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EFFECTS OF TEMPORAL AND SPATIAL VARIATION OF RESOURCES ON THE FORAGING PATTERNS OF HONEY BEES IN THE AGRICULTURAL LANDSCAPE

Dissertação no âmbito do Mestrado em Ecologia, orientada pela Doutora Sílvia Raquel Cardoso Castro Loureiro e pelo Professor José Paulo Filipe Afonso de Sousa e apresentada ao Departamento de Ciências da Vida da Facultade de Ciências e Tecnologia da Universidade de Coimbra

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Abstract

Honey bees are the most important managed pollinators for agriculture globally. With the fragmentation of the natural habitats in intensive agricultural landscapes, the food sources for the honey bees have significantly changed presenting an overall decline in abundance and quality (considering both spatial and temporal scales). These changes are expected to have significant impacts on biodiversity, resulting in the decline of honey bees and other wild or managed pollinators. As global agriculture is becoming more and more dependent on pollination services frequently provided by insects, it is extremely important to design pollinator-friendly solutions that addresses the key drivers of the population declines. This study analyses the effects of temporal and spatial variation of flower resources on the foraging patterns of honey bees in an intensive agricultural landscape. For this, Albillos in the Province of Burgos (Spain) was chosen as study area, and native subspecies of honey bees *Apis mellifera* ssp. *Iberiensis* as the study subject. Waggle dance decoding was used as the main method to identify the main foraging locations of honey bees and changes in resources were assessed by a monthly flowering species quantification through landscape monitoring in a 10×10km area around the apiary. The importance of plant species for honey bees was classified based on literature data. The study revealed spatial and temporal variability in floral resources in the landscape. In natural areas we have found a diversity of plants species, instead of dominance of a given plant, thus providing diverse food resources. Consequently, the results also show temporal and spatial variability in the foraging locations of honey bees. There were visible differences in foraging patterns of honey bees, foraging closer to the hive in June and farther from the hive later in summer. Honey bees performed waggle dances signalling the abundant wildflower resources in June, a mix of wildflowers and sometimes alfalfa in July, and mostly sunflower and rarely wildflowers in August. We can conclude that honey bees have shown a clear preference for wildflower resources, when available in the landscape. They forage in the agricultural fields only when higher quality floral resources are lacking near the hive. Our results support the need for applying bee-friendly practices in the agricultural landscape and promoting sustainable beekeeping.

Key words: *Apis mellifera*, Waggle dance, Pollination, Melliferous plants, Floral resource availability

Resumo

A abelha melífera é o polinizador domesticado mais importante para a agricultura a nível mundial. Com a fragmentação dos habitats naturais devido às explorações agrícolas intensivas, as fontes de alimento para as abelhas melíferas têm sofrido alterações significativas, apresentando um declínio generalizado em abundância e qualidade (considerando tanto a escala temporal como espacial). E esperado que estas alterações possam ter impactos significativos na biodiversidade, o que poderá levar ao decínio das abelhas melíferas e outros polinizadores, sejam eles salvagens ou domesticados. Com o aumento da dependência da agricultura mundial dos serviços de polinização frequentemente providenciados por insetos, é de extrema importância criar soluções que beneficiem a polinização, tendo como foco os principais fatores do declínio das populações. Neste estudo analisaram-se os efeitos da variação temporal e espacial dos recursos florísticos exercem nos padrões de forrageamento da abelha melífera numa paisagem agrícola intensiva. Para esse propósito, foi escolhido como área de estudo o município de Albillos, na província de Burgos (Espanha), e como objeto de estudo a subespécie nativa de abelha melífera, *Apis mellifera* ssp. *iberiensis*. O método principal para identificar os principais locais de forrageamento por parte das abelhas foi a descodificação de "waggle dance". Por sua vez, as alterações nos recursos foram avaliadas por uma quantificação mensal das espécies em floração através da monitorização da paisagem numa área de 10x10 km em redor do apiário. A classificação da importância das espécies de plantas para a abelha melífera foi baseada em dados bibliográficos. Este estudo revelou variabilidade espacial e temporal dos recursos florísticos na paisagem. Nas áreas naturais encontrou-se uma diversidade de espécies de plantas, em vez da dominância de uma determinada planta/espécie, proporcionando dessa forma diferentes recursos alimentares. Consequentemente, os resultados também mostraram variabilidade temporal e espacial nos locais de forrageamento das abelhas melíferas. Existiram diferenças notórias nos padrões de forrageamento das abelhas, forrageando mais perto da colmeia em Junho e mais afastado ao longo do verão (Julho e Agosto). As abelhas realizaram danças sinalizando locais com abundância de flores silvestres em Junho, uma mistura de flores silvestres e algumas vezes alfalfa em Julho, e predominantemente zonas com girassol e escassas zonas com flores silvestres em Agosto. Podemos concluir que as abelhas mostraram clara preferência por recursos de flores silvestres, quando estes se encontravam disponíveis na paisagem. As mesmas forragearam em campos agrícolas apenas quando recursos florísticos de alta qualidade escasseavam nas redondezas da colmeia. Os nossos resultados suportam a necessidade de aplicar práticas mais favoráveis às abelhas nas paisagens agrícolas em conjunto com a promoção da apicultura sustentável.

Palavras-chave: *Apis mellifera*, Polinização, Plantas melíferas, Disponibilidade de recursos florais.

Abbreviations

CCD – Colony Collapse Disorder

EMMC-IMAE - Erasmus Mundus Master Course - International Master in Applied Ecology

EFSA – European Food Safety Authority

FAO - Food and Agriculture Organization (United Nations)

GIS – Geographic Information System

IPBES – Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

LED – Light emitting diodes

NIV – Nectar Importance Value

OPERA – Observatory for Productivity and Efficient use of Resources in Agriculture

PIV – Pollen Importance Value

UK – United Kingdom

USA – United States of America

Acknowledgements

I want to dedicate this thesis to my parents who have always been supporting my every goal throughout the life and teaching me the importance of education.

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1. Introduction

The honey bees (*Apis mellifera*) are social insects, having high ecological and economic importance. They are a generalist species in the sense that they explore multiple plant species for food resources (Pankiw & Page, 2000). Honey bees are naturally found in most of Europe, except the Azores and northern regions such as Iceland, the Faroe Islands and northern Scandinavia (De la Rúa et al., 2014). There are 10 subspecies of *A. mellifera* described in Europe and 28 recognized cross-fertile *Apis* species around the world (Engel, 1999). Honey bees provide people with several products such as honey, pollen, wax, royal jelly, and propolis (Mortensen et al., 2013). Because of their economic value, European honey bees can be found everywhere around the globe, except in Antarctica (Mortensen et al., 2013). In 2016 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) has reported around 81 million hives registered globally, producing 1.6 million tonnes of honey annually (Potts et al., 2016). But above all, they are the most important managed pollinator for agriculture globally, because of its current broad distribution area (Mortensen et al., 2013; Potts et al., 2016). Only in the United States of America (USA) crops pollinated by the bees have been assessed to be worth $15 billion (Mortensen et al., 2013). The value of insect pollination for agriculture in Europe has been assessed to be around 20 billion € (Gallai et al., 2009; OPERA, 2013), while the direct value of the honey production is only 140 million € (Moritz et al., 2010). Worldwide, and considering impacts on agriculture only, the estimated economic value of the pollination services is 153 billion € (Gallai et al., 2009; Hein, 2009).

Pollination is a regulating ecosystem service critical to human livelihood by supporting the food production (Hein, 2009). The vast majority of pollinator species are wild animals (Williams, 2002), but besides *Apis mellifera*, there are also some managed species of bees, including bumble bees, stingless bees, eastern honey bees (*Apis cerana*) that are also important pollinators (Hein, 2009). In general, more than 30% of the global food production depends on bee pollination (Mortensen et al., 2013). In Europe, it has been estimated that 84% of the crops are insect pollinated, with bees being very important for numerous varieties (Williams, 1996). The Food and Agriculture Organization of the United Nations (FAO) reported that 90% of the food worldwide is bee-pollinated, depending entirely or partially on bees to achieve pollination (Kluser et al., 2011).

For last 50 years, honey bee hives have increased by 45%, but in some parts of the world, namely in Europe and North America, their numbers have been declining (Kluser et al., 2011; Potts et al., 2016). During the same 50-year period, non-animal pollinated crop production has doubled, whilst animal pollinated crop production has increased four times. Consequently, the global agriculture is becoming more and more dependent on pollination, whilst pollination service has been declining (Aizen et al, 2008; Kluser et al., 2011; Potts et al., 2016).

With the increasing importance of honey bees for pollination services, their decline is more alarming. Land-use change negatively affects honey bee populations through different factors. Fragmentation of the natural habitats and the decrease of flower-rich biotopes due to ploughing are among the main factors leading to decreases of honey bees, as well as other pollinators (Kluser et al., 2011; Kryger et al., 2011). Simplification of the habitats results in reduction of the amount and diversity of food sources for resident animals (Kluser et al., 2011). In several parts of Europe, crops have become the main food source for the honey bees as the wild flower resources are lacking. In United Kingdom, rapeseed (*Brassica napus)* has become the main flower source for honey bees (Kluser et al., 2011). However, due to the simplification of the agricultural landscapes, particularly those dominated by large monoculture crops, bees have difficulty obtaining quality resources, such as sufficient pollen with essential amino acids, and also mineral salt and proteins (Hendriksma & Shafir, 2016). Availability of wild flower resources and a diversified diet is crucial for successful larva development and their survival during the winter (Hendriksma & Shafir, 2016; Kluser et al., 2011). When there are small but diverse patches of floral resources close to the hive, bees are profiting from the diversity of resourced provided by this vegetation, collecting distinct food sources at short distances. Moreover, in a diversified resource landscape, flowering does not occur simultaneously on all species, allowing bees to profit from resources over larger periods. Contrary, if there are extensive monocultures close by the hives, foragers either have to stay close, save energy and forage on existing low diversity of resources for a shorter time (even if they have high quality) or fly farther, use more energy in order to get diverse resources (Beekman & Ratnieks, 2000). Habitat simplification and the decrease diversity in floral resources ease the development of parasites and diseases, affecting the populations of wild pollinators as well as managed populations (Kluser et al., 2011). Scientists have mentioned that likelihood of “Colony Collapse Disorder”[1] (CCD) increases with low-protein pollen such as blueberries and sunflowers (Kluser et al., 2011). So, ultimately, landscape structure and the consequent spatial and temporal distribution of resources significantly affects the behaviour and fitness of honey bee colonies.

[1] Colony collapse disorder is the phenomenon when the number of worker bees drastically decrease, while queen bee and sufficient food stays in the colony, with a few nurse bees taking care of immature bees, and is associated with multiple stressors impacting honey bee colonies.

In addition to the simplified and depauperated landscape by intensive farming, systemic insecticides used in agriculture may cause toxic exposure of non-target pollinators, including honey bees. Laboratory studies have shown lethal effects on honey bees of the highly toxic chemicals such as Imidacloprid, Clothianidin, Thiamethoxam and associated ingredients (Kluser & Peduzzi, 2007). There have been cases of population mortality by the unsustainable use of above-mentioned chemicals as well as *Varroa* treatment. In addition to that, there have been some examples of losing of sense of direction, impairing memory and brain metabolism (Kluser et al., 2011). Herbicide spraying also have indirect negative effects on honey bee populations as important plants and habitats are destroyed (Kluser et al., 2011). Air pollution is another issue honey bee population has to face to find available flower resources. Due to the effects of air pollution on the insect attracting chemical production in flowers, the scents now can only travel 200m from the plants when in the 1800s it could reach 800m distance (McFrederick et al., 2008), with expected significant effects of foraging efficiencies of honey bees and other wild pollinators.

Honey bees live in large families. They are eusocial insects, meaning they create casts consisting one queen, some males (drones) and thousand worker bees (Seeley, 1995). Honey bees, as other insects undergo complete metamorphosis. Meaning that their lifecycle consists of four life stages: egg, larva, pupa and adult. Worker bees are the ones doing most of the work in the hive. At different stages of adulthood, they have to clean up the hive, feed the larvae and the queen, produce honey, and at the latest stage of their life they become the foragers, collecting pollen, nectar and water (Seeley, 1995).

Because of the large size of the colony, honey bees need large amount of food and diverse food sources. To share information with other individuals about the food locations, the method honey bees use is a “waggle dance” or a “round dance” depending on the distance to the food source. The waggle dance is used to share details about the found resources (further then 100 m) such as nectar, pollen, water and propolis (von Frisch, 1967) and possibly nest sites too (Couvillon et al., 2012). The dance has two main phases, the waggle run and a return phase, where the bee goes back to the starting point to keep doing the next waggle run (Grüter & Farina, 2009) (Figure 1). In the waggle run, duration determines the distance, the orientation relatively to gravity – the direction to the resource (von Frisch, 1967).

