers did not prefer mass-flowering OSR compared to mixed floral resources in SNH, whose importance as a pollen resource was influenced by landscape composition. Foraging frequency on SNH increased in spring and in summer with decreasing SNH area in the landscape. Our findings have general implications for the understanding of honey bee foraging in agricultural landscapes and for agri-environmental management to foster pollen resources for bees. While our results underpin the importance of SNH as pollen sources for honey bees, they also indicate a strong increase of foraging frequency in simple agricultural landscapes, possibly resulting in resource competition with wild bees.

Pollen foraging distances and landscape composition

Mean pollen foraging distances in this study (1 km) are in the range of previous reported distances of 0.7 km (Waddington et al. 1994; suburban landscape), 0.8 km (Danner et al. 2014; agricultural landscape), 1.1 km (Couvillon et al. 2015; suburban/agricultural

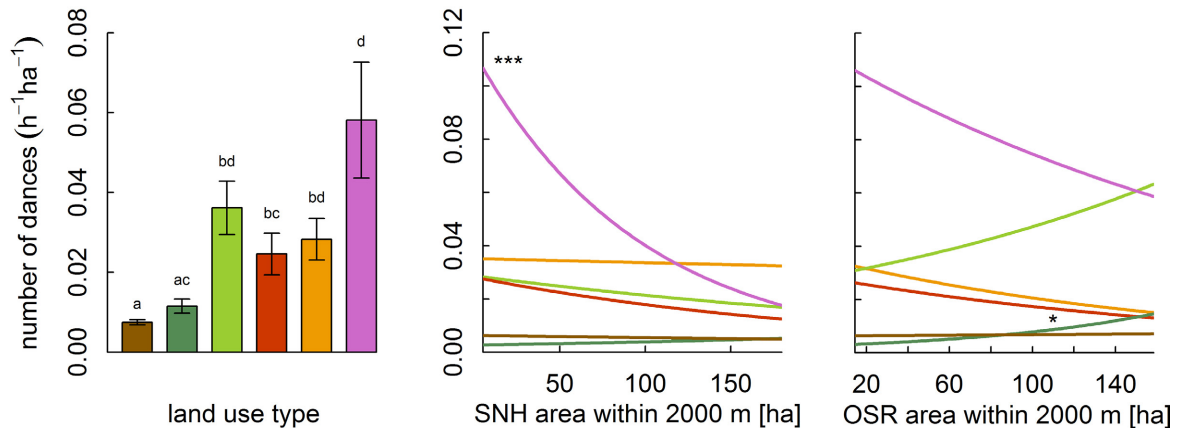
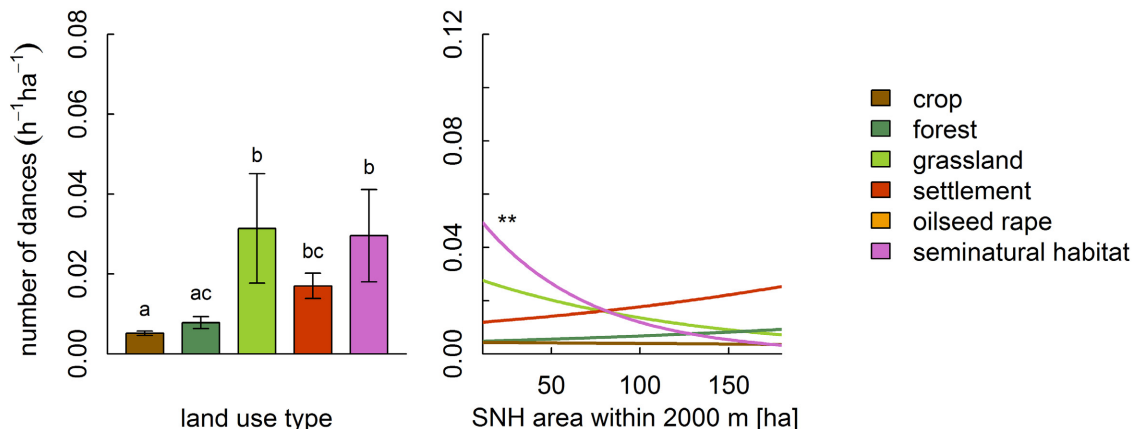
A spring**B summer**

FIG. 4. Effects of seminatural habitats (SNH) on pollen foraging for different land use types in spring (A) and summer (B). Bar plots show mean dance frequencies \pm standard error of the mean (SEM) measured as number of dances per hour and hectare. Different lowercase letters above the bars indicate significant differences ($P < 0.05$). Other plots show the effect of SNH and oilseed rape (OSR) area within 2000 m on dance frequency. Crops in spring excluded OSR, in summer included former OSR fields. Asterisks indicate slopes significantly different from zero (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; see Table S2 for post hoc tests for slopes). Model estimates were back-transformed for plotting fitted lines.

