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Temporal Analysis of Honeybee Interaction Networks based on Spatial Proximity



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Berlin, den April 16, 2017

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Abstract

TODO

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Chapter 1

Introduction

A social insect society is formed by thousands of individuals that continuously interact with each other inside a dark nest. Honey bees are organized in colonies, which are a complex and dynamic system. Observing individual honey bees and their interactions with each other is vital for understanding collective behavior and the organization of tasks within the colony.

Within the BeesBook project of the Biorobotics Lab of Freie Universität Berlin, Wario et al. [48] developed technologies to automatically track all individuals of a honey bee (*Apis mellifera*) colony that are inside the honeycomb. Shortly after hatching, each bee is marked with a circular 12-bit tag (Figure 1.1) on their thorax and then added to the observation colony. Several cameras observe the colony over a period of nine weeks. An image analysis pipeline evaluates each frame automatically. The resulting data set contains the exact position of each detected bee on the honeycomb and its age for each frame.

In this thesis, worker-worker interaction networks, based on spatial proximity, are derived from the described data set. Each node in the network is a bee and a link between two nodes results if two bees are located close to each other for a specified period. The networks are time-aggregated, which means that one network represents the data of multiple frames. After extracting the static networks, social network analysis methods are applied to determine the characteristics of the resulting networks and its social structure.

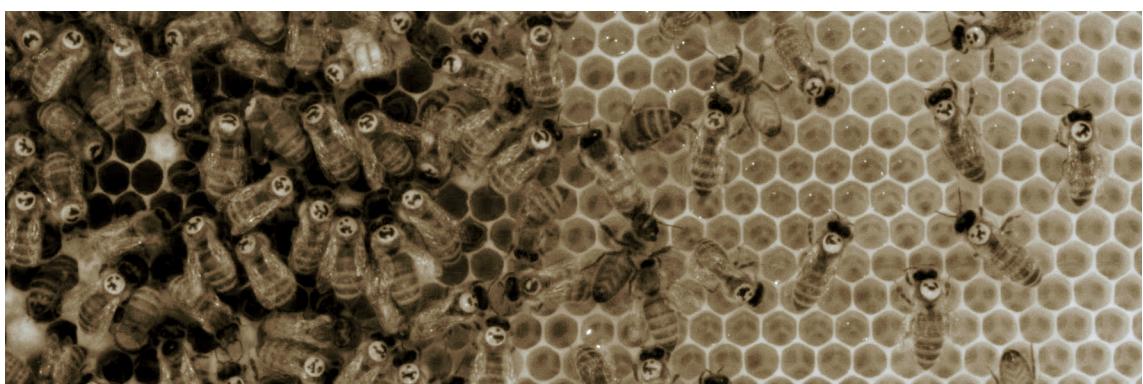


Figure 1.1: Tagged bees inside the observation hive.

1.1 Motivation

Manual insect tagging and tracking is widely applied in the behavioral sciences. Animals are marked using colored paint or numbered tags to distinguish individuals and then they are observed using a video recorder or by taking photos. The interaction data is obtained by repeatedly watching the video files and manually extracting events. Consequently, labeling only a subset of the colonies' individuals, short observation periods, a low sampling resolution, or limiting the observation to only a small area of the hive is very common. Most insect related studies, in the field of animal social network analysis, analyze only a limited subset of the life of a colony. Due to technical limitations, the majority of social insect interaction networks studies aggregate temporal tracking data into a single static network [22, Chapter 15].

Recently, automated tracking of insects has become technically feasible [48, 10, 14]. Using automated high resolution tracking data, which includes all individuals of the complete hive over an extended period, allows for more advanced analysis focusing on temporal dynamics. [TODO: some better motivation]

1.2 Research Goal and Method

The aim of this thesis is to investigate whether the BeesBook data of tracked honey bees is useful for creating worker-worker interaction networks using spatial proximity as an indicator for interactions between bees. Thus, I will implement a pipeline to extract networks out of the given data. Furthermore, I will investigate if the resulting networks are suitable for social network analysis.

I want to achieve my research goals by answering the following questions:

1. *Is it possible to infer temporal networks with the provided honey bee tracking data?*
What challenges and limitations arise from using this data? What pipeline parameters are necessary?
2. *What kind of worker-worker interaction networks emerge and how are they structured?*
What is their topology? What are the properties of the networks and how do they differ from randomly generated networks?
3. *Does the network display a meaningful community structure?*
How are the identified communities characterized? Do they reflect already known colony behavior concerning age and spatial distribution?
4. *How do these communities develop over time?*
Do the communities have stable properties? How do members move between communities?

This work is meant to establish the foundation for future research using a network science approach to study the complex system of honey bee colonies and their col-

lective behavior.

The methodology of this work consists of two parts, described in detail in Chapter 3. The first part details the approach to infer and define spatial proximity networks using the honey bees tracking data. The second part analyzes properties, communities, and the development of the identified networks.

1.3 Outline

This thesis is organized as follows. Chapter 2 is a short introduction into social network analysis (SNA). I define network measures, terms, and algorithms used throughout this work and provide a brief summary of the current state of research concerning social insect networks, temporal networks and community detection in animal social networks. In Chapter 3 I describe my research approach in general and how the pipeline infers networks out of the given dataset, what steps are needed and what parameters it uses. Also, I explain and justify what decisions I took during the network analyses and community detection process. In Chapter 4, I report the results of the network analysis and the characteristics of the extracted communities. Finally, in chapter 5, I summarize the results, discuss limitations and conclude with directions for future work.

Chapter 2

Theoretical Background for Network Analysis of Insect Colonies

The following chapter gives a short introduction into social network analysis (SNA) and introduces social insect interaction networks, as a specific type of a biological network. It defines terms and concepts used throughout this work and explains the used network metrics and algorithms. Further, I summarize the most relevant studies, which use a network analysis approach to investigate interaction networks of social insect colonies.

2.1 Social Network Analysis

A *social network* is a representation of a social structure comprising actors such as individuals, affiliations, as well as their social interactions. The network model conceptualizes social, economic, or political structures as lasting patterns of interactions between actors [49]. In mathematical terms, networks are graphs and thus consist of *nodes* (vertex, representing individuals), and *links* (edges, relationships or interactions). Social network analysis provides a set of methods, measures, and theories, borrowed from network and graph theory, to investigate social structures and its dynamics.

This work focuses on the special case of social insect networks, where individuals are nodes and edges represent interaction events between individuals. Those networks are called *interaction networks* and sometimes also association networks. According to Charbonneau et al. [9] those interactions used as an edge can be of four different types when looking at social insect networks: spatial proximity, physical contact (usually with antennae, “antennation”), a food exchange event (trophallaxis¹), or specific communication signals.

Edges can be directed (e.g. trophallaxis) or undirected, weighted or unweighted. The edge weights represent the strength of the relationship; commonly the number or duration of interactions is used [13].

¹The mouse-to-mouse transfer of fluids is called trophallaxis and is used by social insects.

2.1.1 Temporal Networks

When modeling *temporal* or so-called *dynamic networks*, two main approaches exist: (1) time-aggregated (discrete), where the data is aggregated either in a disjoint, overlapping or cumulative snapshot, and (2) the time-ordered (continuous) approach, with interactions having a start and end timestamp [26, 35, 7].

The time-aggregated approach cumulates the data for each snapshot and reduces the available information per edge. In contrast, the time-ordered approach retains the information about when interactions occurred and how long they lasted. It provides a detailed insight when timing and order of interactions are important. It can be used to model the topological flow of information through a network.

Choosing a suitable time interval for data aggregation is challenging [35], but many methods for analyzing time-aggregated networks already exists, whereas, for time-ordered networks, only a limit toolset is available. To model nodes and edge weights in time-aggregated networks can be challenging when taking into account that interactions, which occurred earlier or later in time should be weighted accordingly.

2.1.2 Network Measures and Metrics

The following definitions are mainly taken from Barabási [2] and Newman [30]. The gray box below summarizes the basic variables and terms used in the course of this work.

Network size N is the total number of nodes, respectively animals in a network.

Number of links L is the total number of links in a network, representing social interactions.

Edge weight w_{ij} of an edge between node n_i and n_j is an indicator of how important that edge is.

Component is a subnet of nodes in a network so that there is a path between any two nodes that belong to the component.

Degree k_i of a node n_i represents the number of other animals this focal animal interacts with.

Average Degree $\langle k \rangle$ is the number of interaction partners an animal has on average in the network.

Path length (distance) d_{ij} is the shortest number of links between the nodes n_i and n_j .

Average path length $\langle d \rangle$ is the average of all shortest paths between all pairs of nodes.

Diameter d_{\max} represents the length of the longest shortest paths, respectively the longest possible path length in the network.

Density D is the number of realized links divided by the number of theoretically possible links is defined as:

$$D = \frac{2L}{N(N - 1)}$$

Strength s_i of a node $n - i$ is also called the weighted degree. It measures the total weight of edges connected to that node. The average strength is denoted as $\langle s \rangle$. According to Barrat et al. [4] it is defined as:

$$s_i = \sum_{j=1}^n w_{ij}$$

Global clustering coefficient (gcc) C_Δ is also called transitivity. According to Wasserman and Faust [49] it is defined as:

$$C_\Delta = \frac{3 \times \text{number of triangles}}{\text{number of connected triples}}$$

Local clustering coefficient (lcc) c of a node n quantifies how close its neighbors are to being a clique.

Centrality When looking at the node level structure of a network, it is possible to identify nodes, which are important or central to the network, regarding different aspects. This concept is called *centrality* and measures the influence of a node in a network.

Degree Centrality C_D^i is the normalized degree k_i of a node n_i in relation to the whole network. Its is calculated as follows:

$$C_D^i = \frac{k_i}{N - 1}$$

Closeness Centrality C_C^i of a node n_i measures how close this node is to all other nodes in the network. It is the average length of shortest paths between node n_i and all other nodes in the network.

$$C_C^i = \frac{N}{\sum_j d_{ij}}$$

Betweenness Centrality C_B^i of a node n_i measures the extent to which a node lies on paths between other nodes. Nodes that occur on many shortest paths between other nodes have a higher betweenness than those that do not.

2.1.3 Community Detection

To understand the large-scale structure of networks, one can look at the network's community structure. Communities are naturally occurring groups within a network, usually also called clusters, cohesive groups or modules and have no widely accepted, unique definition [34]. For my work, I adapt the definition according to Barabási [2, p. 322]: "In network science, we call a community a group of nodes that have a higher likelihood of connecting to each other than to nodes from other communities." In contrast to a simple graph partition, the number and size of communities is not predetermined or set in advance.

Communities in animal social networks refer to groups of individuals that are associated more with each other than they are with the rest of the population. These communities reflect an intermediate level of social organization, which is located between the individual and population level [11].

There are a lot of different approaches and algorithms that address the detection of communities. Fortunato [16] gives an extensive overview of the various types of community detection algorithms. Explaining any of those would be beyond the scope of this work. For example, traditional methods include algorithms based on graph

partitioning, hierarchical clustering, and spectral clustering. There are also divisive and agglomerative algorithms. The algorithms used in this work are described in the following sections and include the leading eigenvector [31] and walktrap [37] algorithm.

Modularity

Modularity is a quantity that measures the quality of a partitioning. It can be used to compare a community partition to another and decide for the better one. Modularity optimization is also used for community detection algorithms. A high modularity of a network indicates more connection between nodes within a community and fewer connections between nodes of different communities. The basic idea is: If the fraction of links inside the community is higher, than expected in the same community of a corresponding random graph having the same degree distribution, then it is a community in the sense of modularity. This difference is summed up and normalized. If all nodes fall into one community, the modularity is 0. Fewer links inside the community than expected result in a negative value, otherwise positive.

Leading Eigenvector and Walktrap

The *leading eigenvector* algorithm was proposed by Newman [31]. It uses the eigenvectors of matrices for finding community structures in networks. It is a top-down hierarchical approach that optimizes modularity. The algorithm starts with all nodes inside one community (modularity is 0). In each step, the network is split into two parts, so that the modularity of the new separation increases. The splitting is done by first calculating the leading eigenvector of the modularity matrix and then splitting the graph in a way that maximizes the modularity improvement based on the leading eigenvector. The algorithm stops if the modularity does not further increase.

The *walktrap* algorithm by Pons and Latapy [37] is based on random walks. The authors consider random walks as a tool to calculate the similarity between nodes of a network. It uses a bottom-up hierarchical approach, that means the algorithm starts with each node in a single community. The basic idea of walktrap is that short distance random walks (the step size is a parameter) tend to stay in the same community because there are only a few links that lead outside a given community. The results of these random walks are used to merge separate communities. Again modularity can be used to cut the dendrogram at an optimal place.

2.2 Related Studies

Relevant for my work are studies using a network analysis approach focusing on interaction networks² to investigate the behavior of social insects, especially honey bees. I mainly reviewed studies mentioned in the survey papers of Pinter-Wollman et al. [35], Krause et al. [22, chapter 15] and Charbonneau et al. [9].

The most relevant studies were classified by:

- type of analysis: temporal or static analysis (using automated or manual tracking over a long or short term); and
- studied species: honey bees or other social insects.

Additionally, I inspected their shortcomings regarding time, space, and the number of tracked individuals, and thus, examined the following characteristics: total duration of study, observation period, sampling resolution, the number of colonies and marked individuals and space limitations. Table ?? (Appendix ??) summarizes the selected studies and their characteristics. I also recorded whether the studies included the aspect of age cohorts in their analysis and I listed the used software tools for network analysis.

Within the scope of my literature review, I found a lot of studies in the field of static network analysis of ants [17, 36, 38, 15, 50, 45], wasps [27] and bumblebees [33], but only a few related to honey bees [3, 28, 41, 29]. Also, I found several studies focusing on temporal aspects of ant colonies [25, 6, 20], but I didn't find any for honey bee colonies.

2.2.1 Static Network Analysis of Honey Bee Colonies

The most advanced work studying honey bees using a network science approach is by Baracchi and Cini [3]. Their studie revealed a highly compartmentalized structure inside the honey bee colony: Depending on the age, bees occupy separate areas of the comb and perform different tasks. Also, there is limited contact between different age groups.

Generally, the theory that bees change tasks over the course of their lifetime, starting as nurses in the nest and ending as foragers outside, termed as temporal polyethism, is widely accepted and has been studied for a long time [42, 21, 23]. Johnson [21] observed two groups of within-nest bees: young bees responsible for the brood care and middle-aged bees specialized on nectar processing and nest maintenance. Instead, Seeley [42] distincts four age subcastes among worker bees besides the queen cast: cell cleaning, brood nest, food storage, forager. Lindauer [23] defined certain tasks a bee can perform at any given age. Also, a bee can perform several different tasks per day. The bee is flexible and responds to the given needs of the hive. Young

²Studies using worker-task, worker-nestarea, nestarea-nestarea or other bipartite networks are excluded.

bees mostly clean cells and old bees mainly forage, instead middle-aged bees perform several tasks.

Baracchi and Cini [3] used the frequency of interactions between bees as weights for edges in an undirected worker-worker interaction network. The body length of a bee defines the radius of spatial proximity. Baracchi and Cini make use of the node level measures strength (weighted degree), closeness and eigenvector centrality to investigate the networks. Furthermore, they perform a cluster analysis using the dissimilarity measures 'average linkage between groups' and 'squared Euclidian distance among network values.' The main drawback is that they marked only 211 bees from three predefined age cohorts out of one colony with 4000 individuals and observed only one side of the observation hive for ten hours by capturing with a low resolution of one frame per minute. [TODO: explain drawback of clustering in a better way, ask somebody!]

Scholl and Naug [41] investigate the mechanism behind the emergence of organizational immunity of honey bee colonies by using unweighted, undirected physical contact and trophallaxis networks. In their case, the observation is limited to one hour per day, with three days of observation spread over three weeks. In the field of network analysis they investigated the interactions between three predefined age groups.

Naug [28] inspects the network structure of weighted, directed trophallaxis networks using four age cohorts. He evaluates the changes in transmission dynamics produced by experimental manipulation. The data set is limited to one hour and only first- and second-order trophallaxis interactions are considered.³

2.2.2 Temporal Network Analysis of Insect Colonies

Regarding the used methods, the study of Mersch et al. [25] is very close to my work. They automatically tracked all individuals of six ant colonies over a period of 41 days using a resolution of two frames per second. For each observation day, the authors extracted time-aggregated weighted contact networks per colony, using antennation as the physical contact event. They applied the Infomap community detection algorithm to each daily network and thus revealed three distinct and robust groups. Each group represents a functional behavioral unit, with ants changing groups as they age. Except for community detection, they did not use any other network science methods to investigate the network properties.

Another work, using automatic tracking, is by Jeanson [20]. It focuses on the investigation of the temporal stability of spatial proximity networks in four ant colonies over three weeks. Here, proximity is defined as $\frac{4}{3}$ of an ant's body length. Per week and colony they generated weighted time-aggregated networks, using the total duration of interaction as the edge weights. They investigated the strength, betweenness and closeness centrality and found out that the networks are stable over time, without

³The food transfer from the forager to a worker bee is called first level interaction, the food transfer from that worker bee to other bees is called second-order.

2.2. Related Studies

the queen contributing to the network structure. Also they state that individuals with long lasting interactions seem to have a reduced tendency to move, while mobile ants interact homogeneously with their nestmates. The size of the observed colonies ranges from 55 to 58 individuals.

In these studies each of the observed ant colonies contained a maximum of 200 individuals. This number is relatively small compared to the size of honey bee colonies used in the static analysis approaches.

