Foraging and Drifting Patterns of a Highly Eusocial Neotropical Stingless Bee Species Assessed by Radio-frequency Identification Tags

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Foraging and drifting patterns of a highly eusocial neotropical stingless bee species assessed by radio-frequency identification tags

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Abstract

Bees play a key role in ecosystem services as the main pollinators of numerous flowering plants. Studying factors influencing their foraging behaviour is relevant not only to understand their biology, but also how populations might respond to changes in their habitat and to the climate. Here, we used radio-frequency identification tags to monitor the foraging behaviour of the neotropical stingless bee *Melipona fasciculata* with special interest in drifting patterns, i.e. when a forager drifts into a foreign nest. In addition, we collected meteorological data to study how abiotic factors affect bees' lifespan and behaviour. Our results show that only 35 % of bees never drifted to another hive nearby, and that factors such as temperature, humidity and solar irradiation affected the foragers drifting rates and/or lifespan. Moreover, we tested whether drifting levels would decrease after marking the nest entrances with different patterns. Contrary to our predictions, there was an increase in the proportion of drifting, indicating that this could be a deliberate strategy rather than an orientation mistake. Overall, our results demonstrate how managed bee populations are affected by both nearby hives and climate factors, offering unprecedented insights on their biology and potential commercial application as crop pollinators.

Keywords: Radio-frequency Identification; stingless bee; Melipona, foraging, drifting behaviour

Introduction

Ecosystem services encompasses a wide range of goods and services provided by nature functioning resulting in increased wellbeing and/or economic benefit to human societies[1,2]. Pollination services, i.e. direct economic benefits derived from natural or managed animal pollinators, are among the most important ecosystem services, with a yearly valuation estimated between US$235-577 billion worldwide[2]. It is estimated that ca. 90% of flowering plants and ca. 75% of crops depend to some extent on animal pollination[3,4], of which, bees play a major role. Nevertheless, despite the remarkable importance of bee pollination, most studies are focuses on only a handful of bee species, notable the honeybee *Apis mellifera,* and the effect of other native bee populations are often overlooked and underestimated[5]. In fact, wild pollinators enhance fruit set of crops regardless of honeybee abundance[6]. This scarcity of studies from many bee species in terms of their contribution to ecosystem services is possible a consequence of a general lack of knowledge about basic aspects of their biology and natural history.

Stingless bees are a highly diverse group of social bees native to the tropical and subtropical regions of the world that form perennial colonies composed of hundreds to thousands of workers that are common visitors of many flowering plants, including a number of crop species[7,8]. Despite the great potential[9], the large scale application of stingless bees as crop pollinators is still not as developed when compared to honeybees and bumblebees[10-12]. It is nonetheless important to understand basic aspects of their biology such as foraging activity patterns and lifespan, and also their viability to be managed prior to any potential application of stingless bee populations. Several species of stingless bee species are already managed successfully in small scale, notably those from the genus *Melipona* that have been traditionally used for honey production in the Americas, with several other stingless bee genera used in Africa, Asia and Oceania[13-15].

Studying the foraging patterns in bees can help to not only increase the knowledge about these important providers of ecosystem services but also to better formulate beekeeping strategies such as colony density and proximity to both natural areas and crops. As yet, little is still known about many aspects of their foraging patterns. In natural conditions, colonies of a single species are usually located somewhat distant from each other with densities ranging between 0.014-16 hives/ha[16,17]. In managed populations, in contrast, there is usually a large number of colonies aggregated next to each other, resulting in increased competition for resources and high levels of orientation mistakes, namely drifting behaviour, when foragers return to their hives. This drifting behaviour is well studied in honeybees but still poorly understood in stingless bees[18], and it is an important factor to be considered for both honey production and crop pollination, since diseases and pathogens may spread across colonies via drifted workers[19,20].