landscape), and 1.6 km (Steffan-Dewenter and Kuhn 2003; agricultural landscape). Foraging distances of honey bees are variable and depend on temporarily occurring patches of food resources, landscape structure, and dominant habitat types (Visscher and Seeley 1982, Steffan-Dewenter and Kuhn 2003). In intensively used landscapes, mass-flowering crops like OSR in particular might reduce foraging distances since they massively enhance the availability of resources, at least for a short time period, but empirical data are mainly lacking so far. Our study demonstrates that in spring OSR area within 2000 m around the hives reduced overall pollen foraging distances (Fig. 3A). Lower distances in landscapes with high OSR area confirm that OSR has the potential to reduce pollen foraging effort in terms of flight distances. However, our study and others indicate that OSR is not as preferentially used as expected by its dominance (Odoux et al. 2012, Woodcock et al. 2013, Garbuzov et al. 2015, Requier et al. 2015).

Seminatural habitat area was a relevant factor for pollen collection on smaller scales than 2000 m. Our results show that SNH areas close to the hive (within 200 m) reduced overall pollen foraging distances and consequently foraging effort in summer. The effect of SNH might differ depending on specific plant communities. However, our study provides more general information about the significance of SNH in agricultural landscapes. Comparing single scale models during the scale selection and modeling procedure (see *Materials and Methods: Statistical analysis*) reveals small differences between models ($\Delta AIC < 2$; Table S1), suggesting that the influence of SNH does not strongly depend on its scale. It is therefore most relevant on small scales like 200 m but probably still important on larger scales as well.

Similarly, in a study with African honey bees foraging ranges increased during a shortage of resources (Schneider and McNally 1993). A larger foraging range of a colony is assumed to raise the probability of discovering more

suitable food source patches (Visser and Seeley 1982). Shorter flight distances in turn should point out that the available resources like OSR and SNH are suitable for honey bee colonies. Steffan-Dewenter and Kuhn (2003) found no significant differences of overall mean foraging distances between simple (assumed to supply resources less continuous) and complex landscapes. However, pollen foraging distances were significantly higher in simple landscapes after OSR bloom. Assuming that a simple landscape would most likely correspond to one with low SNH area in our study, this is in accordance with our results.

Oilseed rape raises the pollen offer in the landscape for a short time period in spring and might reduce energy effort of honey bee colonies. In contrast a landscape with SNH provides pollen continuously with positive influence on energy effort. Requier et al. (2015) suggest that honey bees use a wide variety of pollen resources, even during OSR flowering, in order to ensure colony health. According to our observed effect of SNH area on foraging distance this is of relevance especially in summer when resources in our studied landscapes tend to be scarce compared to spring. In summer, profitable resources (comparable to OSR in spring and besides SNH) would be sunflower (*Helianthus* spp.) and maize (*Zea mays*) that were barely grown in these landscapes. The missing effect of SNH area on foraging distances in spring might be due to the higher demand for pollen in the stage of colony growth. Apparently even high amounts of SNH close to the hive do not meet the complete demand for pollen (quantity or quality/diversity) in spring, resulting in high foraging distances. A poor availability of pollen resources might have negative consequences for colony development and health (Keller et al. 2005).

Very few published studies quantitatively measure colony success in response to landscape variables (Sponsler and Johnson 2015). Besides foraging distance as a measure of colony success, honey production or colony size can be related to landscape variables, e.g., colony size was positively correlated with forest land cover in an intensively managed agricultural landscape in France (Odoux et al. 2014). A study performed in Denmark reveals that colonies situated in agricultural landscapes were significantly less productive than colonies situated in urban areas (Lecocq et al. 2015), pointing out the poor suitability of certain agricultural landscapes for honey bee colonies.

To overcome obvious shortages in pollen resources after periods of mass-flowering crops and in landscapes with low SNH, a suitable landscape management is needed. Accounting for about one-third of foraging flights (Fewell and Winston 1992) makes pollen foraging a relevant part of energy effort that can be shaped by landscape composition. We emphasize the importance of SNH in the neighborhood of honey bee colonies. Further, the establishment of flower strips, organic farming and diversifying flowering crops are possible

agri-environmental schemes for a pollinator supporting landscape management (see Decourtye et al. 2010 for a review). However, to answer questions like how much resources in the agricultural landscape are actually needed for optimal colony development depending on season, further studies are needed.

