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Temporal Analysis of Honeybee Interaction Networks based on Spatial Proximity



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Berlin, den April 14, 2017

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Abstract

TODO

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Chapter 1

Introduction

A social insect society is formed by thousands of individuals, which continuously move and interact with each other inside a dark nest. Honey bees are organized in colonies, which form a complex and dynamical system. Observing individual honey bees and their interactions with each other is, therefore, 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 on their thorax by using circular 12-bit tags (figure 1.1) and then added to the observation colony. Four cameras observe the comb over a period of nine weeks, by capturing approximately three frames per second. An image analysis pipeline evaluates each frame automatically. The resulting data set contains, for each frame, the exact position of each detected bee on the honeycomb, and its age.

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 over a specified period. The networks are time-aggregated, which means one network represents the data of multiple frames. After extracting the temporal networks, social network analysis methods are applied to determine the characteristics of the resulting networks and its communities.



Figure 1.1: Tagged bees inside the observation hive.

1.1 Motivation

Colonies of social insects consist of a vast number of individuals. The technique of manual insect tagging and tracking is widely applied in the behavioral sciences: First animals are marked using colored paint or numbered tags to distinguish individuals. 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, a short observation period, a low number of frames, or limiting the observation to only a small area of the hive is very common. Accordingly, most studies in the field of animal social network analysis, related to insects, analyzed only a reduced subset of a colonies' life. The majority of social insect interaction networks studies, due to previously technical limitations, 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 comb over an extended period allows for more advanced analysis focusing on temporal dynamics. Therefore, automatic tracking allows shifting more towards the temporal and dynamic investigation.

1.2 Research Goal and Method

The aim of this thesis is to investigate whether the provided data set of tracked honey bees is useful for creating worker-worker interaction networks using spatial proximity as an indicator for interactions between bees. Thus, I need to implement a pipeline to extract networks out of the given data set. Furthermore, I want to find out 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 does the data set imply? What pipeline parameters are necessary?

2. *What kind of worker-worker interaction networks emerge and how are they structured?*

What is their topology? What properties are characteristic 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?*

Are they stable regarding their properties? How do members move between communities?

This work is meant to be the foundation to answer further more specific biological research questions using a network science approach to study the complex system of honey bee colonies and their collective behavior.

The methodology of this work consists of two parts, described in detail in Chapter 3. The first part deals with the approach to infer and define spatial proximity networks using the given tracking data of honey bees. It serves as a prerequisite for analyzing the resulting networks concerning its network properties, communities and its development in the second part.

1.3 Outline

This thesis is organized as follows. Chapter 2.1 gives a short introduction into social network analysis (SNA) and defines network measures, terms, and algorithms used throughout this work. In chapter 2.2, a brief summary of the current state of research concerning social insect networks, temporal networks and community detection in animal social networks is given. Chapter 3 describes 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. Chapter 4 reports the results of the network analysis and the characteristics of the extracted communities. Finally, in chapter 5 I explore 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). It introduces social insect interaction networks, as a special type of a biological¹ network. It defines terms and concepts used throughout this work and explains used network metrics and algorithms. Furthermore, I reviewed and classified the most relevant studies using a network analysis approach focusing on interaction networks of social insects.

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 is focusing on the special case of social insect networks, where individuals are nodes and edges are defined as interaction events between individuals are called *interaction networks*, sometimes called 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 (trophallaxis), 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].

¹Maybe more precise: within species interaction network.

2.1.1 Temporal Networks

When modeling temporal or so-called dynamic networks two main approaches exists (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 aggregates the data for each snapshot and therefore reduces the available information per edge. In contrast, the time-ordered approach keeps the information for each edge, when the interaction occurred and how long it lasted. It provides a detailed insight when timing and order of interactions are important. And therefore it can be used to model the topological flow information through a network.

Choosing suitable time intervals for aggregating is challenging [35], but a lot of methods for analyzing those networks already exists, whereas for time-ordered networks, only limit toolset is available. In time-aggregated networks, the modeling nodes and edge weights can be challenging when taking into account that interactions, which took place earlier or later in time are weighted accordingly.

2.1.2 Network Measures and Metrics

The following definitions are mainly taken from Barabási [2] and Newman [30]. the gray box summarizes the basic variables and terms of this work. [TODO: Box referencing as table and align bottom.]

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

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

Edge weight w_i of an edge l_i 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 edges a node has; so the number of other animals this animal interacts with.

Average Degree $\langle k \rangle$, the number of animals one animal interacts with on average.

Path length d the shortest number of links between two nodes.

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

Diameter d_{\max} is the longest of all path length. The distance between the two furthest nodes, 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

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

Is it independent from the edge weights.

Strength s_i of a node is also called the weighted degree. It measures the total weight of edges connected to a node n_i and is definded as

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

according to Barrat et al. [4]. The average strength denoted as $\langle s \rangle$.

Global clustering coefficient C_Δ 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 c_i of a node n_i quantifies how close its neighbours are to being a clique (complete graph).

Centrality When looking at the networks local structure (node level), 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. [30] In the course of analysing networks and their local node level structures, you will find and encounter the most important (central) nodes and vertices by indicators of centrality. These indicators give values to the nodes and therefore they can be listed in a way of importance.

The the weighted versions of betweenness and closeness using Dijkstra and the inverse of the edge weights.

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

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

Eigenvector Centrality The eigenvector centrality x_i of a node n_i is the sum of its connections to other nodes, weighted by their centrality.

$$x_i = \frac{1}{\lambda} \sum_j A_{ij} x_j$$

It is like a recursive version of degree centrality. So a nodes importance (centrality) is increased by having neighbours that are themselves important. Eigenvector centrality gives each vertex a score proportional to the sum of the scores of its neighbours. [30]

Closeness Centrality Is is the average length of the shortest path between node n_i to all other nodes in the network. The more central a node is the closer it is to all other nodes. Mean distance from a node to other nodes. [30]

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

Betweenness Centrality It measures the extend to which a node lies on paths between other nodes. Nodes that occur on many shortest paths between other nodes have 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 who address the detection of communities. Fortunato [16] gives an extended 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 related 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, therefor a modularity of 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 modularity improvement is maximised based on the leading eigenvector. The algorithms stops if the modularity is not increasing anymore.

This *walktrap* algorithm by Pons and Latapy [37] is based on random walks. The authors consider random walks as a tool to calculate similarity between nodes of a network. It uses a bottom-up hierarchical approach, that means the algorithms start with each node its own 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 in 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 A.1 (Appendix A) 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 study 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.

The frequency of interactions between bees is used 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!]

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

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 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.

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.

Chapter 3

Methodology

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

3.1 Inferring Spatial Proximity Networks

To yield the first set of functional and non-functional requirements concerning the pipeline, I conducted a data analysis of the given tracking data, and a literature review, already mentioned in section 2.2. The data analysis supported the forming of a general understanding of the given dataset, its structure, characteristics and estimation of its quality. The purpose of the review was to get an overview of the common methods and approaches regarding network analysis in this field of research. Both results are then used to decide for a network type and its definition of nodes and edges. Furthermore, I inferred specific pipeline parameters and decided for the procedure of network extraction.

This pipeline was developed, tested and then 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 derives 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 permanently. Figure 3.1 illustrates the camera setup. The *recording period* lasted nine weeks (63 days), from 19.07.2016 until 19.09.2016, with

3.1. Inferring Spatial Proximity Networks

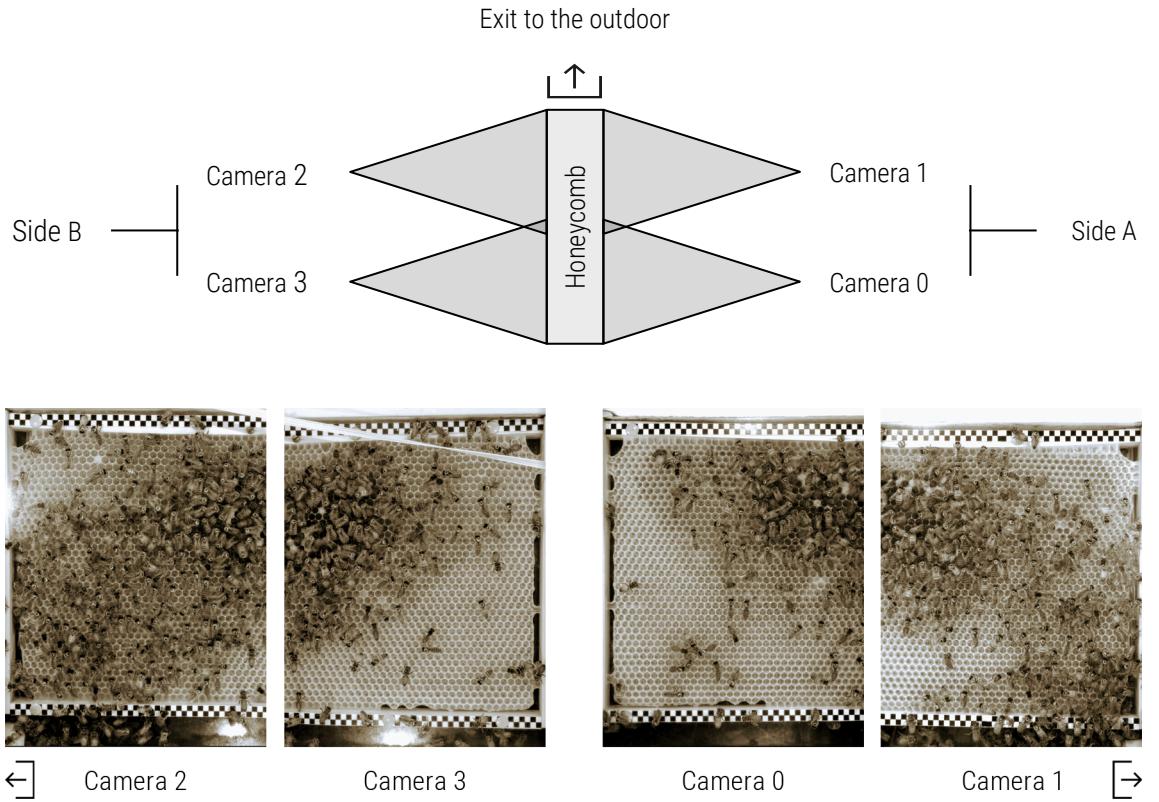


Figure 3.1: Observation setup Each side of the honeycomb is filmed by two cameras. The two cameras per side overlap, so bees inside this area are detected from both cameras.

some interruptions due to maintenance work and technical failures. An overview about the complete recording period is given in figure A.5 in appendix A.

All four cameras, each with a resolution of 4000×3000 pixel, record 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 days long *tagging period* started 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, about noon each day. Figure A.4 (Appendix A) shows the frequency of tagged bees per day. The hatching day for each bee is documented; 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]. Hence, the maximum number of present bees in the hive is about 1,600.

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

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

Data Scheme

The data is organized in so-called *frame containers*. Each frame container corresponds to one video file of a certain camera and consists of about 1024 frames. Each *frame* holds a list of bees, which were detected by the image analysis pipeline.

A bee *detection* has, among others, the 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 is not a one or zero but 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, which remains for further processing.

