Assessing nest sites, survival rates and population dynamics of free-living honeybee colonies in Germany: A comparative study using personally collected and Citizen Science data

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ABSTRACT

Our understanding of the western honeybee (*Apis mellifera*) predominantly stems from studies conducted within beekeeping environments, leaving the presence and characteristics of honeybees outside managed settings largely unexplored. This study focuses on free-living colonies, examining their habitats, nesting sites, and survival rates, thereby highlighting the liminal state of the species in Europe. Through the BEEtree-Monitor project, we personally monitored (PM) nest sites in Munich (N=107) and coordinated Citizen Science (CS) monitoring across Germany (N=423), resulting in 2,555 observations on 530 colonies from 311 participants over 7 years. While habitat preferences differed between urban, rural and forested areas, we found that 31% of the occupied nest sites were in buildings and 63% in mature trees with cavities, including lime (*Tilia* spp., 18%), beech (*Fagus sylvatica*, 14%), oak (*Quercus* spp., 13%), and ash (*Fraxin*us excelsior, 11%). On average, only 12% of the PM colonies in Munich survived annually, according to model predictions based on observed data. Consequently, we found a minimum free-living colony density per km² of 0.06 in spring but 0.42 in summer, accounting for at least 4% of the total Munich population during the summer. Comparing the two monitoring approaches (PM vs. CS) and published data revealed significant discrepancies: survival rates reported by CS were markedly higher (model prediction: 28%), than PM and other published studies. We found that CS not only yielded significantly fewer updates per colony, but also that 76% of CS reports noted active colonies compared to 42% from PM, indicating an underreporting of abandoned sites. To ensure the reliability of survival data in CS projects, regional swarming should be monitored, and the timing of reports needs particular attention as 46% of reports about overwintering were too late (i.e. after the onset of the swarming season; 11% in PM). CS data proved to be highly valuable for nest site and habitat analysis but require a strict validation protocol for survival statistics. This study enhances our understanding of the ecological dynamics and conservation needs of free-living honeybee cohorts, addresses potential monitoring biases, and suggests standardized data collection protocols for future monitoring projects.

KEYWORDS

wildlife monitoring, *Apis mellifera*, urban ecology, wild pollinators, liminal species, wildlife conservation, wild-living honeybees, multi-species studies

INTRODUCTION

The western honeybee (*Apis mellifera*) holds a significant place in the European entomofauna, facilitating the reproduction and genetic diversity of countless plant species, including many agricultural crops (Garibaldi et al., 2013; Breeze et al., 2014; Hung et al., 2018). Among researchers and beekeepers alike, *Apis mellifera* tends to be perceived solely as a domesticated animal, found and researched under managed conditions. Consequently, most of our comprehensive understanding of the western honeybee as a species, its behaviour, and its ecology predominantly stems from research conducted with colonies under beekeeping conditions, while wild honeybee populations have been neglected in the modern apidological tradition (Stoeckhert, 1954; Kohl and Rutschmann, 2018; Seeley, 2019; Requier et al., 2019). The introduction of the parasite *Varroa destructor* (Anderson and Trueman, 2000) from Asia to Europe in the 1970s intensified this oversight, as the mite's infestations suggested that only human-managed colonies receiving miticide treatment could survive (Rosenkranz et al., 2010; Meixner et al., 2015).

Yet, this belies the fact that the western honeybee is also present outside the realms of beekeeping and human husbandry (Grindrod and Martin, 2021; Visick and Ratnieks, 2023a) and how little is known about the formation and dynamics of this cohort. Currently, stable wild honeybee populations within their original range are known to exist in Africa and the Southern Ural, and outside their original range in the Americas and Australia (Schneider and Blyther, 1988; Moritz et al., 2007; Ilyasov et al., 2015b; Ratnieks et al., 1991; Seeley, 2007; Oldroyd et al., 1997). Studies on these populations usually focus on habitats where managed and non-managed colonies are relatively separated, or where the density of wild colonies matches or surpasses that of managed colonies (Visick and Ratnieks, 2023a). However, the situation in Europe is different: Due to the fragmented landscape (Ibisch et al., 2016; Lesiv et al., 2019) and the high density of managed colonies (Phiri et al., 2022; Jones, 2004), there likely isn't a spatial or genetic barrier between managed and free-living colonies in most parts of Europe. Hence, the key differences between free-living colonies and managed ones lie in their nest site ecology and their modus vivendi. Therefore we refer to both as *cohorts* of one local honeybee population, that is neither *wild* nor *domesticated*, but in a yet *liminal* state.

Recently, news about stable populations of western honeybee colonies outside beekeeping raised the interest of beekeepers in how to escape treatment (Seeley, 2019; Remter, 2021a) and spurred considerable research in this field. Free-living colonies have been discovered in

various environments, ranging from forests, to electric power poles in agricultural landscapes and rural and urban areas (Oleksa et al., 2013; Kohl and Rutschmann, 2018; Requier et al., 2020; Oberreiter et al., 2021; Kohl et al., 2022; Rutschmann et al., 2022; Hassett et al., 2018; Browne et al., 2020; Moro et al., 2021; Bila Dubaić et al., 2021; Lang et al., 2022; Visick and Ratnieks, 2023b; Cordillot, 2024). Due to their hidden locations in cavities high above the ground, free-living colonies lead secretive lives (Kohl and Rutschmann, 2018; Remter, 2021b): finding them and repeatedly collecting data in numbers high enough for statistical inference is extremely time-consuming and requires specialized skills and equipment (Kohl and Rutschmann, 2018; Kohl et al., 2022).

One approach that has garnered significant attention in the study of wild animals and biodiversity monitoring in general is the utilization of Citizen Science (Pocock et al., 2018; Fraisl et al., 2022; Koffler et al., 2021; Weissmann et al., 2023). As in the case of free-living honeybee colonies Citizen Science offers the advantage of enlisting the help of many individuals who share the task of finding and monitoring colonies, thus extending the geographic and temporal scope of the research beyond what researchers could achieve alone (Henneken et al., 2012; Lesiv et al., 2019; Hsing et al., 2022). To understand the free-living honeybee cohort more completely, it is crucial to examine not only their nesting sites but also the survival rates which are critical for assessing their genetic contribution to the local honeybee population. However, most of the studies on free-living honeybees in Europe have not systematically monitored individual colony survival, and have instead reported on nesting sites without comprehensive knowledge of the life histories of individual colonies (but see (Rutschmann et al., 2022; Kohl et al., 2022; Lang et al., 2022; Cordillot, 2024). Also, although previous studies have acknowledged the importance of Citizen Science in data collection (Moro et al., 2021; Bila Dubaić et al., 2021), none have yet investigated the quality of the data generated by Citizen Science and how to validate such reports.

We present data from a web-based monitoring scheme (BEEtree-Monitor) developed to study the habitats, nesting sites, and life histories of free-living honeybee colonies. In a parallel undertaking we collected data in the Munich region personally and via Citizen Science in Germany, both according to the same protocol. Over a span of seven years (2016-2023), we collected various parameters of 530 nest sites together with longitudinal occupation data: 107 nest sites monitored by ourselves and 423 by citizen scientists. We compare survival rates between these two groups to evaluate the validity and potential biases of in the Citizen

Science reports and methodology. Through this study, we aim to provide a broader understanding of honeybees as a species existing outside human husbandry and offer guidelines to leverage future Citizen Science projects for effective monitoring of free-living honeybee colonies.

METHODS

Data collection and data curation

The monitoring and data collection process for this study was implemented through a combination of personal monitoring, (PM) and reports by volunteering supporters with highly diverging skill levels and knowledge sets (citizen science monitoring, CS). Leveraging our own experiences in surveying free-living honeybee colonies and third-party reports, we developed an advanced monitoring scheme tailored to our target groups. Initially, participants were asked to fill in a designated form and send it to us via email (BEEtrees HOBOS form, supplementary material (SM)). Later on, we constructed an online platform specifically tailored for Citizen Science monitoring, launched as a website (BEEtree-Monitor; www.beetrees.org) in 2018. This platform was created entirely from open-source software (see SM for further information on the software and online form).