Chapter 3

Methodology

This chapter describes the methodology I applied to reach my research goals. In the first section, I describe the data and the approach to infer networks. The network inference was driven by a combination of an exploratory data analysis and an iterative pipeline development process. It serves as a prerequisite for the network analysis part of this thesis. The second section explains the methods I used to analyze the properties, communities, and development of the resulting networks.

3.1 Inferring Spatial Proximity Networks

To generate functional and non-functional requirements of the pipeline, I conducted an analysis of the tracking data and a literature review, presented in section 2.2. The analysis led to a general understanding of the data, its structure, characteristics and an estimation of its quality.

The purpose of the literature review was to get an overview of the common methods and approaches regarding network analysis in the field behavioral insect studies. Both results are then used to select a network type and to define its nodes and links. Furthermore, I inferred specific pipeline parameters and decided for the procedure of network extraction.

The pipeline was developed, tested and refined in an iterative process. Accordingly, the results of the evaluation lead to new or changing functional requirements. The evaluation is conducted by reviewing the pipeline parameters' effects on network properties and checking the validity and quality of the networks by investigating the age of bees in the resulting network.

3.1.1 Describing the Dataset

The dataset is derived from high-resolution video files that capture tagged honey bees of one colony in a single frame observation hive. The bees are uniquely tagged with circular 12-bit markers (figure 1.1, section 1). Two cameras per side filmed the complete honeycomb. Figure 3.1 illustrates the camera setup. The *recording period* lasted nine weeks (63 days), from 19.07.2016 until 19.09.2016, with some interruptions due to maintenance work and technical failures. An overview about

3.1. Inferring Spatial Proximity Networks

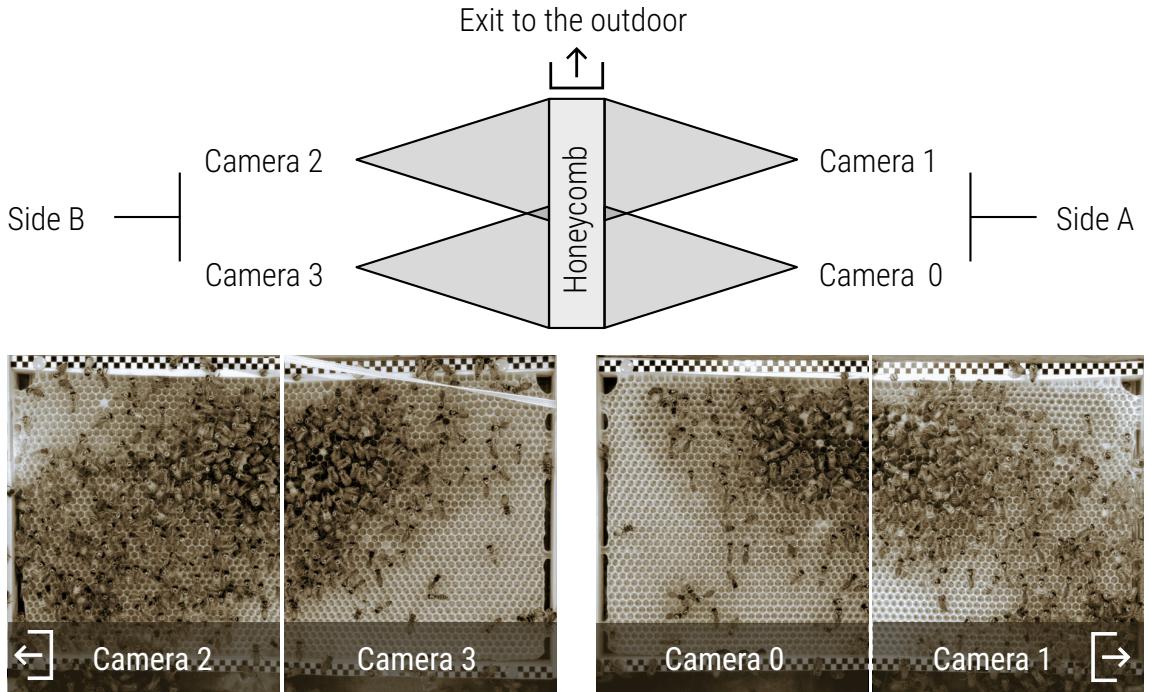


Figure 3.1: Observation setup Each side of the honeycomb is filmed by two cameras. The two cameras per side overlap, so bees inside this area are detected from both cameras.

the complete recording period is given in Figure B.2 in Appendix ??.

All four cameras, each with a resolution of 4000×3000 pixel, recorded 3.5 frames per second. An image analysis pipeline [48] detects all bees in each frame. The resulting detection data is stored in a binary file format. A python library¹ provides a frame-level access to those binary files. The size of the dataset is 470 GB, about 7.5 GB of binary data per day.

The 67 day *tagging period* began on 28.06.2016 and lasted until 02.09.2016, resulting in 3.191 tagged bees. The young bees, which were raised in a separate incubator, were tagged and then added to the observation hive at noon each day. Figure B.1 shows the frequency of tagged bees per day. The hatching day for each bee is documented and therefore the age of each bee at a particular point in time can be calculated. The life expectancy of a honey bee during summer ranges from 30 to 60 days, according to Menzel and Eckoldt [24, p. 27]. The maximum number of present bees in the hive is about 1,600.

Data Scheme

The data is organized in *frame containers*. Each frame container corresponds to one video file from a particular camera and contains approximately 1024 frames. Each *frame* contains a list of bees, which were detected by the image analysis pipeline.

¹The library is called `bb-binary` and is created by the Biorobotics Lab. It can be found on GitHub: https://github.com/BioroboticsLab/bb_binary; Last accessed: 2106-02-16, 04:28PM

Table 3.1: XXX XXX [TODO: good title and ref in text]

Frame container	Contains all frames, which belong to a specific video file of a certain camera.
Frame	Includes all detections of one frame at a certain point in time.
Detection	Detection of a bee at a certain point in time.
Decoded ID	Identifier of a bee consisting of 12 probability values, representing 12 bits.
Confidence	Value between 0% and 100%.
ID	Decimal representation of a decoded ID.
Bee time series	Binary sequence, indicating the absence and presence of a certain bee in a particular time interval.
Pair time series	Binary sequence, indicating whether or not two bees are close to each other, in a particular time interval.

A bee *detection* includes following attributes:

- xpos:** x coordinate of bee with respect to the image in pixel
- ypos:** y coordinate of bee with respect to the image in pixel
- decoded ID:** decoded 12-bit ID
- cam ID:** ID of the camera 0, 1, 2, 3
- timestamp:** unix timestamp with milliseconds

The data can be accessed by iterating on the frame level, using a start and end timestamp for specifying a time interval. The complete data scheme can be found on GitHub².

ID Probabilities, Confidence Level, and Quality

Twelve bits can encode the identity of 4096 bees. Each bit of the decoded ID represents a probability between 0 and 255, normalized to a value between 0 and 1. Therefore, a bit indicates the confidence of the image analysis pipeline for that specific bit. I define the confidence c for a bit b , analogously to Leon Sixt [47, p. 14], as

$$c(b) = 2 \cdot |b - 0.5|$$

The confidence of a decoded ID is, accordingly, the minimum of all twelve bits' confidences. Detections with a confidence below a certain level are removed from the data set. Consequently, a high level of confidence reduces the amount of data available for further processing.

I use the age of the bees to check the quality of the remaining data. If the pipeline detected a code that has not been assigned a bee will have a negative age value.

²https://github.com/BioroboticsLab/bb_binary/blob/master/bb_binary/bb_binary_schema.capnp; Last accessed: 2106-02-16, 04:46PM

³Data set: 26.07.2016, 4 p. m., 10 minutes, all cameras

3.1. Inferring Spatial Proximity Networks

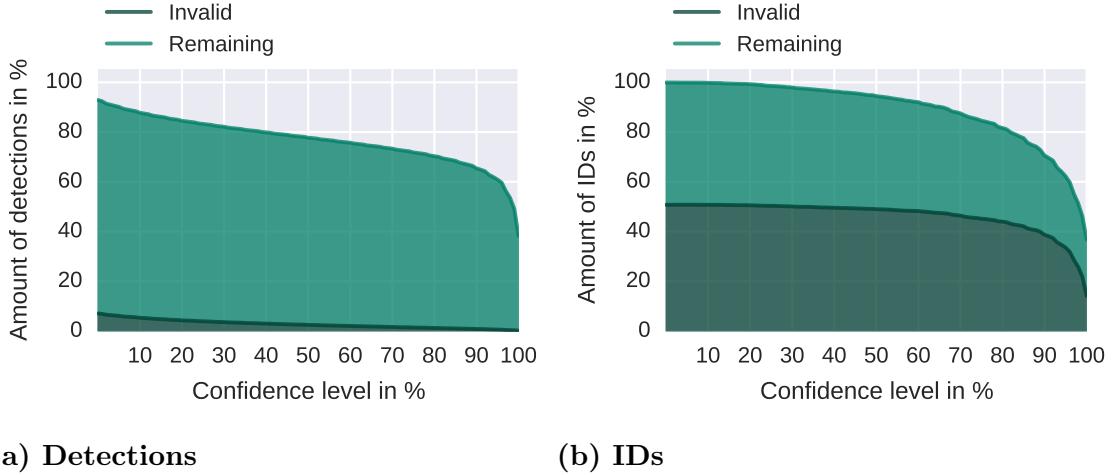


Figure 3.2: Quality of detections and IDs Light green represents the number of remaining detections and IDs (from 4096 possible IDs). Dark green indicates the fraction of invalid detections and IDs and in relation to the remaining number of detections and IDs.³

A bee has a negative age, if the pipeline detected a code, that was not used yet. I examined the number of remaining bee detections and IDs, depending on the chosen confidence by calculating the age of each bee detection and ID. A bee detection with a negative age is counted as an *invalid detection* and an ID with a negative age is counted as an *invalid ID*.

As expected, with increasing confidence levels, the number of remaining detections and IDs decreases (Figure 3.2), as does the fraction of invalid detections and IDs. With a confidence level of 100%, the fraction of invalid detections reaches 2.5%. However, the fraction of invalid IDs remains at the high value of 30.2%. Consequently, selecting a high level of confidence is not sufficient. To obtain a more reliable dataset, invalid detections need to be filtered out.

Detection Frequency Filter

A good indicator if a bee detection represents a real bee on the comb is the detection frequency of its ID. Individuals with a very low detection rate may be detection errors. To check this hypothesis, I investigate the correlation between the detection frequency of bees and their age. Figure 3.3 shows that bees with a negative age are observed less often than bees with a positive age.

During my analysis, I noticed the existence of a group of bees with a negative age and a high detection frequency. I inspected the corresponding photos and confirmed that those bee detections correspond to living individuals and are not artifacts. This results likely from a mistake in the reported hatching date for each bee. Consequently, I excluded bees from this analysis, which had a negative age, but a detection fre-

⁴Data set: 20.08.2016, 24 hours, number of total frames: 302400



Figure 3.3: Detection frequency of IDs Orange corresponds to bees with a negative age and green displays bees with a positive age.⁴The gray line represents the 99th percentile of bees with a negative age.

quency over 10,000 frames. Also I excluded bees ($n = 10$), whose age is unknown⁵. For each analysis day, the number of detections per ID is calculated, excluding the mentioned IDs. To obtain a reliable dataset, I filtered invalid detections, by discarding all detections with an ID frequency below the 99th percentile of negative IDs.

Time Series of Bees and Bee Pairs

I investigated the quality of the initial data regarding its completeness of bee tracks. A bee track represents the movement of an individual over time. I transformed the initial data set into binary *bee time series*, depicted in Figure 3.4 left and middle. A bee time series, similar to a track, represents the absence and presence of a bee over a specified sequence of frames. For further processing I use the bee time series to extract *pair time series* of bees that are spatially close (Figure 3.4, right). A one indicates that a pair of bees is detected and both bees are spatially close in a certain frame.

By analyzing the resulting pair time series, I noticed that the sequences of ones are often interrupted by short sequences of zeroes. As stated before, the higher the level of confidence, the more data is discarded. This data reduction leads to more zeroes in both time series. I assume that those short gaps do not refer to any meaningful behavior of the bees. Bees are not able to approach each other and move apart within a second because they simply do not move that fast. Therefore, I concluded, that those gaps originate from detection errors and consequently need to be treated in an appropriate way during further data processing.

git

⁵id= [2, 74, 2045, 3172, 3764, 3796, 3827, 3836, 3844, 3940]

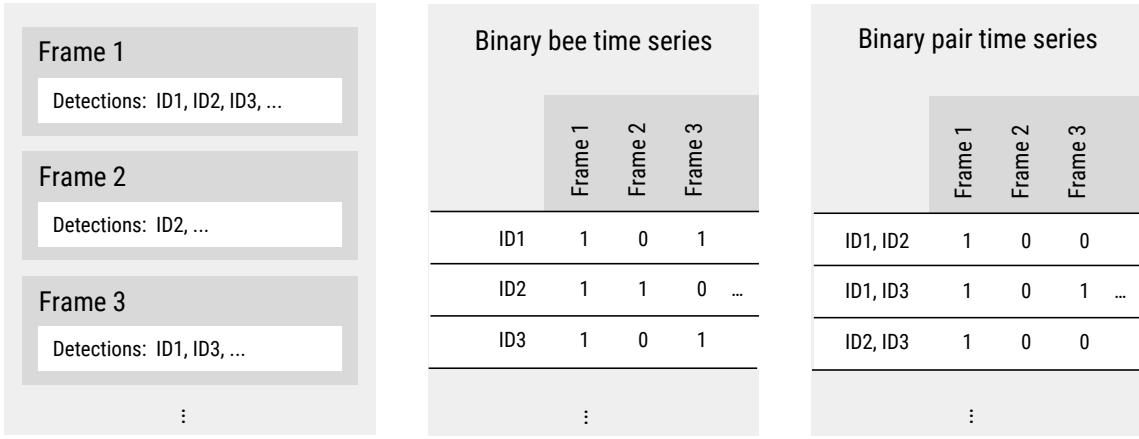


Figure 3.4: Structure of dataset *Left*: original dataset - containing a sequence of frames with bee detections; *Middle*: binary bee time series - zero and one indicate absence and presence of a bee; *Right*: binary pairs time series - zero and one indicate the absence and presence of two bees in the same frame.

3.1.2 Defining the Network and its Parameters

As this work constitutes the first step towards network analysis using this tracking data I chose to infer a time-aggregated spatial proximity network. Accordingly, the interactions are undirected but weighted. A node in the network is a bee, identified by an ID. The network consists only of bees that interact with other bees at least once, during the specified time interval.

Two bees are associated (spatially close to each other) if their distance is smaller than a *maximum distance*. Using only this criterion leads to many interactions, resulting in a very dense network, because an interaction could only last for 0.33 seconds. Therefore, an additional parameter, the *minimum contact duration*, is introduced. It specifies the minimum time two bees have to spend close to each other to be called associated.

Edges are assigned two attributes. The first one is the frequency of contacts, meaning how often they share a close position. The second parameter refers to the total duration of contact, so the total time they spend nearby.

Pipeline Parameters

The network pipeline takes two types of parameters. The first set of parameters defines the resulting network and the exact type of spatial proximity. The second set relates to the given data set. Both parameter types are described below.

Chosen Parameter Values for Network Analysis

[TODO: muss das nicht zu Method Network Analysis (als ersetzen Teil?)]

For network analysis, I chose three days: 20 August, 22 August, and 24. August.

3.1. Inferring Spatial Proximity Networks

Maximum distance	level of closeness between two individual bees (in pixel)
Minimum Contact duration	the number of frames two individuals need to spend close to each other to count it as an interaction (in frames)
Start timestamp	starting point of the network aggregation (as UTC string)
Window size	size of time window for aggregating the network (in minutes)
Confidence	level of confidence, as described in section ID Probabilities, Confidence Level, and Quality (in percent)
Valid IDs	list of valid ids within a specified time interval, as described in section Detection Frequency Filter (in CSV file format)
Gap Size	for correcting, filling gaps in, the time series of bee pairs (in frames)
Number of CPUs	number of used CPUs for parallelization
Year	calculate bee IDs and stitching of camera images according to the observation period (2015 or 2016)

These days were selected because bees from a wide range of age groups were present and older bees, which are likely to be foragers, were more represented in the hive during these days. Additionally, no data is missing due to camera failures. The following values are chosen according to biological constraints and similar to other studies, for better comparability.

I chose the length of a bee body, according to Baracchi and Cini [3], as the maximum distance between two bees (figure 3.5). The average bee length of 212px ($\pm 16\text{px}$) was determined by manually measuring the length of all bees ($n = 337$) of four camera images using the tool ImageJ⁶. The minimum contact duration is set to three frames (one second). This value corresponds to Mersch et al. [25], they also exclude interactions below one second. The networks are aggregated for ten hours during daylight; this corresponds to the biological rhythms of bees.