Here, we used state-of-the-art radio frequency identification (RFID) tags to monitor the long-term foraging behaviour of the stingless bee *Melipona fasciculata* in a research institute breeding facility, with special interest in the drifting patterns between different colonies. In particular, we tested whether the proportion of drifting behaviour observed would decrease after marking the colony entrances with different geometric patterns, i.e. workers would make fewer orientation mistakes, since different patterns can be used as recognition cues to the hive entrances[21]. In addition, we tested if the position of the colonies had an influence in terms of the direction of the drifting rates and, finally, we correlated the data collected with the RFID system with meteorological data to understand how abiotic climatic factors affected both the bees' lifespan and drifting rates.

Results

Bees foraging activity and lifespan

Our results show that the tagged workers lived on average for 9.3 days, ranging from a minimum of 1.2 to a maximum of 72.5 days after being tagged (figure 1a). In addition, bees began foraging on average 2 days after being tagged, with some more extreme cases where workers only started foraging after 25 days and beyond, as registered by the first reading of their tags at the colony entrance (figure 1c). Foragers were active throughout the day, with the highest foraging activity being recorded during the early morning hours (figure 1d). Furthermore, our data show that workers in colony four lived significantly less, while in colony one and two significantly more than the average (Poisson GLM, colony four: Wald Z score = -7.602, $p < 0.001$; colony one: Wald Z score = 2.373, $p = 0.047$; colony two: Wald Z score = 5.478, $p < 0.001$). Figure 2 illustrates the reconstructed foraging activity of all 2880 bees during the four-month experimental period.