Pollen foraging frequency and landscape composition

To gain insight into the intensity of resource use on different land use types in different seasons we analyzed dance frequencies, i.e., the number of dances (resource locations advertised by dances) per hour and hectare (Danner et al. 2014). Overall, we observed a lower dance frequency in summer compared to spring. Since we controlled for colony size throughout the experiment by removing bees when necessary, there was no natural colony growth that could have influenced dance frequency. The colony regulates its pollen foraging intensity in accordance with changing colony needs, which derive from the amount of stored pollen and the demand of adult bees and larvae (Camazine 1993). A lower dance frequency in summer might therefore reflect a decreasing demand for pollen after the intensive larval rearing in spring.

Comparing dance frequencies for different land use types revealed that grassland, settlements (gardens), and SNH were frequently foraged for pollen regardless of the season. OSR is a rewarding pollen resource in spring, which is underlined by its influence on pollen foraging distances, but OSR was not as preferentially visited as could be assumed for a mass-flowering crop. OSR is known to be foraged intensively for nectar (Nedić et al. 2013) while there is only little known for pollen. In a study in an agricultural landscape in western France, OSR pollen never represented more than 29% pollen weight of a weekly pollen load sample while other single weed species represented up to 98% (*Sinapis*; Odoux et al. 2012). Although it is not known whether pollen input from a certain plant species correlates with its related dance frequency, this result indicates that OSR pollen is not a dominating species in the pollen harvest of honey bees. In accordance Woodcock et al. (2013) and Garbuzov et al. (2015) report a low probability of pollen foraging on OSR, based on observed visitation rates in OSR fields and dance decoding, respectively. While the study of Garbuzov et al. (2015) was performed in a single landscape, our study allows the independent comparison of OSR and SNH landscape gradients. Similarly, a preference of other pollen than OSR in intensive farmlands was indicated by analyzing pollen samples from traps in front of the hive (Requier et al. 2015). This is also consistent with general low proportions of OSR pollen in nests of solitary bees (Holzschuh et al. 2013). The frequent utilization of SNH and grassland in spring and summer suggests that honey bees try to recruit nest mates for collecting a diverse pollen diet throughout the year, instead of only concentrating on mass-flowering crops. However, the influence of mass-flowering crops on pollen

foraging pattern appears to be crop and season specific. In a previous study analyzing pollen foraging in landscapes during bloom of maize we detect a different pattern with a significantly higher pollen foraging frequency on mass-flowering maize fields compared to all alternative habitat types including grassland and settlement (Danner et al. 2014). In temperate regions, maize is in bloom during summer when alternative resources are scarce compared to spring which might also be a cause for the observed difference.

As a further new aspect in our study we incorporated the effect of landscape context on foraging frequencies. Foraging on SNH was concentrated in both seasons when SNH area within the landscape decreased, while this effect was absent for other land use types as well as for the influence of OSR area in spring. Interestingly, OSR area had a positive but relatively small effect on foraging on forest. Since foraging frequency on forest was generally very low compared to other land use types, this effect could be biologically less important. However, Requier et al. (2015) report that woody plant species (which are only partly forest species) are important pollen resources during OSR bloom. In order to clarify a possible relationship between OSR and foraging in forest habitats individual studies should be designed. Nevertheless, our results showed the importance of SNH as a pollen resource for honey bees especially when its proportion in the landscape is rather limited (Steffan-Dewenter et al. 2002). Furthermore, as wild bees are known to prefer SNH (Rollin et al. 2013), the interspecific competition for pollen resources between honey bees and wild bees might be more severe in such landscapes (Holzschuh et al. 2013, Härtel and Steffan-Dewenter 2014), an aspect not considered in the few studies on honey bee–wild bee competition (Steffan-Dewenter and Tscharnkte 2000, Hudewenz and Klein 2013). Integrating SNH in landscape management would benefit honey bees but also other pollinators like wild bees (Rollin et al. 2013) or butterflies (Ockinger and Smith 2007). Rollin et al. (2013) suggest to support different bee groups with distinct management strategies, e.g., promoting mass-flowering crops to benefit honey bees and seminatural herbaceous habitats to benefit wild bees. We emphasize the cross-group effectiveness and importance of SNH, particularly regarding the continuous provision of diverse pollen resources.

In conclusion, our study provides clear evidence that landscape composition has an influence on foraging distances and consequently energy effort of honey bee colonies. SNH in the vicinity to honey bee colonies reduced foraging distances in summer and was one of the most important pollen sources with even increasing importance in landscapes with low SNH cover. While OSR is an important nectar source it was not an outstanding pollen forage which suggests that diverse pollen sources within the foraging range are very important for honey bee colonies. Maintaining SNH and promoting agri-environmental schemes to provide diverse and

continuously available pollen resources will improve the wellbeing of honey bee colonies, the coexistence with wild bees and the provisioning of crop pollination services in agricultural landscapes.

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