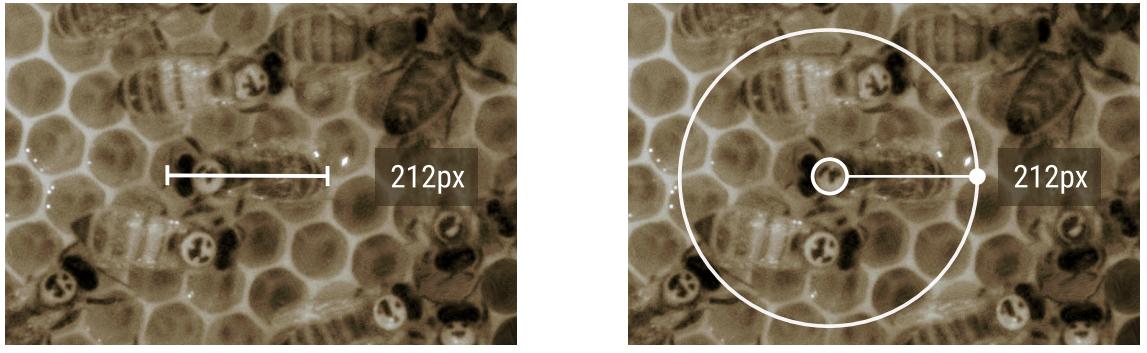
The confidence level confidence is set to 95%, to keep about 60% of the data. The gap size is set to two frames. This value corresponds to the median gap length in the time series of bee pairs.

3.1.3 Implementing the Network Pipeline

This section describes the pipeline for generating spatial proximity networks out of honey bee tracking data. The network pipeline takes as input a path to the data and a set of parameter previously described and outputs a network in graphML file format. I parallelized the pipeline on the frame level. That means each process gets a fraction of the data and extracts interactions for a time interval of five minutes. The main process accumulates the resulting interactions and creates a

⁶<http://imagej.net/Welcome>; Last accessed: 22.02.2016

3.1. Inferring Spatial Proximity Networks



(a) Body length of a bee

(b) Contact radius

Figure 3.5: Maximum distance of bees: A length of a bee body is chosen as the maximum distance between two bees.

Table 3.2: Chosen parameters for network analysis The maximum distance corresponds to the length of a bee body and the minimum contact duration is about one second. The networks are aggregated for ten hours.

Parameter	Value	Unit
Maximum distance	212	px
Minimum contact duration	3	frames
Window size	600	minutes
Confidence	95	percent
Gap size	2	frames

final network.

The pipeline consist of the following steps:

1. Prefilter detections

All detections below the chosen level of confidence are filtered out.

2. Simple stitching

For each camer positioned on the right hand side of the hive (camera 1 and 3), the x -coordinates of each detection is offseted to the right ($2 \times \text{maximum distance}$), to combine all detections per side into one coordinate system.

3. Synchronize cameras

The cameras do not capture all images synchronously and sometime take more or less than 3.5 images per second. Therefore, the cameras pers side need to be synchronized. In the normal case the difference between consecutive frames should be about 0.332 seconds, due to technical problem this value can be lower (0.003) and higher (2.932) at certain times. The frames of cameras 3 and 2 and cameras 1 and 0 are matched, frames without a match are discarded.

4. Discard detections with certain IDs

All bee detections with an ID contained in a valid ID list are kept, all other

detections are discarded.

5. Extract close pairs

For each side of the hive, all close bee pairs according to the maximum distance parameter are calculated using an KDE-tree and then combined.

6. Generate time series of bee pairs

The data structure (frames and pairs of bees) is transformed to time series of bee pairs.

7. Correct pair time series.

The time series of bees are corrected by filling in the gaps of a certain length (gap size parameter).

8. Extract interactions

The edges and its attributes (frequency and duration) are extracted from the time series of bees using the minimum contact duration parameter. A sequence of ones with a length of at least minimum contact duration are evaluated as an interaction . The frequency of those series and the total duration (number of ones) are the attributes.

I used python to implement the network pipeline, because the library to access the tracking data is only available in python. The data analysis is done with pandas⁷ and numpy⁸ using the web-based environment Jupyter Notebook⁹. The networks are saved in graphML format and are created using the python library networkX¹⁰ in version 1.11. iGraph¹¹ was used for community detection and for network analysis.

3.1.4 Summary and Results

The goal, as mentioned in 1.2, was to answer the question whether it is possible to infer temporal networks with the provided honey bee tracking data and to work out challenges and limitations regarding the provided data set. Furthermore, it was a goal to identify the parameters necessary for the pipeline.

Pipeline Parameters

This analysis results in two types of pipeline parameters. The first category specifies the resulting network, concerning the definition of spatial proximity, duration of interaction and size of the aggregated time window. The second type represents parameters resulting out of the characteristics of the dataset.

1. Pipeline parameters for network

⁷<http://pandas.pydata.org/>

⁸<http://www.numpy.org/>

⁹<http://jupyter.org/>

¹⁰<https://networkx.github.io/> Last accessed: 2017-02-17, 08:07PM

¹¹<http://igraph.org/python/>

3.2. Methods for Analyzing Spatial Proximity Networks

maximum distance, minimum contact duration, window size

2. **Pipeline parameters for data**
confidence, list of valid IDs, gap size

Limitations

It is possible to infer networks, but a complex preprocessing of the dataset is essential with two major steps:

1. **Reduction of data**
Reduce the amount of data to obtain a reliable data set, by filtering out detections with a low confidence value or by IDs with a low detection frequency.
2. **Combine camera data**
This step consists of the time synchronization of each of the two cameras and the joining of the data per frame.

A tradeoff between the remaining amount of data that can be used for network inference and the data's quality had to be found. A high confidence value reduces the amount of data and produces gaps, whereas the gap size parameter tries to fix this problem.

It is also possible to infer time-aggregated networks, but with restrictions. When limiting the window size for network aggregation to the biological rhythms of day and night¹², then due to a large number of interruptions, only a small amount of useful analysis days remain.

3.2 Methods for Analyzing Spatial Proximity Networks

This section outlines the methods I used to investigate the networks on a global, intermediate and local level. It explains the choice of network measures used for the global analysis. Also, I report the decision for a community detection algorithm and illustrate the methods to examine the segregation of communities concerning age and spatial distribution. Furthermore, I explain what approach I used to study the development of communities.

3.2.1 Investigating the Topology and Network Characteristics

I summarized the network analysis methods of the reviewed studies (chapter 2.2) to gain an overview of established procedures in the field of social insect networks.

¹²Any other window size entails the inclusion of the duration of biological processes related to honey bees, I would need to know beforehand. Alternatively, I would need to apply a method to infer an appropriate window size out of the given data, this it out of scope.

3.2. Methods for Analyzing Spatial Proximity Networks

I grouped the methods by global measures, node level measures and other network analysis methods. Table A.3 summarizes the used network analysis methods of the reviewed studies. The network measures I chose for the global and node level analysis are listed in table 3.3 and were defined in chapter 2.1.2.

Each edge in the network is attributed with the frequency of interactions and total duration of interactions between the two individuals. Figure 3.6 shows a strong positive correlation between those two values. For further analysis I decided to use the frequency of interactions as the weight for edges, analogously to [25, 3].

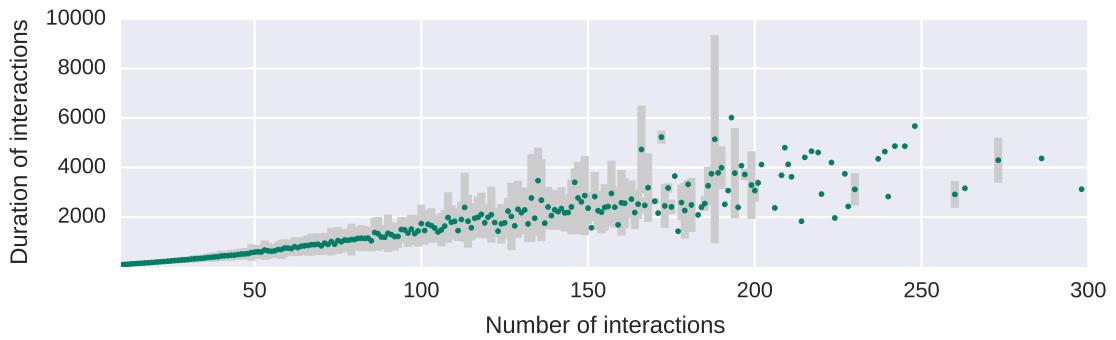


Figure 3.6: Frequency and total duration of interaction The two edge weight values show a strong positive correlation. The data of the three snapshots is aggregated.

The degree of a bee represents the number of other bees this focal animal interacts. Bees with a high number of interaction partners, have a high degree. This measure was chosen because it reveals a lot about the general topology of a network. The strength of a bee is the sum of its edge weights. A high strength refers either to a large number of interaction partners with a low edge weight or a low number of interaction partners with high edge weights. Especially for aggregated networks this measure accumulates valuable information regarding the interaction activity of bees. The local clustering coefficient (lcc) of a bee indicates how close its interaction partners are to being a clique¹³. A large lcc shows that most of its interaction partners interact with each other. A low lcc indicates the absence of those interactions. It is a good indicator for the embeddedness of single bees.

The betweenness of a bee measures, how many shortest paths go through that bee. A bee with a high betweenness would be central or important for the network in the sense of information flow. Removing this bee from the hive would lead to the breakdown of information or food flow and would negatively affect the robustness of the network. The closeness of a bee measures how fast this bee can reach all others in the network. A high closeness would indicate a very short path to every other bee. Regarding information flow, a bee with high closeness can spread e.g. information to all other bees very fast. I selected these centrality measures exemplarily.

I examined all node level metrics concerning the age of bees and their detection frequency. The global network properties are compared to an Erdős-Réniy random network, by averaging over 100 runs.

¹³A clique is a complete subgraph.

Table 3.3: Measures used for analysis Each measure is explained in chapter 2.1.2

Global level measures	Node level measures
Number of nodes N and edges E	Degree k
Average degree $\langle k \rangle$	Strength s
Average strength $\langle s \rangle$	Local clustering coefficient c
Density D	Closeness Centrality C_C
Diameter d_{max}	Betweenness Centrality C_B
Number of components	
Global clustering coefficient C_Δ	
Average path length $\langle d \rangle$	
Edge weights	

3.2.2 Detecting Communities

For finding an appropriate community detection algorithms, I checked the reviewed studies for applicable methods and scanned papers, which compare various community detection algorithms. Finally, I checked a subset of algorithms, which I identified as suitable in this context.

The reviewed studies only include two examples of community respectively cluster analysis. Mersch et al. [25] used the infomap [40, 39] algorithm. According to the authors, this algorithm only works with sparse networks and is therefore not applicable in my case of densely connected spatial proximity networks. Baracchi and Cini [3] use a hierarchical clustering to infer groups of bees within the network that are similar regarding the measures strength, eigenvector, and betweenness centrality. In contrast to the resulting groups of community detection, groups identified by hierarchical clustering do not automatically refer to dense subgraphs of the network.

Much literature on the comparative analysis of community detection algorithms exist, e.g. [51, 18]. Some studies seem to be promising, but assume either a power law degree distribution or evaluate networks with a low density, which is not applicable here. Thererfore, I tested community detection algorithms implemented in python, to find an algorithm, which works well for my case of animal social networks. The three most common python libraries for network analysis were reviewed: NetworkX¹⁴, igraph¹⁵, and graph-tool¹⁶) The algorithm needs to fulfill the following criterias:

- Support for large and very dense networks ($N = 1000$, $D > 50\%$)
- Support for weighted edges
- Fast runtime

Table 3.4 gives an overview about the algorithms reviewed. Five algorithms did not

¹⁴<https://networkx.github.io/>; Last accessed: 16.03.2016, 6:36 p.m.

¹⁵<http://igraph.org/python/>; Last accessed: 16.03.2016, 6:38 p.m.

¹⁶<https://graph-tool.skewed.de/>; Last accessed: 16:03.2016, 6:39 p.m.

3.2. Methods for Analyzing Spatial Proximity Networks

terminate after 15 minutes and were therefore excluded from further investigations. Infomap and label propagation tend to partition all nodes into a single community, this is known especially in dense graphs [51, 16]. The Louvain algorithm ¹⁷ (networkX) is the same as multilevel (iGraph), but takes longer producing almost the same communities and therefore was also excluded. Walktrap was tested for different step size parameters, as suggested in [37], the communities remained almost the same, only a few nodes switched communities.

I examined the number and size of detected communities for the algorithms fast-greedy, leading eigenvector, multilevel, and walktrap for all three snapshots. Table 3.5 gives an overview about the results. All algorithms found at least two communities. Except for leading eigenvector, most tend to find three communities.

I decided to use two algorithms for community detection: leading eigenvector and walktrap. Farine and Whitehead [13] explains that leading eigenvector is often used with animal social networks and works well. Walktrap is chosen for also examining the third community.

Table 3.4: Comparing community detection algorithms Comparison of algorithms implemented in python. Criterias are the support of weighted edges, runtime and number of communities. A runtime indicated by “–” means no termination after 15 minutes.

	fastgreedy ¹	leading eigenvector ¹	louvain ²	multilevel ¹	walktrap ¹	infomap ¹	label propagation ¹	edge betweenness ¹	k-clique communities ²	optimal modularity ¹	spinglass ¹	statistical inference ³
Edge weights	×	×	×	×	×	×	×	–	–	–	–	–
Runtime in sec	3.6	6.3	11.7	0.7	19.4	13.2	0.2	–	–	–	–	–
Communities	3	2	2	3	2	1	1	–	–	–	–	–
Size	473 434 15	488 434	469 453	462 427	490 431	922 33 (1)	922	–	–	–	–	–

¹ igraph, ² NetworkX, ³ graph-tool

¹⁷Implemented in python for networkX: <http://perso.crans.org/aynaud/communities/api.html>

3.2. Methods for Analyzing Spatial Proximity Networks

Table 3.5: Number of community members per algorithm and snapshot Four algorithms were tested and compared regarding their number of detected communities and size.

	fastgreedy	leading eigenvector	multilevel	walktrap
Snapshot 1	473	488	462	490
	434	434	427	431
	15		33	(1)
Snapshot 2	504	503	481	372
	467	475	439	311
	7		58	294
				(1)
Snapshot 3	534	537	505	310
	388	385	415	390
			(2)	231

Age and Spatial Distribution of Communities

To answer the question whether communities reflect different age groups, I studied the average age and the general age distribution of communities. I also investigated whether the age division persists in each snapshot. A two-sample Kolmogorov-Smirnov test was used to determine the statistical difference of the age distribution between communities.

To investigate whether communities reflect groups of bees working in different areas of the comb, I used heat maps to determine the core regions per group and snapshot visually. I stored the positions of all bees present within the ten hour time windows in an SQLite database to faster access the data and to eliminate the time-consuming parsing.

3.2.3 Development of Community Members

According to Aynaud et al. [1] and Bródka et al. [8] there are three main approaches for community detection in temporal networks (sometimes referred to as community tracking): (1) using a static community detection algorithm on several snapshots and then solving a matching problem, (2) using algorithms that are directly suited for temporal networks and (3) using incremental or online algorithms when processing data streams. For each of the three approaches, several methods already exist. As community tracking is not the main focus of this work, I chose to apply the most natural method out of approach (1): detecting static communities for each snapshot and then matching those communities using set theory.

Two communities at successive time steps are matched if they share enough nodes. The *match value* between two communities C and D according to Hopcroft et al. [19] is defined as:

$$\text{match}(C, D) = \min \left(\frac{|C \cap D|}{|C|}, \frac{|C \cap D|}{|D|} \right) \quad (3.1)$$

This value is between 0 and 1. A high match value occurs when two communities share many nodes and are of a similar size. Communities with the highest value are matched, respectively represent the same community to different points in time. The author suggests applying a threshold to more precisely define what “share enough nodes” means. Otherwise, a matching could occur between communities with only 0.1% of overlapping nodes.

To investigate the total number of bees, that remain in the network over the three snapshots, I inspected the match value of bees in consecutive snapshots. Also, I calculated all match values between communities in consecutive snapshots and additionally calculated the number of intersecting bees. I visualize the dynamic movement of bees between groups of different snapshots with a flowchart diagram using the JavaScript library D3.js¹⁸.

¹⁸<https://d3js.org/>

Chapter 4

Results of Network Analysis

This chapter summarizes the analysis results of the temporal, spatial proximity network of honey bees, consisting of three consecutive time-aggregated snapshots. The first section describes my results related to static aspects of the network and the second section focuses on the temporal network aspects. The last section of this chapter summarizes the main results and discusses the findings.

4.1 Static Perspectives of Honey Bee Networks

The networks are examined on three levels. First of all, I examine the networks' global structure and derive properties of the overall colony (global level). Following I study the characteristics of individual bees (local level), and its' relation to detection frequency and age. Additionally, I investigate the intermediate level of the colonies social organization by detecting communities and inspecting their practical meaning. I analyzed a temporal network, consisting of three time-aggregated snapshots; these are referred to below as snapshot 1 ($N = 922$), snapshot 2 ($N = 978$) and snapshot 3 ($N = 922$). The snapshots are aggregated for ten hours (108,000 frames) starting at 8 a.m. and lasting until 6 p.m, see Table 4.1 for details about the added bees per day. Figure 4.1 shows the proportion of intersecting bees between consecutive snapshot. This figure illustrates the stability of the network concerning its size.

Table 4.1: Sampling period Overview of the chosen aggregated daily snapshots including the number of added bees and the time they were added to the hive.