I use the age information of the bees to check the quality of the remaining data. A bee has a negative age, if the pipeline detected a code, that was not used yet. I

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

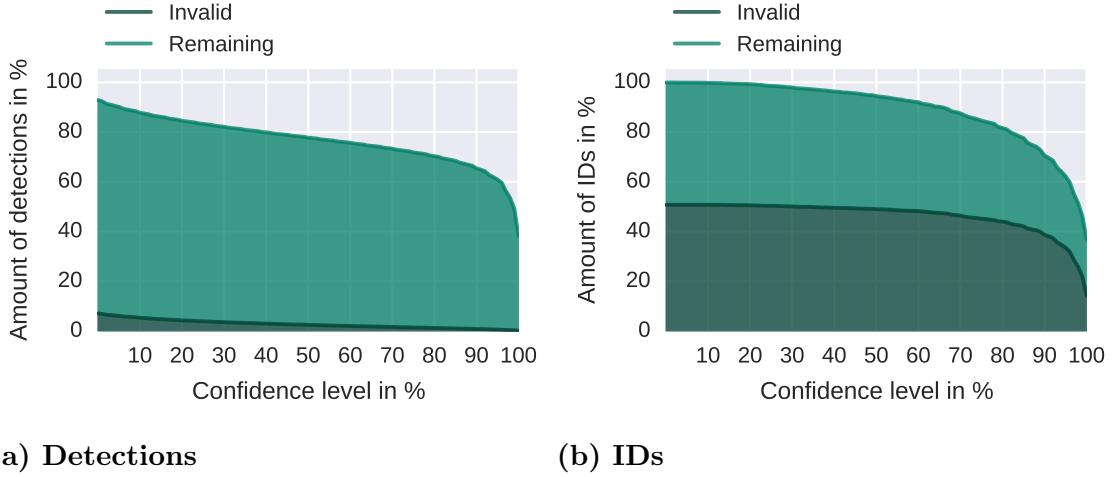


Figure 3.2: Quality of detections and IDs Light green represents the number of remaining detections and IDs (from 4096 possible IDs). Dark green indicates the fraction of invalid detections and IDs and in relation to the remaining number of detections and IDs.³

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*. Also, an ID with a negative age is counted as an *invalid ID*.

As expected, with increasing confidence, the number of remaining detections and IDs decreases (figure 3.2), as well as the fraction of invalid detections and IDs. With a confidence level of 100%, the fraction of invalid detections reaches the value of 2.5%. However, the fraction of invalid IDs stays at the high value of 30.2%. Consequently, selecting a high level of confidence is not sufficient for obtaining a high data quality. Therefore, to obtain a more reliable dataset, invalid detections need to be filtered out, in addition to choosing a good level of confidence.

Detection Frequency Filter

A good indicator, whether a bee detection represents a real bee on the comb is its detection frequency. The hypothesis is: Individuals with a very low detection rate seem to be detection errors and lead to the assumption that those bees do not exist. 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 on average less detected than bees with a positive age.

During my analysis, I noticed the existence of bees with a high detection frequency attributed with a negative age. I inspected the corresponding photos and confirmed that those bee detections correspond to living individuals and are no artifacts. Probably this result from a mistake in the table, which reports the hatching days for each

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

3.1. Inferring Spatial Proximity Networks



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.

bee. Consequently, I excluded bees from this analysis, which had a negative age, but a detection frequency 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 tracks represent 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 consequently 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.

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

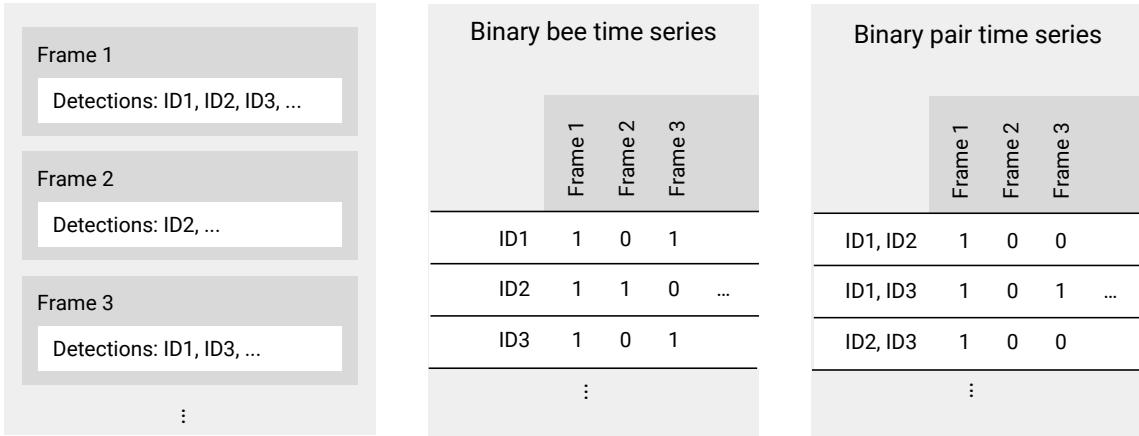


Figure 3.4: Structure of dataset *Left:* original dataset - containing a sequence of frames with bee detections; *Middle:* binary bee time series - zero and one indicate absence and presence of a bee; *Right:* binary pairs time series - zero and one indicate the absence and presence of two bees in the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

For further network analysis, I chose three days: 20., 22., and 24. August. Those days were selected because a wide range of age groups was present at this time. The hive especially contained older bees which are likely to be foragers. Besides, no data

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)

is missing on those days. 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 (± 16 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.

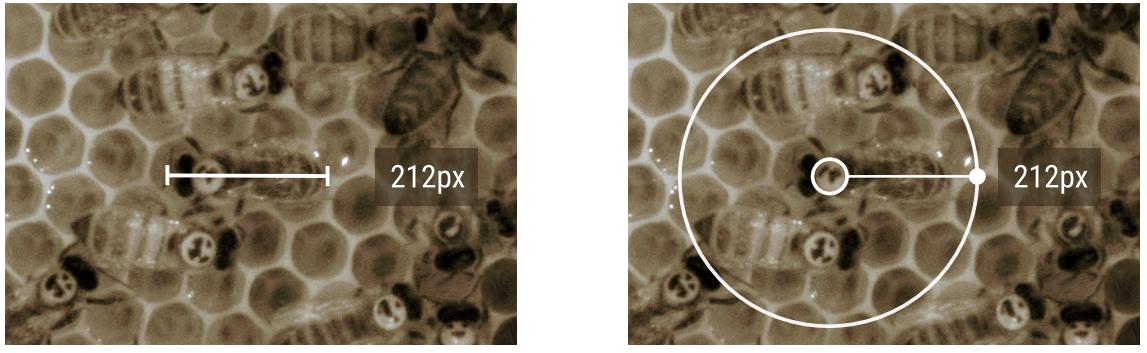
The confidence level confidence is set to 95%, to keep about 60% of the data. The gap size is set to two frames. This value corresponds to the median gap length in the time series of bee pairs.

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 parameters 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 final network.

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 3.1: 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

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 in general.

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

maximum distance, minimum contact duration, window size

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/>

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

[TODO überarbeiten]

This section explains the what measures I used to investigate the properties of my temporal networks and justifies my choice. Also I explain how I chose a community detection algorithm and which one I picked. Explains method to examine age and spatial segregation of communities and how I study the development of communities.

3.2.1 Investigating the Topology and Network Characteristics

[TODO: überarbeiten]

Table A.2 (or figure A.1 summarized the used network analysis methods in the reviewed studies mentioned in chapter 2.2. The table includes global level measures, node level measures and other network analysis methods the authors used in their

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

Table 3.2: 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	

studies. I chose the measures for my own analysis, because of XY. [TODO: do I need to explain, why I used this and not that?] Therefore, I am going to analyse the global network properties and local node level properties listed in table 3.2. The node level metrics are investigated also in relation to the bees age. The global network properties are compared to an Erdős-Rényi random network, by averaging over 100 runs [TODO cite?].

The degree k of a bee represents the number of other bees this focal animal interacts. Bees with a high number of interaction partners, therefore, have a high degree. Bees with a low number of interaction partners consequently a low degree.

The strength s of a bee is the total number of all its interactions. A high strength indicates that this bee has either a high number of interaction partners (with a low interaction frequency, low edge weight) or interaction partners, with a high interaction frequency (high edge weight).

The local clustering coefficient (lcc) c of a bee indicates how close its interaction partners are to being a clique¹³. A high lcc indicates that its interaction partners all interact with each other. A low lcc shows the absence of those interactions.

The betweenness of a bee measure how many shortest paths go through a bee, meaning how many information would flow through a bee or how many foods is transferred. A bee with a high betweenness would be central or important for the network in the sense of information flow. Removing this bee 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 it can reach all others in the network. A high closeness indicated a very short path to every other bee. A low closeness consequently a long path to all other bees. Regarding information flow, a bee with high closeness can spread information to all other bees very fast.

¹³A clique is a complete subgraph.

3.2.2 Detecting Communities

[TODO: überarbeiten]

(1) check reviewed studies, (2) check comparative analysis, (3) check algos by myself. The reviewed studies only include two examples of community and cluster analysis. Mersch et al. [25] used the infomap [40, 39] algorithm. As they explain this algorithm only works for sparse networks, it is not applicable in my case. Baracchi and Cini [3] use a clustering algorithm. [TODO explain and why not want to use] I want to perform community detection instead of cluster analysis. [TODO: difference?] There are comparative analysis of community detection algorithms, e.g. [51, 18]. They seem to be promising, but assume either a power law degree distribution or evaluate networks with a low density, which is not applicable here.

Therefore, I tested all 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 criteria:

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

Table 3.3 gives an overview about the twelve algorithms reviewed. Five algorithms did not 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 is the same as multilevel, 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 had a closer look at fastgreedy, leading eigenvector, multilevel, and walktrap regarding the number of detected communities and community size for all three networks. Table 3.4 shows the results. All algorithms found at least two communities. Except for leading eigenvector, there is a tendency that a third community exists. 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 possible third community.

Age Distribution of Communities [TODO überarbeiten]

For each community I investigated the age distribution and the average age for. I

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

Table 3.3: 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 – mean 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	–	–	–	–	–
	473	488	469	462	490	922	922					
	434	434	453	427	431							
	15			33	(1)							

¹ igraph, ² NetworkX, ³ graph-tool

Table 3.4: Chosen algorithms for community detection These four algorithms were tested, and the comparison of their results are displayed for all three snapshots.

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

also investigated whether the age division persists in each snapshot. A two sample Kolmogorov-Smirnov test was used to determine the statistically difference of the age distribution between communities. Answer the question: Communities reflect different age groups? For hypothesis (2) the data is stored as a csv file of birth dates of each bee. For testing if age gups are different the Kolmogorov Smirnov Test was used.

Spatial Distribution of Communities [TODO überarbeiten]

Communities occupy different areas of the comb (similar to [3]). Do they stay at the same in each snapshot? Answer the question: Communities reflect groups of bees working in different areas of the hive? The data which was used to test the hypothesis (1) is saved in a sqlite database for faster access, because using bb_binary (parsing the data over and over again) was to slow.

3.2.3 Evolving Communities

[TODO: Change to intersection and flowcharts] 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. The author suggests applying a threshold to more precisely define what “share a lot of nodes” means. Otherwise, a matching could occur between communities with only 0.1% of overlapping nodes. I matched all communities, but excluded values below 3%.