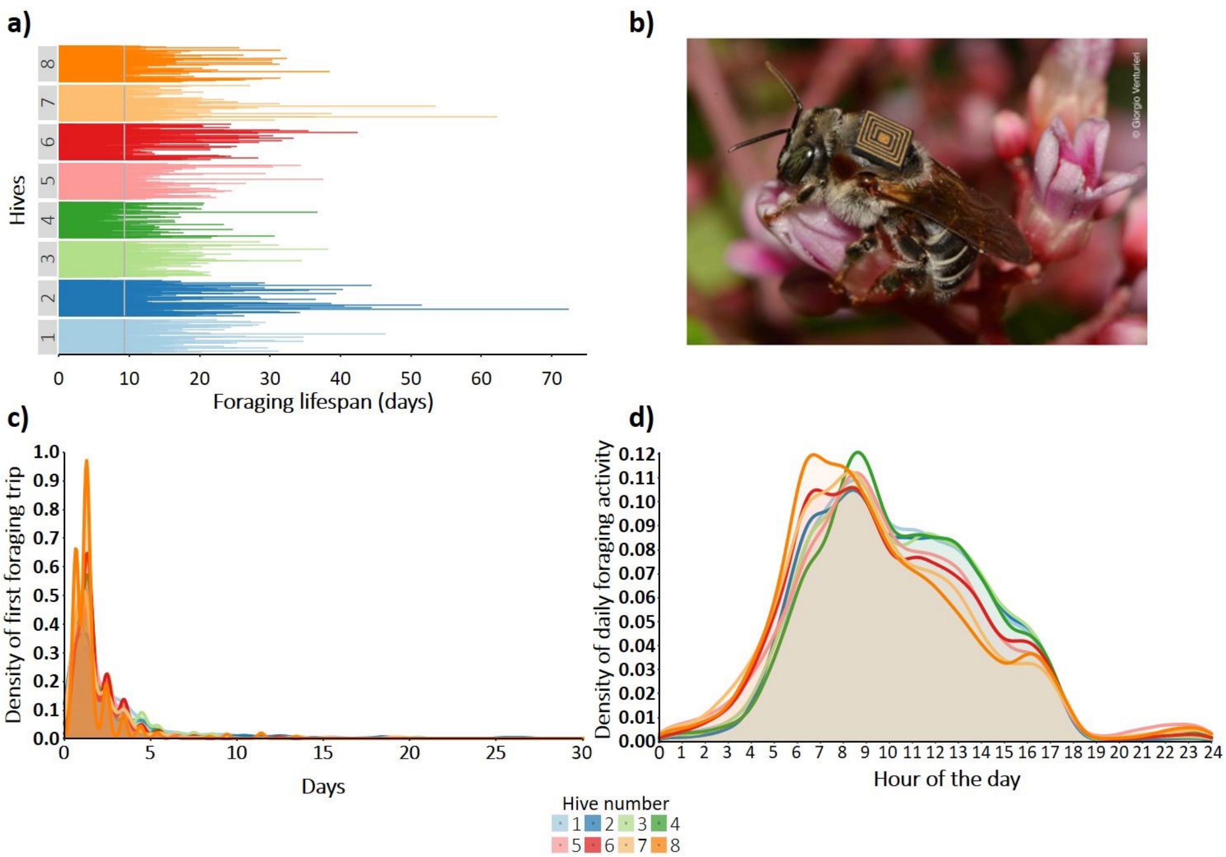

Figure 1. a) Worker bees' lifespan based on the difference between the last reading on the RFID system and the day they were tagged. Different colonies are plotted on the y axis with every row corresponding to an individual bee. The vertical grey line represents the mean lifespan of 9.3 days. **b)** Picture of a *M. fasciculata* forager with a RFID tag on her thorax. Photo by Giorgio Cristino Venturieri. **c)** Density plot of the bees' first foraging trip calculated as the difference between the tagging data and the first record on the reader. **d)** Density plot displaying the foragers activity throughout the day. Peak activity was recorded between 5:00 to 10:00 in all colonies.

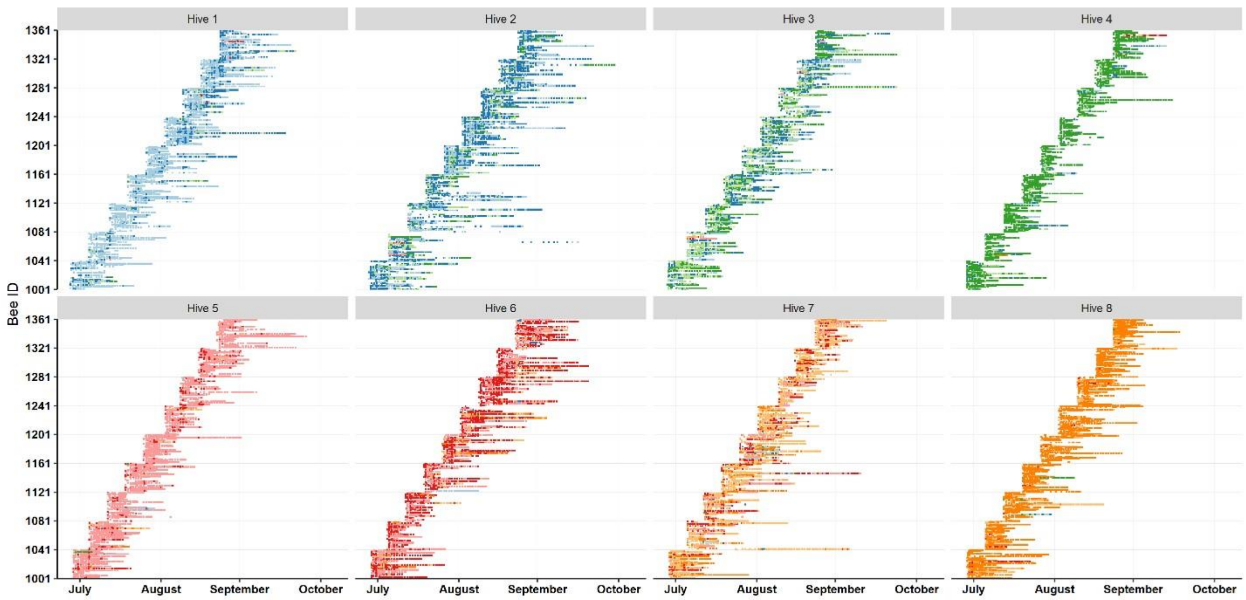

Figure 2. Foraging activity of all bees during experimental period. Each row represents the RFID scans of an individual bee, with the colours corresponding to their respective natal hives. In total 2880 bees were tagged in nine separate sessions demonstrated by the ladder-like appearance along the y axis. That is, at every session 40 tagged bees were introduced per colony.