	20.08.16	21.08.16	22.08.16	23.08.16	24.08.16
Snapshot ID	1	–	2	–	3
Number of added bees	0	0	110	60	0
Time added	–	–	2 p.m.	6 p.m.	–

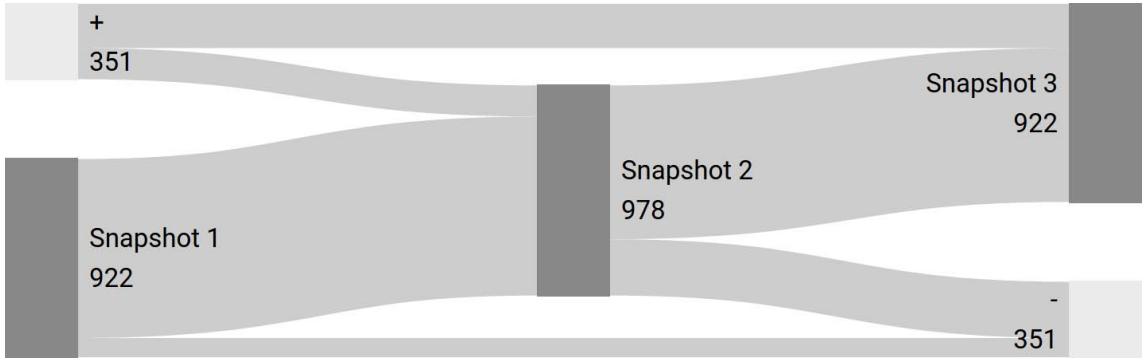


Figure 4.1: Number of bees per snapshot [TODO: bessere Beschreibung] This figure shows the amount of bees for each snapshot and the proportion of intersecting.

4.1.1 Properties of the Bee Colony

Each snapshot consists of one component. The density D is over 50% for all snapshots (69%; 54%; 61%). The diameter $\langle d_{\max} \rangle$ 3 and the average shortest path $\langle d \rangle$ length between 1 and 2. The global clustering coefficient (gcc) C_Δ of all snapshots is higher than compared to an Erdős-Rényi random graph, averaged over 100 runs using the same number of nodes and edges. On average, each bee is connected to at least 50% of the colony (68%; 52%; 61%). During the ten-hour observation period, a bee interacts on average over 4,000 times (5,680; 3,978; 4,206). Table 4.2 summarizes those basic network properties for each snapshot and lists the values of its corresponding random graph.

For further analysis, I select snapshot 3 because no young bees were added to the colony during that day and unlike snapshot 1 bees below the age of five days were part of the colony (Figure C.10). Figure 4.2b shows the age distribution of the further investigated snapshot 3. This distribution corresponds to the artificial tagging of the bees. Consequently, bees of certain age groups are simply not present. The detection frequency of an individual bee is negatively correlated with its age (Figure 4.2a).

The edge weight distribution is shown in Figure 4.2c. Most edges have a low weight; only a few edges have a high weight. It seems that bees do not prefer individuals for interaction.[TODO. figure out what it means.]

4.1.2 Characteristics of Bees

I inspected the properties of each honey bee concerning its degree k , strength s , local clustering coefficient (lcc) c , betweenness centrality C_B and closeness centrality C_C for snapshot 3, and derived characteristics and properties of the honey bee colony.

Low Hierarchical Structure

The degree is normally distributed (a in Figure 4.3). Therefore most bees have the same high number of interaction partners. The absence of hubs, a small num-

4.1. Static Perspectives of Honey Bee Networks

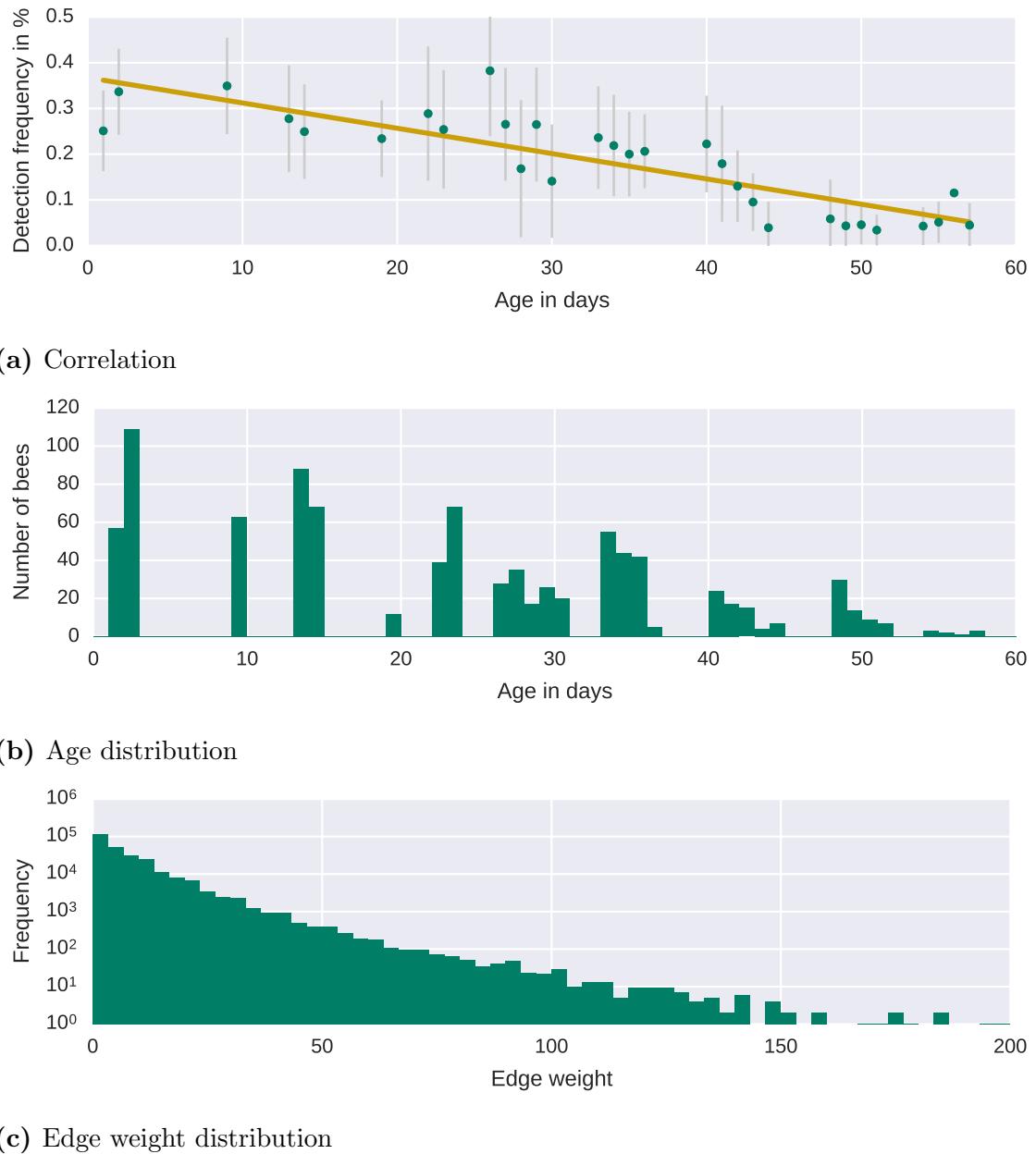


Figure 4.2: Age distribution, correlation with detection frequency and edge weight distribution of snapshot 3 (a) Detection frequency and the age of a honeybee seem to be negatively correlated. (b) The age of bees ranges from 1 to 60 day, but some age groups are missing. (c) The edge weight distribution decays exponentially.

4.1. Static Perspectives of Honey Bee Networks

Table 4.2: Global network properties N number of nodes, L number of edges, D diameter, $\langle d_{\max} \rangle$ average path length, $\langle d \rangle$ diameter, C_Δ global clustering coefficient, $\langle k \rangle$ average degree and $\langle s \rangle$ represents the average strength, as introduced in section 2.1.2.

	N	L	D	$\langle d_{\max} \rangle$	$\langle d \rangle$	C_Δ	$\langle k \rangle$	$\langle s \rangle$
Snapshot 1	922	291179	0.69	3	1.32	0.79	631.62	5680.17
Random 1	922	291179	0.69	2	1.31	0.69	631.62	-
Snapshot 2	978	256066	0.54	3	1.46	0.72	523.65	3977.94
Random 2	978	256066	0.54	2	1.46	0.54	523.65	-
Snapshot 3	922	259421	0.61	3	1.39	0.75	562.74	4205.99
Random 3	922	259421	0.61	2	1.39	0.61	562.74	-

ber of highly connected bees, indicates a low hierarchical structure of the network. Strength and lcc are also normally distributed (d and g in Figure 4.3). That also shows the absence of extreme values and confirms that bees are similar to each other regarding those properties. Betweenness and closeness centrality (j and m in Figure 4.3) also follow a normal distribution. This distribution leads to the assumption that no central or important bees exist. However, this could be a consequence of the definition of interaction (spatial proximity). All bees are similarly close to all other bees in the network, and every bee can reach any other bee with a few steps. That also corresponds to the low average path length, and the small diameter of the network described in section 4.1.1. The absence of bees with a high betweenness suggests that the colonies functionality is robust concerning the disappearance of single individuals.

Local Network Measures and Detection Frequency

Degree, strength, closeness and betweenness (b, e, k, and n in Figure 4.3) are positively correlated with the detection frequency. A low value corresponds to a low detection frequency. In contrast, the lcc (h in Figure 4.3) and detection frequency are negatively correlated.

Local Network Measures and Age of Bees

The histograms of degree, strength, betweenness, and closeness show a normal distribution with a tendency for bimodality. The lcc distribution is instead right skewed, with one peak at 0.75

There is no sharp border between the two modes in the degree distribution plot (a), but a value around 0.4 can be estimated. The strength histogram (d) seems to have a border at 1000. For closeness (j) and betweenness (m), a border can be seen at 0.6 and 0.0001. All distributions indicate a small group (100 bees) and a second larger group containing the rest of the colony. The correlation between all measures

is depicted in the scatter plot in Figure C.9.

The first small group interacts on average with 20% of the colony and has a very low strength (number of total interactions below 250). The closeness value is compared to the second group smaller but still over 0.5. The betweenness has a small range and is close to 0 for the first smaller group. The second group interacts with about 80%, corresponding to almost the entire colony and an average strength of 5000. A high strength can result from lots of neighbors with low edge weights or a few neighbors with high edge weight. As only a few edges with high weight exists (Figure 4.2c) the second option can be excluded. The second group is characterized by a very high closeness (0.75) and a still very low betweenness but higher than the first group (0.0005).

All age-correlation plots show a separate group of bees older than 45 days, corresponding to the first smaller group of bees described above. This older group is characterized by a low degree, a low strength, and low closeness and betweenness. In contrast, a high lcc, compared to the younger group is noticeable. The younger group relates to a high degree and strength, as well as a high betweenness and closeness compared to the first group, but a lower lcc. A high lcc of the old group indicates a high connectivity within the younger group and less connectivity between bees of the older group.

4.1.3 Functional Groups within the Colony

The leading eigenvector (LE) community detection algorithms revealed two communities with a similar size (modularity score of 0.25). The walktrap algorithm (WT) discovered three communities instead, also evenly distributed (modularity score of 0.23). Table 4.3 lists the precise number of members per community and algorithm for snapshot 3.

For both algorithms the communities correspond to different age groups. For LE, the average age of the young community is 13.2 days, and for the old community 28.7 days. For WT, the average age of the young community is 6.6 days and 29.3 days for the older community. The third middle-aged community of WT is on average 25.1 days old. The age distribution for each algorithm is represented in figure 4.4a and 4.4b. The two sample Kolmogorov-Smirnov test confirmed that the age distributions per community are significantly different. The corresponding *p*-values are listed in table 4.4.

Each community occupies a different region of the comb. Figure 4.4 shows that the young communities spend the most time in the comb center and the old communities closer to the hive exit. The middle-aged community is positioned between the young and old community and in the periphery of the comb.

4.1. Static Perspectives of Honey Bee Networks

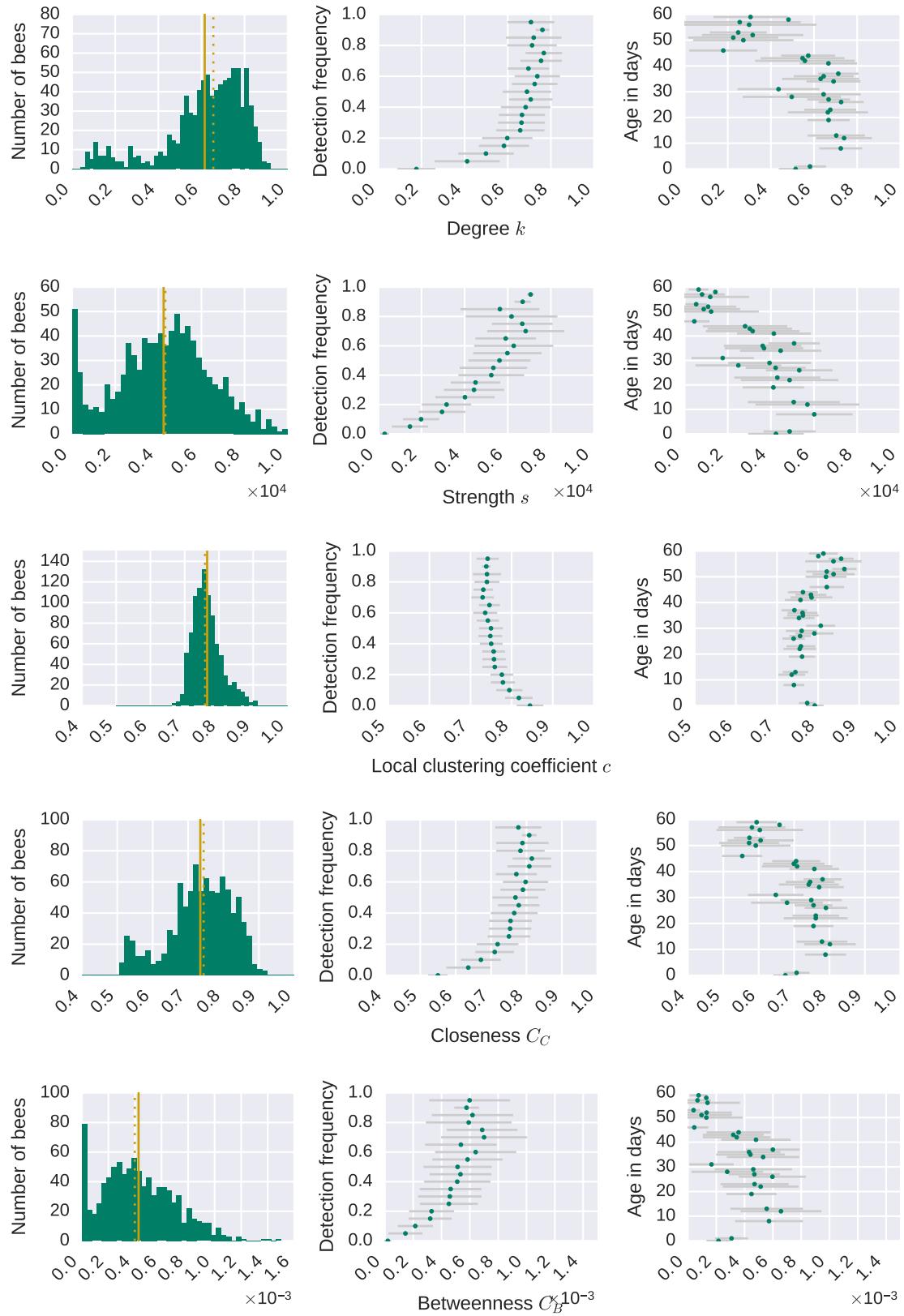


Figure 4.3: Local measures of snapshot 3

4.2. Temporal Perspectives of Honey Bee Networks

Table 4.3: Communities per algorithm Communities marked with * contain the queen. Age and standard deviation (SD) are measured in days. The queen and nine bees with a negative age are excluded from this analysis.

Community ID		Members	Proportion	Age	SD
LE	CY	*381	41.78%	13.15	± 13.50
	CO	531	58.22%	28.70	± 11.67
WT	CY	*229	25.11%	6.55	± 10.36
	CM	298	32.68%	25.08	± 11.97
	CO	385	42.21%	29.29	± 11.44

Table 4.4: Kolmogorov-Smirnov test p -values for leading eigenvector (LE) and walk-trap (WT)

Communities	LE p-value	WT p-value
CY, CO	5.10e-66	5.51e-67
CY, CM		1.10e-95
CM, CO		1.98e-05

4.2 Temporal Perspectives of Honey Bee Networks

I investigate the stability of local and global properties, as well as the stability of functional groups of bees concerning age and spatial distribution. Furthermore, the dynamics of individual bees regarding their group membership over time is examined.