I calculated the match value between consecutive snapshots, to investigate the number of bees, which stay the same over time. Also, I calculated all match values of all communities per snapshot.

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 results related to static aspects of one snapshot 3. I investigate the snapshot on three levels. First I examined the networks global structure and derived properties of the overall colony (global level). Second I studied the characteristics of individual bees (local level), and its relation to detection frequency and age. Additionally, I investigated the intermediate level of the colonies social organization by detecting communities and inspecting their practical meaning.

The second section focuses on the temporal network aspects of all three snapshots. I investigated 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. The last section fo this chapter summarizes the main results and discusses the findings.

4.1 Static Perspectives of Honey Bee Networks

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 and figure A.11 for the age distributions. Figure 4.1 shows the proportion of intersecting bees between each 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.	-

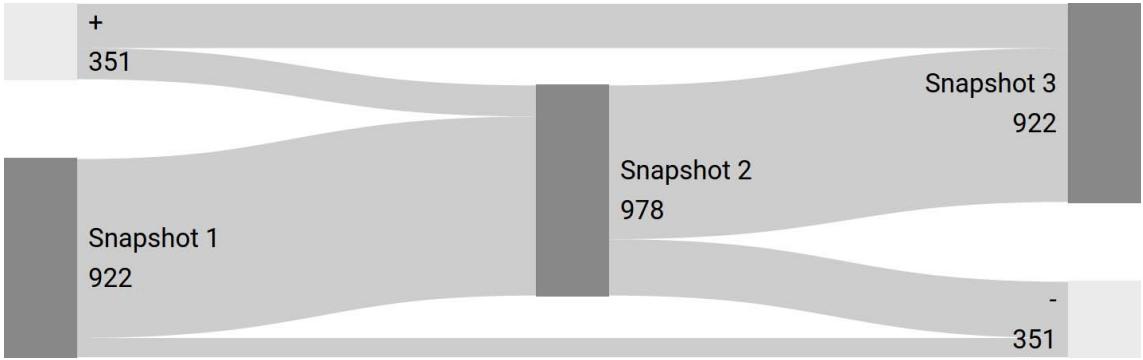


Figure 4.1: Number of bees per snapshot This figure show the amount of bees for each snapshot and the proportion of intersecting.

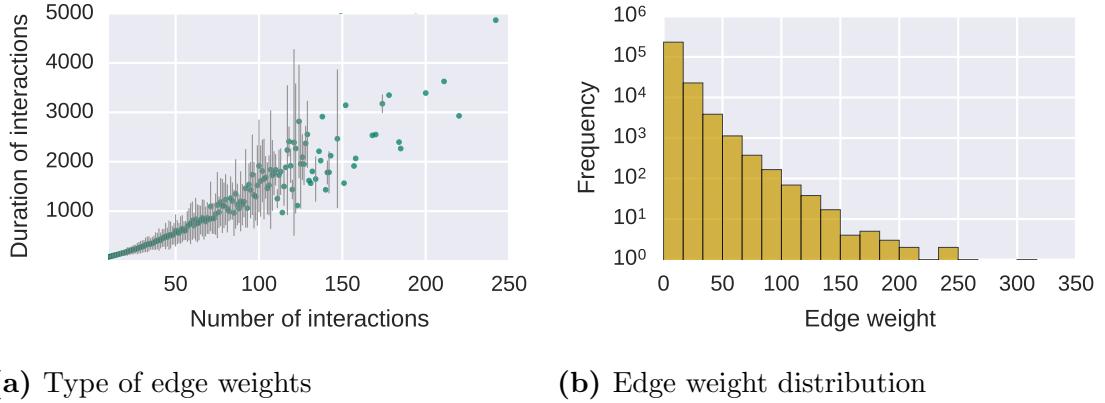
4.1.1 Properties of the Bee Colony

Each snapshot consists of one component. Table 4.2 summarizes the basic network properties for each snapshot. The density D is over 50% for all snapshots. The diameter $\langle d_{\max} \rangle$ is three and the average shortest path length $\langle d \rangle$ is below two. The global clustering coefficient 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. The high clustering coefficient and the small diameter suggest a small-world network type. On average, each bee is connected to at least 50% of all other bees.

Figure 4.2a shows a positive correlation between the frequency of interactions and the total duration of interactions. I chose the frequency of interactions as the weight for edges. The edge weight distribution is shown in figure 4.2b. Most edges have a low weight; only a few edges have a high weight. It seems that bees do not prefer individuals bees for interaction. Figure 4.3b shows the age distribution of the investigated snapshot 3. This distribution does not seem to follow any known distribution. It corresponds to the artificial tagging of 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 4.3a).

Table 4.2: Global network properties N number of nodes, L number of edges, D diameter, $\langle d_{\max} \rangle$ average path length, 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.

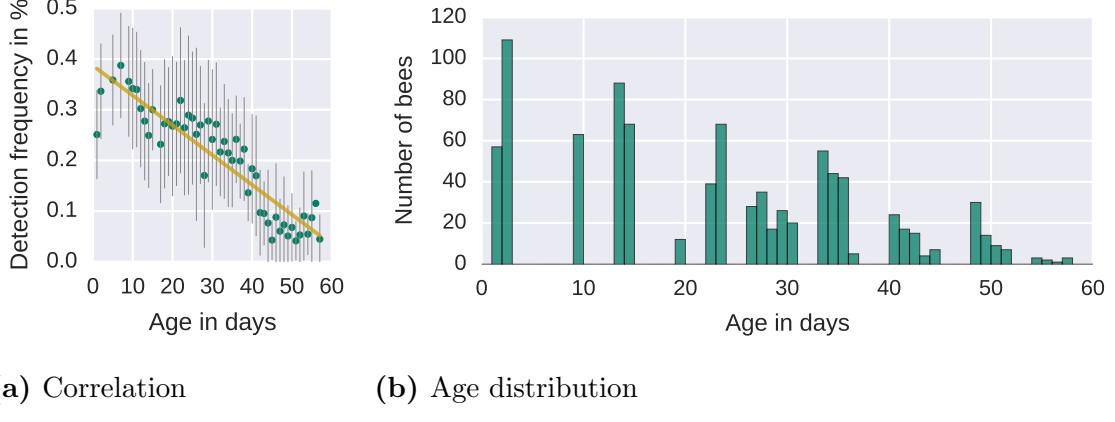
	N	L	D	$\langle d_{\max} \rangle$	$\langle d \rangle$	C_Δ	$\langle k \rangle$	$\langle s \rangle$
Snapshot 1	922	291179	0.69	3	1.32	0.79	631.62	5680.17
Random 1	922	291179	0.69	2	1.31	0.69	631.62	-
Snapshot 2	978	256066	0.54	3	1.46	0.72	523.65	3977.94
Random 2	978	256066	0.54	2	1.46	0.54	523.65	-
Snapshot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



(a) Type of edge weights

(b) Edge weight distribution

Figure 4.2: Edge weights (a) Correlation between number of interactions and total duration of interactions. The number of interactions is chose as the edge weight. (b) The edge weight distribution decays exponentially.



(a) Correlation

(b) Age distribution

Figure 4.3: Age distribution and correlation with detection frequency of snapshot 3 (a) Detection frequency and the age of a bee seem to be negatively correlated. (b) The age of bees ranges from one to 60 day, but some age groups are missing.

4.1.2 Characteristics of Bees

For snapshot 3, 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 and derived characteristics and properties of the honey bee colony.

Low Hierarchical Structure

The degree is normally distributed (a in figure 4.4). Therefore most bees have the same high number of interaction partners. The absence of hubs, a small number of highly connected bees, indicates a low hierarchical structure of the network. Strength and lcc are also normally distributed (d and g in figure 4.4). 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 4.4) also

4.1. Static Perspectives of Honey Bee Networks

follow a normal distribution. This leading to the assumption that no central or important bees exist. 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 4.4) show a positive correlation with the detection frequency. A low value corresponds to a low detection frequency. In contrast, the local clustering coefficient (h in figure 4.4) 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 local clustering coefficient distribution is instead right skewed, with one peak at 0.75

There is no clear border between groups 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 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. The second is rather unlikely, looking at the edge weight distribution (figure 4.2b). 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 plot show a separate group of bees older than 45 days, seeming to correspond 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. Static Perspectives of Honey Bee Networks

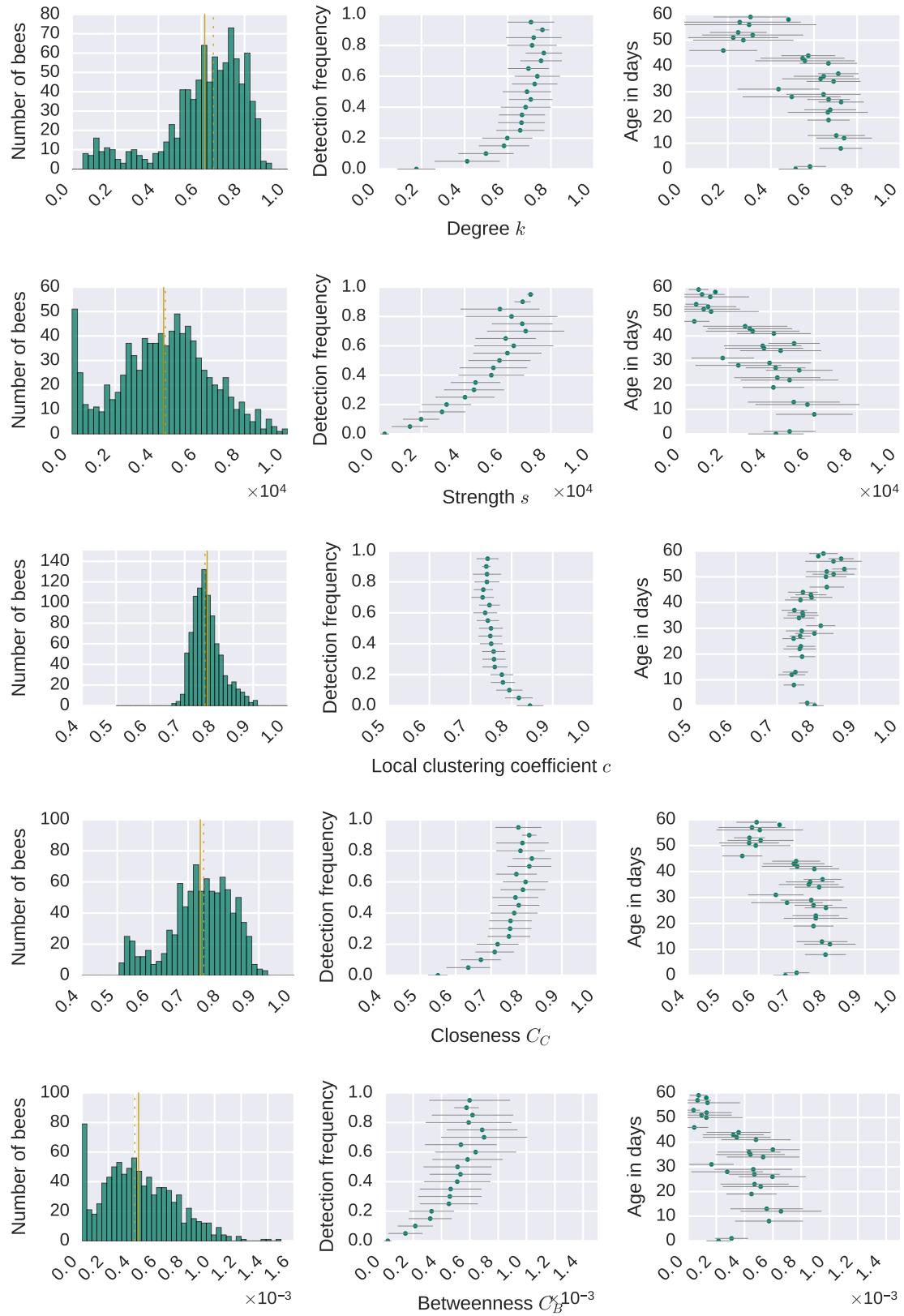


Figure 4.4: Local measures in relation to age and detection frequency

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.