The CS recruiting was facilitated through social media outreach, presence in public media and beekeeping journals. The community was maintained via regular newsletters with guiding and motivating information. To enable as many volunteers as possible without offering a special training, our protocol focused on location, easily measurable nest site parameters, and continuous, repeated observations with specific date, time and focus. The citizen scientists therefore contributed by collecting part of the data that we used but did not contribute to the analysis and interpretation of that data. In total only 36 nesting sites were found by the authors (and 494 by citizen scientists), however 107 locations were actively monitored by us (and 423 by citizen scientists). Our primary analysis focused on colonies located in Germany and several nearby Central European countries, including Switzerland (N=9), Austria (N=3), Czechia (N=2), and Luxembourg (N=3). To mitigate the influence of markedly different environmental conditions that could confound our study's findings, we excluded observations of ten free-living colonies from geographically distant countries like France, the UK, Italy, Spain, Norway, and Ukraine.

Precise GPS coordinates allowed us to investigate the nesting and foraging habitats of the colonies, and the nest site parameters were used to analyse the swarms' preferences for different nest types such as hollows in building structures (e.g., chimneys, window blind boxes or facade compound insulations) or hollows in different tree species. Additionally, we sought information on entrance directions and height, as well as the trunk diameter for trees. The online platform also featured an open-text/commentary field for participants to provide other relevant information.

To further understand the survival and behaviour of these colonies, we applied two distinct monitoring approaches (Figure 1A):

PM: This method entailed meticulous checks for visual signs of pollen import (indicating brood production, marking the colony as live) and frequent short-term observations of nest sites exhibiting ambiguous flight patterns or no observed foraging for pollen. We filmed some of the typical or ambiguous situations to collectively analyse and relate them to continuous observations at the site. This monitoring protocol substantiated our classification of flight patterns and the ideal standard we aimed to achieve with CS.

CS: This approach involved providing participants with protocols and guidance to e.g. prioritize pollen import observation. Accessible explanations in the online form and regular emails encouraged detailed reporting during key observation periods.

<u>Analysis of nesting and foraging habitats of reported free-living colonies</u>

To classify the nesting and foraging habitats of the reported free-living colonies, we imported the coordinates of each colony's location into QGIS version 3.16.2 (QGIS Development Team, 2020) and performed intersections (using point layers for nesting habitats and 2 km buffers for foraging habitats) with the land cover classes from the CORINE Land Cover map 2018 (European Environment Agency, 2018). We grouped different land cover types together and quantified the proportional contributions of five major land cover types: urban areas, cropland, grassland, deciduous forest, and coniferous forest (see SM for further details). These land cover types were for some of the analysis further grouped into three broader categories: Urban (urban areas), rural (cropland and grassland), and forest (deciduous and coniferous forests). In the case of the foraging habitat, we chose a radius of 2 km as approximately 80% of honeybee foraging occurs within this distance (Rutschmann et al. 2023). Moreover, the landscape within the 2 km scale has been shown to measurably

influence honeybee colony performance, affecting factors such as foraging rate, colony growth, and winter survival (Steffan-Dewenter and Kuhn, 2003; Sponsler and Johnson, 2015; Rutschmann et al., 2022, 2023).

Observation scheme for colony survival statistics: Timing, pollen import and flight patterns

We defined survival as an instance when a cavity occupied from summer (during or after the swarming season) remained occupied until the following spring before the next swarming season commenced (Figure 1B). One valid report of an active colony before the start of the swarming season (1st Check) would be proof for an overwintering survival. Additionally, we implemented and encouraged participants to conduct one or two more annual checks: right after the end of swarming (2nd Check) and in Autumn before the winter (3rd Check). Post-swarming checks at all known cavities (including the recently unoccupied ones) served finding the new founder colonies for the further monitoring while the Autumn check (3rd Check) detects summer deaths. In our study, colonies that died in summer/autumn were attributed as perished to the survival statistics of the following year. For assessing overwintering, observations typically take place in March or early April where it is crucial that weather conditions are suitable for honeybee foraging (e.g. no rain and temperatures above 12° C. [Kevan and Baker, 1983]). Consequently, observations without suitable weather conditions for honeybee foraging were excluded. As only life histories recorded in the database were considered for our analysis, oral reports or in retrospect reports (of colonies living for "several years" in the same cavity) were considered hearsay and not included. Data pre winter 2016/2017 were discarded due to small sample sizes , and nesting sites that were destroyed were not considered for the survival statistics.

A potential pitfall of reporting mere flight activity at the entrance is that certain behaviours such as robbing, or the presence of scout bees may be erroneously interpreted as signs of a living colony by less experienced observers. Therefore pollen import into a colony was used as an indicator of brood production, hence designating it as a live colony. However, if pollen deposition is not visible, a death is not generally evident, either because pollen is scarce, not needed for the bees or due to the difficulty in observing pollen import in colonies with nest entrances that are high above ground level. Consequently, under certain conditions, even in the absence of visible pollen import, we still considered the colony to be alive. These criteria included:

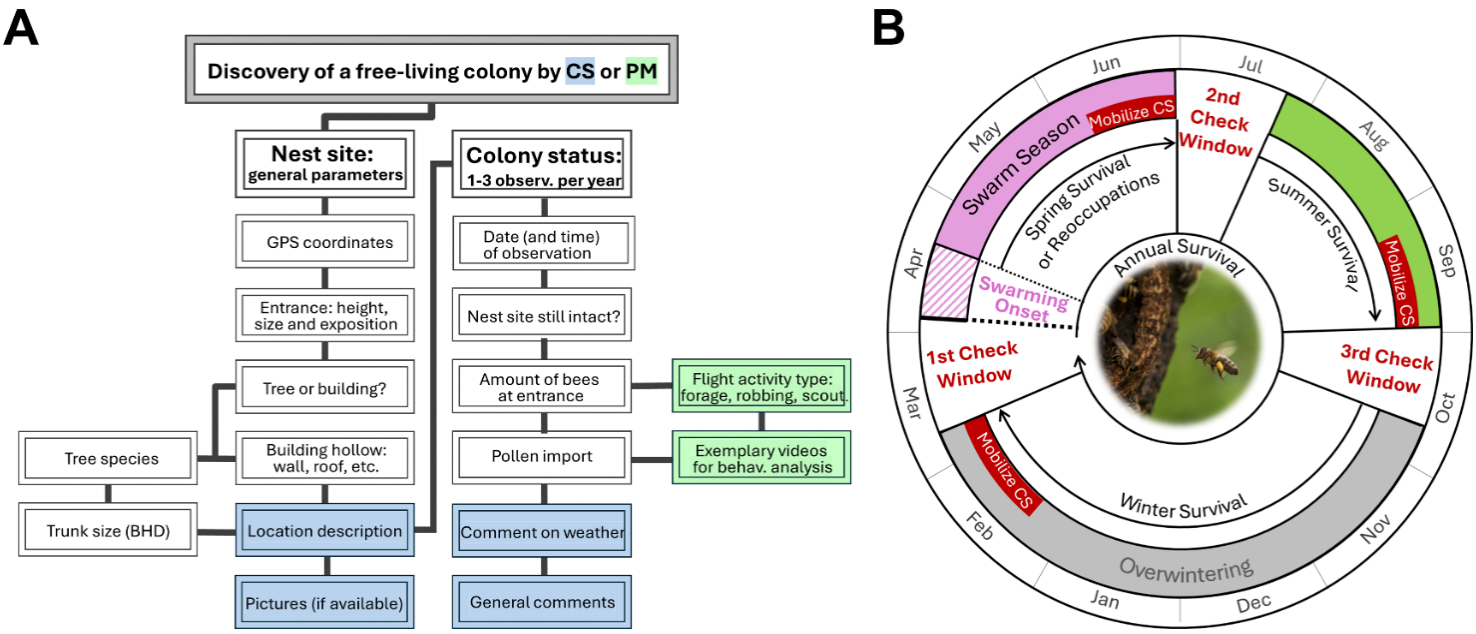

Figure 1: A) Flowchart of the monitoring protocol for Citizen Science (CS) and personal monitoring in Munich (PM). The workflow details the steps for recording nest site parameters and colony status. The inclusion of location descriptions, weather comments, general comments, and supplementary materials like pictures and videos helps ensure comprehensive and accurate data collection in CS (light blue). Personal monitoring yielded reliable information regarding flight activity types, which were further analysed with video analysis (light green). B) Annual monitoring schedule for free-living honeybee colonies. The monitoring schedule outlines three critical observation windows: 1st Check Window (before the onset of the swarming season in late March and April), 2nd Check Window (post-swarming season in July), and 3rd Check Window (in autumn, September). These checks focus on different survival metrics: Spring survival and reoccupations, summer and winter survival, respectively. Citizen scientists (CS) are mobilized before each check window to ensure timely data collection. The onset of swarming shifts each year and must be monitored closely to ensure accurate data on colony survival. The inlet picture shows pollen import into the colony an indication for brood production (photo: Felix Remter).

1. <u>Observation of foraging flight patterns:</u> Colonies were classified as active if regular and/or directional flight activity was reported convincingly in the commentary section. These behaviours are differentiated from non-foraging activities based on specific patterns observed in PM:
    - Scout bees typically exhibit distinct behaviours such as taking time to land, thoroughly exploring the entrance before entering the cavity, performing slow orientation flights during departure, and might defend the entrance against other scouts when near swarming.
    - Robbing bees display violent interactions with defenders if attempting to rob a living colony. Initially, robbers perform orientation flights akin to scouts but may also demonstrate a distinct 'bouncing off' landing pattern. Although robbers can temporarily mimic regular foraging patterns, these are distinguishable by experienced observers.
2. <u>Reliability of observer comments:</u> Assessments were also based on the reliability of observers' comments. If the observer was suspected to credibly discern differences in

flight patterns indicative of foraging rather than robbing or scouting due to a competent comment given, the colony was considered active.

3. Frequency and timing of observations: Multiple observations made at short intervals that consistently indicated foraging behaviour, as opposed to scouting or robbing, supported the classification of a colony as active.

Survival rates of free-living honeybee colonies and the impact of monitoring type and year

To analyse colony survival statistics across different years in Germany we merged datasets from this study (CS and PM) and from two published studies (Kohl et al., (2022) and Lang et al., (2022)). Each dataset employed a distinct monitoring approach (see SM for further details). To ascertain the influence of various predictors on the odds of colony survival, we compared several mixed-effects logistic regression models. These models were constructed using the glmmTMB package in R (Magnusson et al., 2017). Model 1 included 'monitoring type' as a fixed effect (with the factor levels CS, PM , Kohl et al. 2022 and Lang et al. 2022) and 'colony id' nested within 'year' as a random effect to account for repeated measures on the same subjects across years. Model 2 included both 'monitoring type' and 'year' (from 2016 till 2023) as fixed effects, with 'colony id' as a random effect. Model 3, which did not converge, included the interaction between 'monitoring type' and 'year' as fixed effects, with 'colony id' as a random effect. The model selection process was guided by the Akaike Information Criterion (AIC) and the 'emmeans' package (Lenth and Lenth, 2018) was used for post-hoc comparisons. Residuals of the models were inspected with DHARMa package (Hartig and Hartig, 2017).

Exemplary estimation of free-living honeybee colony density

Estimating the density of free-living honeybee colonies poses challenges due to the likelihood of substantial underreporting. To address this, we concentrated our density estimation efforts on the city of Munich, where the majority of our known free-living honeybee colony locations are situated (further details on the density estimation can be found in the SM).

Onset of regional swarming

In 2019, two of the authors (SR and FR) established a website across Germany and a hotline in Munich for the discovery of honeybee swarms and their potential capture. This enabled us to amass substantial data (N=376) on the initiation of swarming activity in the years from

2019 to 2023 within the geographic extent of the study. These years also represent the period during which most of the nest sites presented in this study were found (N=378 out of 530 colonies) and monitored (N=307 out of 350 life history reports) for of this study. For each year, the first reported swarm served as a conservative estimate of the commencement of the swarming season. We observed variability in the yearly onset of swarming over the five-year period from 2019 to 2023. Specifically, swarming began on 17 April in 2019, 6 April in 2020, 8 May in 2021, 28 April in 2022, and 23 April in 2023 . Hence, the time difference between the earliest and the latest recorded yearly swarming onset was more than one month (32 days), suggesting it should be taken into account in planning of CS initiatives and survival analyses of free-living honeybees. Especially critical are years where swarming occurs unexpectedly early (e.g. year 2020). A small subset of the free-living colony reports in this study stem from years before 2019 in which we lacked empirical data on the beginning of the swarming season. Hence, we conservatively selected mid-April as the presumed start of swarming for these years (Henneken et al., 2012).

Statistical analysis of directional and height preferences in cavities

To evaluate directional preferences of honeybees when selecting cavities, we recorded the entrance orientation of nesting sites occupied by free-living colonies in the eight cardinal and intercardinal directions (N, NE, E, SE, S, SW, W, NW) for both tree cavities and cavities in buildings and assessed whether the distribution of orientations was non-random by employing the Rayleigh test for circular statistics using Directional package in R (Tsagris et al., 2016). The height of cavity entrances in trees and building structures was investigated with a non-parametric Mann-Whitney U Test.

Further information on statistical analysis regarding number of reports per colony, reported colony status and timing of the reports can be found in the supplementary material.

All statistical analyses were performed using R software (version 4.3.1; R Core Team, 2016). For data wrangling and graphical representation of the results, we utilized 'tidyverse' and 'ggplot2' (Wickham, 2017, 2016).

RESULTS

Nesting and foraging habitat of reported free-living colonies

We garnered responses from 311 participants (including the authors), providing us with 2,555 observations on 530 colonies (Figure 2A). Using landcover data to assess the habitat of the free-living colonies we found 57 percent of the reported colonies to dwell in urban areas with high human density, 14 percent in deciduous forest, 14 percent in cropland, 9 percent in grassland and 5 percent in coniferous forest (Figure 2B). The distribution of nesting habitats for free-living honeybee colonies was significantly different from the proportional distribution based on land cover types in Germany[1] ($\chi^2 = 99.81$, df = 4, $p < 0.001$). Specifically, colonies were disproportionately more often found in urban areas relative to the habitat availability in Germany. Calculating the available foraging habitat 2 kilometres