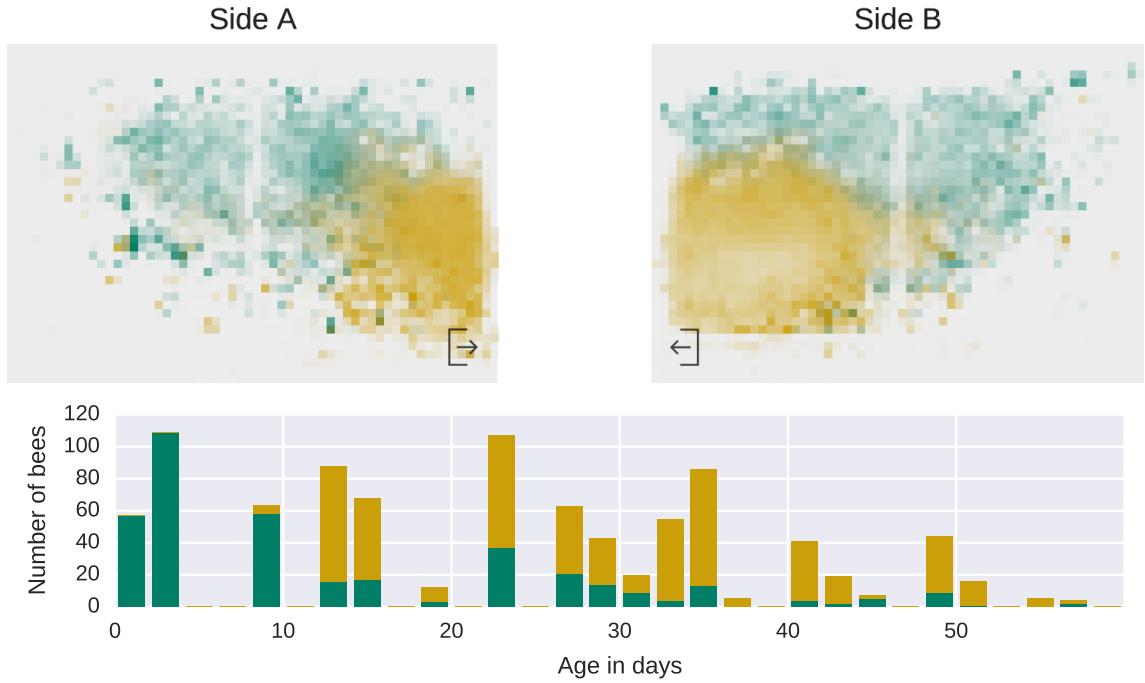
For all three snapshots, the same exponential decay regarding the edge weights can be seen in Figure C.4a. The analysis of snapshot 1 and 2 showed that the same characteristic distribution of degree, strength, lcc, betweenness, and closeness for snapshot 1 C.7 and snapshot 2 C.8 exists. They also follow a normal distribution. The correlation between the local measure and detection frequency and age remains. All of this shows that the characteristics described in section 4.1.2 apply for all three snapshots and are therefore stable for the investigated time interval. A low hierarchical structure and the correlation with age and detection frequency seem to be global properties of the colony.

4.2.1 Stability of Functional Groups

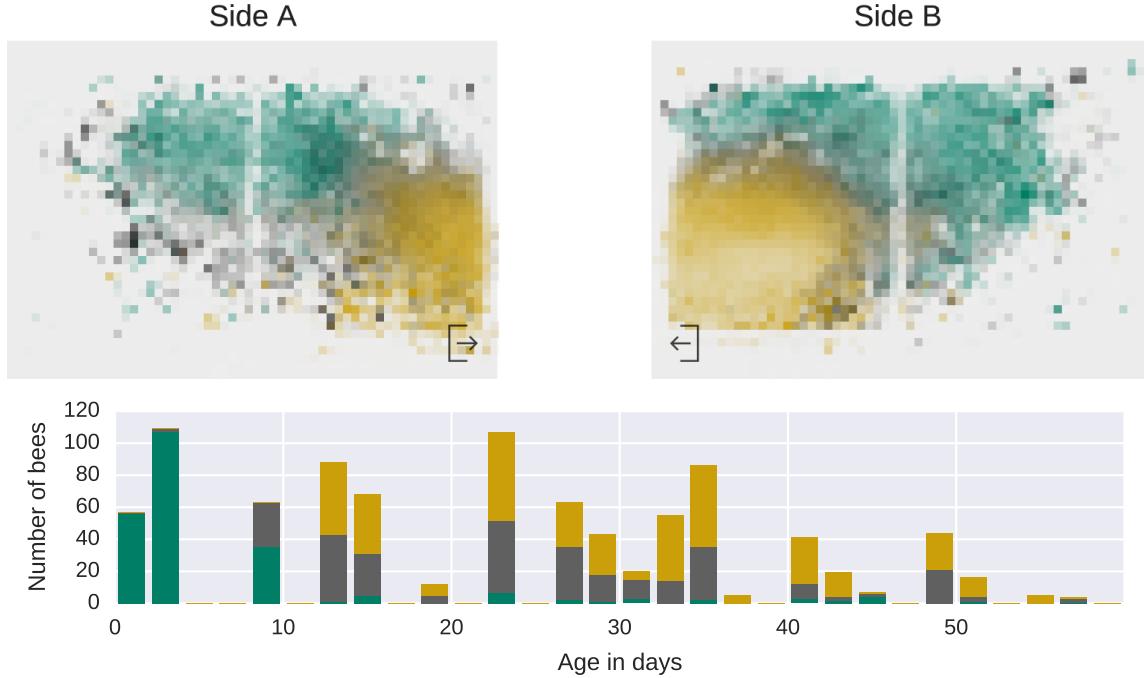
Table 4.5 lists the exact number of bees per community for each algorithm and snapshot. For each snapshot, LE detected two communities with about the same number of bees. The first communities CY(1,2,3) contain the queen and on average younger bees than the second communities CO(1,2,3).

In comparison, WT identified three communities, but two for the first snapshot.

4.2. Temporal Perspectives of Honey Bee Networks



(a) Leading eigenvector communities



(b) Walktrap communities

Figure 4.4: Age and spatial distribution of communities *Green* represents the young community occupying the center area of the comb and *orange* the old community, which is situated closer to the hive access. For walktrap the *gray* middle-aged community is positioned between the other two and in the periphery of the comb.

Again the first communities CY(1,2,3) consist of the queen and on average younger bees than the second CM(2,3) and third communities CO(1,2,3). The bees in CM2

4.2. Temporal Perspectives of Honey Bee Networks

Table 4.5: Overview about communities per snapshot Communities marked with * contain the queen. Age and standard deviation (SD) are measured in days. For each network the queen and bees with a negative age are excluded: snapshot 1: 12 bees, snapshot 2: 119 bees, snapshot 3: 10 bees.

	ID	Members	Proportion	Age	SD
Leading eigenvector (LE)					
Snapshot 1	CY1	*430	47.25%	17.12	± 10.97
	CO1	480	52.75%	27.24	± 10.96
Snapshot 2	CY2	*392	45.63%	20.24	± 12.01
	CO2	467	54.37%	28.10	± 10.88
Snapshot 3	CY3	*381	41.78%	13.15	± 13.50
	CO3	531	58.22%	28.70	± 11.67
Walktrap (WT)					
Snapshot 1	CY1	*427	46.92%	17.07	± 10.92
	CO1	482	52.97%	27.23	± 11.00
Snapshot 2	CY2	*263	30.62%	18.23	± 11.46
	CM2	305	35.51%	25.20	± 11.47
	CO2	291	33.88%	29.47	± 10.06
Snapshot 3	CY3	*229	25.11%	6.55	± 10.36
	CM3	298	32.68%	25.08	± 11.97
	CO3	385	42.21%	29.29	± 11.44

and CM3 are on average younger than the bees in CO2 and CO3. Figure C.3 depicts the age distribution for each community and snapshot.

A two-sample Kolmogorov–Smirnov test showed that the age distributions are significantly different ($p < 0.001$) for both algorithms. However, the p -values for the WT communities CM2, CO2, and CM3, CO3 are lower. The spatial segregation of the communities is very similar in all three snapshots. For further reference see the heat maps in C.2 and C.1. The detected communities seem to differ in their respective age and occupy different areas of the comb, but remain stable over this inspected time interval.

4.2.2 Dynamic of Individual Bees

Figure 4.5a (LE) and figure 4.5b (WT) show the flow of bees between consecutive snapshots and communities. For LE-communities, the majority of bees stay in their age group, and a small fraction of bees switches to older communities. Only a few bees change to younger communities.

The new middle-aged communities (CM2) of WT is formed equally by members of the young (CY1) and old (CO1) communities. The switching behavior of individuals

Table 4.6: Kolmogorov-Smirnov test p -values for leading eigenvector (LE) and walktrap (WT) for each snapshot and its communities.

		LE p-value	WT p-value
Snapshot 1	CY1, CO1	2.18e-33	1.52e-32
Snapshot 2	CY2, CO2	2.99e-20	2.3e-32
	CY2, CM2		4.72e-10
	CM2, CO2		1.00e-04
Snapshot 3	CY3, CO3	5.10e-66	5.51e-67
	CY3, CM3		1.10e-95
	CM3, CO3		1.98e-05

between communities is similar to LE. Individual bees change communities as they age.

4.3 Discussion of Results

In the following chapter, I summarize and discuss my results considering the current state of research. This part is structured according to the research goals, listed in section 1.2. First I discuss the topology of the spatial proximity networks of honey bees and its characteristic properties. Secondly, I compare the discovered communities and their development over time with existing theories regarding temporal polyethism.

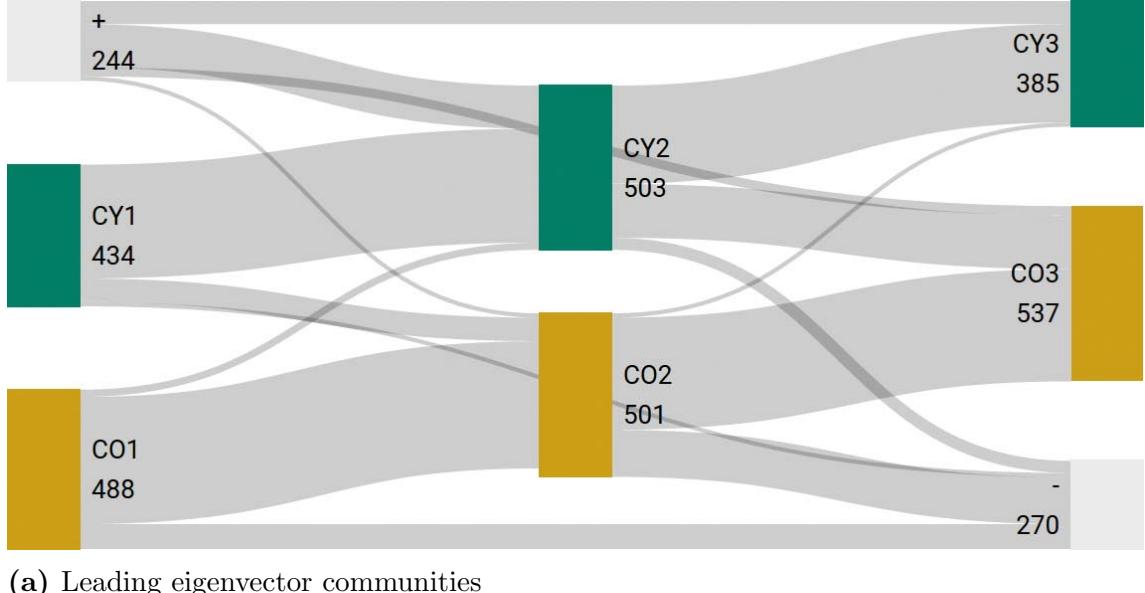
4.3.1 Network Topology and Properties of Honey Bee Colonies

The investigated honey bee spatial proximity networks are characterized by a high density (69%, 54%, 61%), which means the bees encounter many nestmates during the ten hours of data aggregation. That results either from a high activity or the fact that the comb is simply very full. The latter increases the probability that two bees are close to each other. Comparing to the ant contact networks of Mersch et al. [25] ($D = 72\% \pm 5.3$), the values are similar. In contrast to Baracchi and Cini [3] ($D = 0.15$) the density is higher, probably due to their lower observation resolution of one frame per minute.

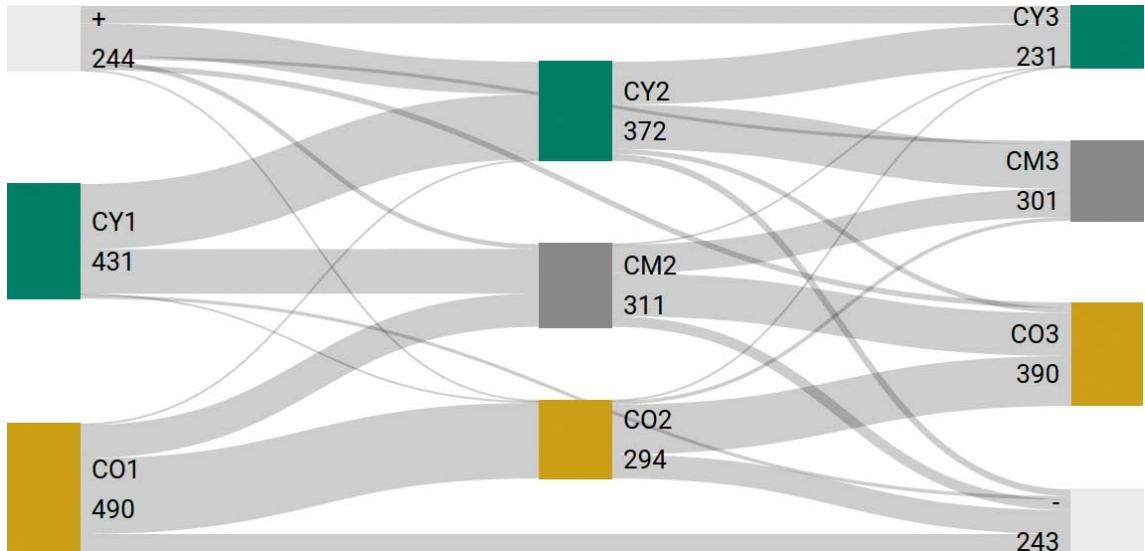
The small diameter ($d_{\max} = 3$) of my investigated networks and the low average shortest path of 1.4 in combination with a high global clustering coefficient (0.79, 0.72, 0.75) are characteristic for a class of networks known as small-world networks. This type of networks allows for rapid and efficient communication between individuals.

Charbonneau et al. [9] state that it is assumed for many biological networks, including insect colonies, to approximate scale-free networks. For some of them, the

4.3. Discussion of Results



(a) Leading eigenvector communities



(b) Walktrap communities

Figure 4.5: Dynamics of bees Each column represents a time step, the colored rectangles represent the communities for each step, and the height of the rectangles corresponds to the number of its community members, as referenced by the number. *Green* indicates the community containing young bees and the queen, *gray* represents the community containing middle-aged bees (only for WT), and *orange* the community containing old bees. This figure shows that the major part of the bees either stays in the same aged community or switch to an older group. The *light gray* boxes represent the number of bees that are added to the colony and bees that disappear.

4.3. Discussion of Results

scale-free property has been shown, but for social insect networks, this question remains open. The authors justify this by the fact that the so far investigated social insect colonies are often small and therefore the methods for the recognition of scale-free phenomena are limited. They do not specify the type of social insect networks, whether the inference of interactions is based on spatial proximity, physical contacts, or food transfer events.

The size of the network I explored is large compared to present studies (section 2.2). The degree distribution of the investigated spatial proximity network of honey bees does not follow a power-law: The absence of hubs and a non-hierarchical structure characterizes this network. This result corresponds to the decentralized structure of a honey bee colony, and the absence of a central authority described by Seeley [44].

I noticed bimodal degree, strength, closeness and betweenness distributions and a right skewed lcc distribution, corresponding mainly to bees older than 45 days. While inspecting this group of bees, I found out that this group has a very low detection rate and is not part of any other following snapshot. Probably this group of bees dies during that day. Bees who are present in the hive earlier that day and are then absent for the rest of the day have very low network measure values. The total number of old bees is relatively small compared to other age groups. Consequently, low network measure values strongly affect the mean of that old group and should be excluded in future studies.

Generally, I observed a correlation between the detection frequency of a bee, its age, and its corresponding network measure value. Older bees are detected less often than younger bees and therefore differ regarding their network measures. The age-based task division of bees in a colony observed by Seeley [43] might be an explanation; namely, old bees are foragers, the middle-aged bees relate to several tasks inside the hive but mainly they store resources, and young bees are primarily nursing. Baracchi and Cini [3] also assumed that the time which bees spend outside the hive, probably affects their connectedness within the interaction network and.

4.3.2 Characterization of Functional Groups and its Dynamics

According to the definition of communities in section 2.1.3, I found two to three communities, depending on the used algorithm.

The algorithms (LE and WT) detected communities, despite a high density and without thresholding edges of low values, as opposed to Mersch et al. [25]. They reduced the network's density artificially to 25% to apply the infomap algorithm.

I also studied the spatial fidelity of the revealed communities and their age composition, similar to Baracchi and Cini [3]. I found out that bees that are on average younger are located close to the brood (upper center of the comb); bees that are on average older are situated closer to the hive exit, and the on average middle-aged bees are placed between the two groups and around the brood, where the cells for honey storage are positioned.

4.3. Discussion of Results

I inspected three snapshots over a period of five days and found out that the detected communities are stable over time. Age-division and spatial fidelity can be observed in all the snapshot. Bees from younger communities move to older communities as they age. Only a few bees changed from older to younger communities.

It is surprising that my results align with Baracchi and Cini [3], because they did not use a community detection algorithm. The authors conducted a hierarchical clustering based on the network measures strength, eigenvector and betweenness centrality of individual bees. Moreover, their colony contained bees of three predetermined age cohorts, instead of representing all age groups ranging from 0 to 60 days, as in my study.

[start - TODO: put into related work part]

Generally, the theory that bees change tasks over the course of their lifetime, starting as nurses in the nest and ending as foragers outside, termed as temporal polyethism, is widely accepted and has been studied for a long time [42, 21, 23]. Johnson [21] observed two groups of within-nest bees: young bees responsible for the brood care and middle-aged bees specialized on nectar processing and nest maintenance. Instead, Seeley [42] distincts four age subcastes among worker bees besides the queen cast: cell cleaning, brood nest, food storage, forager. Lindauer [23] defined certain tasks a bee can perform at any given age. Also, a bee can perform several different tasks per day. The bee is flexible and responds to the given needs of the hive. Young bees mostly clean cells and old bees mainly forage, instead middle-aged bees perform several tasks. [end - TODO: put into related work part]

The communities I detected relate to the groups of bees formed by temporal polyethism. The old bees are positioned closer to the hive exit, probably relate to the group of foragers, the middle-aged group spatially close to the storage cells relate to food storage bees and the group of young bees relate to the cell cleaning and brood care because they are located close to the brood. My findings are very close to the ones of Baracchi and Cini [3].