The communities correspond to different age groups. The young community is 13.15 days old (6.55 days for WT), and the old community is 28.70 days old (29.29 days for WT). The third middle-aged community of WT is 25.08 days old. The age distribution for each algorithm is represented in figure 4.5a and 4.5b. 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 4.5 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.

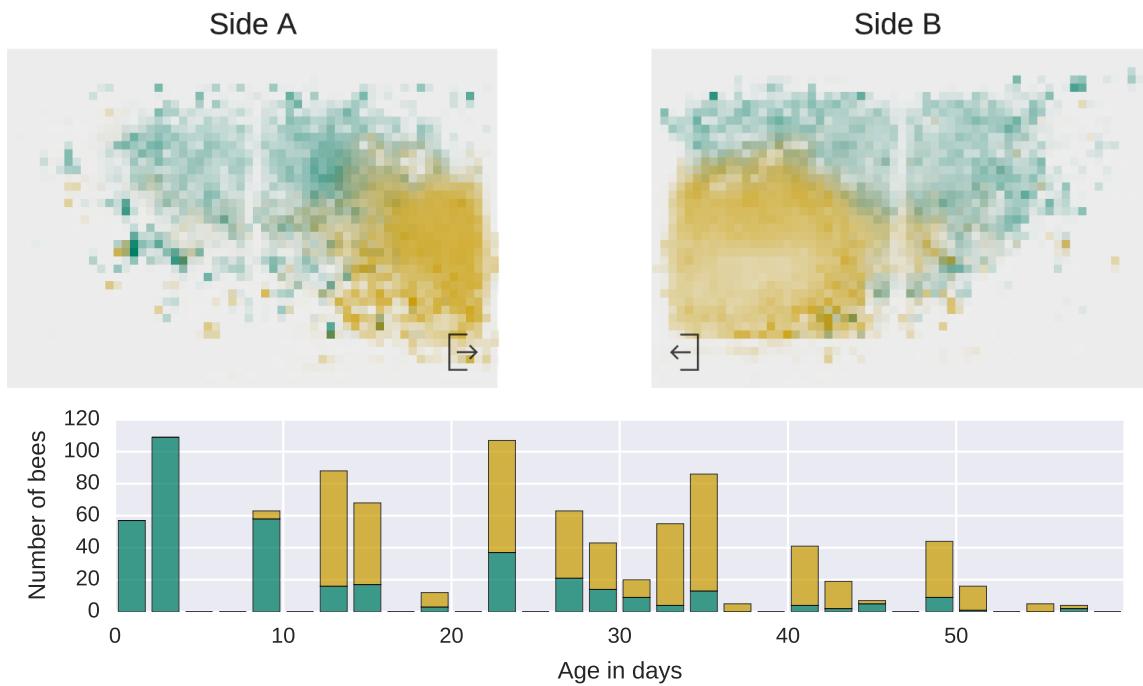
Table 4.3: Communities per algorithm Communities marked with * contain the queen. Age and standard deviation (SD) are measured in days. The queen and nine bees with a negative age are excluded from this analysis.

	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

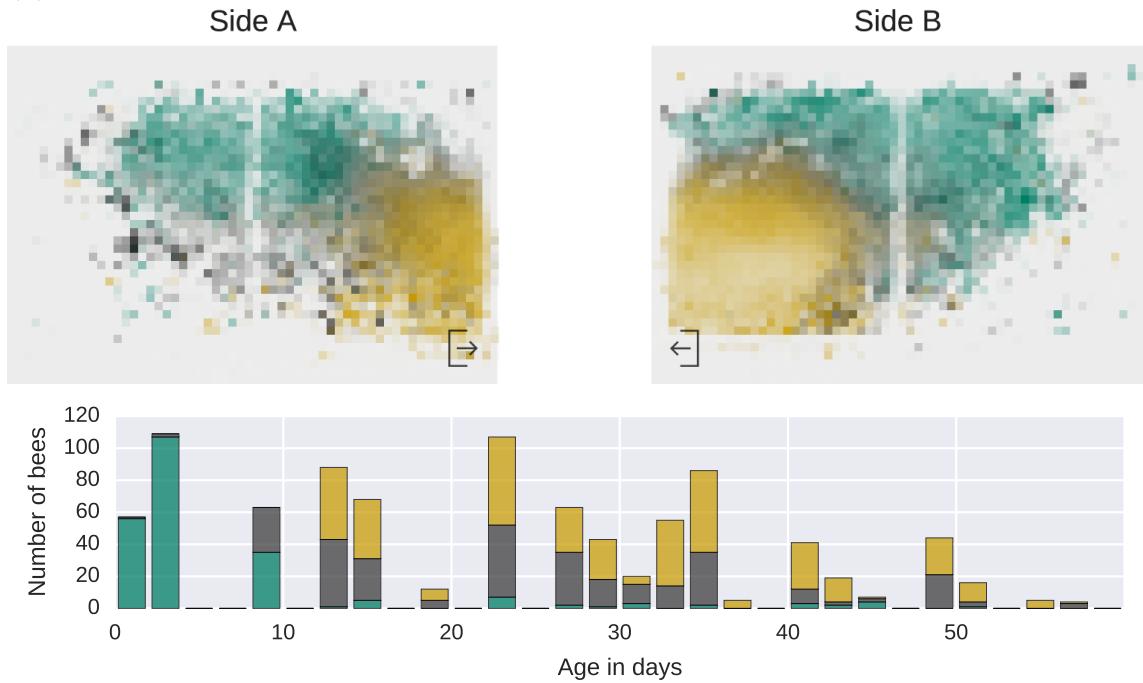
Table 4.4: Kolmogorov-Smirnov test p -values for leading eigenvector (LE) and walktrap (WT)

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

4.1. Static Perspectives of Honey Bee Networks



(a) Leading eigenvector communities



(b) Walktrap communities

Figure 4.5: 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.

4.2 Temporal Perspectives of Honey Bee Networks

For all three snapshots, the same exponentially decay regarding the edge weights can be seen in figure A.9a. The analysis of snapshot 1 and 2 showed that the same characteristic distribution of degree, strength, lcc, betweenness, and closeness for snapshot 1 A.12 and snapshot 2 A.13 exists. They also follow a normal distribution. The correlation between the local measure and detection frequency and age remains. This shows that the characteristics described in section 4.1.2 applies for all three snapshots and is, therefore, stable for this investigated time interval. A low hierarchical structure and the correlation with age and detection frequency seem to be a global property 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, the leading eigenvector 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, walktrap identified three communities, but two for the first snapshot. 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 and CM3 are on average younger than the bees in CO2 and CO3. Figure A.8 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 walktrap 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 A.7 and A.6. 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 4.6a (LE) and figure 4.6b (WT) show the flow of bees between consecutive snapshots and communities. For leading eigenvector 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 and CM3, detected by walktrap, consist partly of young (CY1) and old (CO1) bees. The switching behavior of individuals between communities is similar to leading eigenvector. Individual bees change communities as they age.

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					
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					
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

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

4.3. Discussion of Results

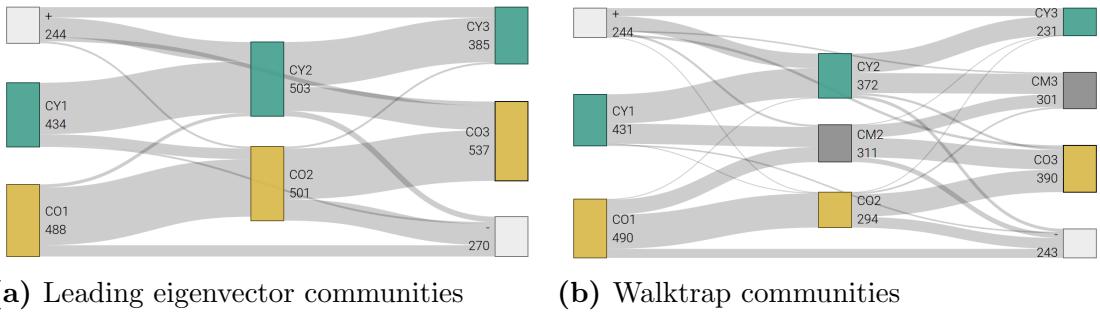


Figure 4.6: Dynamics of bees Each column represents a time step, the colored rectangles represent the communities for each step, and the height of the rectangles corresponds to the number of its community members, as referenced by the number. *Green* indicates the community containing young bees and 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.

4.3 Discussion of Results

In the following chapter, I summarize and discuss my results concerning 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 many biological networks, including insect colonies, are thought to approximate scale-free networks. For some of them, the scale-free property has been shown, but for social insect networks, this question remains open.

4.3. Discussion of Results

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, regarding interaction networks based on spatial proximity, physical contacts or food transfer. 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. Consequently, hubs are absent and accordingly a non-hierarchical structure is typical for 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 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. Baracchi and Cini [3] also assumed that the time, which bees spend outside the hive, affects their connectedness within the interaction network and, hence, their findings might be trivial. 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.

I noticed a bimodal degree, strength, closeness and betweenness distributions and a right skewed local clustering coefficient distribution, corresponding 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 network, therefore this group of bees probably 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. This strongly affects the mean, especially of the old group, because the number of old bees is very low.

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 (leading eigenvector and walktrap) 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.

I inspected three snapshots over a period of five days and found out that the detected

4.3. Discussion of Results

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, they used three predetermined age cohorts, instead of representing all age groups ranging from 0 to 60 days, as in my study.

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] distinct 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, middle-aged bees instead perform several tasks

The communities I detected relate to those functional groups of bees. 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 the provided high-resolution honey bee tracking data. Moreover, the resulting weighted undirected spatial proximity networks of three consecutive time steps were analyzed regarding their network topology, community structures and the development of community members.

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 those networks allows efficient communication within the bee colony. The detected communities within the honey bee colony, relate to 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 relate to distinct tasks.

The global network structure of the honey bee colony is stable over time, but its local structure is highly dynamic as individual bees change communities as they age. My results are aligned with established state of research and directly relate to 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. It can be stated, that 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 the restrictions, which result from the high density of the networks, are pointed out.

Despite a complex preprocessing procedure, the quality of the extracted networks could be higher. Although I filtered out erroneous detections before network generation, a few number of 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.

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

Spatial proximity is an indicator for interaction but 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, where space is limited. It leads to many edges and a high density of the network resulting in high noise. This noise provokes 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, which profits by the aggregation, all other measures are less meaningful. Due to the high density and size of the network, the methods I can apply concerning 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 change regarding 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. Moreover, a simple global threshold for excluding edges below a certain value could be used.