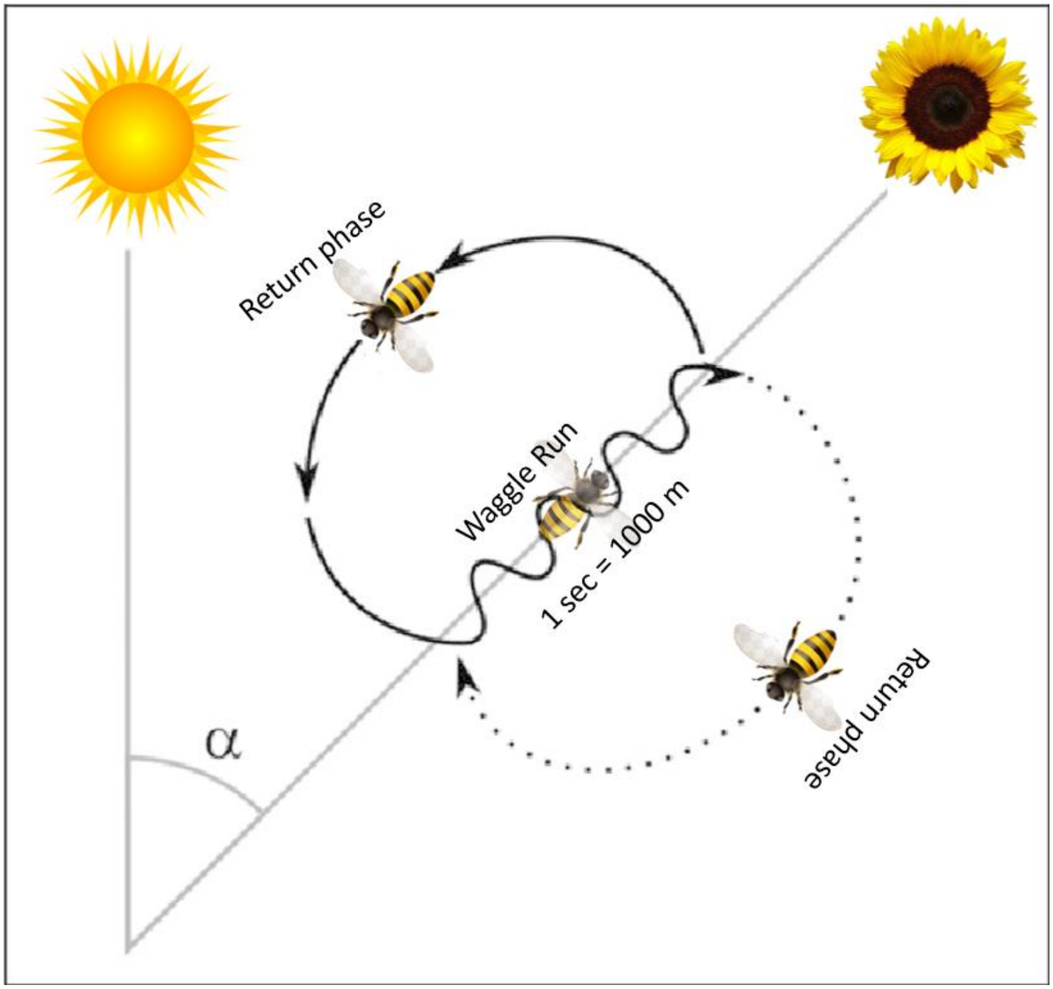

Figure 1. Waggle dance consists of waggle runs and return phases. Distance to the resource source is determined by the duration of the waggle run and the direction is determined with the orientation relatively to gravity (α). Adapted from "Bees algorithm for effective supply chains configuration." A. Lambiase, R. Iannone, S.Miranda, A. Lambiase, & D. Pham. 2016. International Journal of Engineering Business Management. https://doi.org/10.1177/1847979016675301

If resources are found close to the nest (around 100m) dance is a sequence of running circuits with bee changing directions after completing rounds (von Frisch, 1967). The number of circuits of waggle runs increase with better resource quality and the speed of dance increases with the necessity of resources (Seeley et al., 2000). Honey bees mostly choose resources within a 2-3 km distance from the hive, however they can fly up to 10 km distance for food (Seeley, 1995).

There is still a lot in the waggle dance that we do not understand completely, and it is not 100% precise method to study exact foraging locations of honey bees (Al Toufailia et al., 2013; Couvillon et al., 2012; Preece & Beekman, 2014; Schürch et al., 2013). Studies have found that there are some variations (intra-dance variation, inter-specific variation and miscalibrations) implying the spread of the forager bees over a patch of the landscape (Couvillon et al., 2012; Preece & Beekman, 2014; Schürch et al., 2013). However, it can still be used to assess the general foraging patterns, because bees dance the best they can to share information with their nestmates (Couvillon et al., 2012; Preece & Beekman, 2014; Schürch et al., 2013).

The flying distance for resources is conditioned by their qualitative and quantitative availability (Beekman & Ratnieks, 2000). The quality of each patch changes temporarily due to the vegetation phenology (Beekman & Ratnieks, 2000). When the landscape close to the hive yield low quality resources, bees tend to forage at a far-away patches for nectar with a high sugar concentration (Seeley, 1995). For example, this occurs during summer when bees have to fly to farther distances to find resources (Couvillon et al., 2014a). In the study by Beekman *et al.* (2004) in urban environment in Yorkshire, UK, the mean values of foraging distances were different for small and large colonies. Small hives forage at smaller distances, while large hives forage to further distances most probably to respond to higher resource needs. In July, mean value for small hive was 670m, while the value in August was 1430m; for larger hives these values were 620m and 2850m for July and August, respectively (Beekman et al., 2004). In intensive agricultural landscape, finding resources can be harder for small colonies, as they cannot search the farther distances for quality resources.

Due to climate change, flower growing periods have been shortening, and flowering periods shifting. Spatial and temporal changes in the floral resource availability may hinder the livelihood of pollinators (Steltzer & Post, 2009). Bee community composition depends on floral composition and resources offered by flowering plants (Potts et al., 2003). Honey bees use different sources throughout the season in response to shifts in the availability of the different plant species (Meneguetti, 2013). However, when honey bees find a good source, they try to exploit it completely, having it easier due to good communication system (Dupont & Jørgensen, 2017). In some regions, the occurrence of drought events, or even a shift in seasonal rainfall might cause asynchronization between pollinators and plant life-cycles, affecting the seasonal availability of different plant species used by the pollinators, and consequently affecting the life-cycles of the pollinators as well.

The conservation of pollinators requires a holistic approach. Preservation of honey bees, being a single most important managed pollinator for agriculture, is an urgency and requires integrated studies from a local to a landscape level, including the analysis of the spatial distribution of resources and their temporal changes. This study was performed within the framework of the POOL-OLE-GI project, funded by the European Union through the Interreg SUDOE programme (reference SOE1/P5/E0129), with the aim to see how the implementation of enhanced green infrastructures influences pollination services on oleaginous crops. The study was conducted at the Burgos province (Spain), in a landscape dominated by crop areas, and using an apiary that was regularly monitored for bee health. Flower resources were spatially assessed on a monthly basis between May and September, and the foraging locations were derived via waggle dance decoding (see details in the Materials and Methods section).

The major aim of this study was to analyse how honey bees use floral resources in an intensive agricultural landscape. More specifically we aim (i) to understand which resources were collected by honey bees and their preferences for crop and wild flower resources, and (ii) to study if temporal and spatial variation of resources in the landscape affected the bee foraging patterns. We hypothesize a shift in foraging locations over time due to the flowering phenology of the most abundant resources in the landscape, namely legumes, alfalfa, sunflower and fruit trees.

2. Materials & Methods

2.1. Observation hive and setup

The honey bee subspecies chosen for this study was a native subspecies to the Iberian Peninsula, *Apis mellifera* ssp. *iberiensis*. Healthy, adequately fed and disease-free colony was obtained from a certified producer. The observation hive used to acquire the movies of the waggle dances (see details below) was placed in an apiary installed within the "Princípe Felipe" Agricultural School in Albillos, province of Burgos, Spain (42.280634 N, 3.767428 W) with an elevation of 882 m above sea level.

Burgos province is characterized by a continental climate. The summer months are dry with temperatures varying between 8 ^{0}C and 25 ^{0}C in June and 11 ^{0}C and 27 ^{0}C in July and August (Weather Spark, 2016). The precipitation is scarce, within 380-480 annual mm in the region in the plain where the apiary was located but presenting higher values in the mountain areas of the province. The observation hive was located within a distance of 1 km from river of Los Ausines (Diccionario de ALEGSA, 2015).

The observation hive consisted fundamentally of a modified Langstroth hive (Figure 2) and was monitored for the waggle dances of honey bees across the beekeeping season. The hive was specially designed for this study by teams from the University of Coimbra and Aarhus University within the framework of an ongoing project funded by the EFSA (European Food Safety Authority). The observation hive and the recording box were connected so that no additional direct sunlight entered the box. A simple pendulum (Figure 2E) was used to create the gravitational reference. Under these circumstances, bees will use gravity as a reference point instead of sunlight, with the cord equalling the sun's position (Dyer, 2001; von Frisch, 1974).

The observations were conducted periodically during the 2018 beekeeping season, from March to September. However, only the data from June to September was analysed in this work. Raspberry Pi 3 model B+ with camera module V2 was used to record bee behaviour (Figure 2D). Greenwich Mean Time and the date were also recorded. Recordings of 28 minutes with a 15 minutes interval were obtained. Procedures and intervals were the same every day, except the starting and ending time because the activity period varies according to the season and weather conditions. Most of the recordings were performed between 08:30 to 17:30 approximately, except the 12th of July and the 6th of September, when the recordings started at 10:30 due to the low air temperatures in the early morning. In the end, there were 12 videos each day. Waggle dances were recorded monthly during three consecutive days. Recording throughout the entire day allowed the understanding if there were diurnal shifts in dances and consequently, shifts in foraging locations. This gave a diverse and complete picture of the variations of the colony's foraging activity.

Meteorological data such as temperature, solar radiation, rainfall, wind speed and direction were also collected (Figure 3). Sunny days without rain and wind were ideally selected for the experiment.

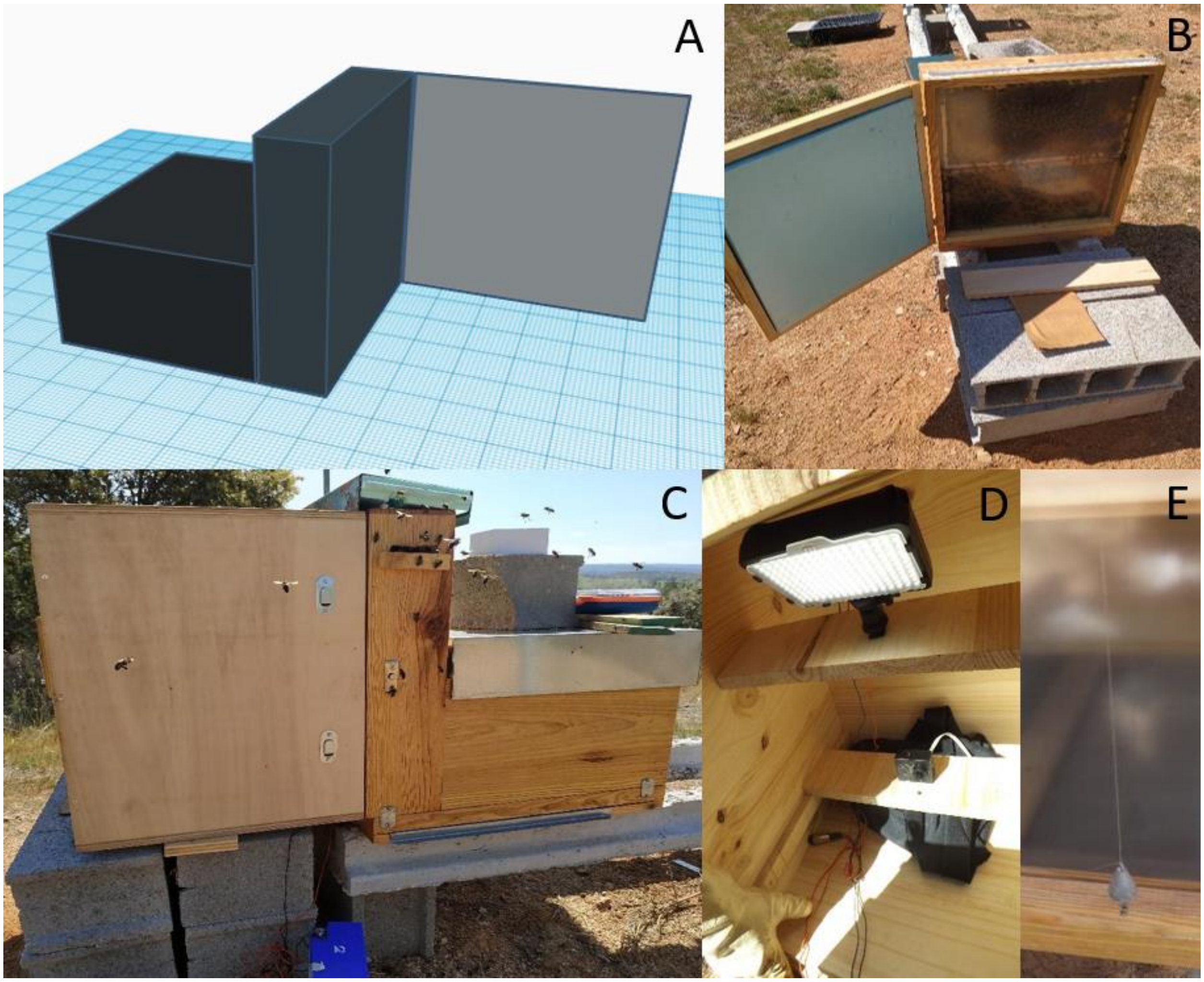

Figure 2. Structure of the modified observation hive. A. The hive is a mixture of a Langstroth hive with 10 frames (black) and a 4-frame observation hive (dark grey). The outer wall of the observation box is made from non-reflective glass, that is covered by a door with isolating material (grey) to close the hive when we are not recording. B. Real life version of the box. C. Langstroth hive while recording; D. materials used for recording: camera, power bank and LED light; E. Pendulum creating gravitation line equalling to the sun's position.

Figure 3. Meteorological station at the apiary.

2.2. Analysing recordings of waggle dances

From all the records, the waggle dances were analysed in the following days: 14th of June; 12th of July; 9th of August; 4th, 5th and 6th of September. Days were chosen based on the meteorological data and recording quality. In total, there were five hours and 40 minutes (12 videos of 28 minutes) of recordings for each day analysed.

First, videos were screened to identify which waggle dances could be decoded and afterwards the waggle dances were listed with day and hour. Afterwards, the videos were observed in slow motion (0.13X) enabling the decoding of the dance. The angle for dances to natural food sources was measured against the gravitational lines manually (Figure 4). Duration of waggle run was measured in milliseconds using Media Player Classic Home Cinema (MPC-HC X64 v1.7.13). After obtaining this information, an Excel macro developed by Peter Borgen Sørensen (Aarhus University) was used to calculate the azimuth and later, endpoint coordinates of a waggle dance. The macro makes an estimate of the direction and distance flown using the coordinates of the observation hive, date (year, month and day), time of the day, azimuth and duration of the waggle dance. For the analysis, the protocol described by Couvillon *et al*. (2012) was used.

As studies have shown that a mean of four waggle runs, not including the first and the last run, give the most precise estimate, only dances with a minimum of six waggle runs without interruption were decoded (Couvillon et al., 2012). The dance followers take a mean value to determine the distance and the direction to the food source, due to the variation in the duration and angle within the waggle runs (De Marco et al., 2008; Dyer, 2001; Tanner & Visscher, 2010; von Frisch & Jander, 1957).

All the bees in the videos that performed the complete dance (six waggle runs at least) and were consistent and visible, were measured. If there was an interruption in the video, or the "dancer" bee was covered by other bees or had left the frame throughout the process, the dance was not decoded, to keep the observation less biased possible. However, there is a chance that some of the dances were performed by the same bee for the same resource. In June, decoding only one day (14th of June) resulted in 183 usable dances, in July (12th) 32 dances, in August (9th) 22 dances and in September no dances were recorded.