The two approaches discovered the same functional groups of the bee colony, on the one hand by node level network measures (hierarchical clustering) and on the other hand by a higher than expected density of nodes (community detection). That acknowledges the existence of the age-based division of labor in honey bee colonies as well as the higher communication frequency within groups than between groups. Nevertheless, the low modularity score indicates that the segregation of groups is not that obvious and strict; therefore much interaction between groups exists.

Mersch et al. [25] revealed that the behavioral maturation of ants is a slow and noisy process. Instead of investigating the transition of individuals day wise, they grouped 41 days in four periods. For each period they assigned each ant to a community if it was found in this community 70% of the time. It seems that honey bee transitions are in contrast to ants faster and smoother.

Chapter 5

Conclusion

The purpose of this thesis was to investigate worker-worker interaction networks of a honey bee colony. To achieve this, I implemented a pipeline for the extraction of time-aggregated networks using high-resolution honey bee tracking data. The topology, community structures and development of community members were examined from the resulting weighted, undirected, spatial proximity networks of three consecutive time steps.

As opposed to most real-world networks, the examined honey bee interaction networks are not scale-free. They are characterized by a non-hierarchical topology and a decentralized structure. The small-world characteristic of honey bee networks allows for efficient communication within the bee colony. The observed communities within the honey bee colony, are formed of age-based functional groups with a spatial fidelity towards different areas of the comb. There are different types of cells (e.g. brood, honey, and pollen) and honeybees occupying different areas have distinct tasks.

The global network structure of the honey bee colony is stable over time, but its local structure is highly dynamic. Individual bees change communities as they age. My results align with the established state of the research: the absence of a central authority and the decentralized organization of honey bee colonies shaped by temporal polyethism.

My network analysis results verify the network pipeline, my definition of spatial proximity networks and the initially chosen parameters. The network pipeline provides an excellent foundation for further investigations.

5.1 Limitations

The following section outlines limitations concerning the accuracy and quality of the resulting networks. Especially, consequences of the networks' high density are pointed out.

Despite a complex preprocessing procedure, several shortcomings concerning the quality of the extracted networks still exist. I filtered out erroneous detections before network generation; however a few individuals remain in the extracted networks that should not exist according to the tagging and hatching documentation. Besides this,

bees which are dying at some point during the aggregation period, are part of the network. This fact needs to be considered depending on the research context.

The prefiltering of detections, as well as the synchronization of four cameras, reduces the amount of data that remains for the extraction of interactions. The gap size parameter was an attempt to compensate for this shortcoming of the data but does not perfectly solve the problem. I believe that some observed interactions are shorter than they are in reality, which distorts the networks.

Spatial proximity is an indicator for interaction but it does not capture actual interactions. The definition of spatial proximity by a maximal distance and a minimum contact duration is very loose, especially on a honeycomb with limited space. It leads to many edges and a high density of the network resulting in high noise. This noise creates a blurred image of real interactions between bees. My choice of aggregating the networks for ten hours fosters this noisiness, resulting in a global state of the colony, rather than capturing finer granular dynamics.

In this context, the network property strength is the only measure, that profits from the aggregation. All other measures are less meaningful. Due to the high density and size of the network, the methods I can apply for community detection are limited. The selection of an algorithm for detecting communities is restricted to algorithms finding only non-overlapping structures.

5.2 Recommendations

This sections list recommendations for improving the applied methods. I am focusing on concepts to reduce the noise within the network.

More Dynamic and Temporal Analysis Lowering the window size of the aggregated network and investigating different granularities could allow more dynamic analysis of the networks. Instead of using time-aggregated networks, one could shift towards the use of time-ordered networks by using time-stamped interactions.

Focusing on Important Interactions The space on the honeycomb is limited and crowded. For reducing the number of edges to only meaningful interactions, I see three main approaches. For the time being, it is an option to fine tune the pipeline parameters by lowering the size of the maximum distance and by raising the number of frames for minimum contact duration. Instead of keeping the definition of spatial proximity, I would recommend extracting contact events (e.g. by including an angle, so bees facing each other) or trophallaxis events for defining the edges, especially when using those networks to investigating more specific biological research questions.

Using the Potential of Weighted Edges A simple global threshold for excluding edges below a certain value could be used. Instead of applying a global threshold to

reduce the density, a network reduction algorithm could be implemented to extract the backbone structure of the network. Serrano et al. [46] propose a disparity filter algorithm, which seems promising but needs further investigation. The disparity measure characterizes the level of local heterogeneity of edges [5]. For all network measures utilized in this work, weighted versions exist. The weighted measures (e.g., closeness and betweenness) implemented in iGraph and networkX favor edge weights over the number of links and simply apply Dijkstra for calculating the shortest paths. Opsahl et al. [32] propose weighted network measures by providing a generalized degree and shortest path algorithm. The tuning parameter, Opsahl et al. introduce, has to be chosen. This parameter defines whether to emphasize the number of links or the weights of edges and must be selected according to a predefined research question.

Normalizing by the Detection Frequency of Individuals Depending on the topics of further research a normalization of the networks regarding the detection rate of individuals could be useful. I propose two options: either normalize the edge weight by applying the simple ratio index¹ (SRI) [15] or normalize the particular node level measure by taking the detection frequency of that focal individual into account.

Random Geometric Graph Instead of comparing the honeybee network to an Erdős-Rényi graph a new model could be implemented. As the starting point, a random geometric graph [12] can be used. In each frame, the nodes could be placed not completely randomly, preferably by modeling the behavior of a bee as a random walker. The direction of movement could be chosen randomly, but the distance of a step might be selected according to the average speed of bees.

5.3 Outlook

To fine tune the pipeline parameters for the network, one should systematically investigate the parameters effects on network properties. I started to analyze this, but only for a few combinations of values and for window sizes up to one hour. Similarly, the robustness of the detected communities regarding the pipeline parameters is worthy of further study. In addition, the provided dataset facilitates the investigation of seasonal change in honey bee colonies using network analysis methods. Long-term dynamics offer a high potential for further studies. It would be interesting to compare my network analysis results of domesticated honey bees to the social networks of wild honey bees, to discover differences regarding individual behavior and global colony organization.

¹Dividing the edge weight by the proportion of times two individuals were seen together out of the total number of times those individuals were observed.

5.4 Closing Remarks

The automatic tracking of a vast number of animals over an extended observation period with a high sampling resolution leads to an enormous amount of data. The simultaneous observation of not only more individuals but also several colonies under distinct conditions becomes possible in an efficient way. The availability of this data, which was not collected for a specific study, opens the space to investigate the data in an explorative way and to discover the unexpected.

Studying non-human animal data in an explorative way that fosters the framing of a novel biological hypothesis demands a profound domain knowledge or the constant support of experts of the studied species. Valuable information which is beneficial for data analysis and understanding the context of research is gained during the process of manual data collection by observing the animals face to face. An automatic observation process veils this part and therefore increases the abstraction level and encourages alienation between the researchers and observed animals.

Applying network analysis methods to novel datasets carries the risk of either simply describing network structures of various species or leading to the restating of well-known facts. Framing biological research questions that benefit from network science methods or the development of new techniques in the field of network analysis with the help of this unique dataset should be the overall goal, but requires profound knowledge in both areas of research.

Nevertheless, my work was an important first step to gain trust in the data and to identify limitations. It lays the foundations for further exploratory network analysis.

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Appendix A

Literatur Review

Table A.1: Properties of conducted studies XXX

	Temporal Analysis			Static Analysis										
	blonder2011time	jeanson2012long	mersch2013tracking	naug2007	otterstatter2007contact	naug2008structure	naug2009structure	sendova2010	pinter2011effect	scholl2011ofactory	waters2012information	baracchi2014socio	greenwald2015ant	quevillon2015social
Tracking														
automatic	x	x		x				x				x		
manual	x			x	x	x	x	x	x	x	x	x	x	
Species	A	A	A	HB	BB	HB	W	A	A	HB	A	HB	A	A
(1) Time														
Total duration of study	3w	3w	41d	1d	40d	24d (6)	1d	1d	3w	1d	1d	1d	8d (5)	
	2x	3x7x	41x		40x	24x			2x				9x	
Observation period	30m	24h	24h	1h	12h (4)	1h	45x5m	30m	5m	1h	2h	10h	30m	30m
Sampling resolution***	v/e	1 f/s	2 f/s	v/e	30 f/s	v/e	v/e	1 f/m	30 f/s	v/e	15 f/s	1 f/m	v/e	v/e
(2) Space*												x (3)		
1-frame hive														
2-frame hive				x (2)	x(4)					x				
(3) Size														
Number of colonies	4	4	6	1	7	1	9	4	2	1	2	1	2(1)	2
Colony size**	6-90	55-58	122-192	4000	5-7	1000	8-40	42-95	131, 72	1500	89	4000	50-100	75
Marked individuals	x	x	x		x		x	x	x		x	211	x	x
Marked cohorts					6		4			3				
Age		x		x		x			x		x			
Analysis Tools in R											x		x	
igraph	x													
t-net		x												
timeordered	x													
Other Tools: netdraw, cytoscape, UCINET, FANMOD														

(1) two species

(2) only video for one side

(*entrance designed so foragers should unload here)

(3) only one side observed

(4) 6 day and 6 night"

(5) night

(6) Each sampling day consisted of three sessions of 2 h each between 0630 and 1830 hours. in each session 15 5-min all-occurrence samplings were carried out resulting.

A = Ant

BB = Bumble Bee

"HB = Honey bee

W = Wasp"

* only for honey bees

** Mean or range if > 2

**** v=video, e=event, if no resolution given or manual video analysis was used

Table A.2: Type of network XXX

	Temporal Analysis			Static Analysis																																
	blonder2011time	jeanson2012long	mersch2013tracking	naug2007			ottersatter2007contact			naug2008structure			naug2009structure			sendova2010			pinter2011effect			schol2011olfactory			waters2012information			baracchi2014socio			greenwald2015ant			quevillon2015social		
Type of network	ta/to	ta	ta	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s	s									
Weighted Network																																				
duration of interaction	-	x	-	-	x	x	-	-	-	-	-	-	-	-	-	-	v (2)	-	-	-	-	-	-	-	-	-	-									
number of interactions	-	-	x	-	x	-	x	-	x	-	x	-	x	-	-	-	x	-	-	x	-	-	-	-	-	-	-									
Directed Network																																				
directed	x- (1)	-	-	x	-	x	-	x	-	x	-	-	-	x	-	-	x	-	x	-	x	-	x	-	-	-										
Type of interaction																																				
spatial proximity (body(B) length)	4/3xBL									2/3xBL >0.2s						1xBL																				
physical contact	A-B	A	B-B	ex (3)						A						x			x			x			> 1s											
food exchange (throphallaxis)	> 5s			> 5s																																

(1) both

(2) volume corresponds to duration

(3) except dominance interactions

ta = time-aggregates, to=time-ordered, s=static

A = antenna

B = body

BL = bodylength

Table A.3: Network measures XXX

	Temporal Analysis	Static Analysis					score
	blonder2011time jeanson2012long mersch2013tracking	naug2007 ottensatter2007contact naug2008structure naug2009structure sendova2010 pinter2011effect	scholl2011olfactory waters2012information baracchi2014socio greenwald2015ant quevillon2015social				
Global level measures							
Average degree	x			x	x	x	3
Maximal degree					x		1
Average strength		x x					2
Average path length			x		x		2
Density		x x	x		x		3
Diameter					x		1
Node level measures							
Degree	x		x x	x	x	x	5
Strength	x	x x		x	x		5
Betweenness centrality	x x				x	x	3
Closeness centrality	x			x	x		3
Eigenvector centrality				x	x		1
Clustering coefficient			x x				2
Other method							
Burst constraint						x	1
Disparity	x						2
Cluster or Community detection	x				x		2
Fitting of distributions	x			x x	x		3
Compare to random			x x				2
Information flow	x	x			x		2
Interaction between age groups				x			1
Ego network					x		1
Robustness		x					1

Appendix B

Additional Information about the Dataset

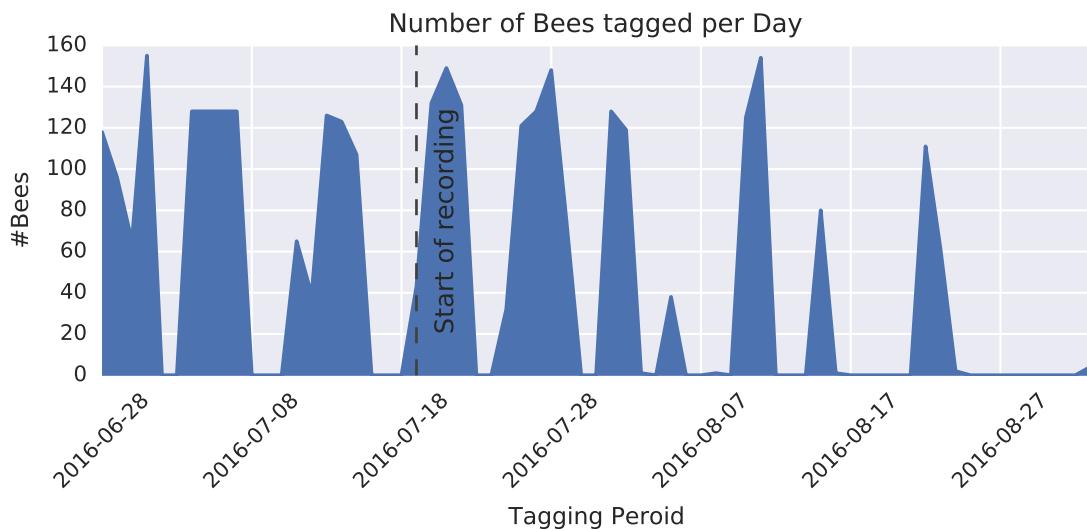


Figure B.1: Tagging frequency The bees were primarily tagged during the week. On average 48 bees were tagged each day, considering only tagging days, the average is about 91. [TODO: combine with other image or make nicer!]

B. Additional Information about the Dataset

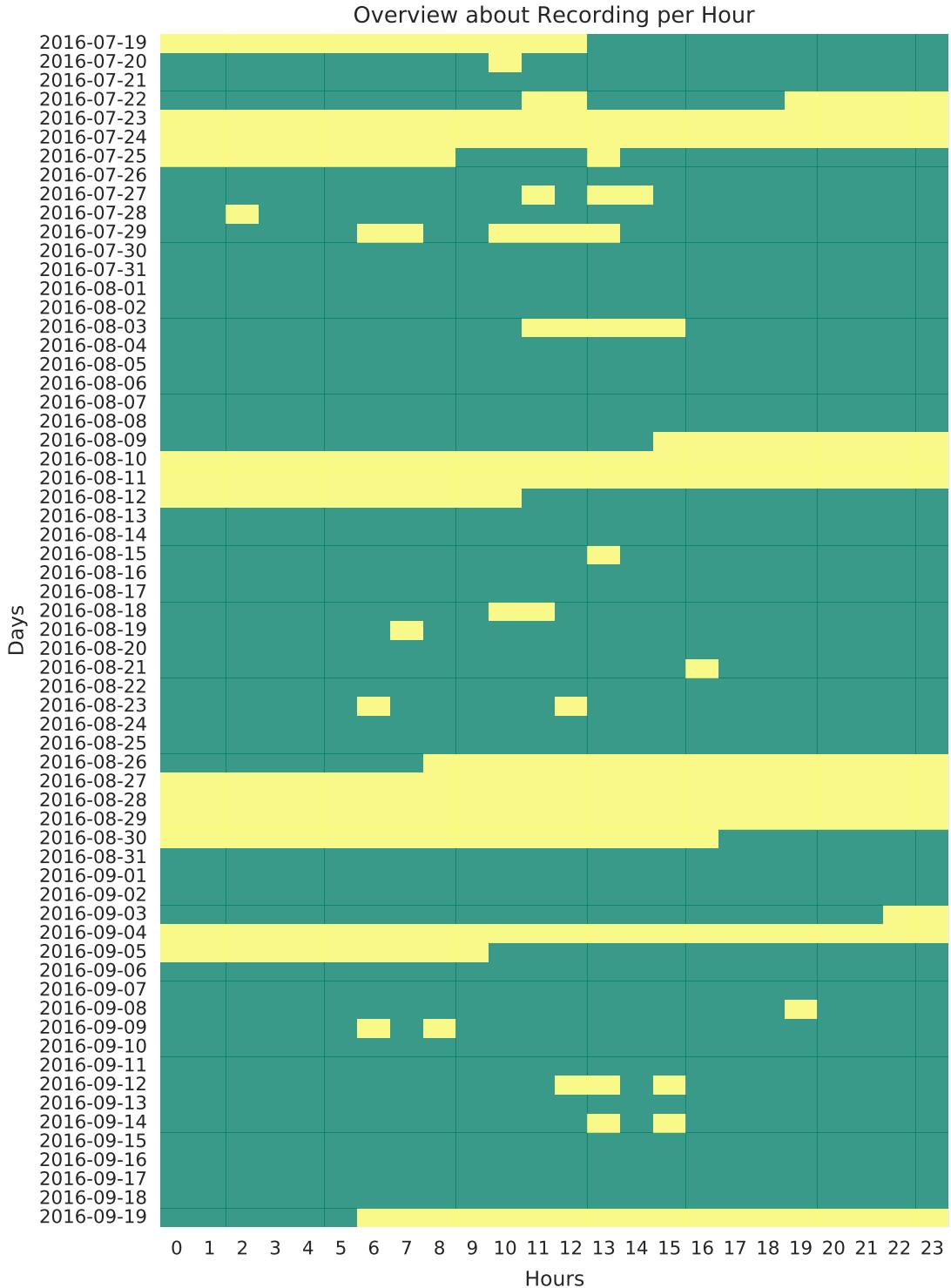


Figure B.2: Recording season with maintainance and failures *Green* indicates recording went without any big interruption; *Yellow* indicates maintainance work or technical failures of one or all cameras. This is calculated using the expected number of files produced by each camera per hour. [TODO, reduzieren auf eine Info pro Tag (keine stuendliche aufloesung), kombinieren mit anzahl der getaggten bienen pro tag, und welchen Zeitraum hab ich nun verwendet], ausserdem Zeit von links nach rechts!, evtl. kein Datum, sonder Tage durchnummerieren