Using the Potential of Weighted Edges Instead of applying a global threshold to reduce the density, a network reduction algorithms 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 already implemented weighted measures (e.g., closeness and betweenness) 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 purposeful. I propose two options: either normalize the edge weight by e.g. 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. At 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 already 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 worth to be studied further systematically. In my work, I tested the robustness just for some values, but there are more to investigate. In the case of robustness, I focused more on different algorithms. 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 is not targeted towards a specific study purpose, opens the space to investigate the data in an explorative way and to discover the unexpected.

The prerequisites for studying non-human animal data in an explorative way that fosters the framing of a novel biological hypothesis are either a personal, 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 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.

Bibliography

- [1] Thomas Aynaud et al. “Communities in evolving networks: definitions, detection, and analysis techniques”. In: *Dynamics On and Of Complex Networks, Volume 2*. Springer, 2013, pp. 159–200.
- [2] Albert-László Barabási. *Network science*. Cambridge University Press, 2016.
- [3] David Baracchi and Alessandro Cini. “A Socio-Spatial Combined Approach Confirms a Highly Compartmentalised Structure in Honeybees”. In: *Ethology* 120.12 (2014), pp. 1167–1176.
- [4] Alain Barrat et al. “The architecture of complex weighted networks”. In: *Proceedings of the National Academy of Sciences of the United States of America* 101.11 (2004), pp. 3747–3752.
- [5] Marc Barthelemy, Bernard Gondran, and Eric Guichard. “Spatial structure of the internet traffic”. In: *Physica A: statistical mechanics and its applications* 319 (2003), pp. 633–642.
- [6] Benjamin Blonder and Anna Dornhaus. “Time-ordered networks reveal limitations to information flow in ant colonies”. In: *PloS one* 6.5 (2011), e20298.
- [7] Benjamin Blonder et al. “Temporal dynamics and network analysis”. In: *Methods in Ecology and Evolution* 3.6 (2012), pp. 958–972.
- [8] Piotr Bródka, Stanisław Saganowski, and Przemysław Kazienko. “Community Evolution”. In: *Encyclopedia of Social Network Analysis and Mining* (2014), pp. 220–232.
- [9] Daniel Charbonneau, Benjamin Blonder, and Anna Dornhaus. “Social insects: a model system for network dynamics”. In: *Temporal Networks*. Springer, 2013, pp. 217–244.
- [10] James D Crall et al. “BEEtag: a low-cost, image-based tracking system for the study of animal behavior and locomotion”. In: *PloS one* 10.9 (2015), e0136487.
- [11] Darren P Croft, Richard James, and Jens Krause. *Exploring animal social networks*. Princeton University Press, 2008.
- [12] Jesper Dall and Michael Christensen. “Random geometric graphs”. In: *Phys. Rev. E* 66 (1 2002), p. 016121.
- [13] Damien R Farine and Hal Whitehead. “Constructing, conducting and interpreting animal social network analysis”. In: *Journal of Animal Ecology* 84.5 (2015), pp. 1144–1163.
- [14] Mark Fiala. “Comparing artag and artoolkit plus fiducial marker systems”. In: *Haptic Audio Visual Environments and their Applications, 2005. IEEE International Workshop on*. IEEE. 2005, 6–pp.

- [15] Vincent A Formica et al. “Fitness consequences of social network position in a wild population of forked fungus beetles (*Bolitotherus cornutus*)”. In: *Journal of evolutionary biology* 25.1 (2012), pp. 130–137.
- [16] Santo Fortunato. “Community detection in graphs”. In: *Physics reports* 486.3 (2010), pp. 75–174.
- [17] Efrat Greenwald, Enrico Segre, and Ofer Feinerman. “Ant trophallactic networks: simultaneous measurement of interaction patterns and food dissemination”. In: *Scientific reports* 5 (2015).
- [18] Steve Harenberg et al. “Community detection in large-scale networks: a survey and empirical evaluation”. In: *Wiley Interdisciplinary Reviews: Computational Statistics* 6.6 (2014), pp. 426–439.
- [19] John Hopcroft et al. “Tracking evolving communities in large linked networks”. In: *Proceedings of the National Academy of Sciences* 101.suppl 1 (2004), pp. 5249–5253.
- [20] Raphaël Jeanson. “Long-term dynamics in proximity networks in ants”. In: *Animal Behaviour* 83.4 (2012), pp. 915–923.
- [21] Brian R Johnson. “Within-nest temporal polyethism in the honey bee”. In: *Behavioral Ecology and Sociobiology* 62.5 (2008), pp. 777–784.
- [22] Jens Krause et al. *Animal social networks*. Oxford University Press, USA, 2014.
- [23] Martin Lindauer. “Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat”. In: *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 34.4 (1952), pp. 299–345.
- [24] R. Menzel and M. Eckoldt. *Die Intelligenz der Bienen: Wie sie denken, planen, fühlen und was wir daraus lernen können*. Knaus Albrecht, 2016.
- [25] Danielle P Mersch, Alessandro Crespi, and Laurent Keller. “Tracking individuals shows spatial fidelity is a key regulator of ant social organization”. In: *Science* 340.6136 (2013), pp. 1090–1093.
- [26] James Moody, Daniel McFarland, and Skye Bender-deMoll. “Dynamic network visualization 1”. In: *American journal of sociology* 110.4 (2005), pp. 1206–1241.
- [27] Dhruba Naug. “Structure and resilience of the social network in an insect colony as a function of colony size”. In: *Behavioral Ecology and Sociobiology* 63.7 (2009), pp. 1023–1028.
- [28] Dhruba Naug. “Structure of the social network and its influence on transmission dynamics in a honeybee colony”. In: *Behavioral Ecology and Sociobiology* 62.11 (2008), pp. 1719–1725.
- [29] Dhruba Naug and Brian Smith. “Experimentally induced change in infectious period affects transmission dynamics in a social group”. In: *Proceedings of the Royal Society of London B: Biological Sciences* 274.1606 (2007), pp. 61–65.
- [30] M. Newman. *Networks: An Introduction*. OUP Oxford, 2010.

- [31] Mark EJ Newman. "Finding community structure in networks using the eigenvectors of matrices". In: *Physical review E* 74.3 (2006), p. 036104.
- [32] Tore Opsahl, Filip Agneessens, and John Skvoretz. "Node centrality in weighted networks: Generalizing degree and shortest paths". In: *Social networks* 32.3 (2010), pp. 245–251.
- [33] Michael C Otterstatter and James D Thomson. "Contact networks and transmission of an intestinal pathogen in bumble bee (*Bombus impatiens*) colonies". In: *Oecologia* 154.2 (2007), pp. 411–421.
- [34] Gergely Palla et al. "Uncovering the overlapping community structure of complex networks in nature and society". In: *Nature* 435.7043 (2005), pp. 814–818.
- [35] Noa Pinter-Wollman et al. "The dynamics of animal social networks: analytical, conceptual, and theoretical advances". In: *Behavioral Ecology* 25.2 (2014), p. 242. eprint: /oup/backfile/Content_public/Journal/beheco/25/2/10.1093/beheco/art047/2/art047.pdf.
- [36] Noa Pinter-Wollman et al. "The effect of individual variation on the structure and function of interaction networks in harvester ants". In: *Journal of the Royal Society Interface* 8.64 (2011), pp. 1562–1573.
- [37] Pascal Pons and Matthieu Latapy. "Computing communities in large networks using random walks". In: *International Symposium on Computer and Information Sciences*. Springer. 2005, pp. 284–293.
- [38] Lauren E Quevillon et al. "Social, spatial, and temporal organization in a complex insect society". In: *Scientific reports* 5 (2015).
- [39] Martin Rosvall and Carl T Bergstrom. "An information-theoretic framework for resolving community structure in complex networks". In: *Proceedings of the National Academy of Sciences* 104.18 (2007), pp. 7327–7331.
- [40] Martin Rosvall, Daniel Axelsson, and Carl T Bergstrom. "The map equation". In: *The European Physical Journal Special Topics* 178.1 (2009), pp. 13–23.
- [41] Jacob Scholl and Dhruba Naug. "Olfactory discrimination of age-specific hydrocarbons generates behavioral segregation in a honeybee colony". In: *Behavioral Ecology and Sociobiology* 65.10 (2011), p. 1967.
- [42] Thomas D Seeley. "Adaptive significance of the age polyethism schedule in honeybee colonies". In: *Behavioral Ecology and Sociobiology* 11.4 (1982), pp. 287–293.
- [43] Thomas D Seeley. "Social foraging in honey bees: how nectar foragers assess their colony's nutritional status". In: *Behavioral Ecology and Sociobiology* 24.3 (1989), pp. 181–199.
- [44] Thomas D Seeley. "The honey bee colony as a superorganism". In: *American Scientist* 77.6 (1989), pp. 546–553.
- [45] Ana B Sendova-Franks et al. "Emergency networking: famine relief in ant colonies". In: *Animal Behaviour* 79.2 (2010), pp. 473–485.

- [46] M Ángeles Serrano, Marián Boguná, and Alessandro Vespignani. “Extracting the multiscale backbone of complex weighted networks”. In: *Proceedings of the national academy of sciences* 106.16 (2009), pp. 6483–6488.
- [47] Leon Sixt. “RenderGAN: Generating realistic labeled data - with an application on decoding bee tags”. B.S. Thesis. Freie Universität Berlin.
- [48] Fernando Wario et al. “Automatic methods for long-term tracking and the detection and decoding of communication dances in honeybees”. In: (2015).
- [49] Stanley Wasserman and Katherine Faust. *Social network analysis: Methods and applications*. Vol. 8. Cambridge university press, 1994.
- [50] James S Waters and Jennifer H Fewell. “Information processing in social insect networks”. In: *PLoS One* 7.7 (2012), e40337.
- [51] Zhao Yang, René Algesheimer, and Claudio J Tessone. “A Comparative Analysis of Community Detection Algorithms on Artificial Networks”. In: *Scientific Reports* 6 (2016).