Figure 4. Way of measuring waggle dance direction. Picture represents the sequence of frames in the same waggle run. On the left it is the start and, on the right, the end of a same waggle run. To measure the direction of the waggle dance, a line (red line at the picture) was drawn between the starting and ending point of the waggle run (red points). As thorax does not move in the process, it is the best part of the body for a reference. then the angle (α^0) against the gravitational line was measured

2.3. Assessing flower resource availability

The experimental area consisted of a 10×10 km "landscape window" with the hive located in the centre of the square. This area was mapped by GIS team within the project by identifying all the polygons in the landscape (Figure 5). From the 13 landcover types identified, only eight were sampled for resource availability. The sampled landcover types were: Forests, Fruit trees, Unproductive areas, Pastures with trees, Pastures with shrubs, Pastures and the margins of Water Surfaces and Road Networks.

The resources were assessed at a smaller area, a square of 1.5Km x 1.5Km located at the centre of the landscape window. Five sampling sites were defined for each landcover within this small area and each one was visited monthly to collect information about the plant resources present at that time. The results where extrapolated for 10×10 km area later. These sites were chosen semi-randomly, using an orthophoto, previous field observations and distribution and accessibility throughout the landscape. At each sampling site, the abundance of the available resources was assessed. The floral resources found were identified to species level using available floras (Alejandre Saénz et al., 2006 ; 2014 ; Castroviejo, 1986-2012) and their relative abundance were visually estimated at each sampling point. Then, each landcover type was characterized calculating the mean values of species abundance at the sampled polygons of the correspondent landcover type. The landscape characterization allowed us to compare the information obtained from the waggle dances with the surrounding environment and resource availability. To produce all the maps, GIS specialists used QGIS 3.4.6-Madeira (QGIS Development Team, 2018).

Each plant species recorded in the experimental area was then characterized based on literature analysis. Information such as flowering phenology, resource production quantity and quality and apicultural interest was collected from the bibliography (Flora-On., 2014 ; Castroviejo, 1986-2012). After obtaining all the available information, each plant species was classified from 0 to 3 for their Nectar and Pollen importance, with 0 representing no resource, and 1 to 3 representing low, medium and high resource availability, respectively. The classification in these categories was not always easier and the most comprehensive data sets consisted on a Danish bee calendar (Meneguetti, 2013), manuscripts about plants of apicultural interest in Spain (Carrasco, & Ruiz, 1989; Talavera et al., 1988) and books devoted to bees and honey production (Aguado Martin et al., 2017; Sáenz Laín & Ferreras, 2000). As several sources of information worldwide were used, when there were different values available for the importance of the resources of a given plant species, an average value was given to the species or decision was based on an expert opinion. For example, for *Lotus corniculatus* three different values (all independent from plant abundance) were found in the literature, all of them from Spain (Aguado Martin et al., 2017; Sáenz Laín & Ferreras, 2000). In this case an average value was used as all the data was from the same country (and the country where the study was conducted). For *Echium vulgare*, resource importance value was based on expert opinion given the available literature on pollinator assemblages and bee visitation patterns for this species. Additionally, there were also cases in which there was available information about some species from surveys in Spain (e.g., Carrasco, & Ruiz, 1989); however, the values provided were very different from field observations in the country (Aguado Martin et al., 2017; Sáenz Laín & Ferreras, 2000) as well as from the newest report of the Danish Bee Calendar (Meneguetti, 2013), and thus the values from Danish Bee Calendar were used instead.

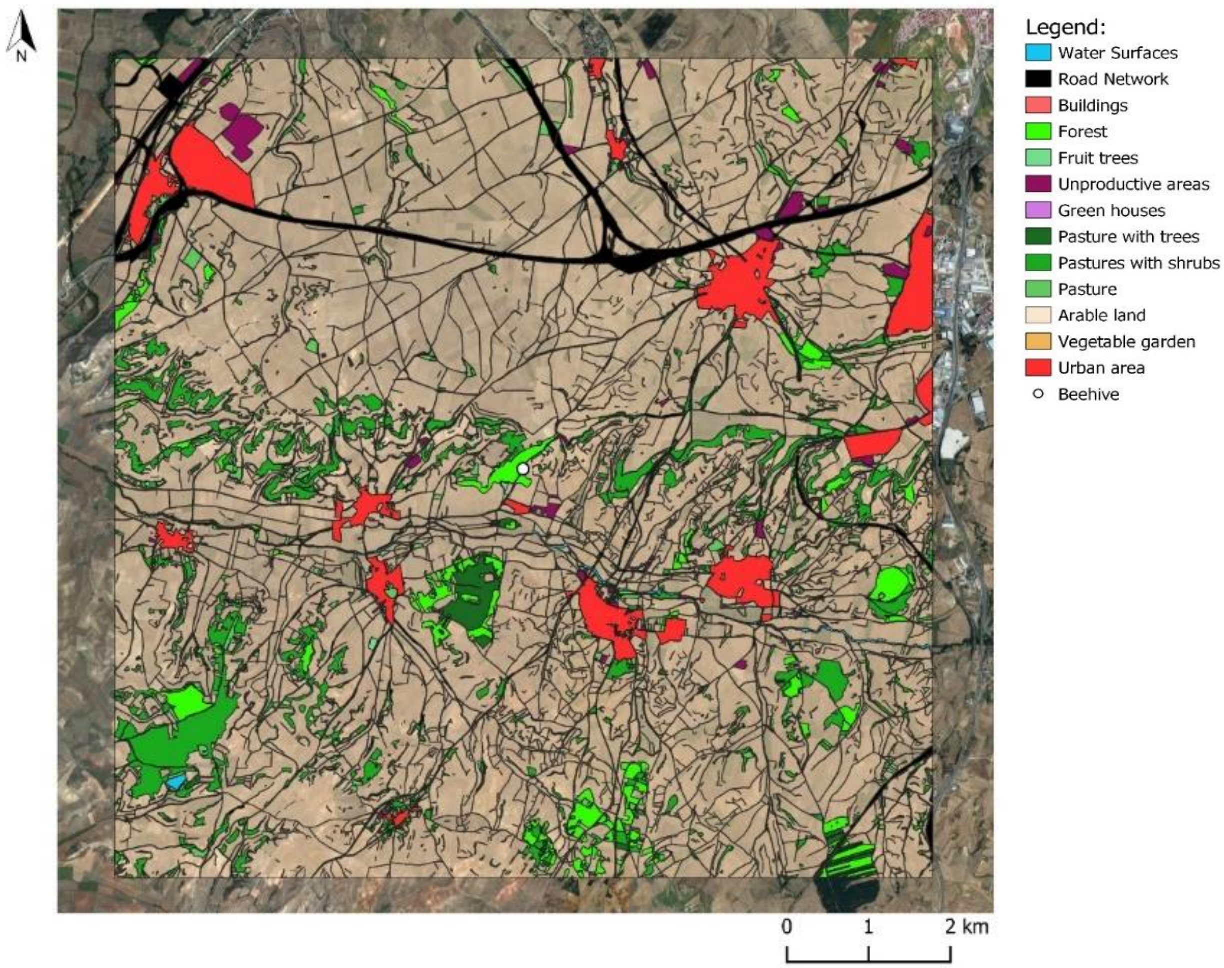

Figure 5.. Spatial variation of landscape around the hive. The experimental area covered a square area of 10×10 km with the hive located in the centre of the square (white dot). The 13 landcover types identified are marked with different colours.

In case information was not available about the value of resources, individual search for floral biology studies was made to assess nectar production and bee visitation and, based on this information, depict its importance as honey and pollen producing plant. Additionally, the species was analysed at a genus level by comparing flower morphology and attributing mean values for the genus. For example, there were five *Centaurea* species found in the landscape, however, information about their resource availability was found only for three of them, namely *C. aspera* subsp. *aspera, C. cyanus, C. jacea* subsp. *angustifolia*. The two species without information (*C. calcitrapa* and *C. cephalariifolia*) were classified using the mean values of the genus based on the three species with information. There were three species identified only to the family level, i.e. Compositae, in the field. In this case, average value of all the available species at the landscape from the same family was attributed to the sample. In the end, a list of all the available flowering species in the landscape was created, with the values attributed for nectar and pollen importance (Annex I).

After species classification, a mean value of nectar and pollen availability were calculated for each landcover type. Formulas used were developed specifically for this work.

Nectar availability was calculated with a following formula:

$$NA_j = \frac{\sum_1^m N_i \times sp_{i\%}}{m} \qquad (1)$$

Pollen availability was calculated with a following formula:

$$PA_j = \frac{\sum_1^m P_i \times sp_{i\%}}{m} \qquad (2)$$

Total Flower Resource availability was calculated with a following formula:

$$RA_j = \frac{\sum_1^m (P_i + N_i) \times sp_{i\%}}{m} \qquad (3)$$

Where:

NA_j – Nectar Availability for a landcover type

PA_j – Pollen Availability for a landcover type

RA_j – Flower Resource Availability for a landcover type

P_i – Value for pollen importance (PIV)

N_i – Value for nectar importance (NIV)

m – number of sampling sites for a landcover type

$sp_{i\%}$ - abundance of the species

Each sampled landcover type got one value that was later used to map the resource availability (final values can be found in Annex II) over space and time (for June, July, August and September). All the agricultural fields with crops were graded according to the flowering phenology. In the periods of flowering, plants were given abundance of 100%, while in other months their abundance was marked as 0%. For example, sunflower fields only got the value of 100% for abundance in August, while rapeseed, green pea and other grain legume fields had value of 100% in June. Alfalfa fields could be flowering any month from June to August, depending on the period they were planted. For the whole summer period we attributed abundance of 100% to all the existing fields of alfalfa in the study area due to the lack of available information about the planting periods.

3. Results

In total, 237 waggle dances were decoded providing useful information on the foraging locations of the honey bees. In June, 183 dances were performed and decoded, while in July this number was 32 and in August it was even smaller with only 22 dances decoded. There were no waggle dances observed in September. Almost all the foraging locations were concentrated to the East from the hive, avoiding sites in the Western part of the landscape (Figure 5-6). Foraging range of honey bees varied from 190 to 6405 metres in June, from 194 to 4985 m in July and from 246 to 3472 m in August. Average foraging distances were 1524, 1599 and 2340 m in June, July and August, respectively. In June, two cases were detected were bees danced for locations further than 6000 m.

Changes in the foraging patterns (foraging location and distance) and number of dances performed were visible between the three studied months. All the foraging locations obtained from the waggle dance decoding are presented in Figure 6, where these different patterns are noticeable. In June, foraging locations were located in several patches close to the hive, but also at higher distances. While in July, they were more scattered around the landscape and only one small patch is signalled by honey bees near the hive (in the North-East to the hive). In August, foraging locations were located at a higher distance from the hive.

Relative frequency of the flight distances is presented in Figure 7 for each month. In June, almost all the decoded waggle dances resulted in coordinates within a three-kilometre zone from the hive, with only 3.3% (six out of 183) of waggle dances resulting in foraging locations at more than 3000 m from the hive. However, it is noticeable that honey bees exploited the eastern part of the landscape evenly at several distances (Figure 5-6). In July, flight distance pattern revealed a slight increase in the number of dances for locations at 1000 and 1500 m distance from the hive with 65.7% of the dances being located within 1500 m, and a slight increase in the flights for distances farther than 3000 m. Foraging pattern in August was considerably different from the previous two months. Honey bees exploited few resources close to the hive and move to the farther distances (3000 m and more; Figure 7). From a total of 22 waggle dances, 18.2% were performed close to the hive (up to 500 m) and 18.1% for the resource locations up to 2500 meters, while 63.4% were made for distance of 3000 m or more.

A detailed landscape structure (with the separation of the different crop types) is presented in the Figure 8 revealing all the polygons classified with landcover types within the 10×10 km experimental area. The study area was mostly agricultural/arable land, with a great dominance of cereal crops. Besides cereals, alfalfa (*Medicago sativa*) and sunflower (*Helianthus annuus*) fields are widely present in the study area.

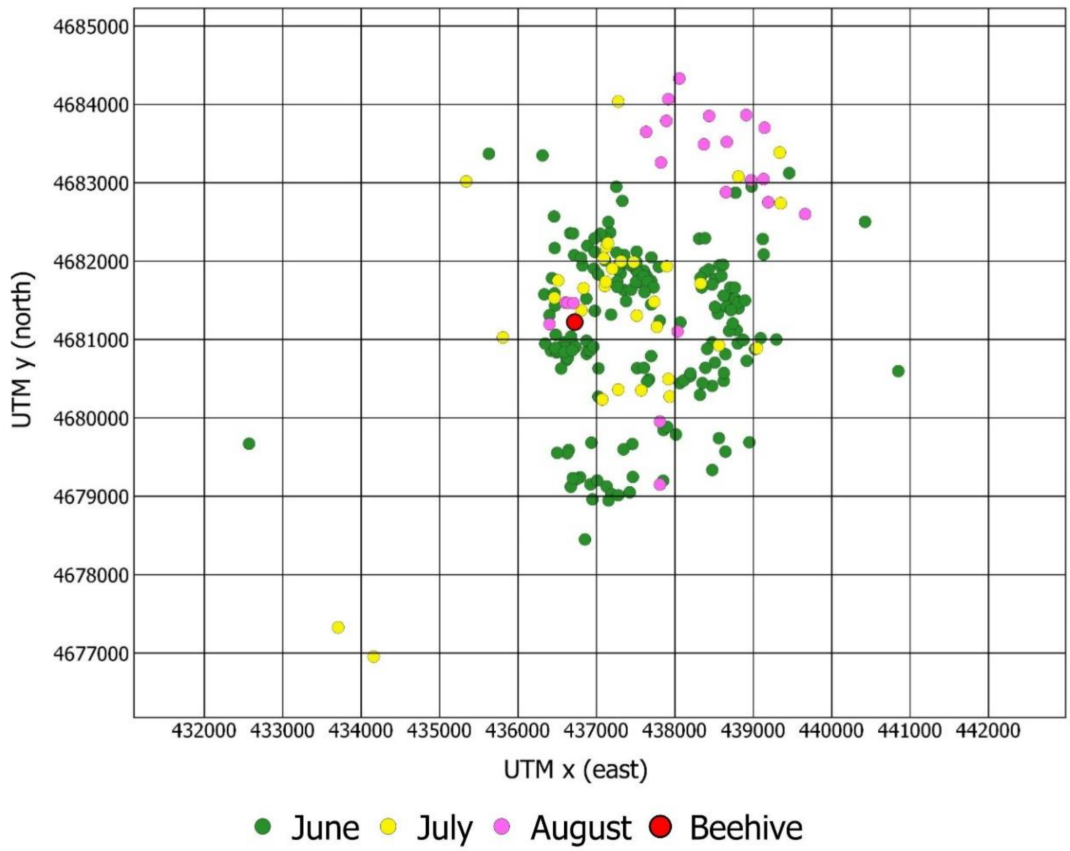

Figure 6. Foraging pattern obtained by decoded waggle dances for June, July and August 2018. The three-month results are separated by colour, respectively green, yellow and pink, allowing to distinguish the patterns from one another.