Appendix C

Network Analysis

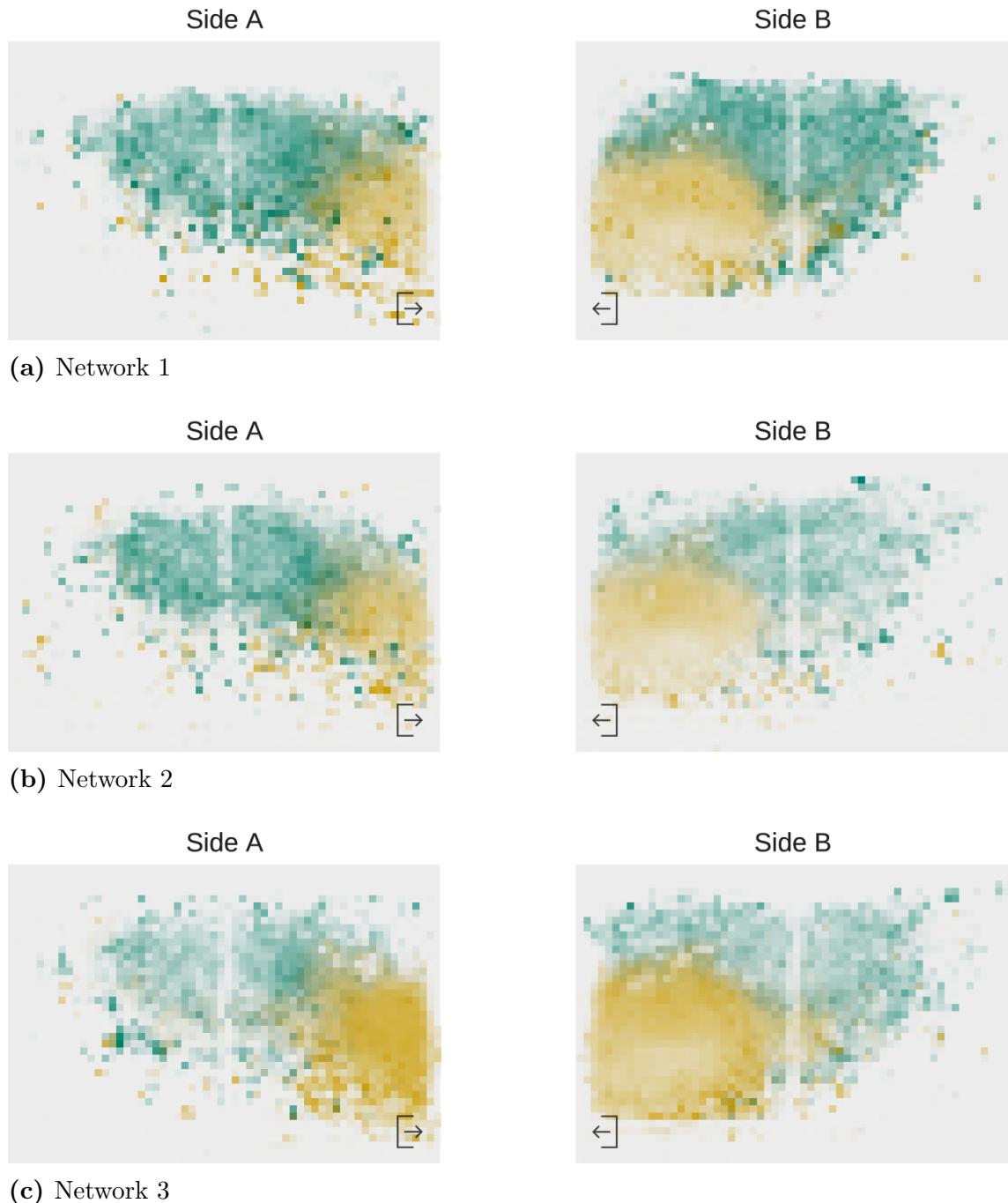


Figure C.1: Communities per network - leading eigenvector The *green* colour represents the younger community, containing the queen. The *orange* color represents the older community. The hive exit on side A is on the bottom right and on side B on the bottom left. The data is aggregated for the complete timeframe of ten hours.

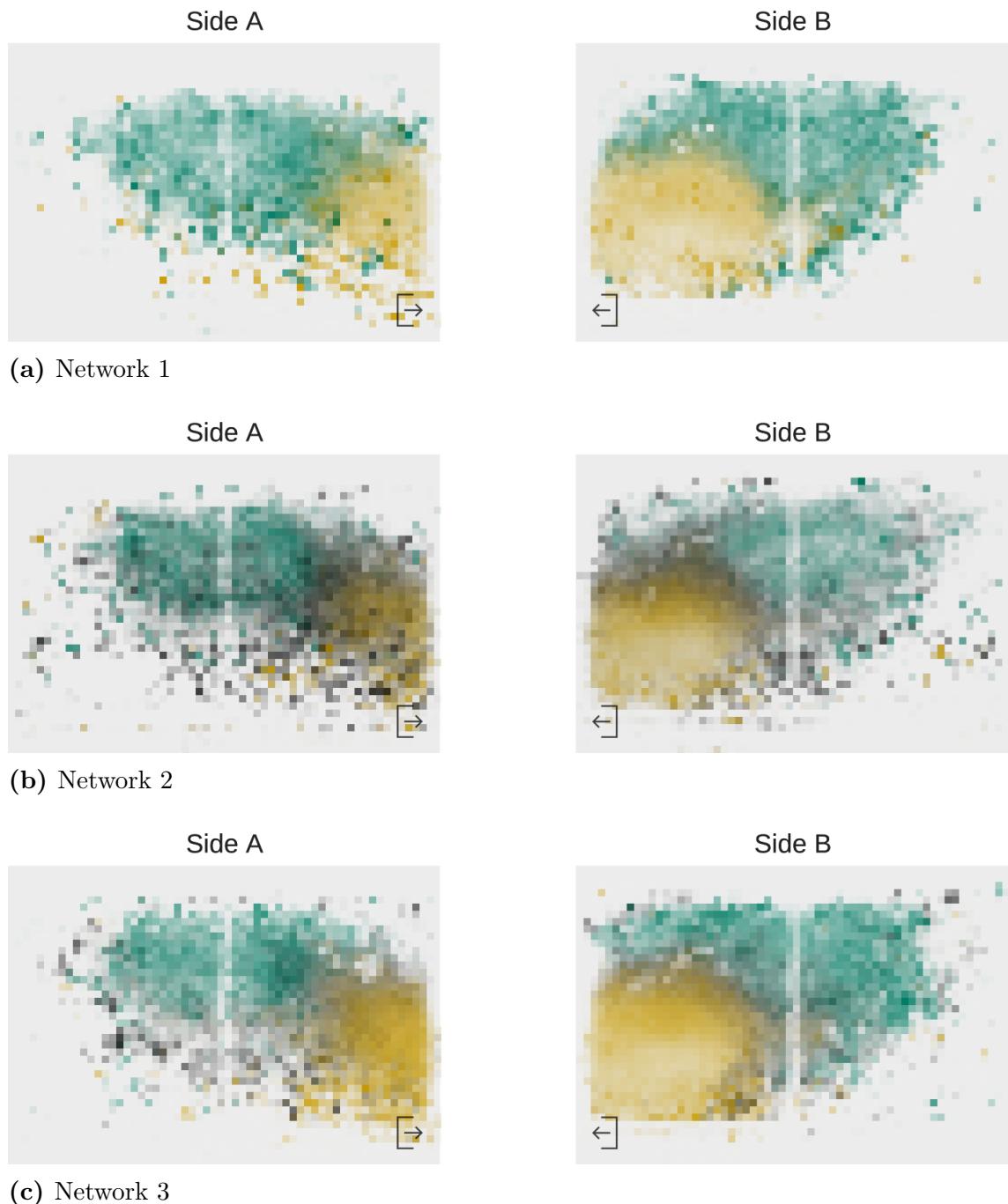
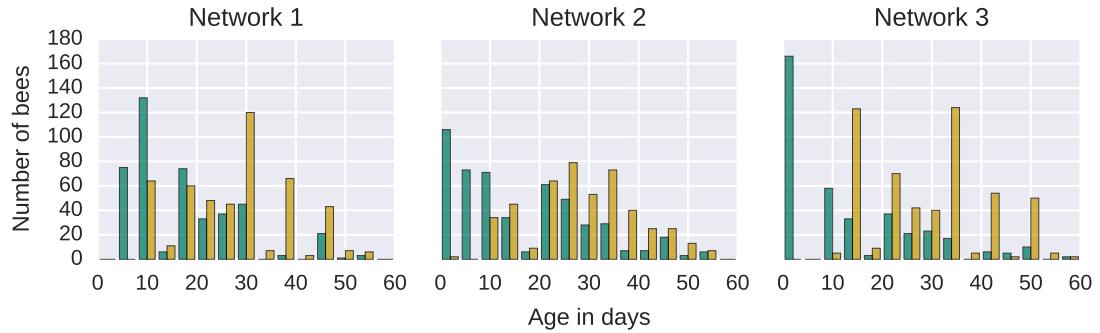
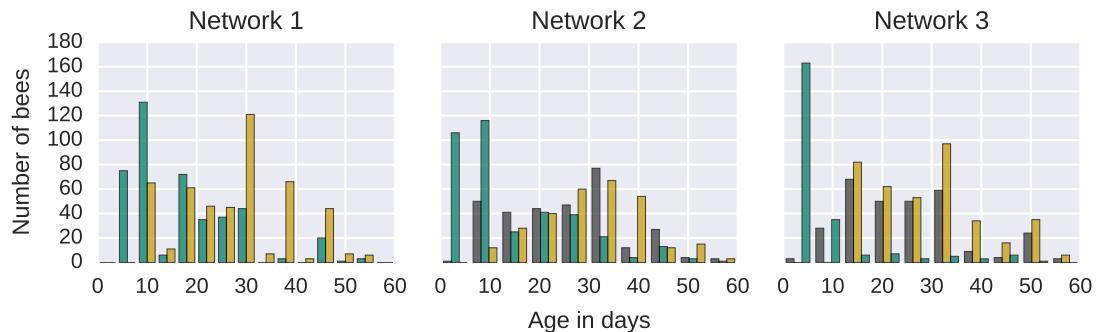


Figure C.2: Communities per network - walktrap The *green* colour represents the younger community, containing the queen. The *orange* color represents the older community. The *gray* represents the middle-age community. The hive exit on side A is on the bottom right and on side B on the bottom left. The data is aggregated for the complete timeframe of ten hours.

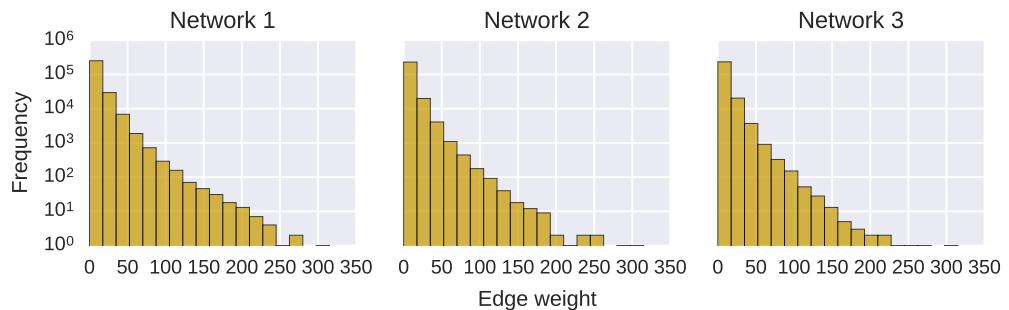


(a) Leading eigenvector



(b) Walktrap

Figure C.3: Age distribution for each community and network The *green* bar is the community containing the queen. The queens age is not included in the statistic. The *orange* bars correspond to the second community, containing older bees. The *gray* bars is a third community only revealed by walktrap and contains middle-aged bees.



(a) Edge weight distribution

Figure C.4: Degree, strength and edge weight distribution [TODO: change figures to snapshots instead of networks]

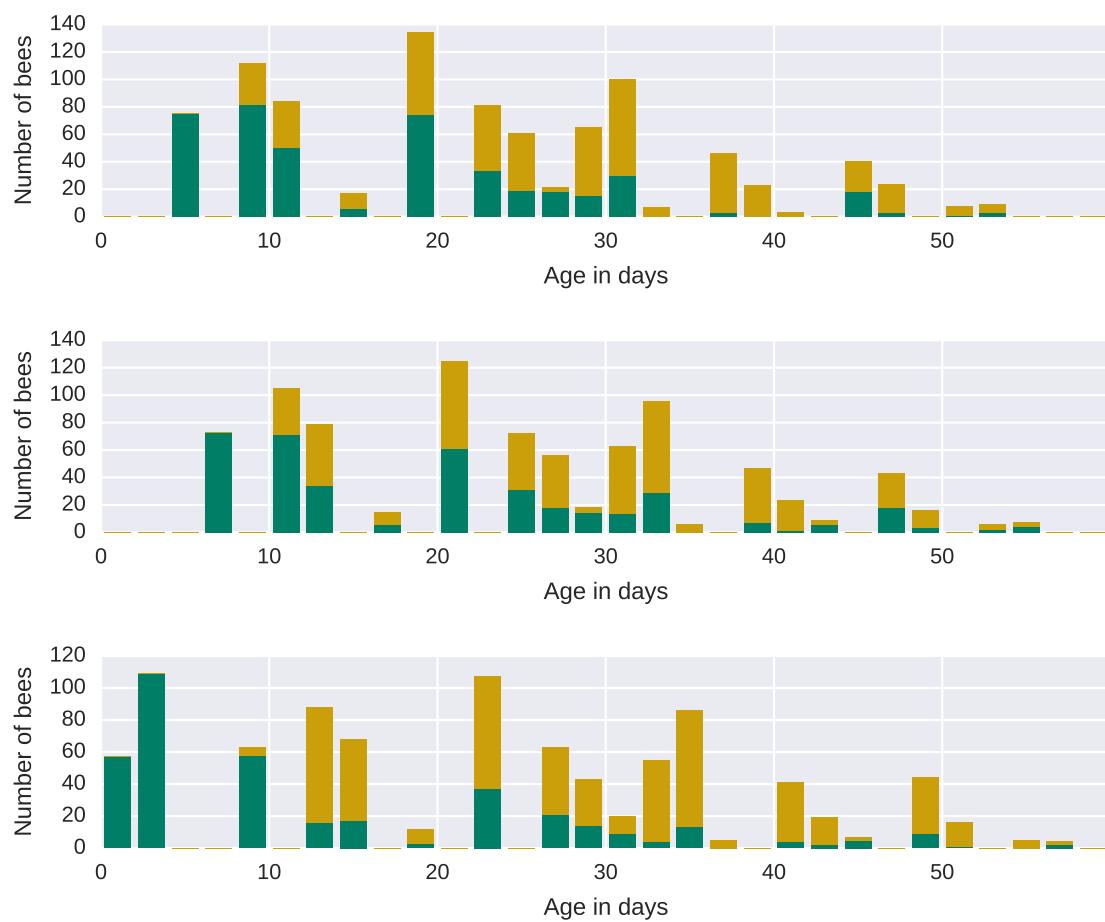
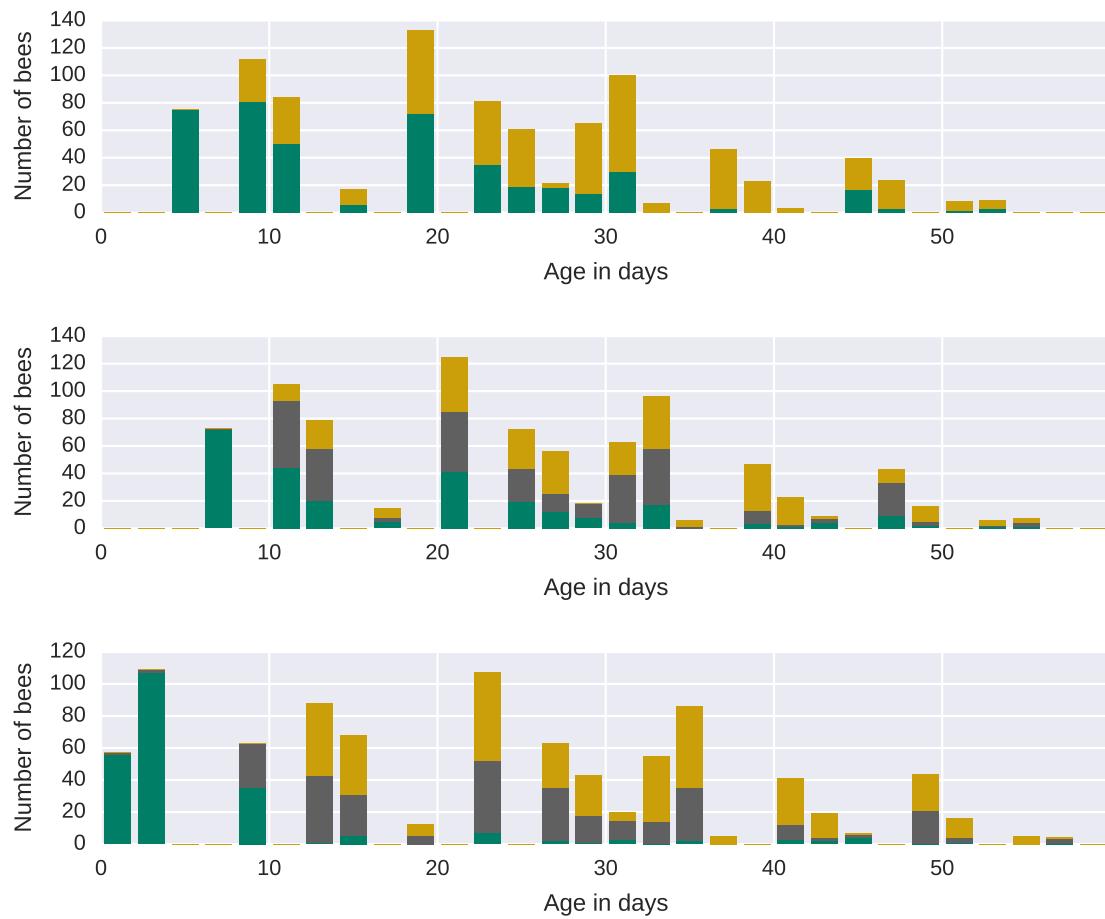