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Appendix A

Appendix Stuff

A.1 Network Analysis

Table A.1: Summary social insect studies https://docs.google.com/spreadsheets/d/1eKuPU-XmqwrHkS_5-TgS8Un050-Hwe1kyRIpareywP4/edit?usp=sharing

TODO	TODO
X	X
X	X

A.1. Network Analysis

Table A.2: Network measures of studies https://docs.google.com/spreadsheets/d/1eKuPU-XmqwrHkS_5-TgS8Un050-Hwe1kyRIpareywP4/edit?usp=sharing

TODO		TODO
X	X	X
X	X	X

Table A.3: Network types of studies https://docs.google.com/spreadsheets/d/1eKuPU-XmqwrHkS_5-TgS8Un050-Hwe1kyRIpareywP4/edit?usp=sharing

TODO		TODO
X	X	X
X	X	X

	Temporal Analysis	Static Analysis					score
blonder2011time							
jeanson2012long							
mersch2013tracking							
Global level measures							
Average degree	x				x	x	3
Maximal degree					x		1
Average strength		x	x				2
Average path length			x		x		2
Density		x	x		x		3
Diameter					x		1
Node level measures							
Degree	x		x	x	x	x	5
Strength	x	x	x	x	x	x	5
Betweenness centrality	x	x				x	3
Closeness centrality	x				x	x	3
Eigenvector centrality					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		3
Compare to random			x	x			2
Information flow	x		x			x	2
Interaction between age groups			x		x		1
Ego network					x		1
Robustness			x				1

Figure A.1: XXX XXX

A.1. Network Analysis

	Temporal Analysis			Static Analysis										
	blonder2011time	jeanson2012long	mersch2013tracking	naug2007	ottensatter2007contact	naug2008structure	naug2009structure	sendova2010	pinter2011effect	scholl2011olfactory	waters2012information	baracch2014socio	greenwald2015ant	quevillon2015social
Type of network	ta/to	ta	ta	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	-	
Directed Network														
directed	x- (1)	-	-	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	A				
food exchange (throphallaxis)		> 5s	> 5s					x	x		x		> 1s	

(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

Figure A.2: XXX XXX

A.1. Network Analysis

Temporal Analysis			Static Analysis											
	blonder2011time	jeanson2012long	mersch2013tracking	naug2007	otterstatter2007contact	naug2008structure	naug2009structure	sendova2010	pinter2011effect	scholl2011factory	waters2012information	baracchi2014social	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)	
Observation period	2x 30m	3x7x 24h	41x 24h	1h	12h (4)	40x 45x5m	24x 30m	5m	3x 1h	2h	10h	30m	8x 30m	
Sampling resolution***	v/e	1 fs	2 fs	v/e	30 fs	v/e	v/e	1 f/m	30 fs	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	x	211	x	x	
Marked cohorts				6		4			3					
Age		x		x		x		x	x	x				
Analysis Tools in R														
igraph	x									x		x		
rNet		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

Figure A.3: XXX XXX

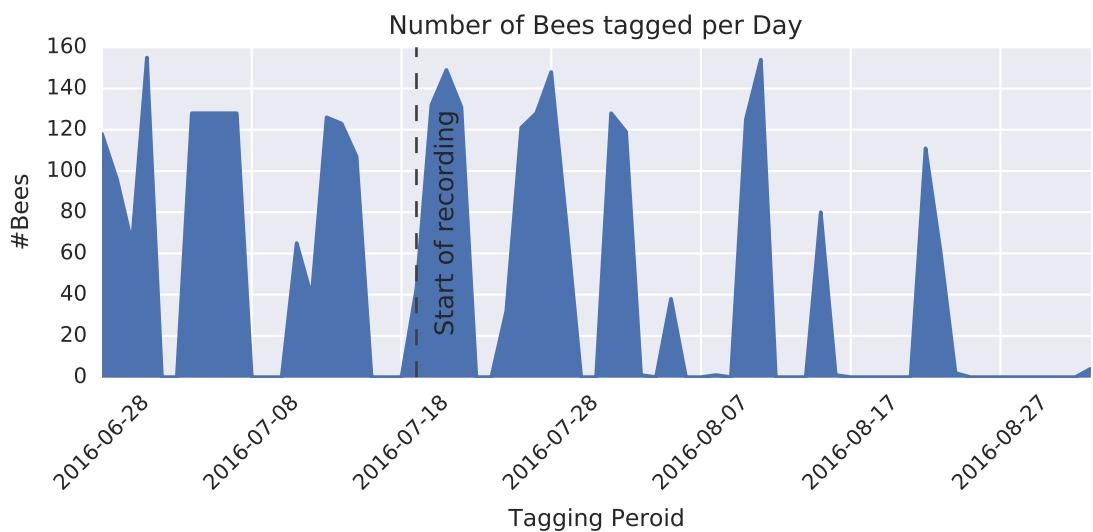


Figure A.4: Tagging frequency The bees were primarily tagged during the week. On average 48 bees were tagged each day, considering only tagging days, the average is about 91. [TODO: combine with other image or make nicer!]

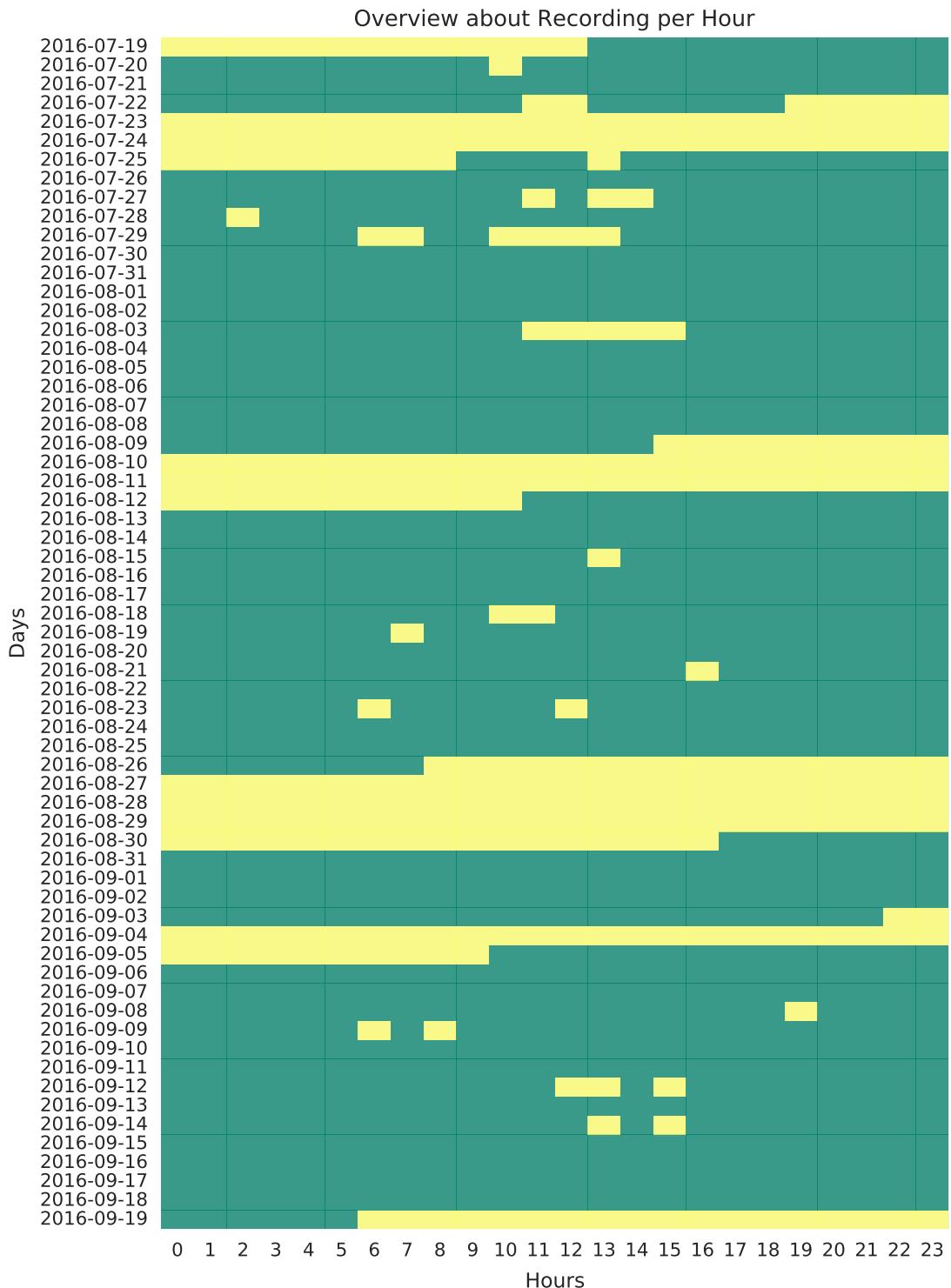


Figure A.5: Recording season with maintainance and failures *Green* indicates recording went without any big interruption; *Yellow* indicates maintainance work or technical failures of one or all cameras. This is calculated using the expected number of files produced by each camera per hour. [TODO, reduzieren 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

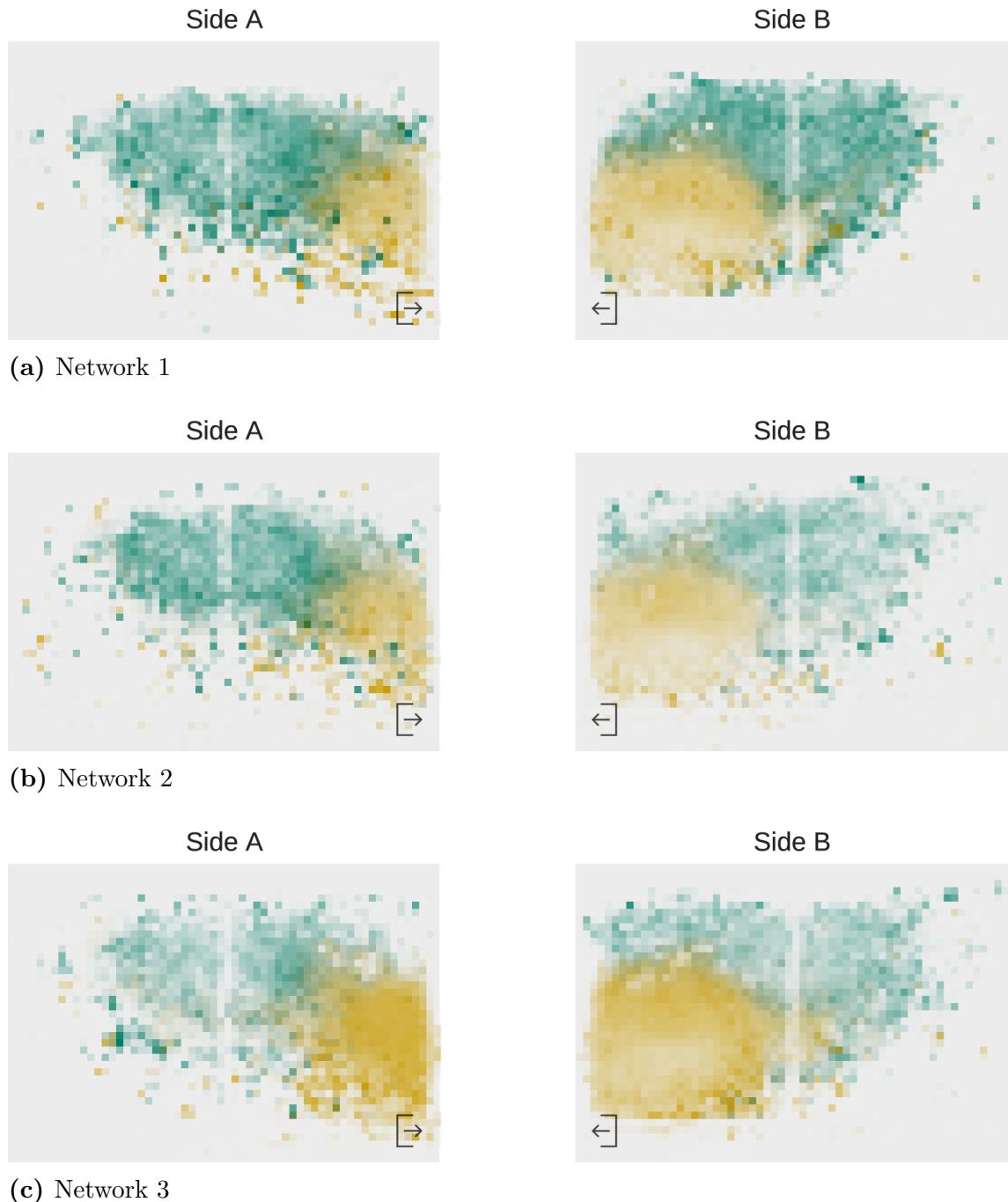


Figure A.6: Communities per network - leading eigenvector The *green* colour represents the younger community, containing the queen. The *orange* color represents the older community. The hive exit on side A is on the bottom right and on side B on the bottom left. The data is aggregated for the complete timeframe of ten hours.