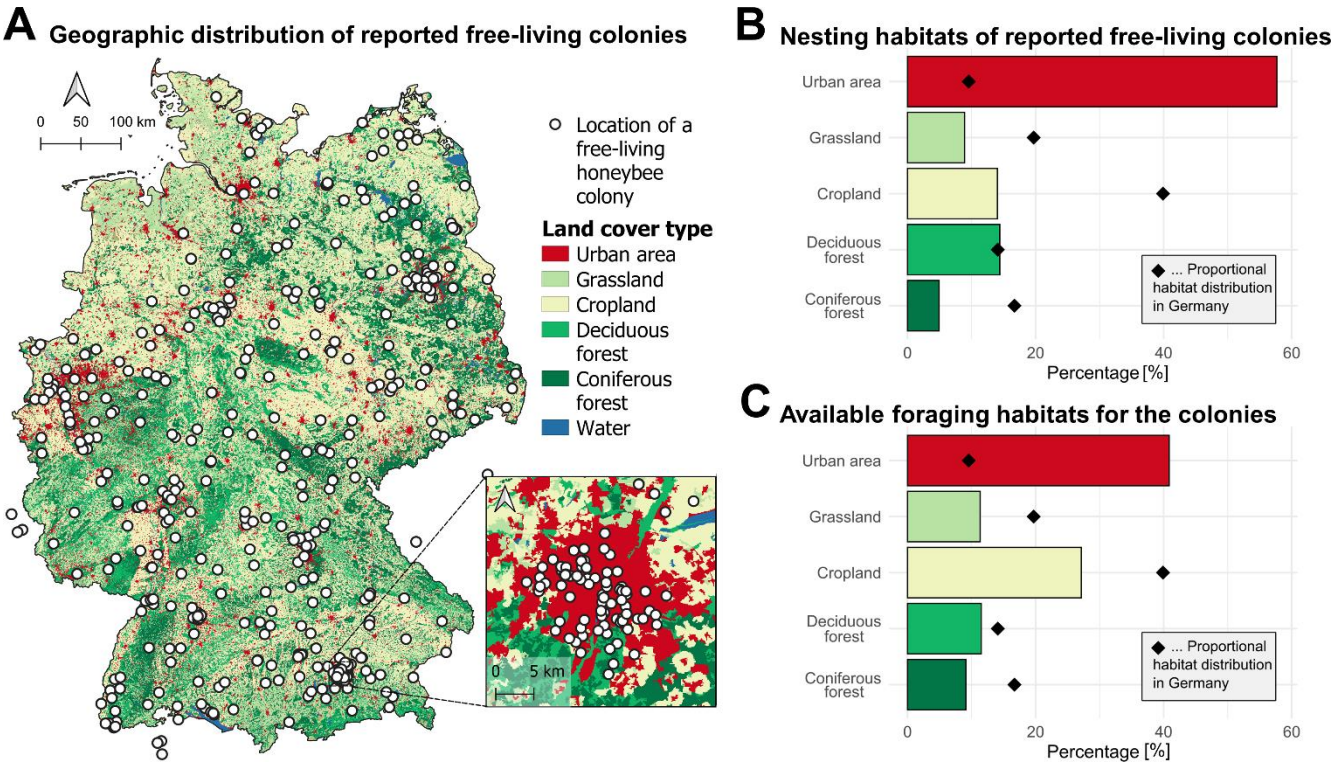

Figure 2: A) Geographic distribution of the free-living colonies reported to the BEEtree-Monitor overlaid on the main land cover types within Germany (CORINE Land Cover map 2018; 3 colonies are hidden by the inlet). The inlet shows the free-living colonies in the Munich region. B) Proportional distribution of nesting habitats where free-living colonies have been reported in comparison to the relative distribution of different land cover types across Germany depicted by black diamond symbols. C) Foraging habitats that is available to the bees (habitat within a 2 km radius around each reported free-living honeybee colony). Again, black diamond symbols show the relative distribution of a land cover type across Germany.

[1] The proportional distribution assumes honeybees have no habitat preferences and their discovery is equally probable in all habitats.

around each nest site, where colonies are operating to find their food, we found similar patterns. We estimated 41 percent of the available foraging habitat of the reported colonies to be urban areas, 27 percent cropland, 12 percent deciduous forest, 11 percent grassland, and 9 percent coniferous forest (Figure 2C).

Nesting sites of the reported free-living honeybees

The ratio of tree cavities and nesting sites in buildings, as well as the occupation rate of different tree species, differed between urban, rural and forest habitats. For the reported colonies in urban areas (N=304), tree cavities comprised 52% of all cavities, while building cavities accounted for 40% (other cavity types: 8%; Figure 3A). In rural areas (N=121), tree

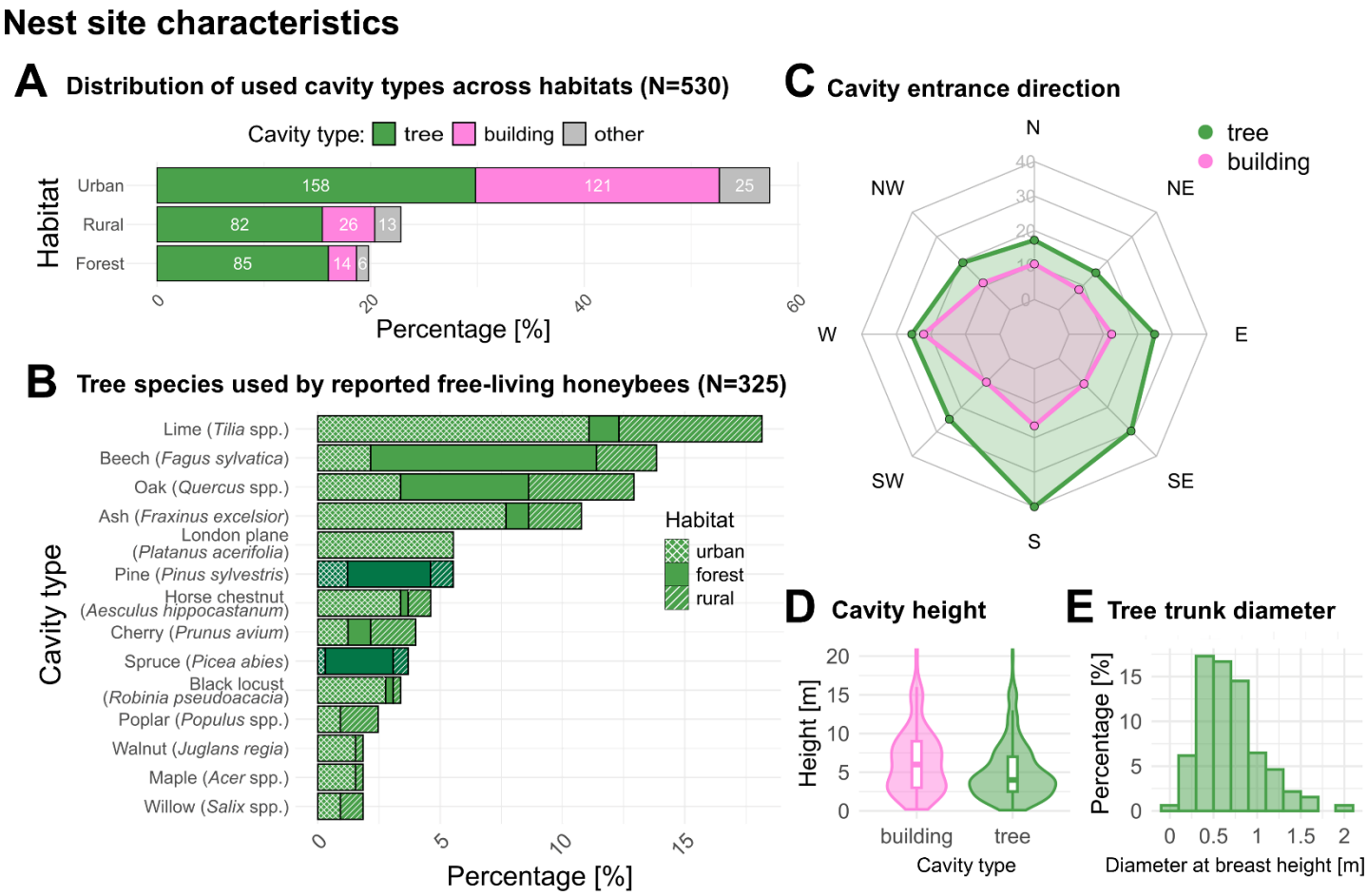

Figure 3: A) Proportional distribution of nesting cavity types (tree, building or other) across the three different habitats. While the x-axis gives the overall percentage, white numbers indicate the count (N) of trees, buildings, and other cavities. B) This panel shows the distribution of tree species used by reported free-living colonies as nesting sites in this study. Pattern fills illustrate the distribution across different habitats. Darker green fill represents coniferous tree species. C) Displays the preferred nesting entrance directions for the two different types of cavities - those in trees and buildings. D) Cavity height distribution: A violin plot with an embedded boxplot that demonstrates the range and distribution of the heights of cavity entrances occupied by free-living colonies, categorized by cavity type. E) Illustrates the distribution of tree trunk diameters (measured at breast height) for trees that hosted free-living honeybee colonies.

cavities were again the most common (68%), followed by building cavities (21%). In forest areas (N=105), tree cavities dominated with 81% of all cavities, while building cavities made up 13 %. Looking at the whole dataset 63% (N=324) of the colonies were found in trees, 31% (N=161) in building structures, and the remaining 6% (N=32) in other types such as rock crevices (N=3) and open nesting (N=15) (Figure SM). Among tree species, Lime (*Tilia* spp.) was the most frequently occupied (N=59; 18%), followed by beech (*Fagus sylvatica*, N=45; 14%), oak (*Quercus* spp., N=41; 13%) and ash (*Fraxinus excelsior*, N=35; 11%) (Figure 3B).