Figure C.5: Age distribution for leading eigenvector



(a) Age distribution for walktrap

Figure C.6: Age distribution per algorithm and snapshot xxx

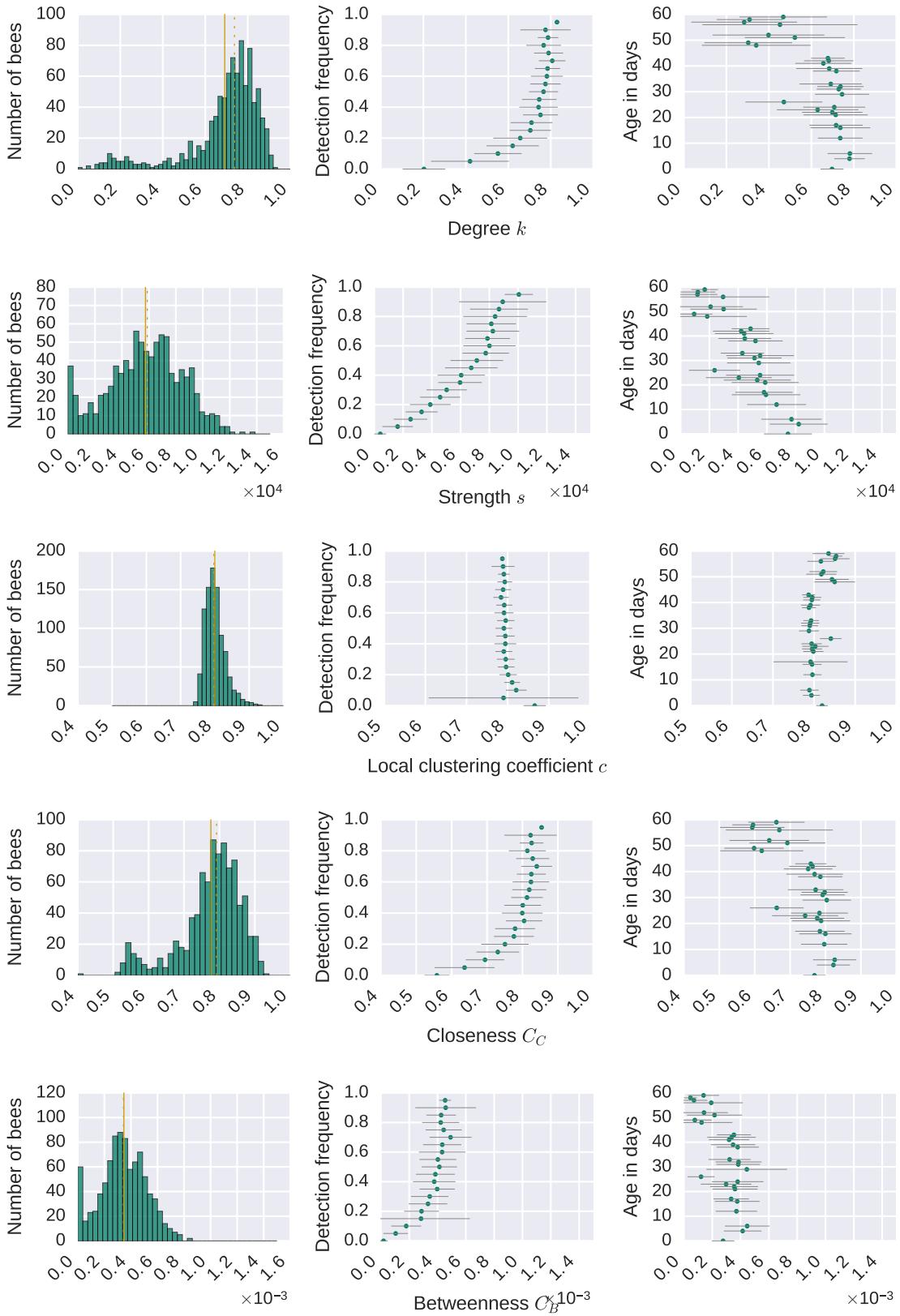


Figure C.7: Snapshot 1: Local measures in relation to age and detection frequency

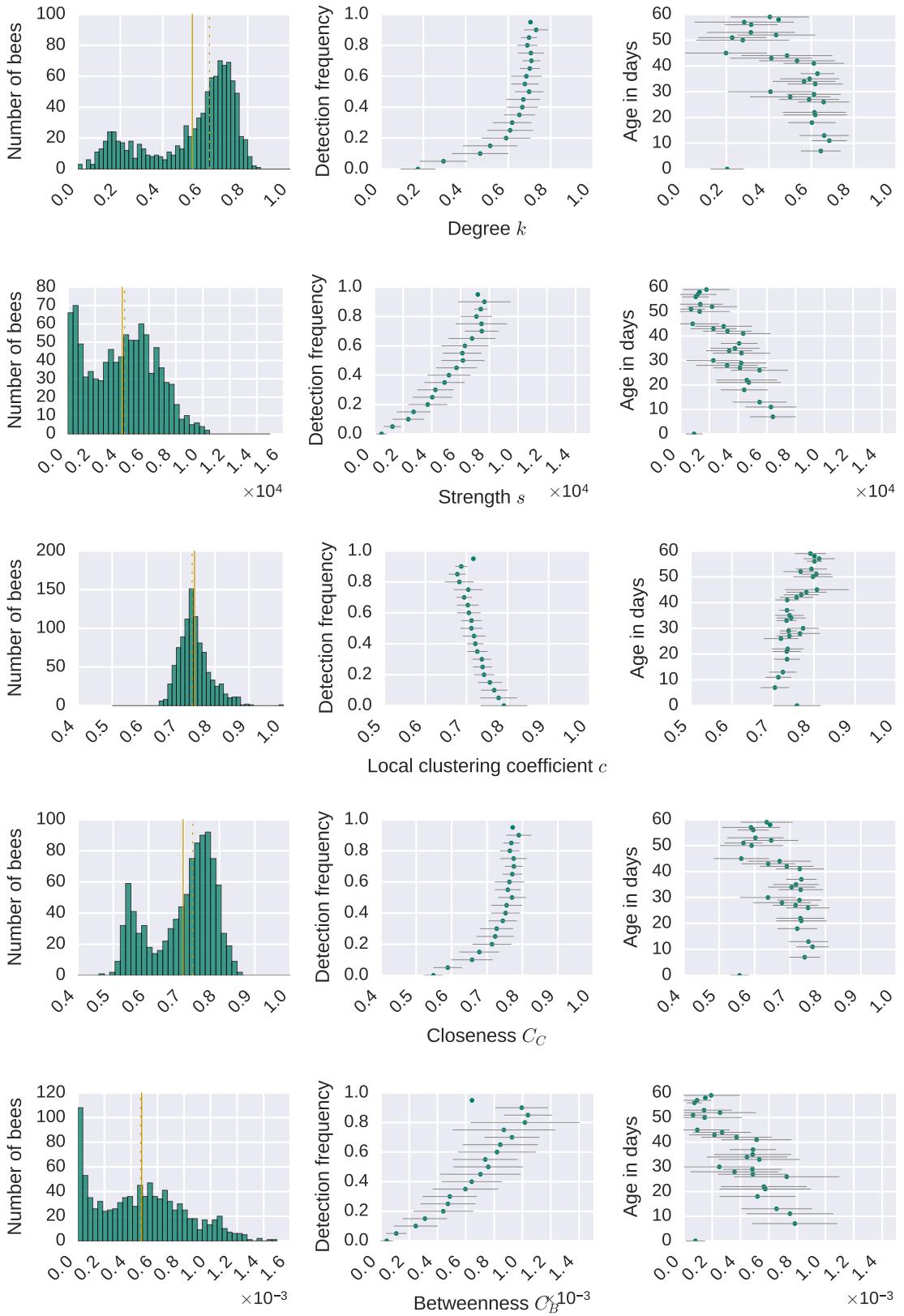


Figure C.8: Snapshot 2: Local measures in relation to age and detection frequency

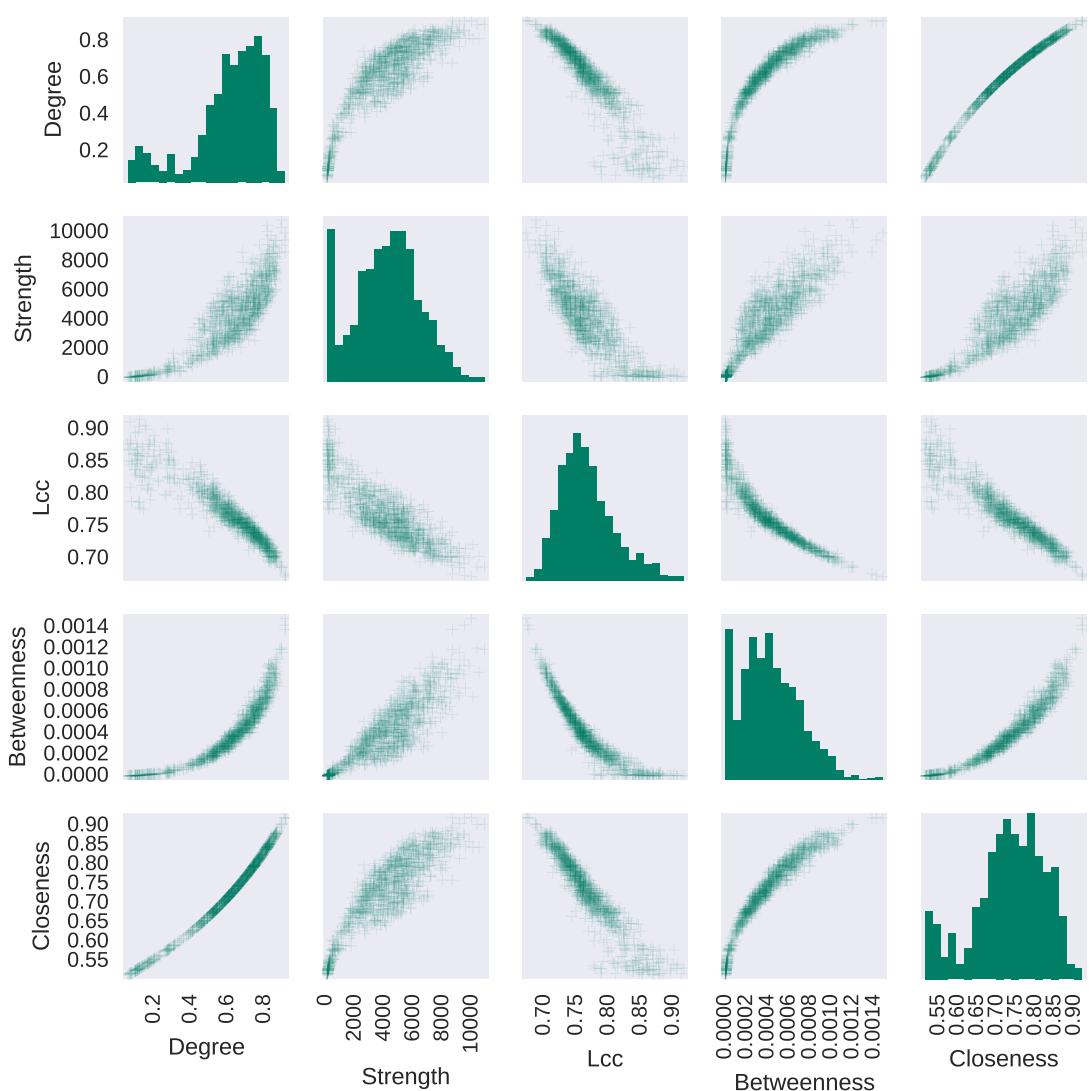


Figure C.9: Scatter plot for node level measure

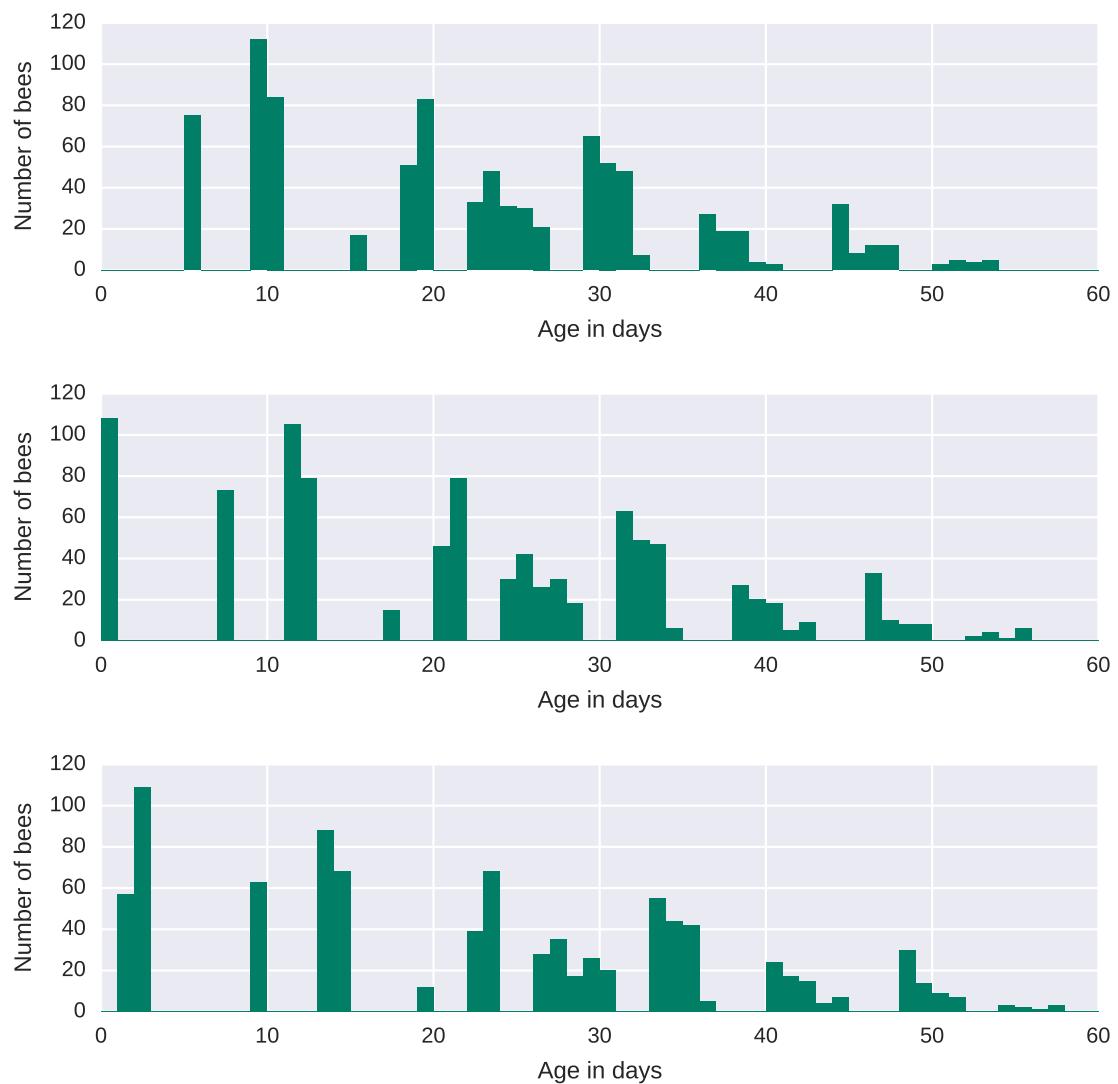


Figure C.10: Age distribution per snapshot