Factors affecting drifting behaviour and lifespan

Throughout the experimental period, only 35.9 % of all tagged workers never drifted to another colony, with 36.6 % drifting to only one, 19.1% to two, 7.6% to three foreign colonies, and the percentage decreasing below 1% as the number of foreign colonies increased up to a maximum of seven colonies, i.e. all non-natal experimental colonies (figure 3a). It is interesting to note that the majority of drifting events was in the horizontal direction, i.e. workers mostly drifted to colonies on their left or right rather than above or below their natal hives (Binomial GLMM, Wald Z score > 8.568, $p < 0.001$ for all colonies, figure 3b). Moreover, colonies placed on both edges produced fewer drifters than colonies placed between other hives. That is, foragers in colonies two, three, six and seven showed significantly higher levels of drifting behaviour (Poisson GLM, hive two: Wald Z score = 11.880, $p < 0.001$; hive three: Wald Z score = 11.499, $p < 0.001$; hive six: Wald Z score = 4.125, $p < 0.001$ and hive seven: Wald Z score = 3.514, $p = 0.001$) while hives four, five and eight had significant fewer drifters (Poisson GLM, hive four: Wald Z score = -5.746, $p < 0.001$; hive five: Wald Z score = -5.250, $p < 0.001$ and hive eight: Wald Z score = -9.716, $p < 0.001$), with hive one being not significant (Poisson GLM, Wald Z score = 0.181, $p = 0.936$). Furthermore, drifting rates were positively correlated with workers' lifespan (Poisson GLM, Wald Z score = 18.113, $p < 0.001$) and the earlier bees began foraging the higher the observed drifting rates (Poisson GLM, Wald Z score = 7.494, $p < 0.001$).

In addition to biotic factors, several meteorological factors influenced the levels of drifting behaviour, with dew point positively affecting the drifting rates (Poisson GLM, Wald Z score = 3.205, $p = 0.001$), while solar irradiation (Poisson GLM, Wald Z score = -2.804, $p = 0.005$), maximum relative humidity (Poisson GLM, Wald Z score = -2.883, $p = 0.002$) and minimum daily temperature (Poisson GLM, Wald Z score = -2.722, $p = 0.006$) were negatively correlated to the drifting rates.

During the experimental period colony entrances received individual markings to test whether foragers would then improve recognition of their own hive and drift to fewer foreign hives i.e. make fewer orientation mistakes. Intriguingly, we observed an increase in the proportion of drifting events after marking the hive entrances, with 63.9 % of tagged bees drifting before and 68.7 % after the hive entrances were marked (Binomial GLMM, Wald Z score = 2.508, p = 0.012), suggesting that drifting behaviour could be a deliberate strategy rather than merely an orientation mistake (figure 3a).