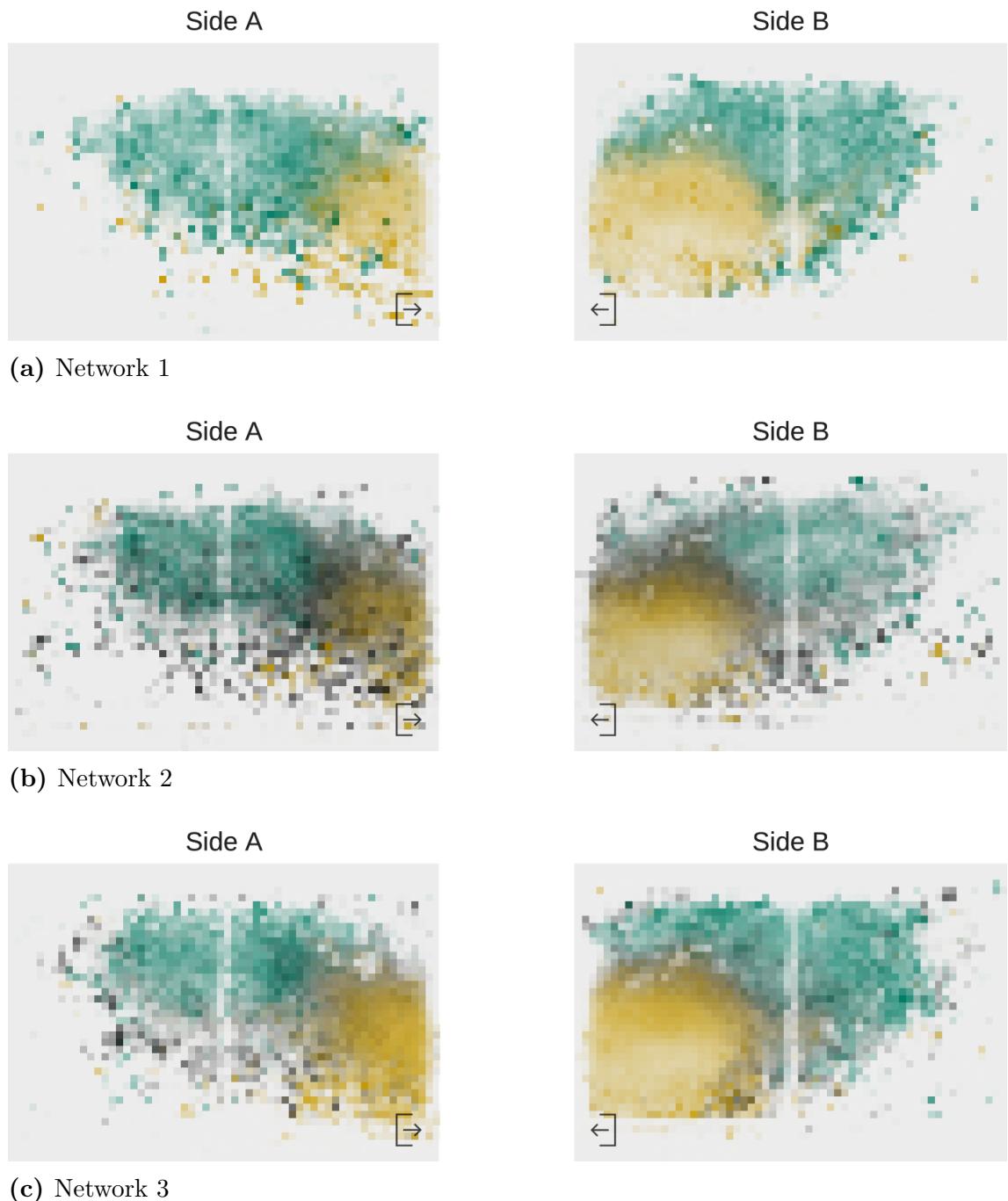
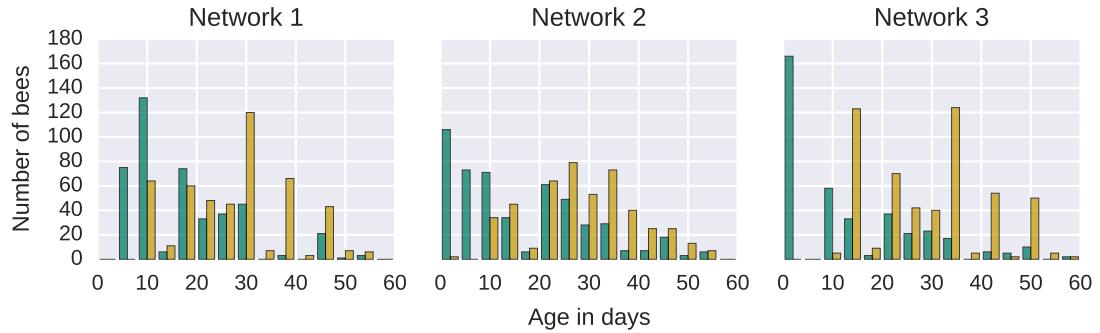
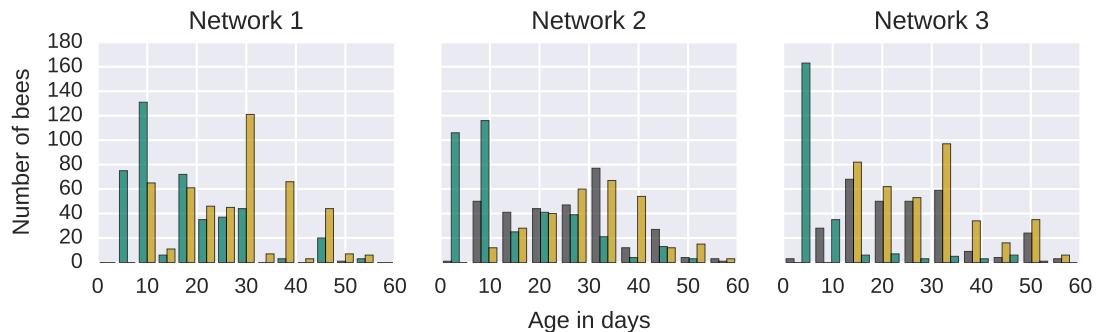


Figure A.7: Communities per network - walktrap The *green* colour represents the younger community, containing the queen. The *orange* color represents the older community. The *gray* represents the middle-age community. The hive exit on side A is on the bottom right and on side B on the bottom left. The data is aggregated for the complete timeframe of ten hours.

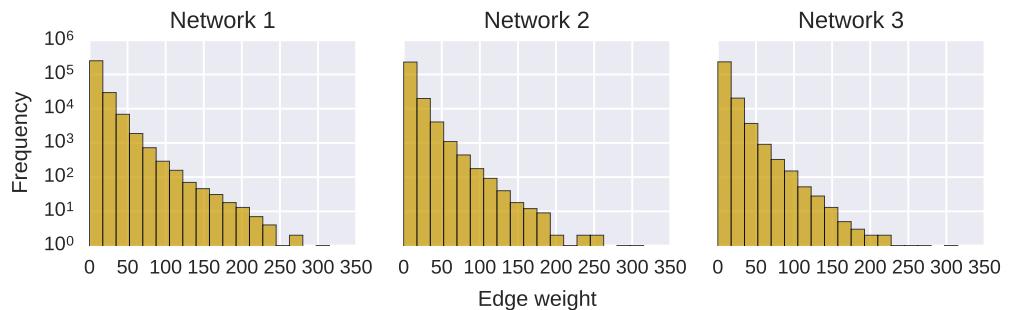


(a) Leading eigenvector



(b) Walktrap

Figure A.8: 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 coresspond 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 A.9: Degree, strength and edge weight distribution [TODO: change figures to snapshots insted of networks]