Our study uncovered clear patterns in common flight entrance directions of nest sites used by free-living honeybees. For colonies situated in tree cavities where the direction was reported, the observed frequency distribution across the eight cardinal and intercardinal directions was significantly non-uniform (Rayleigh Test Statistic = 20.23, Bootstrap p-value = 0.0010; N = 285). Specifically, there was a significant preference for southern directions, with the highest frequency observed in the South direction (N = 58 or 20 %; Figure 3C). Similarly, for colonies located in buildings, the distribution was tested to be marginally non-uniform (Rayleigh Test Statistic = 4.85, Bootstrap p-value = 0.079; N = 146). Unlike tree cavities, cavities in human-built structures showed no clear directional preferences, although the West (N = 32 or 22%) and South (N = 24 or 16%) directions were observed most frequently (Figure 3C).

Our observations indicate that free-living honeybee colonies predominantly use nesting sites far from the ground (mean and median entrance height: 5.7 m and 4.5 m; Figure 3D). There was a statistically significant difference in the height of the cavities entrance in trees and in buildings (Mann-Whitney U Test W = 13482, $p < 0.001$). The entrance heights of cavities occupied in trees ranged from 0.1 to 30 meters, with a median of 4 meters. In contrast, the heights of cavities entrances in man-made structures ranged from 0.2 to 40 meters, with a median of 6 meters.

Additionally, we found that the diameter at breast height (DBH) of trees harbouring free-living honeybee colonies was on average 0.64 meters (median: 0.69 meters, Figure 3E), suggesting that colonies are dependent on trees with a substantial trunk diameter.

<u>Occupation rates and colony density across seasons in Munich</u>

We investigated cavity occupation rates in the city of Munich during three distinct seasonal periods (spring, summer and autumn, see SM for further details). Multiplying these

occupation rates with the density of 0.58 known cavities per square kilometre in Munich (92 nest sites on an area of 160 km², see SM), we estimated the minimum density of free-living honeybee colonies in Munich to be approximately 0.06 colonies per square kilometre in spring, 0.42 in summer, and 0.28 in fall. It is important to note that the reported densities should be viewed as minimum estimates, given the likelihood that a significant number of colonies remain undetected and unreported. Based on these occupation rates, we infer that the number of colonies during summer is roughly seven-fold higher compared to spring. Conversely, the number of colonies in fall is approximately 33% lower than in summer.

Survival rates of free-living honeybee colonies and the impact of monitoring type and year

We analysed the life histories of 343 free-living honeybee colonies over the period from 2016 to 2023. Of these, 151 survival reports were provided by citizen scientists, while 192 were personally observed in Munich. It is important to note that one colony can have multiple survival reports for different years. The yearly survival rates for the two monitoring types are depicted in Figure 4. In most years, survival rates reported by citizen scientists were higher than those observed through personal monitoring. Notably, in the spring of 2019, all PM colonies (N=32) perished.

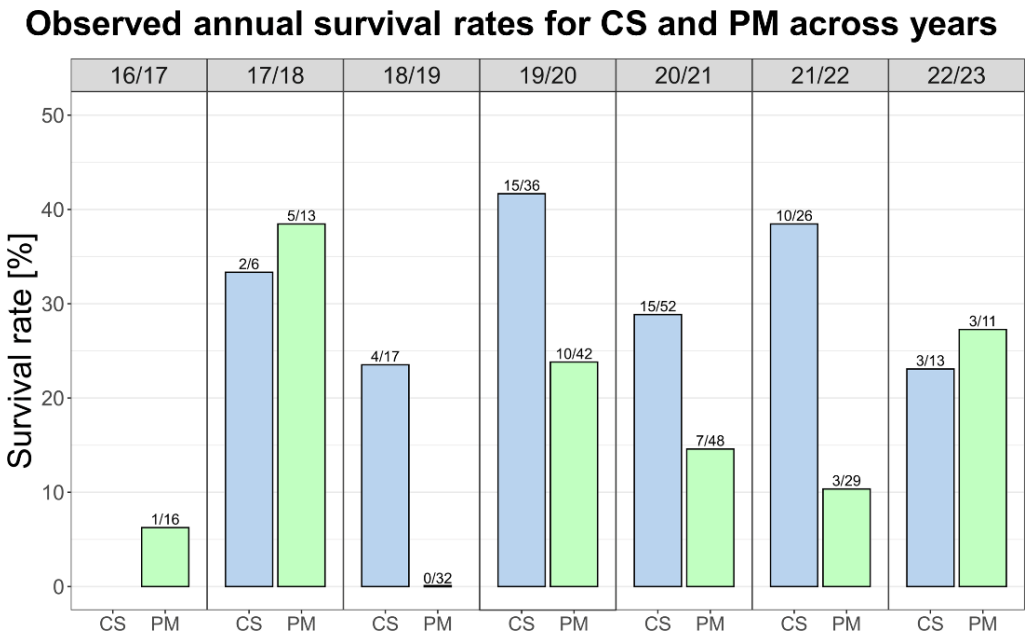

Figure 4: Comparison of observed colony survival rates from Citizen Science monitoring (CS, light blue) and personal monitoring in the Munich region (PM, light green) across the years.

Additionally, we consulted data from two published studies to determine whether the differences between CS and PM were likely due to biases in CS or actual differences. Kohl et al. (2022) focused on 97 overwintering colonies in German managed forest landscapes from

2017 to 2021, while Lang et al. (2022) investigated 24 colonies in Dortmund, Germany from 2018 to 2022 (Figure 5A). More detailed information about the datasets and the reanalysis with the swarming timepoints observed in this study is provided in the SM. To assess the impact of different monitoring types and year on survival rates, we constructed a glmmTMB model. Model selection, guided by AIC values and convergence considerations, favoured including 'year' as a fixed effect alongside the 'type of monitoring' (CS, PM, Kohl et al. (2022) and Lang et al., (2022)). The ANOVA results from the glmmTMB model indicated that both 'monitoring type' (Chi-squared = 14.85, df = 3, p = 0.002) and 'year' (Chi-squared = 17.47, df = 6, p = 0.008) significantly contributed to the model. The estimated probability of survival was notably higher in 'Citizen Science' (28%) than in personal monitoring in the Munich region (p = 0.007) and in 'Kohl et al. 2022' (p = 0.007), but not significantly different from 'Lang et al. 2022' (p = 0.33; probably due to the small number of colonies) (Figure 4B). While minor variations may arise from regional or setting differences, the significant discrepancies observed are likely due to reporting biases in CS compared to systematic surveys by experts. Model estimates placed the survival probability at 12% for PM, 11% for 'Lang et al. 2022', 9% for 'Kohl et al. 2022', and 28% for CS (Figure 5B). These findings suggest that both the type of monitoring and the year of observation have a statistically significant impact on the reported survival rates of free-living honeybee colonies.