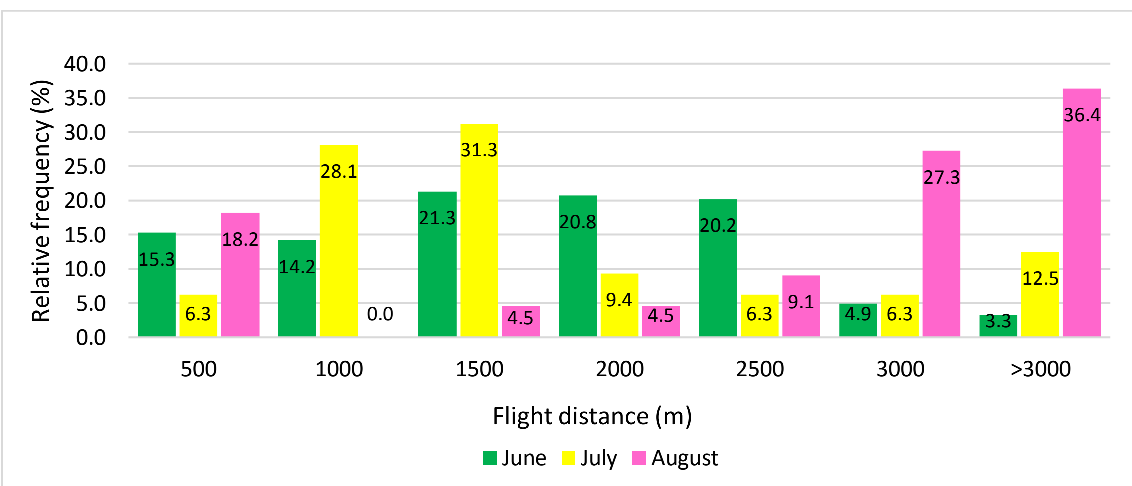

Figure 7. Relative frequency of the flight distances obtained from waggle dance decoding in June, July and August. The three-month results are separated by colour, respectively green, yellow and pink, allowing to distinguish the patterns from one another

From all the crop species around the landscape, only alfalfa, sunflower, rapeseed and legumes could provide floral resources in the summer months. Green peas and other grain legumes flower in May and June, rapeseed flowers in June, alfalfa can be found in the landscape all the time from June to August, and sunflower is mostly present in August, although starting flowering from the end of July. Patches of fruit trees and pastures were also observed, with small urban areas distributed around the landscape. Different types of pastures with shrubs and trees as well as forests can also be seen as small patches around the landscape (Figure 8).

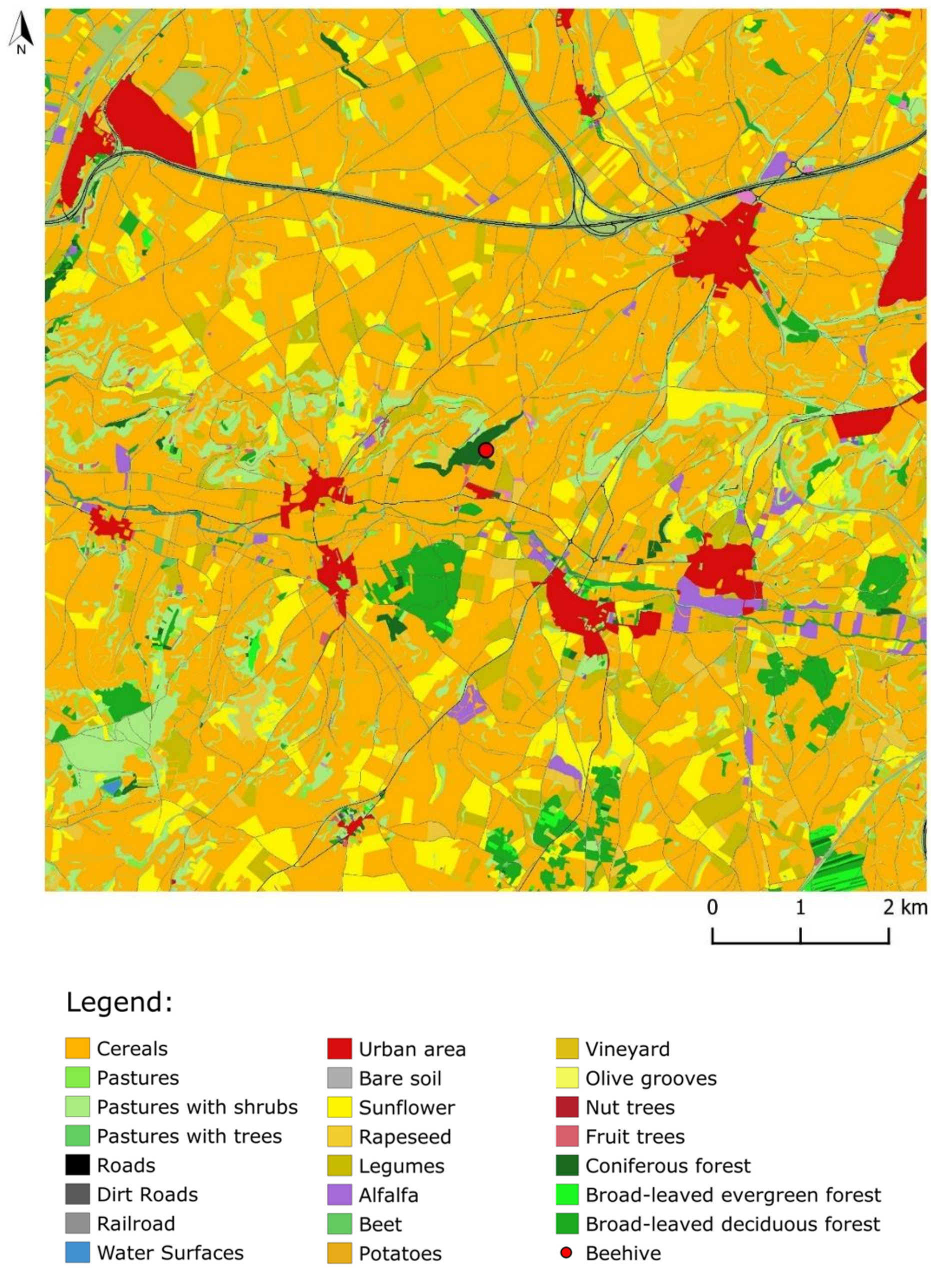

Figure 8.Landscape structure around the hive. The landcover types in natural areas identified previously are marked with different colours. Agricultural fields are also defined by the colours.

The total number of plant species providing resources in the landscape assessed by month where 43, 41 and 13 in June, July and August, respectively. However, the abundances changed between months and in July and August as depicted in Tables 1-3, presenting the lists of the 10 species providing the most abundant flower resources in the three most important landcover types signalled by honey bees for foraging.

In unproductive areas (Table 1) in June, floral resources with very diverse and scattered, and *Rosa canina, Phlomis lychnitis, Papaver rhoeas*, *Cirsium pyrenaicum*, *Vicia sativa* and *Cirsium arvense* were the most abundant floral resources (with abundances of 11.4%), from a total of 17 species observed. In July, *Phlomis lychnitis* and *Papaver rhoeas* continued as most abundant resource, with the addition of new species such as *Phlomis purpurea* and *Santolina chamaecyparissus* (with summing abundances of 6.4%), from a total of 14 species flowering. In August, floral resources were scarcer and this landcover presented only three species providing floral resources such as *Cirsium arvense, Eryngium campestre* and *Carlina corymbose.*

Table 1. List of 10 species providing the most abundant flower resources in unproductive areas and their average abundances in percentage

List of 10 most abundant flower species and their average abundances in unproductive areas					
June		**July**		**August**	
Species	**Abund.**	**Species**	**Abund.**	**Species**	**Abund.**
Rosa canina	2.14%	*Phlomis lychnitis*	2.14%	*Cirsium arvense*	0.71%
Phlomis lychnitis	2.14%	*Papaver rhoeas*	1.43%	*Eryngium campestre*	0.71%
Papaver rhoeas	2.14%	*Phlomis purpurea*	1.43%	*Carlina corymbose*	0.71%
Cirsium pyrenaicum	2.14%	*Santolina chamaecyparissus*	1.43%		
Vicia sativa	1.43%	*Centaurea cephalariifolia*	0.71%		
Cirsium arvense	1.43%	*Centaurea cyanus*	0.71%		
Euphorbia serrata	1.14%	*Cirsium pyrenaicum*	0.71%		
Centaurea cyanus	0.86%	*Globularia vulgaris*	0.71%		
Genista scorpius	0.86%	*Teucrium chamaedrys*	0.71%		
Centaurea cephalariifolia	0.86%	*Convolvulus arvensis*	0.29%		

In pastures with shrubs (Table 2) in June, resources were more abundant than in unproductive areas and *Genista scorpius* was the main species proving floral resources (abundance of 36.0%), followed by the *Lotus dorycnium, Euphorbia serrata, Lavandula stoechas*, *Linum suffruticosum*, *Lotus corniculatus* and *Phlomis lychnitis* (summing abundances of 34.0%), from a total of 15 species flowering. In July, the list of most abundant species in this landcover was completely different from the ones in June, with *Santolina chamaecyparissus, Phlomis lychnitis, Lotus dorycnium, Peucedanum carvifolia*, *Pulicaria odora* and *Helichrysum stoechas* being the main species present in this landcover type (summing abundances of 31,0%), from a total of 11 species. In August, floral resources were again scarce and there were only five species flowering, with *Carlina corymbose, Eryngium campestre* and *Lavandula latifolia* being the most abundant among them.

Table 2. List of 10 species providing the most abundant flower resources in pastures with shrubs and their average abundances in percentage

List of 10 most abundant flower species and their average abundances in pastures with shrubs					
June		**July**		**August**	
Species	**Abund.**	**Species**	**Abund.**	**Species**	**Abund.**
Genista scorpius	36.00%	*Santolina chamaecyparissus*	7.00%	*Carlina corymbosa*	11.00%
Lotus dorycnium	8.00%	*Phlomis lychnitis*	6.00%	*Eryngium campestre*	8.00%
Euphorbia serrata	8.00%	*Lotus dorycnium*	5.00%	*Lavandula latifolia*	2.00%
Lavandula stoechas	6.00%	*Peucedanum carvifolia*	5.00%	*Helichrysum stoechas*	0.20%
Linum suffruticosum	6.00%	*Pulicaria odora*	5.00%	*Mantisalca salvantica*	0.20%
Lotus corniculatus	3.00%	*Helichrysum stoechas*	3.00%		
Phlomis lychnitis	3.00%	*Campanula lusitanica*	2.00%		
Cirsium arvense	2.00%	*Pallenis spinosa*	2.00%		
Rosa canina	2.00%	*Teucrium polium*	2.00%		
Santolina chamaecyparissus	2.00%	*Onobrychis viciifolia*	1.00%		

In forests (Table 3) in June, resources were also more abundant than in unproductive areas and similarly abundant as in pastures with shrubs, and *Genista scorpius, Thapsia villosa* and *Cirsium arvense* were most abundant species followed by *Cistus laurifolius, Crataegus monogyna, Euphorbia serrata, Phlomis lychnitis and Thymus vulgaris* (summing abundances of 42.0%), from a total of 16 species flowering. In July, the list of the most abundant species was different from June, with *Thapsia villosa, Helichrysum stoechas, Phlomis lychnitis* and *Nigella gallica* being the most important resources (summing abundances of 17.2%), from a total of 10 species. In August, again only six species were flowering, with *Jasonia tuberosa, Eryngium campestre* and *Lavandula latifolia* being the most abundant among them.

Table 3. List of 10 species providing the most abundant flower resources in forests and their average abundances in percentage

List of 10 most abundant flower species and their average abundances in forests					
June		**July**		**August**	
Species	**Abund.**	**Species**	**Abund.**	**Species**	**Abund.**
Genista scorpius	8.00%	*Thapsia villosa*	6.20%	*Jasonia tuberosa*	3.00%
Thapsia villosa	8.00%	*Helichrysum stoechas*	4.00%	*Eryngium campestre*	2.00%
Cirsium arvense	6.00%	*Phlomis lychnitis*	4.00%	*Lavandula latifolia*	2.00%
Cistus laurifolius	4.00%	*Nigella gallica*	3.00%	*Carlina corymbosa*	1.00%
Crataegus monogyna	4.00%	*Phlomis purpurea*	2.00%	*Helichrysum stoechas*	1.00%
Euphorbia serrata	4.00%	*Santolina chamaecyparissus*	2.00%	*Mantisalca salvantica*	1.00%
Phlomis lychnitis	4.00%	*Teucrium polium*	2.00%		
Thymus vulgaris	4.00%	*Centaurea cephalariifolia*	1.00%		
Santolina chamaecyparissus	3.00%	*Pulicaria odora*	1.00%		
Achillea millefolium	2.00%	*Achillea millefolium*	0.20%		

These temporal shifts in plant dominance originated a significant decrease in resource availability, as shown by the values for flower resource availability calculated using abundances and species importance (Formulas 1-3) (Table 4). For example, the value for floral resource availability in forests has decreased from 2.625 to 0.982 from June to July, while this number for pastures with shrubs have changed from 2.577 to 1.369 (Table 4 and Annex II).

Table 4. Final values of flower resource (Nectar & Pollen) availability for sampled polygons for the studied months.