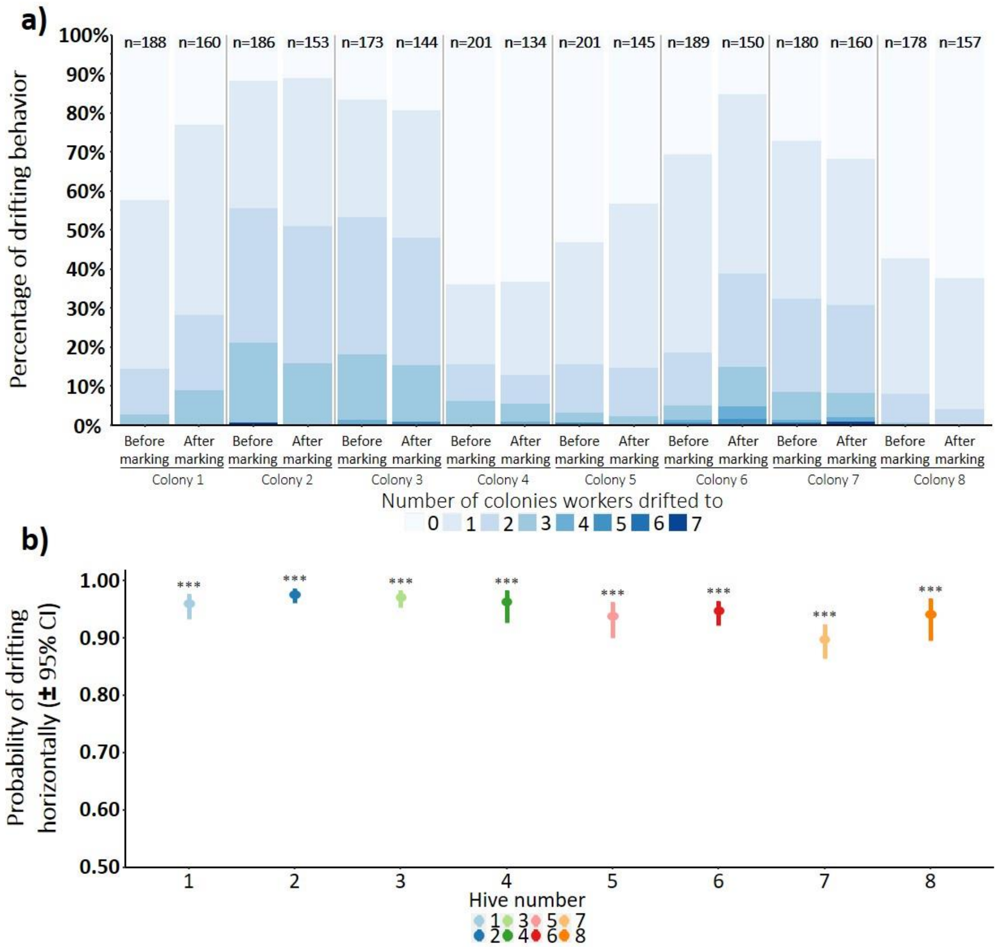

Figure 3. a) Percentages of drifting events to different foreign colonies during the experimental period before and after marking the colony entrances. Hives placed in the middle sections of the shelves presented higher rates of drifting behaviour with some drifters visiting all seven non-natal hives. *n* shows the number of tagged worker drifters per colony per period. **b)** Drifting events were most horizontal, with on average 96% of the drifting events being to colonies placed on the same shelf than the natal hives.

Finally, it was possible to observe that meteorological factors were also correlated with the workers lifespan, whereby maximum daily pressure and temperature, precipitation as well as dew point temperature were positively correlated with lifespan (Poisson GLM, max pressure: Wald Z score = 6.521, p < 0.001; max temperature, Wald Z score = 5.236, p < 0.001; precipitation, Wald Z score = 3.020, p = 0.002; max dew point: Wald Z score = 2.504, p = 0.012; min dew point: Poisson GLM, Wald Z score = 4.710, p < 0.001). Conversely, minimum daily temperature and pressure, humidity and wind speed negatively affecting the bees' lifespan (Poisson GLM, min temperature: Wald Z score = -8.834, p < 0.001; min pressure, Wald Z score = -6.922, p < 0.001; max humidity: Wald Z score = -4.235, p < 0.001; min humidity: Wald Z score = -3.156, p = 0.001; and wind speed: Wald Z score = -9.901, p < 0.001).