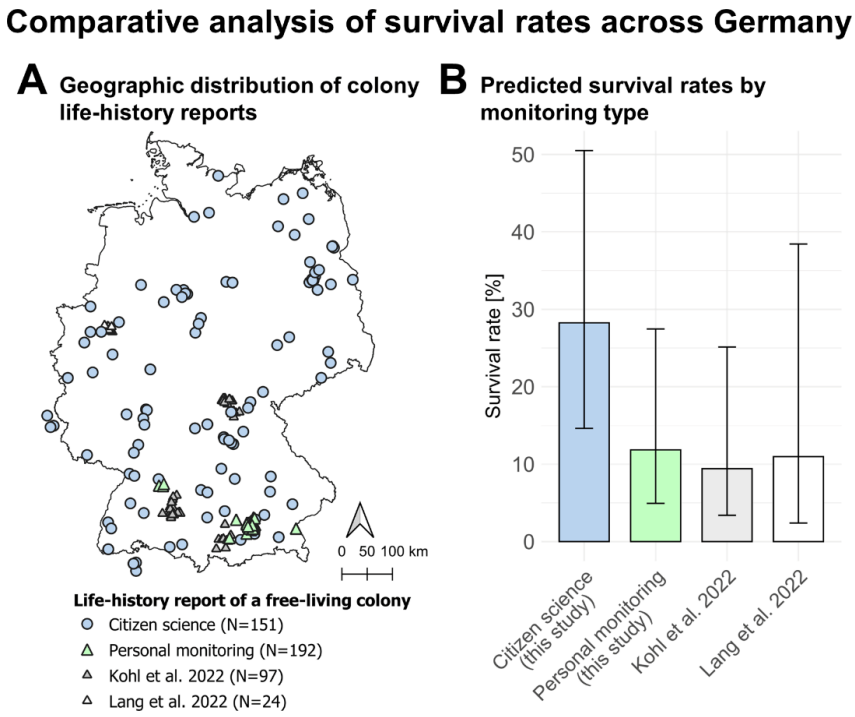

Figure 5: (A) Geographic distribution of life-history reports of free-living colonies from this study (CS and PM) and two published datasets (Kohl et al., 2022; Lang et al., 2022). (B) Model estimates and 95% confidence intervals for colony survival rates for the different monitoring types and studies.

Biases in the different monitoring types

Our dataset comprised 423 nest sites with 1,064 Citizen Science (CS) observations and 107 nest sites with 1,491 personal monitoring (PM) observations. We noted a significantly lower number of CS reports per colony compared to PM (Wilcoxon rank-sum test: $W = 3950$, $p < 0.001$; Figure 6A). Furthermore, we found a stark contrast in the distribution of "alive" versus "dead" colony status reports between CS and PM (Pearson's Chi-squared test: $\chi2 = 176$, $df = 1$, $p < 0.001$; Figure 6B), where 76% of CS reports indicated alive colonies compared to 42% in PM.

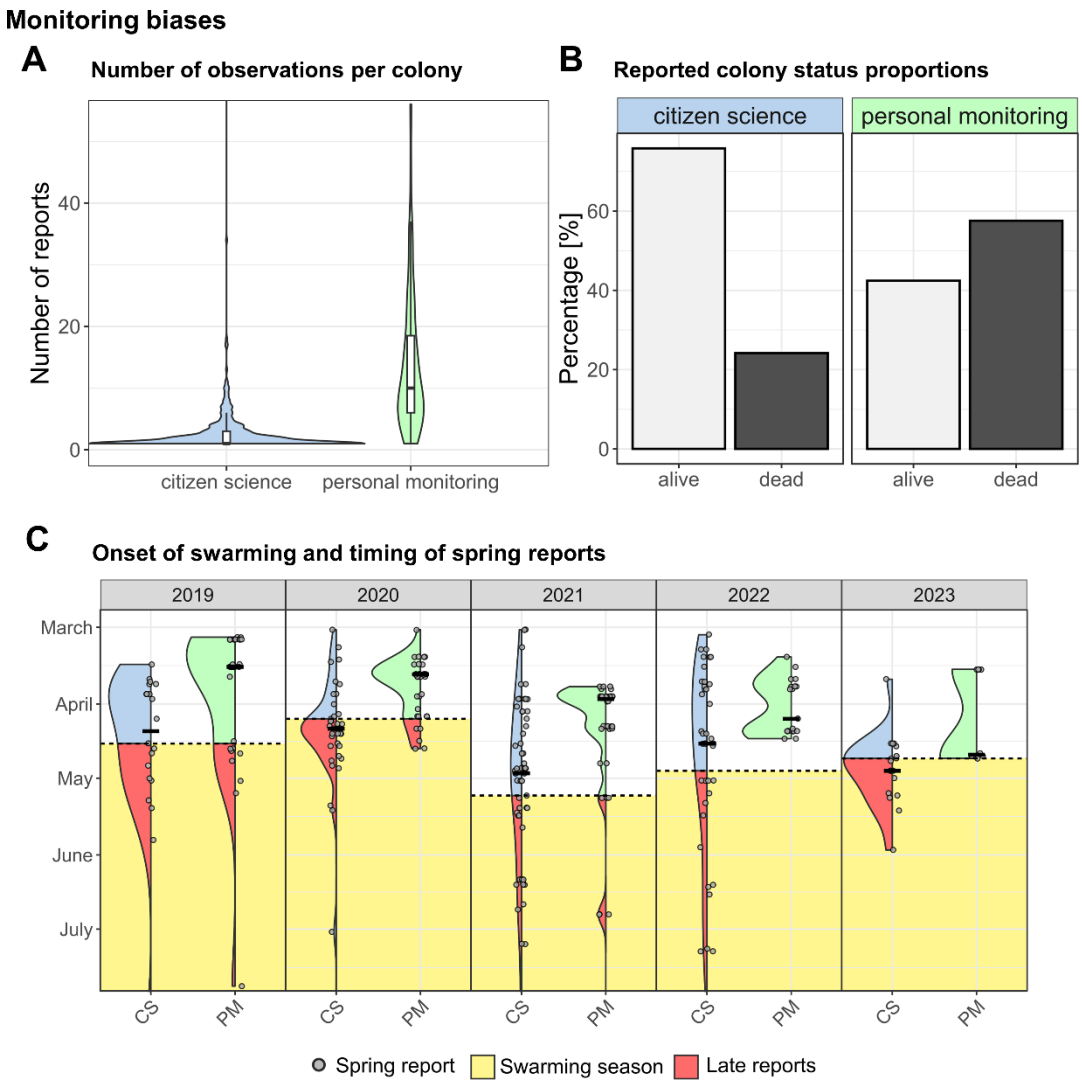

Figure 6: Analysis of reporting biases between Citizen Science monitoring (CS, light blue) and personal monitoring in the Munich region (PM, light green). A) Violin plot with included boxplot illustrating the distribution of the number of observations per colony for the whole monitoring timespan. B) Proportional representation of reported colony statuses ("alive" in light grey, "dead" in dark grey) for CS and PM. C) Temporal variation in colony statuses reported post-winter for the two different monitoring approaches in relation to the swarm season (in yellow) from the years 2019-2023. Note: The dashed line marks the first observed swarm for each year, after which spring reports on colony status may not be reliable anymore (late reports in red colour). Bold horizontal lines indicate median values of the timing of CS and PM reports.

We evaluated the timelines of reports from Citizen Science and personal monitoring, with a particular focus on reports submitted after winter. To assess the effectiveness of the reporting, we quantified the proportion of reports considered 'late reports', defined as submissions after the swarming start date for that year. The median reporting date after winter for CS was consistently later than for PM, specifically 21 April versus 29 March, respectively (mean: 3 April for PM vs. 2 May for CS) (Figure 6C). Consequently, a substantial proportion of CS reports were rendered unusable annually, i.e. around 46 % (84 out of 184) reports of CS could not be used each year, as they were reported too late (compared to 11% in PM, 15 out of 131 reports). These findings suggest an urgent need for improved reporting intensity and timelines within Citizen Science programs to ensure data reliability.