Polygon	June	July	August
Water Surfaces	0.671	0.213	0.110
Road Network	1.101	0.884	0.758
Forest	2.625	0.982	1.075
Fruit trees	1.864	0.970	0.676
Unproductive areas	0.719	0.582	0.750
Pasture with trees	2.010	2.869	0.000
Pasture with shrubs	2.577	1.369	1.368
Pasture	0.927	0.650	0.733

In natural areas, we have found a diversity of plants species flowering, instead of dominance of a given plant species. Pastures with shrubs and forests were the landcover types often signalled by honey bee in their dances, although some dances also signalled for resources in the unproductive areas (Figures 9, 10 and 11). Landscape analysis show visually the temporal shifts in total resource availability at the landscape level (Figures 9, 10 and 11). Though nectar availability is changing in general, there are still high resource patches (darker patches) throughout the whole summer, represent by alfalfa fields (A-III-1, A-III-3, A-III-5). Pollen availability seems to have decreased in July when compared to June, and then increased again in August with the flowering of sunflowers (A-III-2, A-III-4, A-III-6). In general, total floral resources slightly decreases in July, and then, increases in August due to the sunflower flowering in August (Figures 9, 10 and 11), creating more resources, although scattered, around the landscape (Figures 8 and 11).

Landscape analysis also enable us to overlap the foraging points obtained from the waggle dances with floral resources to understand the temporal and spatial foraging patterns of honey bees (Figures 9, 10 and 11).

In June, there are several clusters of points in resource areas close to the hive. Honey bees seemed to forage mainly in forests and pastures. Also, in a few cases in legume and alfalfa fields. Some foraging locations were located in urban areas and on roadside vegetation (Figures 8 and 9).

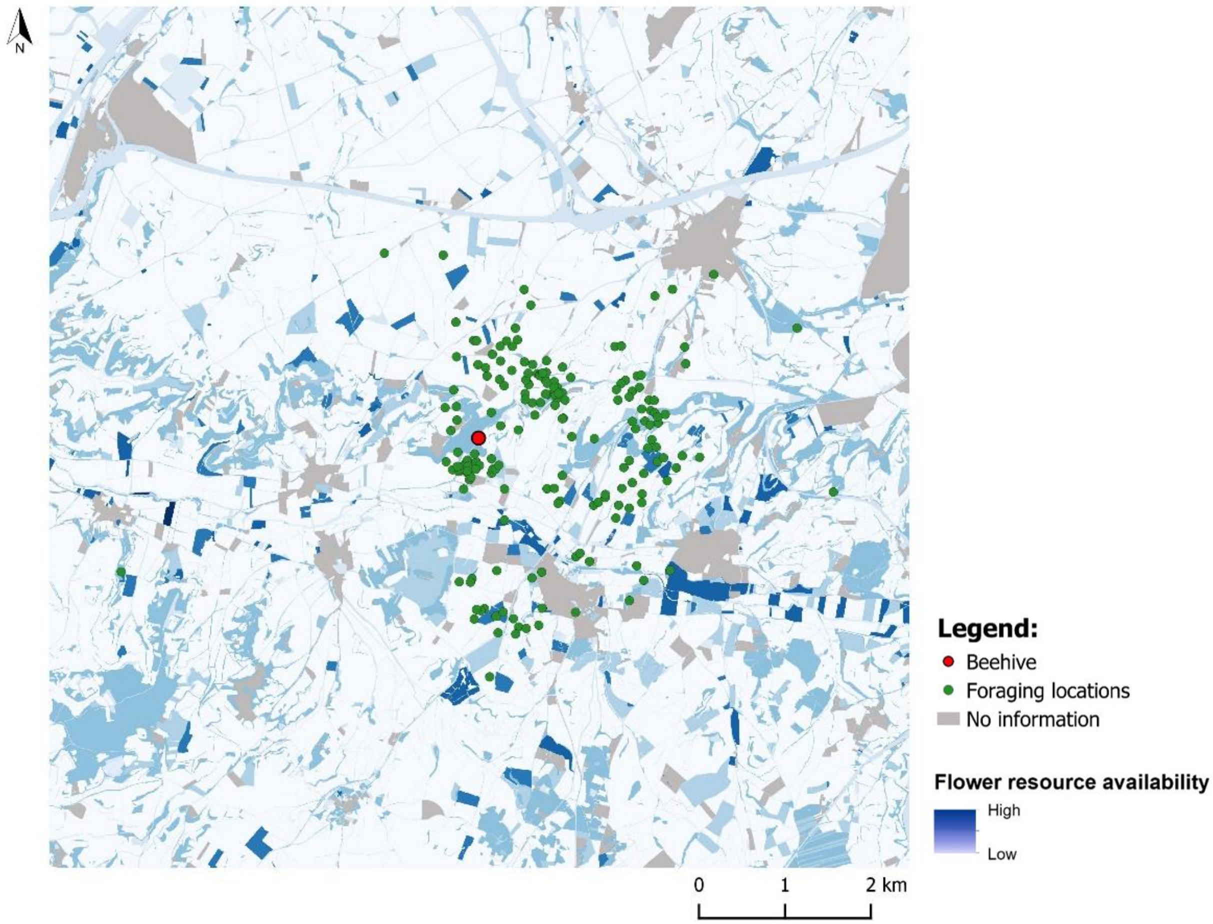

Figure 9. Total Floral Resource availability with the foraging locations obtained by waggle dance decoding in June 2018. Map was created with the polygon values based on the floral resource importance. Foraging locations obtained by waggle dance are represented with green circles. Areas, with no information are in grey. A gradient of blue is representing resource availability (white – no resource, dark blue – high resource availability). Maps representing Nectar and Pollen availability separately, can be viewed in Annex III.

In July, foraging location endpoints were much sparser than in June similarly to the sparse resources available in the landscape (Figures 8 and 10). Resource availability seems to be lower than in June with a decrease of wild resources in most of the landscape, especially in pastures with shrubs and forests. The foraging points appeared mostly near the river edges and by the roads. There were still some foraging locations found in the forest and pasture patches close to the hive. Also, some points were present in or close locations to unproductive areas as well as by urban areas. Although the most common resource present this month was alfalfa, foragers do not seem to have danced for this resource.

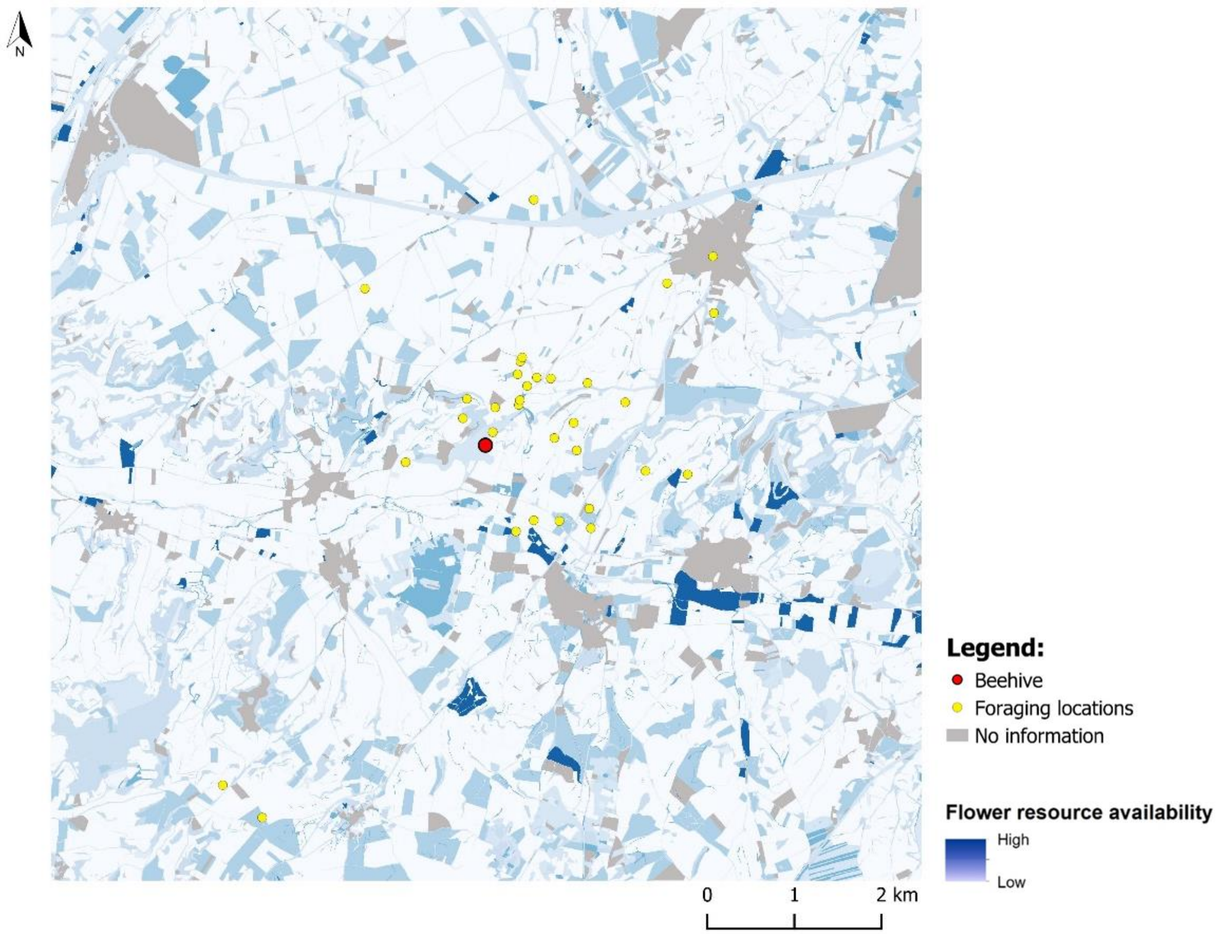

Figure 10. Total Floral Resource availability with the foraging locations obtained by waggle dance decoding in July 2018. Map was created with the polygon values based on the floral resource importance. Foraging locations obtained by waggle dance are represented with yellow circles. Areas, with no information are in grey. A gradient of blue is representing resource availability (white – no resource, dark blue – high resource availability). Maps representing Nectar and Pollen availability separately, can be viewed in Annex III.

In August sunflower created the largest amount of floral resources in the landscape (Figures 8 and 11). Bees seemed to forage mainly in sunflower fields and by the sides of the roads, but also in pasture with shrubs and trees and forests on a few western locations from the hive. They have also danced for the broad-leaved deciduous forest that is following the river throughout the landscape.

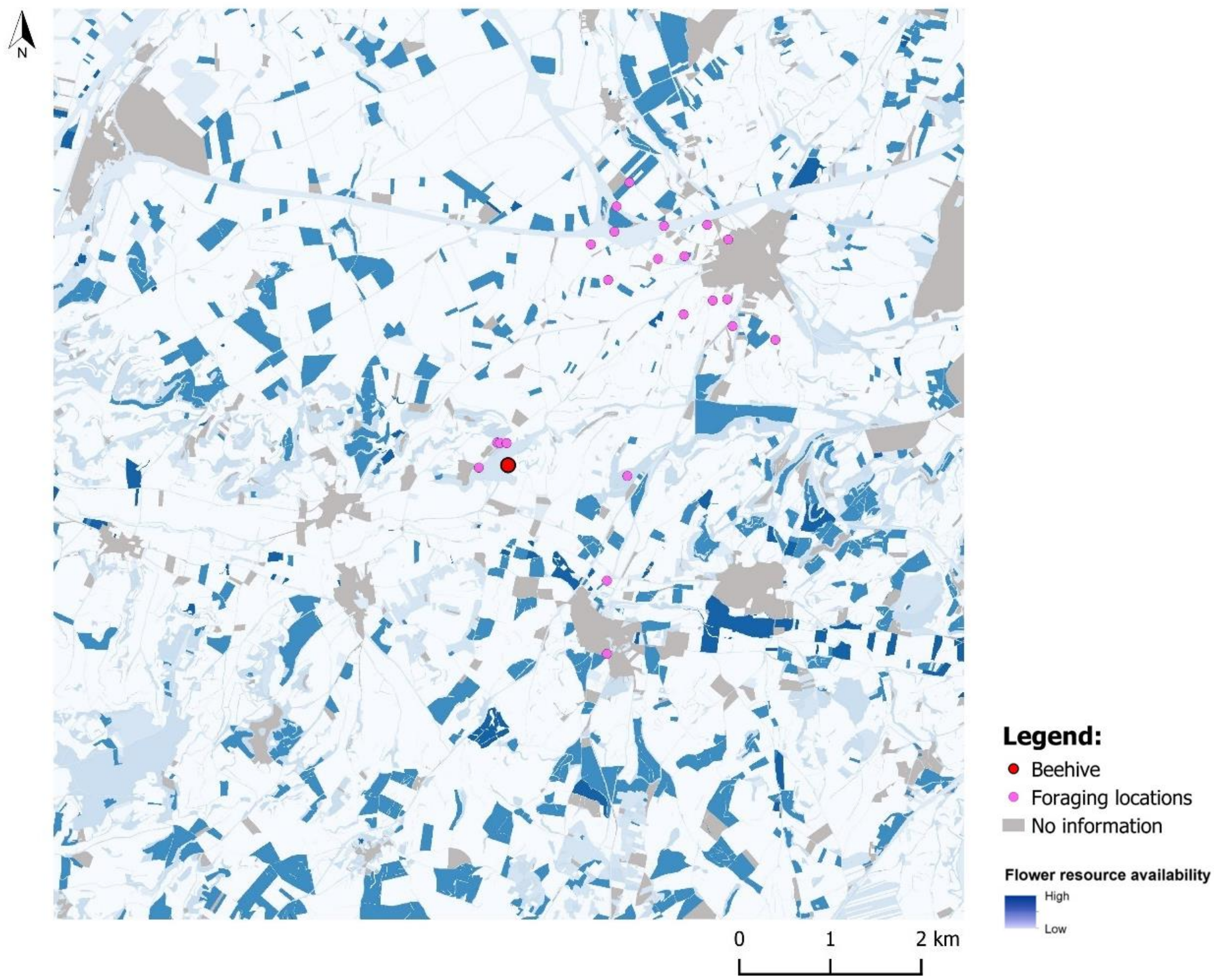

Figure 11. Total Floral Resource availability with the foraging locations obtained by waggle dance decoding in August 2018. Map was created with the polygon values based on the floral resource importance. Foraging locations obtained by waggle dance are represented with pink circles. Areas, with no information are in grey. A gradient of blue is representing resource availability (white – no resource, dark blue – high resource availability). Maps representing Nectar and Pollen availability separately, can be viewed in Annex III.