Discussion

In this study we used radio frequency identification tags to monitor the foraging behaviour of the stingless bee *M. fasciculata* during the dry season in a mosaic of agricultural crops, forest remnants, and human habitations in eastern Amazon. By reconstructing their daily foraging activity, we could observe that bees are foraging during the entire day with the peak activity in early morning hours (figure 1d). Similarly to honeybees, stingless bee workers perform different tasks along their lives, from taking care of the young and cleaning the colony soon after emerging, to carrying out more dangerous tasks such as defending the hive and foraging towards the end of their lives with some degree of specialization in certain tasks[22]. In the congeneric *M. beecheii* it was shown that some foragers collected mostly pollen whereas some were specialized in foraging for nectar, with great impact both in their daily activity and lifespan. Nectar foragers were active during the entire day but died approximately 3 days after they began foraging while pollen foragers were only active for 1-3 hours in the early morning but lived on average 9 days after they started foraging[23]. These patterns could explain the differences observed in our experiments, where we detected a wide variation in their lifespan after they become foragers (1.2-72.5 days). In addition, although we did not quantify the workers precise age, *Melipona* bees usually start foraging around 25-33 days after emergence[22,23], hence we can estimate the life expectance of the bees in our experiments approximately between 25-105 days, which is in line with what is found in the literature for other species of this genus[24].

For most social insects, life-threatening challenges increase when workers leave the security of their nests and start their foraging life. Outside the nest they face an increased chance of predation, death by the elements (e.g. storms), and death by exhaustion[25-27]. Indeed, we observed some climatic factors having strong effects on the bees' lifespan, notably temperature, pressure, and wind speed. An increase in the average daily maximum temperature by one degree during the bee's lifespan corresponded to an increased lifespan by 1.7 days. On the other hand, an increase in the minimum daily temperature had the opposite effect, decreasing the bee's lifespan by 3.3 days. A possible explanation for this observation is that while bees benefit from higher temperatures during daily foraging activity, the same was not true when they were inside their hives during the night, when the minimum temperatures were recorded. A similar pattern was observed for average maximum and minimum atmospheric pressure, where the maximum recorded values had a positive effect whereas minimum values had a negative effect on the bees' lifespan. Finally, average recorded wind speed had a negative impact on their lifespan, likely by impairing the bee's flight ability. Even though further studies are still needed to fully comprehend how climate factors affect the bees' behaviour, our results show that this species is highly susceptible to variations in climate factors with relatively small fluctuations having a significant impact their lifespan, demonstrating that even small changes in the future climate might cause notable implications in their survival.

In terms of the drifting behaviour, our results show that 64 % of the tagged workers drifted to at least one foreign hive, and that some of them were recorded entering all seven foreign hives (figure 3a). High rates of drifting behaviour are not uncommonly observed in apiaries[18,28,29], since the high density of hives next to each other likely results in a larger proportion of orientation mistakes. Although the levels of drifting behaviour observed are likely mainly due to orientation mistakes, nest robbing or social parasitism cannot be completely ruled out, since we observed an increased proportion of drifting behaviour after marking the colony entrances which presumably increased the bees ability to recognize their own colony[21]. In fact, worker social parasitism is well documented in both honeybees[30-34] and bumblebees[35-38], as well as other social insect species including wasps[39]. In addition, one of the few examples of intraspecific queen parasitism in bees is observed in the congeneric *M. scutellaris* and it suggested to occur in other *Melipona species*[40-42]. Whether workers indeed actively drift into foreign colonies and how they manage to avoid being detected as non-nestmates and attacked by guards still deserves further study.

An interesting outcome of our experimental design is the fact the nearly all drifting events took place horizontally, i.e. foragers drifted almost exclusively to colonies placed in the same shelf as their natal hive rather than above or below, and that hives placed in the centre of the rows produced more drifters, similarly to what was observed in honeybees[18]. This finding demonstrates that the spatial distribution of colonies has important management implications for stingless bee populations. Furthermore, ours results also suggest that other factors other than the position of the hives played a role in the rates of drifting behaviour. The average dew point temperature was observed to be positively correlated to the drifting levels, possible because most foraging activity happens in the early morning hours and a higher temperature could be linked with higher metabolic activity. On the other hand, factors like solar irradiation, maximum humidity and minimum daily temperatures were shown to negatively impact drifting rates. These factors are usually linked with lower foraging activity[43], which could explain the lower rates of drifting merely as an outcome of fewer foraging trips.