DISCUSSION

To investigate claims of free-living survivor colonies in Germany, we launched the BEEtree-Monitor project with a low-tech monitoring scheme designed to collectively gather data on free-living honeybee colonies. This initiative resulted in the most extensive database on the topic to our knowledge to date, enabling a comprehensive analysis of the nesting habits and life histories of these colonies over a seven-year period.

Deciduous forests are widely seen as the original habitat of honeybees and offer cavities if mature trees are present. While the reported free-living honeybee colonies relied heavily on tree cavities as nesting sites, our data show that many of the tree species favoured by honeybees are rare in today’s forests and are more likely to be found in settlement areas, along streets, in parks, or in cemeteries. When examining the available foraging habitat around the reported colonies, our findings indicate that forests play a minor role. Additionally, today's German beech forests, for instance, do not provide diverse and rich foraging opportunities throughout the year (Rutschmann et al., 2023). This points to the conclusion that there is no pristine habitat for free-living honeybee colonies in the sense of a “natural environment”. From a conservation perspective, urban landscapes have become crucial refuges for species considered “wild” and those needing to escape rural environments dominated by intensive agricultural land use. These areas are often rich in floral diversity and offer an array of potential nesting sites, such as cavities in buildings and mature trees in parks and gardens (Angold et al., 2006; Threlfall and Kendal, 2018; Gathof et al., 2022). Additionally, urban areas provide an attractive foraging environment for both managed and

free-living honeybee cohorts (Ayers and Rehan, 2021; Baldock, 2020; Rutschmann et al., 2023; Young et al., 2021). Forest aren't "natural" spaces of "wilderness" and the urbanization has unexpected conservational potential. Having entered the Anthropocene, the old dichotomies of natural/artificial of wild/domestic become potentially misleading categorical foundations for research and conservation agendas.

As a case in point, our calculations reveal a notably high density of free-living honeybee colonies in the city of Munich in summer (0.42 colonies/km²), surpassing those in managed German woodlands (0.23 colonies/km²), Polish rural areas (0.1 colonies/km²), and agricultural landscapes in Spain (0.2 colonies/km²) (Kohl et al., 2022; Kohl and Rutschmann, 2018; Oleksa et al., 2013; Rutschmann et al., 2022). This accumulation of free-living colonies in Munich and in cities in general could be attributed to several factors, including those mentioned above, but also to the higher chances of discovering a colony and the prevalence of managed honeybee colonies in urban areas compared to rural areas and forests.

Honeybees living within tree cavities in forested areas rarely share contact zones with humans, while urban environments present a more complex scenario. Here, interactions with humans are more frequent, particularly when colonies establish within building structures. It is also known that higher human population density correlates with higher densities of beekeepers and consequently more escaping swarms searching for cavities (Oré Barrios et al., 2017; von Büren et al., 2019). For example, in Munich, the known density of managed hives is over 12 per km², surpassing the German average density by a factor of 4.3 (personal information from the veterinary office and data from the German Ministry of Food and Agriculture, both in 2022). The dominance of reports from urban areas introduces a bias, potentially skewing perceptions regarding the distribution and density of free-living colonies across different habitats. This issue can be addressed by incorporating systematic approaches with random sampling techniques, such as beelining (Seeley, 2016; Kohl and Rutschmann, 2018; Radcliffe and Seeley, 2018).

High managed honeybee densities in many European regions have sparked ongoing debates about food competition and pathogen transfer among pollinators (Geldmann and González-Varo, 2018; Ropars et al., 2019; Saunders et al., 2018; Herrera, 2020; Iwasaki and Hogendoorn, 2021; Ghazoul, 2005; Casanelles-Abella and Moretti, 2022; Weissmann et al., 2023; Egerer and Kowarik, 2020). Such concerns could be particularly pronounced in urban settings where some endangered solitary bees are present and the density of managed

honeybee colonies is already high (Mallinger et al., 2017; but see Harder and Miksha, 2022; Steffan-Dewenter and Tscharntke, 2000). Yet, our findings suggest that the density of free-living colonies in Munich remains relatively low, at approximately 4% of the density of registered colonies in the city (see SM for more information). While the local densities of managed colonies require careful consideration, free-living colonies should not be considered problematic for urban pollinators nor for managed colonies from urban beekeepers (see Kohl et al., (2023a) for an investigation on the parasite loads of free-living colonies).

Our findings reinforce the understanding that honeybees generally prefer elevated cavities for nesting (Seeley and Morse, 1978; Seeley, 2019). The observed significant difference in the height of nests between building and tree cavities may partially reflect a bias, where colonies in buildings are more likely to be observed despite higher elevation from ground level. Moreover, buildings in urban areas inherently offer more high-elevation spaces suitable for bee colonies, unlike trees, where the likelihood of finding a cavity large enough to accommodate a colony decreases with height.

Interestingly, our data indicate that free-living honeybees exhibit a pronounced directional preference for southern or southwestern exposures when selecting cavities. This preference aligns with the thermoregulatory benefits of southern orientations, which facilitate sun exposure and warmth, particularly beneficial during spring when colonies are emerging from winter. This finding is consistent with some previous studies that noted similar directional preferences (Avitabile et al., 1978; Radcliffe and Seeley, 2018; Cordillot, 2024), though it contrasts with others that reported a random distribution of entrance directions (Seeley and Morse, 1976; Gambino et al., 1990). Additionally, in cities and forests, a high proportion of bee-used hollows in trees and facade insulations are created by woodpeckers. While we cannot exclude an underlying preference of woodpeckers for certain directions and heights, the consistent directional preference observed in our study suggests a genuine selection by the bees themselves.

In German forest environments, spruce (*Picea abies*, 25%), pine (*Pinus sylvestris*, 22%), beech (*Fagus sylvatica*, 15%), and oak (*Quercus* spp., 10%) are the most common tree species by area, collectively representing more than 70% of the trees (Schmitz, 2014). When examining the tree species housing free-living honeybee colonies in German forests, these four species were also the most common, but the distribution was significantly different. While the deciduous species beech (35%) and oak (20%) were highly overused by bees,

colonies were greatly underrepresented in the two most important coniferous tree species in managed forests: pine (13%) and spruce (11%). Although coniferous species are still predominant in managed forests, they do not provide as many suitable cavities for bees and other animals (Requier et al., 2020). Lime trees (*Tilia* spp.), which are of minor importance in managed forests, dominate both the urban and rural landscapes as alley trees and are heavily utilized by honeybees as nesting sites and sources of food. Especially in urban areas, the diversity of tree species used by bees was much higher, with lime (23%), ash (*Fraxinus excelsior*, 16%), plane (*Platanus acerifolia*, 11%), and horse chestnut (*Aesculus hippocastanum*, 7%) being the most frequently occupied. Our observations that ash trees are disproportionately favoured as nesting sites, raises concerns in light of the ongoing threat of *Hymenoscyphus fraxineus*, the causal agent of ash dieback across Europe. In Munich, nearly half of the inhabited trees are ash, and with over half of the city's free-living colonies residing in buildings, the ash dieback could significantly increase human contact with these colonies.

Our study underscores the importance of mature, old-growth trees in providing suitable nesting sites for free-living honeybees (Bütler et al., 2013; Requier et al., 2020; Visick and Ratnieks, 2023b). With an average diameter at breast height (DBH) of 64 centimetres, these large trees in our study are vital for supporting diverse ecological communities. In general, conservation efforts should, prioritize the preservation of old-growth forests and the protection of long-lived tree species -across all habitats- to maintain crucial nesting habitats for many species including free-living honeybees.