4. Discussion & Conclusions

4.1. Honey bee foraging distances and its variation in time and space

As expected, our study revealed spatial and temporal variability in floral resources in the landscape, and consequently also on the foraging locations of honey bees decoded from waggle dances. Honey bees did not forage randomly in the studied landscape. Despite the existence of abundant resources in the western part of the area (especially on pasture patches), honey bees explored locations on the eastern part of the area. This could be attributed to the existence of dense forested areas on the west side of the hive, that could have hampered foraging activity, making it hard for the individual foragers to cross it. Studies have shown that honey bees are sensitive to foraging economics. If there is an option for resources close to the hive that has equal quality as the one far away, honey bees will explore closer resources (Seeley, 1995; Seeley et al., 2000). In June, almost all the decoded waggle dances resulted in coordinates within three-kilometre zone from the hive, showing that most of the foraging activity occurred nearby the hive. In July and August, average distances have increased compared to June, being a result of a decreased food availability around the hive.

A study performed in Sussex, UK has found that the reason why honey bees forage at longer distances from the hive during July and August is due to the scarcity of floral resources in summer (Balfour et al., 2015). Our results follow the same pattern, indicating that the honey bees foraged on nearby abundant resources earlier in the season, increasing the distance as the season advanced and exploring at higher distances later in summer. In June, resource availability is high, thus honey bees explore the landscape within a 2500 m area and collect the multiple resources available. Occasional dances for a distance higher than 6000 m, are probably an indicative of particularly good resource sources. But, because of the wildflower resources available close to the hive, they save energy by foraging close by. In July, there is a decrease of the resource sources such as rapeseed and legumes, as well as wildflowers nearby the hive. There are still alfalfa fields available, but our analyses suggest that honey bees do not seem to be exploiting them. However, there are some points nearby water courses, probably suggesting that they forage in deciduous riparian forests. However, it is important to notice that honey bees can be dancing for any necessary resources for the hive, not only for floral resources (Couvillon et al., 2014b). Thus, for example, these points can be signalling water resources in summer. In August, it is noticeable that there is a higher number of dances with locations further than 2500 m compared to the dances in June and July. Since wildflower resources lack in this period (only 13 species of plants were observed flowering in August) they need to find further resource locations. Also, the main source of the nectar and pollen in August is sunflower fields, being present farther away from the hive. There have been some foraging points near the river in August as well, further strengthening the idea of some dances being for water resources signalling. It is previously known that summer is the hardest period for the honey bees due to the scarcity of resources (Couvillon et al., 2014a). Based on our results, we can conclude that in August resources are scarce close to the hive, that is why 40% of the dances indicate the locations further than 3 km distance.

A few round dances were also observed during all summer months. In these dances, the honey bee simply dances around itself, indicating that food resource is very close to the hive. This would, most probably, correspond to the forest patch on the west side of the hive, or the pasture with shrubs that had diverse floral resources. Also, some cereal crop fields are present around, that could have some wildflowers available thought the field.

Landscape analysis have shown temporal shifts in resource availability. Though nectar availability was changing, there were alfalfa fields available throughout the whole summer. However, alfalfa fields did not seem to be a very attractive resource for honey bees as very few points decoded by the waggle dances overlapped with these fields (Figure 8-10). Pollen and overall floral resource availability seem to have decrease in July compared to June, and then increased again in August (Figure 8-10). This increment in August was mainly due to sunflower flowering season, which provides more resources around the landscape (Figure 8-10). Sunflowers are insect-pollinated plants and the main pollinators are indeed honey bees (Chambó et al., 2011; Morgado et al., 2002). Consequently, honey bees were shown to actively explore sunflower fields, being a resource of major importance in summer.

Every month, some of the dance results indicated the foraging locations in patches that were classified as having no resources or near urban areas. These could possibly be the fruit blossom trees or wild flowers that passed undetected in the field surveys. Indeed, it was not feasible to quantify pollen and nectar sources near town areas, and thus we cannot be sure which fruit trees or other flowering plants were in some of the patches in the landscape. Additionally, agricultural fields with crops such as cereals could have some wildflowers that we have not assessed and that could provide a resource that, once again, passed undetected but was explored by honey bees. This would not affect our results, but the functional diversity of the area could have been different.

4.2. Waggle dances – interpretation and importance

Honey bees showed a clear preference for landscape elements rich in wild flower resources, when available, and a preference for sunflower fields in August. The preference for these landscape elements is explained by the higher quantity of nectar and pollen resources and possibly also resource diversity, as well as the fact that mass-flowering crops such as sunflower fields are particularly attractive especially in August when they represent almost only available food sources.

Some of the previous studies have used less than three km radius area to assess foraging behaviour of honey bees (Couvillon et al., 2014b; Nürnberger et al., 2017). From our results it is clear that considering this distance one cannot capture the complete picture of foraging locations in summer, as honey bees tend to go to farther distances. In June, resources available within three km distance from the hive seemed to be satisfactory to the colony needs, and honey bees stay in the close by locations. But in July and August they tend to dance for the farther locations. Thus, although not necessarily in spring and summer, studies incorporating bigger areas are better for summer analyses. Because of this, 10km×10km landscape, used in this study is more appropriate to get the complete view of the patterns of the use of the landscape.

Honey bees are continuously searching for new food sources due to the seasonal shifts in flowering plants. This way they try to take advantage of the flower-rich fields when in bloom. With the increased distance from the hive, their success of discovering new food sources decrease (Visscher & Seeley, 1982). In our study, from the agricultural fields we clearly see more dances related to legumes in June, some for alfalfa in July and sunflower in August. This could potentially be an indication of the colony identifying in the landscape and valuing these plants as more profitable and therefore generating more dances so that more individuals exploit these resources. This study proves that honey bees are, indeed, good at this, or else they would not have found the better fields in July and August, when main food source from June was not available anymore.

Forest at the west side of the study area was also used for foraging; In these landscape elements, honey bees frequently find a high diversity of wild flowers, including *Genista scorpius* (PIV-3), *Cistus laurifolius* (PIV-3) and *Euphorbia Serata* (PIV-2), which are particularly relevant as pollen sources and *Phlomis lychnitis* (NIV-3) with high relevance as nectar source. In these forests, at different times, species with high nectar and pollen importance have been also described, such as *Cirsium arvense* (NIV-3, PIV-2), *Crataegus monogyna* (NIV-2, PIV-2,5), *Thymus vulgaris* (NIV-3, PIV-2), *Nigella gallica* (NIV-3, PIV-3), *Jasonia tuberosa* (NIV-2, PIV-2), *Eryngium campestre* (NIV-2, PIV-2) and *Lavandula latifolia* (NIV-3, PIV-2).

In August, because of the decrease of resources closer to the nest, bees had to search for food at farther distances. Smaller number of waggle dances in August could also reflect the low resource availability. In the study by Couvillon *et a*l. in 2014, significantly more foragers returned without resources in August and September, then in previous months (Couvillon et al., 2014a). In September, there were no dances implying that the honey bees might not had any resource in the landscape to signalling to other workers.

Waggle dances are very important for an efficient exploitation of the landscape by honey bees, especially in intensive agricultural landscapes such as the ones in Burgos region. Regarding the usefulness of decoding the waggle dance to correctly assess where the honey bees collected their pollen, we can conclude that the decoded waggle dances did, in fact, point towards the most abundant resource locations in the landscape. This corresponds to the contemporary assumption that honey bees upweight costs and benefits before dancing for resources. Together with the landscape analysis, we were able to make an educated guess to where the honey bees found their food sources, although it was not 100% precise.

Bees need diverse flower resources especially as pollen supply (Requier et al., 2015). Within the diverse landscape, bees maximize resource diversity intake, to have sufficient amounts of resources for all functional needs (Kaluza et al., 2017). Study by Filipiak (2019) has found that for nutritional balanced diets bees need not only nectar and pollen rich plants, but also diverse plant species to obtain specific elements. Examples of key plant species providing a dietary stoichiometric balance for bee larvae, found in the study, that were also available in our landscape, were *Sinapis arvensis* and *Rubus ulmifolius* (Filipiak, 2019). Also, species from *Trifolium*, *Vicia* and *Brassica* genera have been identified as important for honey bee dietary needs. For *Osmia bicornis L.* pollen with high quantity of phosphorus, copper and zinc were more demanded for the fitness of the female bees (Filipiak, 2019). For future studies, not only nectar and pollen quantity and quality should be assessed, but specific nutritional needs of the honey bees should also be considered. For example, we have marked dandelions with 3/3 for nectar and pollen importance, even though they lack one of the 10 crucial amino acids for the honey bee nutrition (Keller et al., 2005). More detailed study of the nutritional needs of the honey bees is necessary for the conservational purposes.

Because most of the flower-rich biotopes in agricultural landscapes are slowly decreasing in number and size, it is extremely important for successful and efficient honey bee management to guarantee that there are flower sources available in the landscape both in abundance and diversity. Honey bees need a balanced diet, so for them to successfully thrive we need to develop bee-friendly practices. Practices such as sowing more diverse crops and being careful when ploughing the fields, restoration of field hedgerows or the implementation of floral stripes are just some examples of bee-friendly practices (Delaplane, 2010). Alternating the regime of the trees pruned in the odd or even years, would make it possible to have half of the trees flowering each year (van der Sluijs & Vaage, 2016). Because, bee's dietary needs are still understudied, it is challenging to assess the important resources for the honey bees. However, we know that proteins, amino acids and some chemical elements are especially needed (Filipiak, 2019). The method of our study was to characterize the importance of plant species to honey bees, that in most cases, is based on the flower properties and nectar production information and is useful for having a general overview of available resources and infer about their consequences for colony maintenance and survival.

4.3. Methodological strengths and constrains and alternative solutions

Our analysis showed a good overlap between the foraging points decoded from the waggle dances and the distribution of resources in the landscape surrounding the hive. Thus, foraging distances and floral resource availability are linked, and waggle dance results can be used to determine the conservation areas for the honey bee colonies.

In this study, we succeeded in recording and decoding waggle dances with a simple set-up method. The simplicity of our method contrast to the elaborated implementation of full-automatic methods and their complicated statistical analysis. Our method indeed takes some man hours to decode the dances semi-manually, but this can be taken care by sensible planning and is outweighed by the easier and cheaper set-up. Additionally, the full-automatic method is not necessarily more accurate than human performance. Thus, the need for such method only depends on the type of study. If indications of resources used and their distribution in the landscape is useful enough, then our method is highly recommendable. Main advantage is that it gives us reliable data with a simple set-up directly in the field with no locational nor practical constraints. However, making whole season analysis or even a monthly evaluation, would be far too time consuming. In these cases, fully-automatic methods such as the method developed by Wario *et al*. (2017) could be more comfortable.

Honey bees also grade the resources, including this information in the waggle dance. The dance rate is a measure for the individual bee's subjective evaluation; the higher the dance rate, the higher the importance of resources evaluated by the bee (Waddington, 1982). As we were planning to use plant information to assess the profitability of the species, we did not focus on the bee's subjective evaluation and did not assess the dance rate. This could be interesting to evaluate in the future to explore behavioural features of honey bees.

The decoding of the waggle dances is also very complex and not always straightforward (Couvillon et al., 2012; Preece & Beekman, 2014). The waggle dance contains many variabilities which can make it just as difficult for the bees, as for the biologists, to decode the location danced for. Consequently, we still do not know the bees foraging pattern to a full extent just by decoding waggle dances. However, to a greater extent waggle dance does give an overall picture of where the profitable resources for the colony are located, which are in accordance with our results. Additionally, the method does not avoid the analyses of the same bee twice, as it was impossible to keep track of individual bees.

It is also important to note that it is difficult and very demanding to map the landscape of this size with a high degree of detail. For example, it was unfeasible to quantify all food sources available within the urban areas, and thus we may well have overlooked some important sources in this landscape elements. Moreover, due to time constrains to cover the 10×10 km landscape window, it was not possible to monitor individual agricultural field. Consequently, the classification of these fields was based on inquires to farmers and general phenological information for the crops in the region, which might not have corresponded entirely with the reality. Alfalfa can be flowering any time from June to August, depending on the period it was planted. In all the cases we gave it the abundance of 100% that can create bias in the data. Rapeseed and grain legumes end flowering in June, most probably not having such a high abundance this month. Determining the density of sunflowers in July and August respectively was also challenging due to the same fact.

Honey bees are generalist forager species and the information decoded from waggle dance is informative also to understand foraging patterns for bumble bees, Lepidoptera and many other flower-visiting insects (Balfour et al., 2015). Decoding their waggle dances gives us information not only about the profitable resources, but also about their needs. Waggle dances help colonies reach a balanced diet, definitely giving us relevant information for conservational purposes (Zarchin et al., 2017). The results from this study can be put in perspective to the conservation practices for other pollinators as well.

Future studies should incorporate finer resource evaluations in the landscape, including assessment of floral resources in agricultural fields and assessment of more precise resource classifications based on honey bee nutritional needs. Easy set-up method used in this study was a success for recording and decoding the waggle dances. Waggle dance does give an overall picture of where the profitable resources for the colony are located and can be used for the similar type of studies. All these results will contribute to a better understanding of honey bees, assisting their management and conservation.