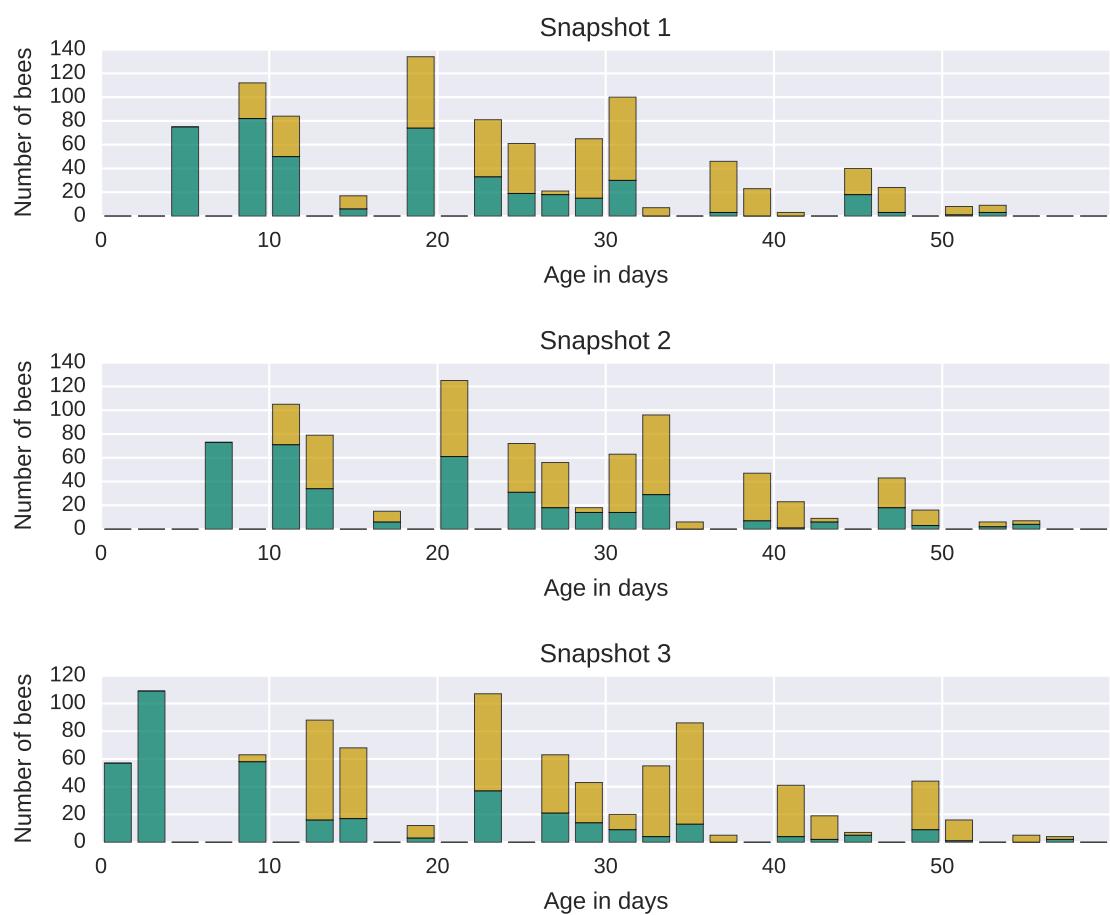
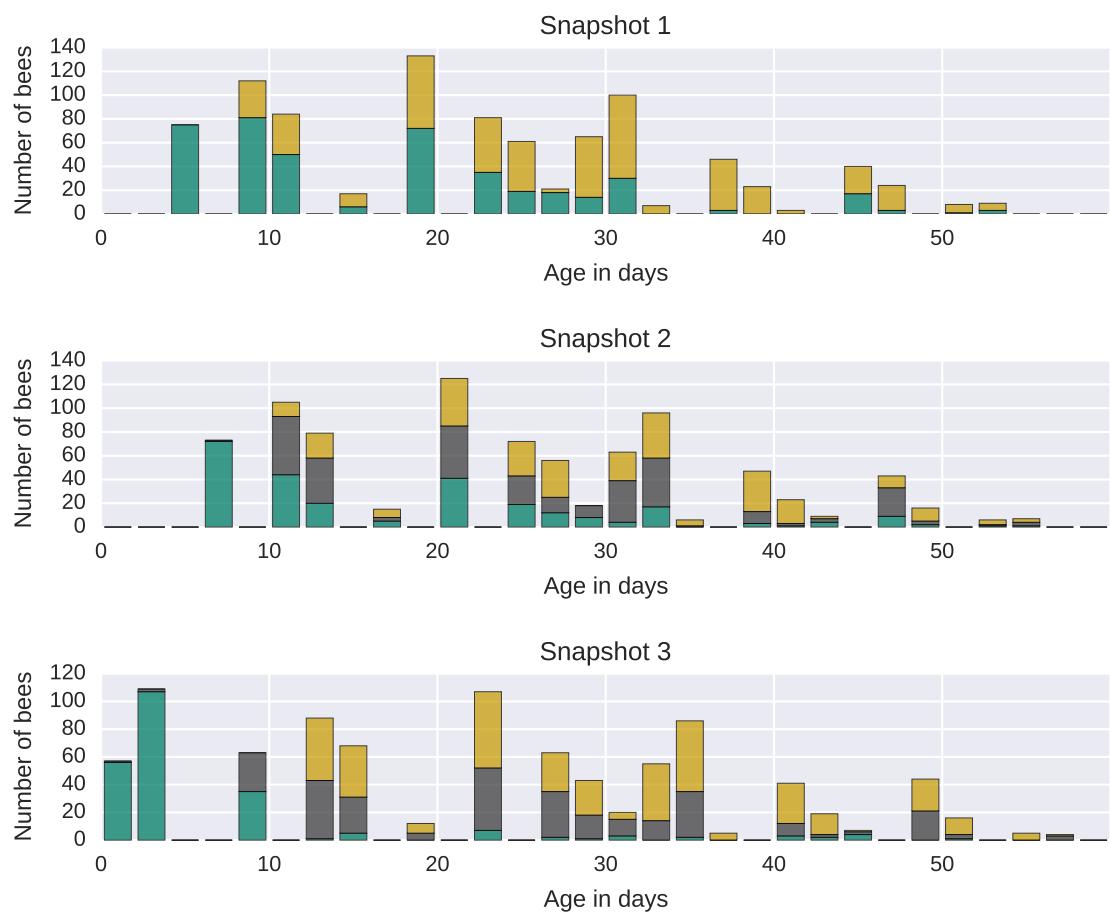


Figure A.10: Age distribution for leading eigenvector



(a) Age distribution for walktrap

Figure A.11: Age distribution per algorithm and snapshot xxx

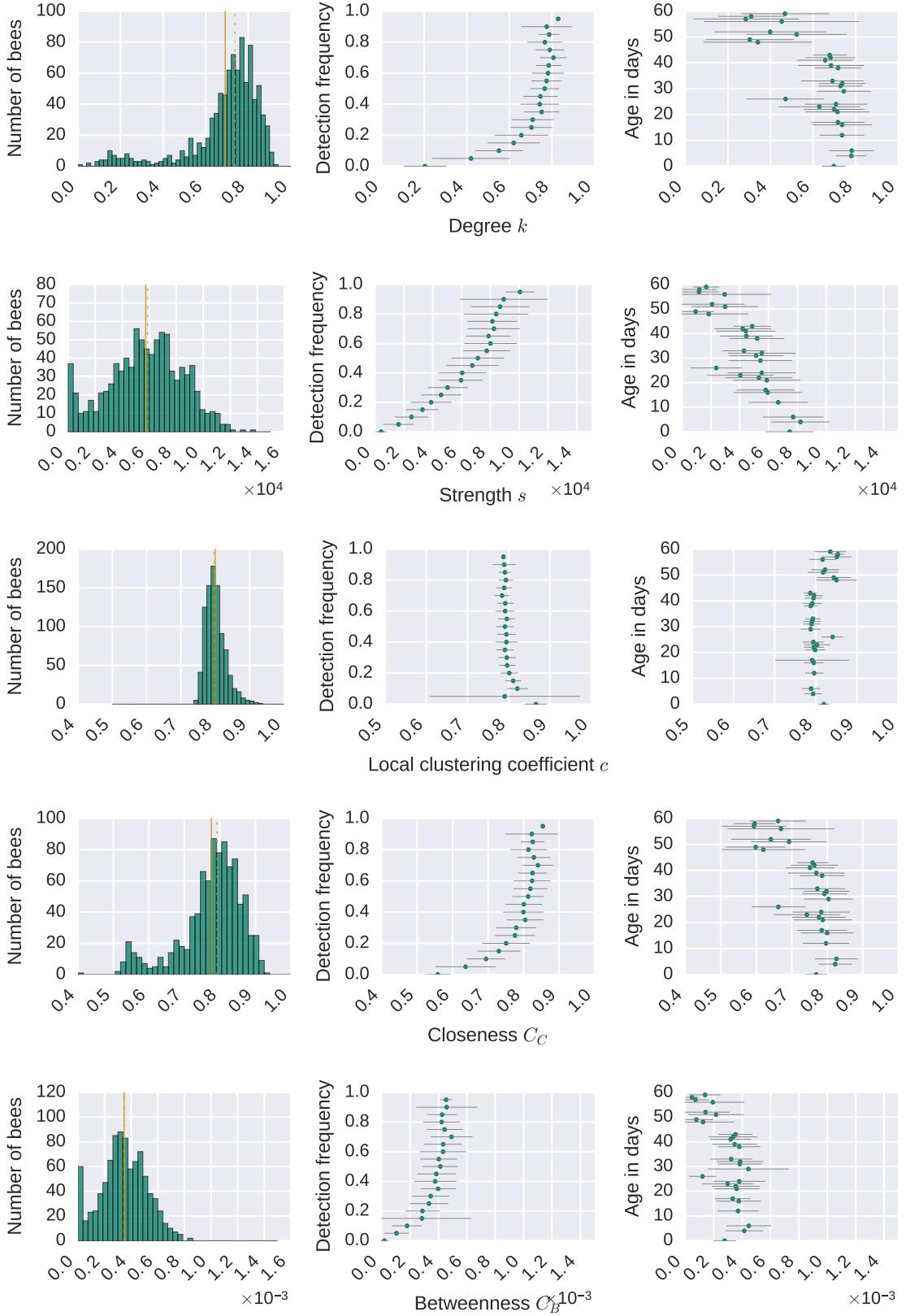


Figure A.12: Snapshot 1: Local measures in relation to age and detection frequency

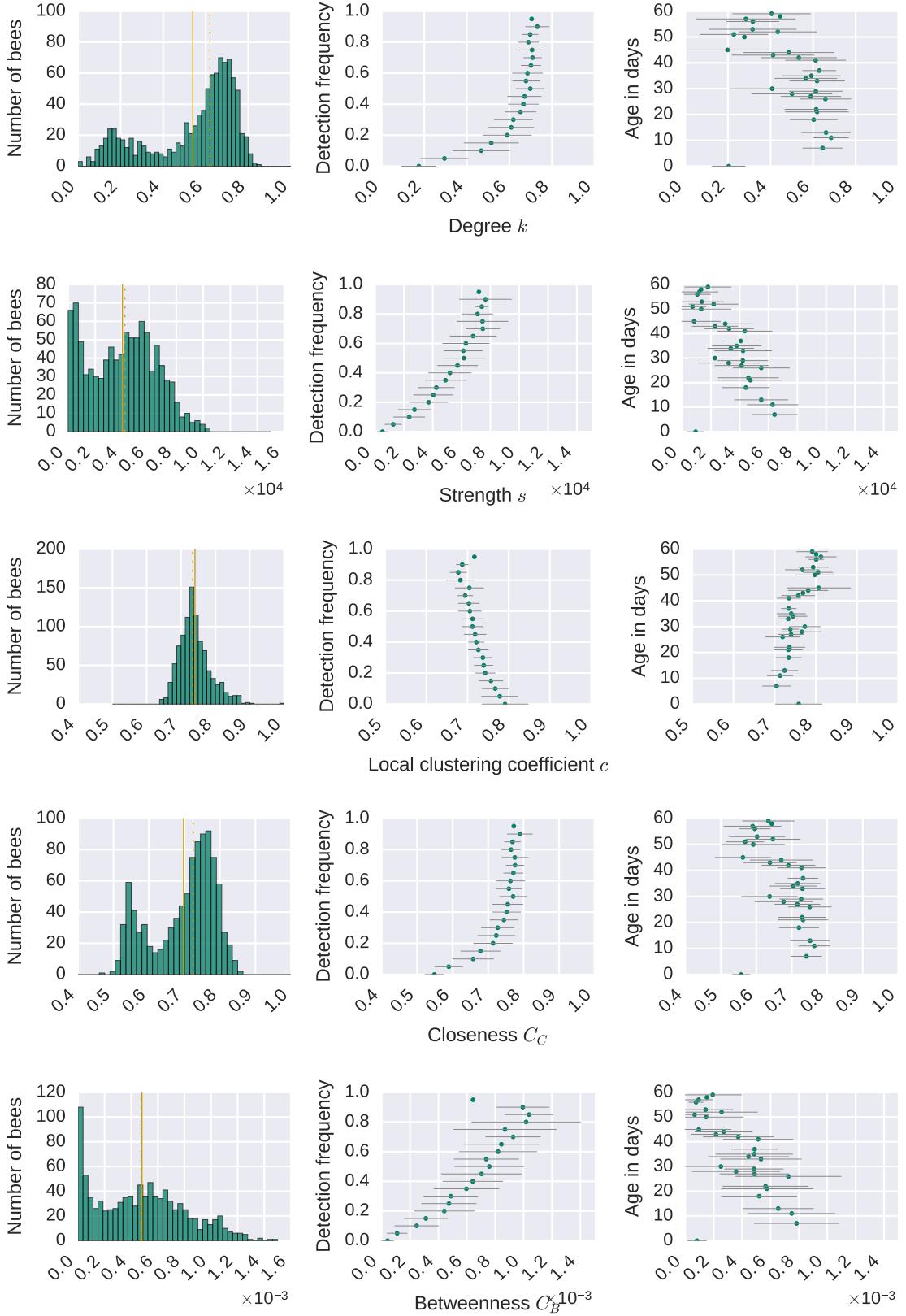


Figure A.13: Snapshot 2: Local measures in relation to age and detection frequency