To assess the self-sustainability of a population is important for the conservations of species with a clear status of being "wild" or "feral". For some species as for the western honeybees in Europe the situation is more complex. Local European honeybee populations consist of deeply entangled managed and free-living cohorts in varying proportions. For centuries, the breeding of the former and the natural selection of the latter have impacted the overall population. With the advent of *Varroa destructor* and the continuing use of acaricides in most beekeeping practices, the ratio might have shifted in some European regions, including Germany. Yet, the species remains in a liminal state, and depending on future conservation strategies, populations might either shift towards full dependency on human care or retain and even enhance their capability to self-sustain by naturally adapting to new environmental circumstances.

In regions such as Spain and the UK, survival rates of free-living honeybee cohorts suggest potential self-sustainability or near self-sustaining populations (Rutschmann et al., 2022; Visick and Ratnieks, 2023b). Notably, in Gwynedd, Wales, the use of acaricides in beekeeping is no longer necessary (Remter, 2015). Our personal monitoring analysis in Munich, however, indicates that the survival threshold required for self-sustaining cohorts—approximately one-third annual survival (Kohl et al., 2022)—is not being met in Germany. This finding aligns with other studies conducted in variable habitats in Germany and neighbouring countries (Kohl et al., 2022; Lang et al., 2022; Cordillot, 2024) , yet contrasts sharply with anecdotal claims from lay observers who report continuous and prolonged occupancy of cavities. These observations do not necessarily confirm extended lifespans of individual colonies; rather, it seems more plausible that many free-living colonies in Germany are recent escapees from managed apiaries, and that monitoring has not been conducted rigorously enough.

The factors contributing to the decline of free-living colonies are varied, encompassing both ecological and evolutionary aspects. From an ecological perspective, challenges such as a shortage of floral resources, lack of suitable and safe nesting sites, and parasite pressure can significantly impact colony viability (Kohl et al., 2023b; Rutschmann et al., 2023). Another aspect to consider is the evolutionary impact of modern beekeeping practices: They focus on breeding for desirable traits such as maximized honey production, reduced swarming tendencies, and docility (Seeley, 2019). Breeding efforts for varroa resistance exist, but they have not yet made a significant impact (Guichard et al., 2023), and the continuous medical treatment of managed colonies prevents tolerance traits from prevailing at the population level (Blacquière et al., 2019; Neumann and Blacquière, 2017). Additionally in Germany, the replacement of the native subspecies *Apis mellifera mellifera* with non-native subspecies might have profound implications on the genetic diversity and adaptability of honeybee populations in this area, potentially influencing their ability to thrive independently (Büchler et al., 2014). Understanding the complex interplay of these factors is crucial for developing reliable conservation strategies for free-living cohorts.

The issue of defining species as “wild” and self-sustaining is significant, especially as organizations like the IUCN assess species status based on these criteria. Emphasizing wilderness and self-sustainability can hinder conservation efforts for liminal species in danger of losing their ability to self-sustain. We suggest understanding honeybees in Europe

as a liminal species, with larger cohorts living under beekeeping conditions and smaller ones living independently, both within a broad and shared geographic range. These cohorts are unlikely to be found independently of each other and are deeply interconnected through genetic exchange via mating and annual swarming. The survival rates of the free-living cohort influence the overall population's genetic diversity in Europe, including the managed cohort.

While the higher number of reports for colonies monitored by PM is partly due to the density of observations applied in the PM to better understand the flight patterns of robbing, scouting or survivor bees, there remains a concern with CS as many colonies in the CS database were reported only once and could not be used for the survival analysis. In fact, it is plausible that citizen scientists primarily report on active, living colonies, and may discontinue monitoring once a colony is no longer present, thereby creating a biased dataset. Our model predictions, incorporating monitoring type and data from CS, PM and two published datasets, also point in this direction, reinforcing the potential bias introduced by CS reporting practices. In our study, approximately 76% of reports from citizen scientists indicated the presence of living colonies, contrasting with only about 42% in the personally monitored dataset meeting the 52% and 43% in two studies by Rutschmann et al. (2022) and Kohl et al. (2022), relying on expert monitoring. This discrepancy between reports on occupied and unoccupied cavities suggests that the ratio of reported colony status indicate inherent biases within the monitoring methods of layperson in contrast to experts. Understanding and addressing these biases is essential for accurately interpreting survival rates of free-living honeybees based on Citizen Science data. Our analysis also revealed a significant delay in reporting by citizen scientists during the spring. This delay rendered a significant proportion of the data unusable for survival analysis. Despite accounting for this factor, the survival rates reported in CS data remained much higher, suggesting a likely bias. These findings indicate that results from CS should be interpreted with caution.

A key challenge of our study, similar to many Citizen Science projects, is its serendipitous nature. While Citizen Science is extremely valuable for identifying the locations of free-living honeybee colonies across huge geographic scales, it presents complexities and significant efforts when it comes to monitoring these colonies coherently over time. Based on our experience in the first years of the study we optimized the monitoring scheme for ourselves and for the applicability in CS. To maximize the contribution of CS to bee research,

we recommend adopting a standardized monitoring scheme (Figure 1B). This approach can be built on the successful protocol employed in our personal monitoring, which consisted of at least three site visits per year to detect pollen import (or typologized flight-patterns) and empirical data on the swarming season (especially its onset). The first visit should occur before the swarming season begins, the second visit after the swarming season to confirm newly established colonies and to include known but previously unoccupied sites to find new founder colonies, and the third visit in autumn to assess summer-deaths and the number of colonies going into winter. Citizen scientists need to be reminded early and often enough and briefed on appropriate timing and weather conditions for observations. Given the average height of the entrances, they should be equipped with sufficiently powerful binoculars or spotting scopes to reliably observe pollen import at each of the three visits. Additionally, observers could be trained to differentiate between various flight patterns, such as normal traffic, robbing, or scouting along the criteria offered in this study. Including a commentary section in the monitoring forms proved valuable, as it allowed observers to describe their observations in detail. This additional information helped us assess the reliability of the data, especially in cases where the data seemed suspicious or lacked information on pollen import. While we could then decide whether to include or exclude such reports in the final dataset, having consistent reports on pollen import is much more time-efficient and should be prioritized.

In essence, structured and standardized monitoring projects are indispensable for thoroughly understanding the mechanisms underlying survival of free-living colonies. Long-term monitoring and more extensive geographic coverage would enhance our understanding of the survival and reproductive success of free-living honeybee colonies in Europe. Collaborative efforts combining scientific research with Citizen Science initiatives could prove beneficial in achieving these objectives. In this sense, overwintering survival serves as a practical and easily recordable indicator for identifying regions in Europe with high survival rates and enlarged free-living cohorts. Such an approach requires minimal investment in monitoring and does not rely on sophisticated kinship analysis, making it accessible for widespread Citizen Science participation.

CONCLUSION

Given the growing trend of citizen science-based knowledge production, particularly for monitoring free-living honeybee colonies, we critically compared the citizen science dataset

with data collected through our personal monitoring efforts. We identified epistemic pitfalls in the collection and interpretation of citizen science data and outlined potential strategies to optimize its use for monitoring purposes. Despite a reporting bias towards more densely populated areas, the combined datasets provide a reliable and comprehensive foundation for assessing nest site parameters of unmanaged colonies across various land cover types in Germany. Importantly, the low-tech approach of our personal monitoring offered a valid foundation for survival analysis. Our findings contribute to filling a gap in our knowledge about the western honeybee and enhance our understanding of its free-living cohort in Germany. Given the low survival rates of free-living colonies in Germany compared to other regions in Europe and abroad, more detailed and comparative research is needed to develop conservation strategies for free-living cohorts.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

Conceptualization: SR-BR-FR
Methodology: SR-FR-BR
Software: SR
Formal analysis: BR
Investigation: SR-FR
Resources: FR-SR-BR
Data curation: SR-BR-FR
Writing - original draft: BR-FR
Writing - Review & editing: SR
Visualization: BR
Administration: SR-FR

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