5. References

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Annex I. Available flowering species in Burgos landscape

Table A-I-1. List of all the available flowering species in the studied landscape of Burgos, with the assessed values of nectar (N) and pollen (P) importance for bees (scale: 0 – no resource, 1 – low importance, 2 – medium importance, 3 – high importance)

Scientific name of species	NIV	PIV	Scientific name of species	NIV	PIV
Achillea millefolium L.	0	3	*Lotus corniculatus* L.	2.5	2
Adonis vernalis L.	0	3	*Lysimachia vulgaris* L.	0	2
Allium sphaerocephalon L.	0	2	*Macrosyringion longiflorum* (Vahl.) Rothm.	2	1
Anacyclus clavatus (Desf.) Pers. (1807)	2	2	*Mantisalca salmantica* (L.) Briq. & Cavill.	2	2
Anchusa azurea P. Mill.	3	2	*Medicago sativa* L.	3	2
Andryala ragusina L. 1763	2	2	*Mentha suaveolens* Ehrh.	3	1
Arctium minus (Hill) Bernh. 1800 not Schkuhr 1803	2	2	*Muscari neglectum* Guss. Ex Ten.	3	1
Argyrolobium zanonii (Turra) P.W. Ball	0	2	*Myosotis discolor* Pers., 1797	2	1
Bellis perennis L.	2	3	*Nigella gallica* Jord.	3	3
Bryonia dioica Jacq. non M.Bieb. non Bojer non Sessé & Moc.	2	2	*Onobrychis viciifolia* Scop.	3	3
Campanula lusitánica L.	2	2	*Ononis spinosa* L.	2	2
Carlina corymbosa L.	3	3	*Onopordum acanthium* L.	2	2
Centaurea aspera L. 1753	3	2	*Pallenis spinosa* (L.) de Cassini	2	2
Centaurea calcitrapa L.	3	2	*Papaver rhoeas* L.	0	3
Centaurea cephalariifolia Willk.	3	2	*Peucedanum carvifolia* Crantz ex Vill.	0.5	0.5
Centaurea cyanus L.	3	2	*Phlomis herba-venti* L.	3	1
Centaurea jacea L.	3	2	*Phlomis lychnitis* L.	3	1
Chondrilla juncea L.	2	2	*Physospermum cornubiense* (L.) DC.	0.5	0.5
Cichorium intybus L.	1.5	1	*Plantago maritima* L.	0	1
Cirsium arvense (L.) Scop.	3	2	*Prunus domestica* L.	3	3
Cirsium pyrenaicum (Jacq.) All.	3	2	*Prunus dulcis* (Mill.) D. A. Webb	3	2
Cistus laurifolius L.	0	3	*Pulicaria odora* L.	2	2
Conopodium majus (Gouan) Loret.	0.5	0.5	*Ranunculus paludosus* Poir.	1	2
Convolvulus arvensis L.	1	1	*Rhamnus saxatilis* Jacq. 1762	2	3
Crataegus monogyna Jacq.	2	2.5	*Rosa canina* L.	2	3
Crepis vesicaria subsp. taraxacifolia	2	2	*Rubus ulmifolius* Schott 1818	3	3
Draba verna L.	1	1	*Sambucus ebulus* L.	2	2
Echium vulgare L.	3	2	*Santolina chamaecyparissus* L.	1	2

Epilobium hirsutum L.	3	3	*Scabiosa atropurpurea* L.	2	1
Eryngium campestre L.	2	2	*Scolymus hispanicus* L.	2	2
Euphorbia serrata L.	0	2	*Scrophularia auriculata* L.	3	3
Fumaria officinalis L.	2	0.5	*Sedum amplexicaule* DC.	2	3
Galeopsis ladanum var. Angustifolia (Ehrh. ex Hoffm.) Gaud.	3	1	*Silene scabriflora* Brot.	3	1
Galium aparine L.	0.5	0.5	*Silene vulgaris* (Moench) Garcke	3	2
Genista scorpius (L.) DC.	0	3	*Sinapis arvensis* L.	3	3
Globularia vulgaris L.	2	2	*Tanacetum vulgare* L.	1.5	1.5
Helianthemum cinereum (Cav.) Pers.	0	3	*Taraxacum obovatum* (Wild.) DC	3	3
Helianthus annuus L.	2	2	*Teucrium chamaedrys* L.	3	2
Helichrysum stoechas (L.) Moench	1	2	*Teucrium polium* L.	3	2
Inula montana L.	2	2	*Thapsia villosa* L.	1	2
Jasione montana L.	2.5	2	*Thymus vulgaris* L.	3	2
Jasonia tuberosa (L.) DC.	2	2	*Thymus zygis* Loefl. ex L.	3	2
Lactuca dissecta D. Don 1825	2	2	*Trifolium dubium* Sibth.	3	3
Lavandula latifolia Medik.	3	2	*Trifolium pratense* L.	3	3
Lavandula stoechas L.	3	2	*Tuberaria guttata* (L.) Fourr.	0	3
Lavatera cretica L.	2	3	*Verbena officinalis* L.	2	1
Leuzea conifera (L.) DC.	2	2	*Veronica hederifolia* L.	2	1
Linum suffruticosum L.	0	0.5	*Vicia sativa* L.	2	3
Lotus dorycnium L.	2	3			

Table A-I-2. List of available flowering species in the agricultural fields in the studied landscape of Burgos, with the assessed values of nectar (N) and pollen (P) importance for bees (scale: 0 – no resource, 1 – low importance, 2 – medium importance, 3 – high importance).

Crop	Latin name	N	P
Sunflower	*Helianthus annuus*	2	2
Rapeseed	*Brassica napus*	3	3
Legumes	*Leguminosae*	2	2
Alfalfa	*Medicago sativa*	3	2

Annex II. Nectar, pollen and flower resource availability in Burgos landscape

Table A-II-1. Final values of nectar availability for sampled polygons in natural areas for the studied months.

Polygon	June	July	August
Water Surfaces	0.303	0.088	0.060
Road Network	0.593	0.479	0.427
Forest	1.044	0.502	0.550
Fruit trees	0.838	0.235	0.361
Unproductive areas	0.264	0.330	0.400
Pasture with trees	1.080	1.595	0.000
Pasture with shrubs	0.655	0.680	0.695
Pasture	0.427	0.300	0.412

Table A-II-2. Final values of pollen availability for sampled polygons in natural areas for the studied months.

Polygon	June	July	August
Water Surfaces	0.368	0.150	0.050
Road Network	0.509	0.405	0.331
Forest	1.581	0.480	0.525
Fruit trees	1.026	0.735	0.315
Unproductive areas	0.455	0.252	0.350
Pasture with trees	0.930	1.274	0.000
Pasture with shrubs	1.922	0.689	0.673
Pasture	0.500	0.350	0.320

Annex III. Nectar and Pollen availability maps in Burgos landscape

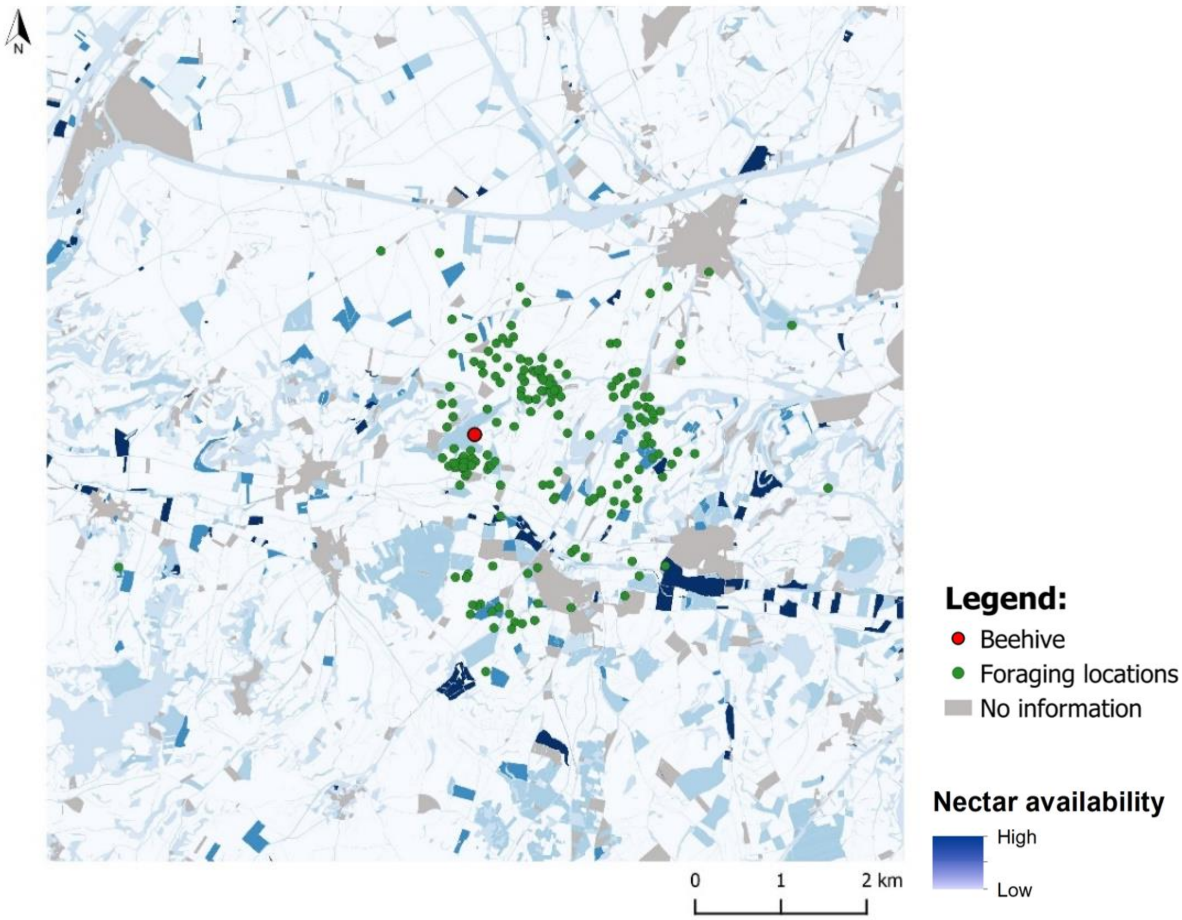

Figure A-III-1. Nectar availability with the foraging locations obtained by waggle dance decoding in June 2018. Map was created with the polygon values based on the nectar importance values. Foraging locations obtained by waggle dance are represented with green circles. Areas, with no information are in grey. A gradient of blue is representing the resource availability (white – no resource, dark blue – high resource availability).

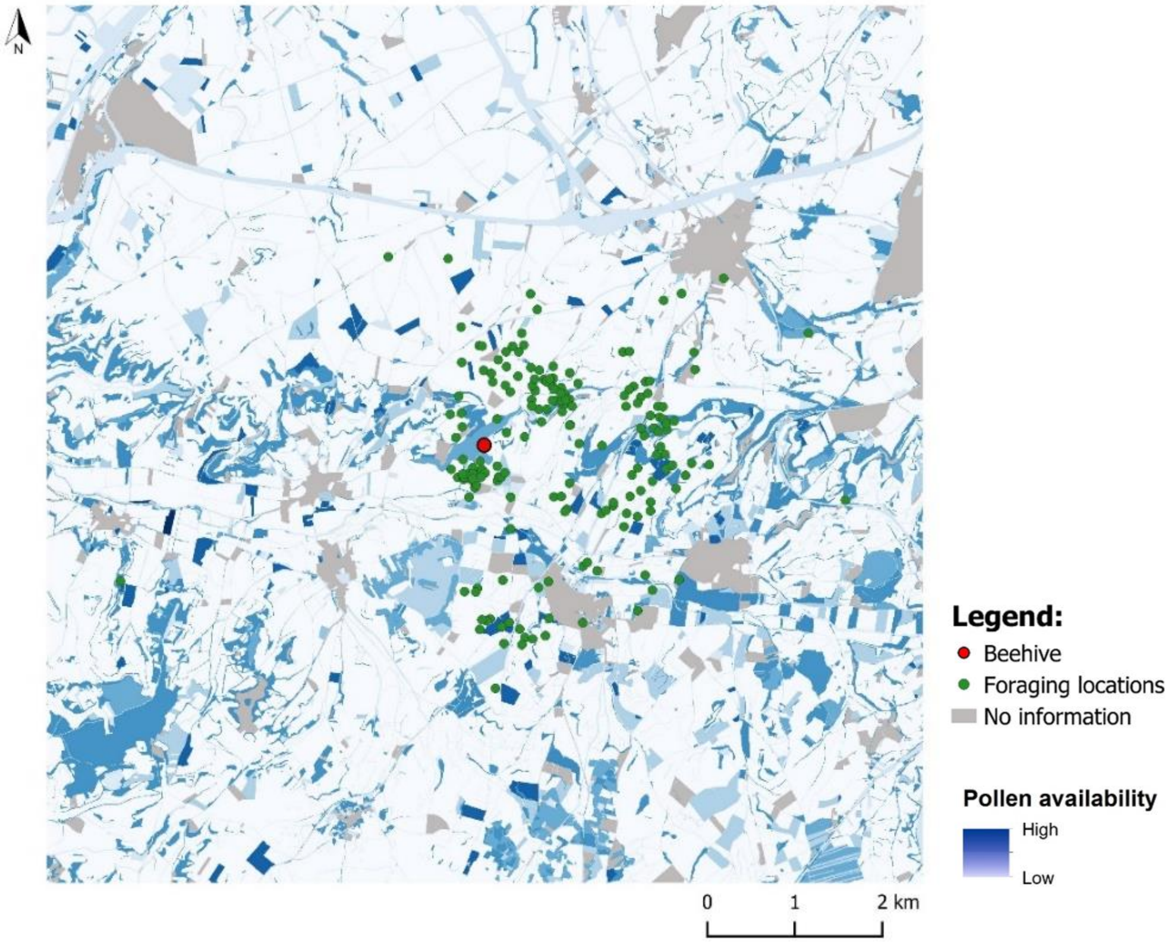

Figure A-III-2. Pollen availability with the foraging locations obtained by waggle dance decoding in June 2018. Map was created with the polygon values based on the pollen importance values. Foraging locations obtained by waggle dance are represented with green circles. Areas, with no information are in grey. A gradient of blue is representing the resource availability (white – no resource, dark blue – high resource availability).

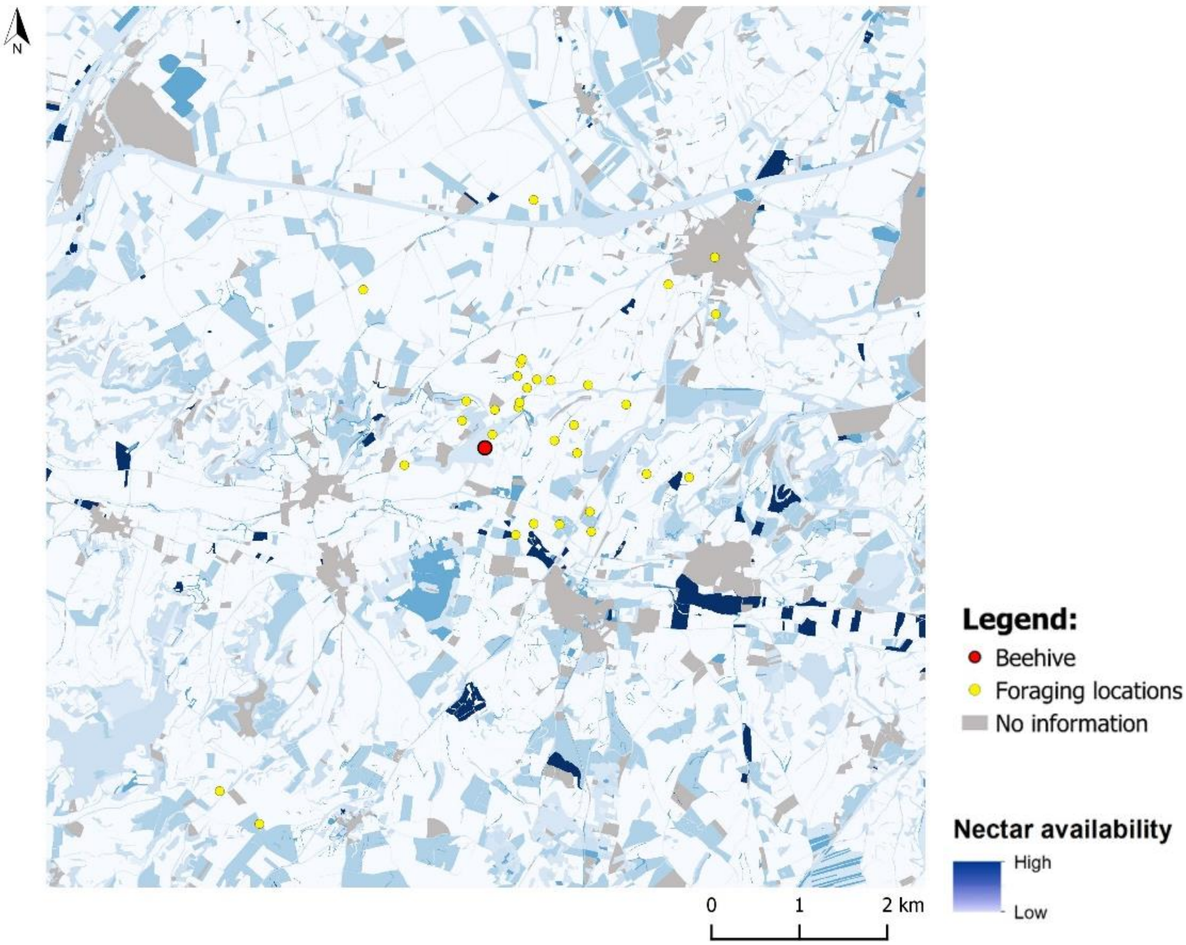

Figure A-III-3. Nectar availability with the foraging locations obtained by waggle dance decoding in July 2018. Map was created with the polygon values based on the nectar importance values. Foraging locations obtained by waggle dance are represented with yellow circles. Areas, with no information are in grey. A gradient of blue is representing the resource availability (white – no resource, dark blue – high resource availability).

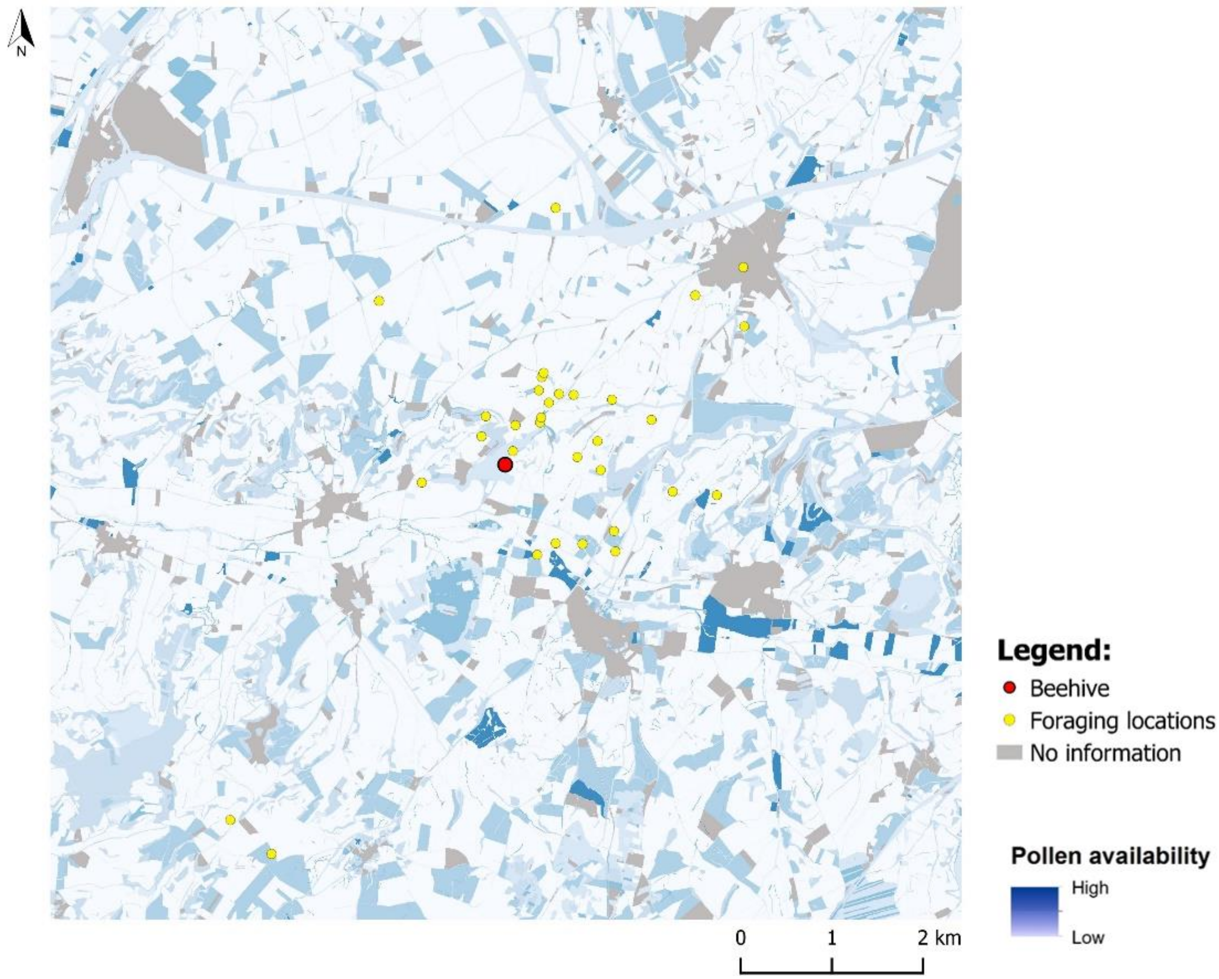

Figure A-III-4. Pollen availability with the foraging locations obtained by waggle dance decoding in July 2018. Map was created with the polygon values based on the pollen importance values. Foraging locations obtained by waggle dance are represented with yellow circles. Areas, with no information are in grey. A gradient of blue is representing the resource availability (white – no resource, dark blue – high resource availability).

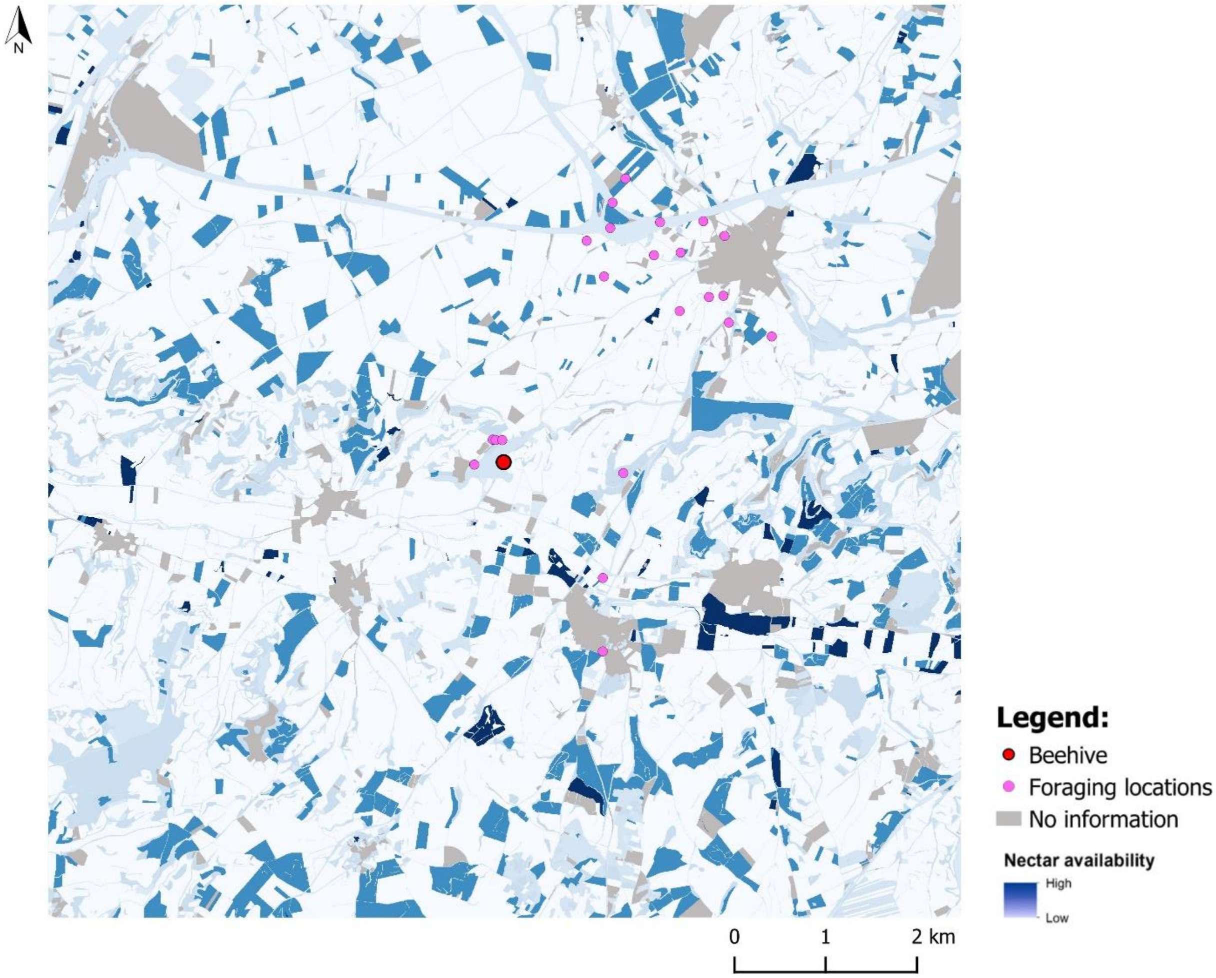

Figure A-III-5. Nectar availability with the foraging locations obtained by waggle dance decoding in August 2018. Map was created with the polygon values based on the nectar importance values. Foraging locations obtained by waggle dance are represented with pink circles. Areas, with no information are in grey. A gradient of blue is representing the resource availability (white – no resource, dark blue – high resource availability).

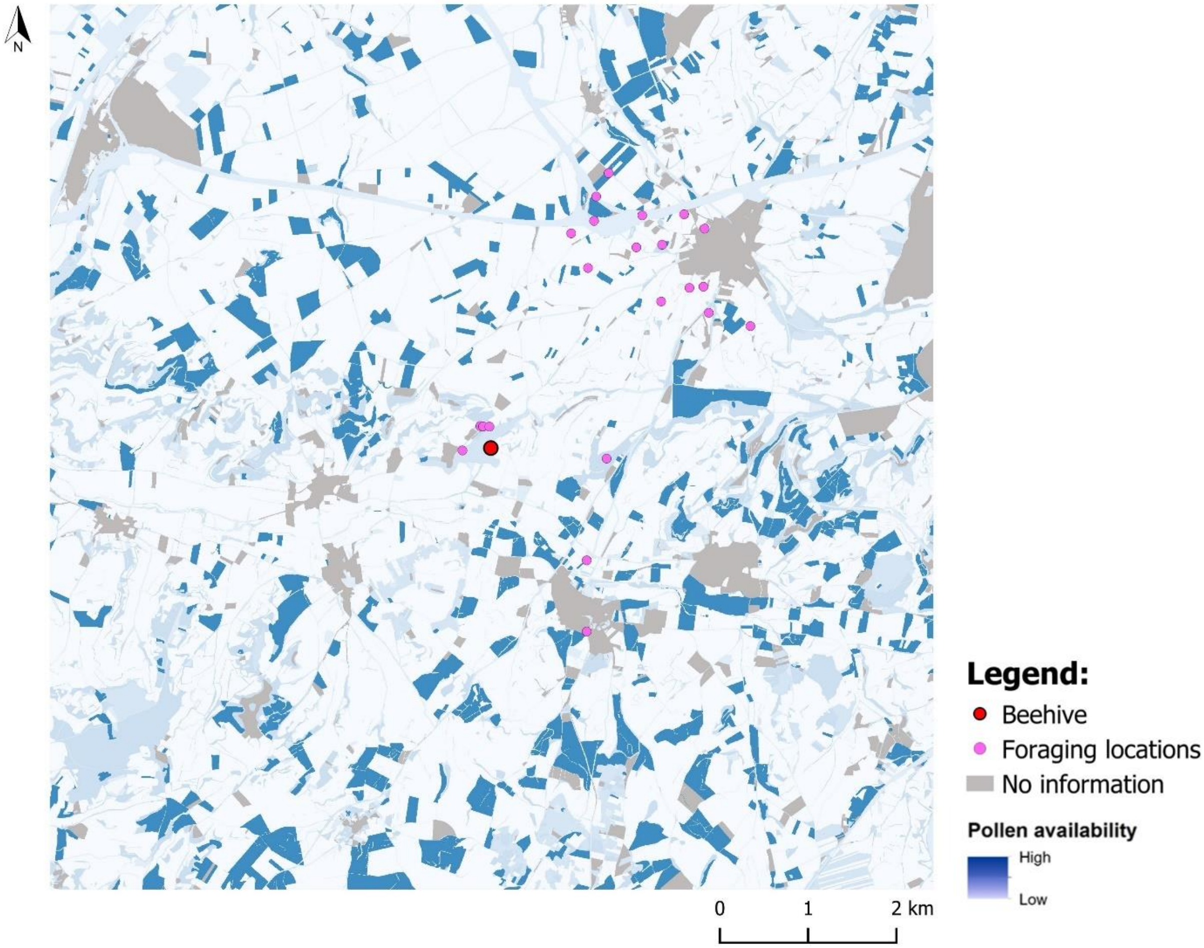

Figure A-III-6. Pollen availability with the foraging locations obtained by waggle dance decoding in August 2018. Map was created with the polygon values based on the pollen importance values. Foraging locations obtained by waggle dance are represented with pink circles. Areas, with no information are in grey. A gradient of blue is representing the resource availability (white – no resource, dark blue – high resource availability).