Stingless bees present great potential to be used in commercial crop pollination[7,44,45]. Indeed, *Melipona* bees have been demonstrated to be efficient pollinators of many economically important fruits and vegetables including tomatoes[46-49], eggplant[9], sweet pepper[50] and annatto[51]. A recent study using the RFID technology with the stingless bee *M. fasciculata* showed that workers of this species can forage up to a distance of 10 km away from their hives[52], suggesting that these bees are well suited for pollination of large scale plantations as well. In addition to their potential to be employed as commercial pollinators, stingless bees are also of great importance as providers of ecosystem services[7,53], being the main pollinators of different ecosystems[54-57]. Our results give support to both applications indicating that stingless bees can be used for extended periods of time in relatively high densities without significant disturbances to both their foraging activities and lifespan.

Overall, this study presents unprecedented data on the foraging activity and drifting patterns of the stingless bee *M. fasciculata*, showing how the presence of nearby hives as well as several abiotic factors have a significant impact on both the rates of drifting behaviour and the bee's lifespan. This is an important step towards a better understanding of stingless bees' biology, suggesting how some factors might affect their application as pollinators in crops as well as in natural areas.

Methods

Study species and experimental design

This study was performed with the stingless bee *Melipona fasciculata*, which has its natural distribution in the northern region of Brazil[58]. The colonies used in the experiment were located at the meliponary of Eastern Amazon Embrapa, in an environment consisting of a mosaic of agricultural crops, forest remnants, and human habitations, where worker bees could forage freely on their expected range of about 2.5km[52,59-61]. The climate at the site is characterized as tropical with daily mean precipitation of at least 60 mm throughout the year[62].

To analyse the foraging and drifting patterns of *M. fasciculata,* eight experimental colonies were housed in hives designed for stingless bees and placed in a shed consisting of two rows with four colonies each (figure 4a). A plastic tube that extended the colony entrance and allowed the positioning of the antennae and microcomputer of the RFID system was placed in the front of the hive. The entire system was enclosed inside a box that protected entrance tubes from direct light in order to not disturb the forager's behaviour (figure 4b). Young worker bees that were not yet foraging were randomly sampled from each hive to receive the RFID tags. Bees were tagged every week for 9 consecutive sessions with 40 workers tagged per week, amounting to 360 bees per colony and 2880 in total. The process consisted in collecting the young workers in the early morning (8:00-9:00) and placing them in a tube with maximum 5 workers per tube prior to tagging them with the RFIDs. The RFID-tags were then glued with cyanoacrylate adhesive onto the worker thorax (figure 1b) and, after all bees were marked and the glue sufficiently dried, they were returned to their original hive. Workers from *M. fasciculata* tolerated well the RFID-tags glued on their thorax without any apparent disturbance to their flight behaviour. Finally, after 42 days of the beginning of the experiment, colonies received individual black and white markings with varying shapes at their entrances in order to test whether foragers would then improve recognition of their own hive and drift to fewer unrelated hives i.e. make fewer orientation mistakes.

RFID-system setup

This study was conducted using the Radio Frequency Identification System Ultra Small Package Tag (USPT) developed by Hitachi Chemical[63]. The system consisted in a single antenna placed below the colony entrance tube connected to an Intel Edison micro-computer to store data (figure 4b). Each tag was recorded with an individual ID that included the bee number and her colony of origin prior to being glued onto the bees. Therefore, whenever a tagged bee passed through the entrance tube both worker ID and time of the day were recorded. A caveat of the experimental design was that our system consisted of only one reader per colony, hence the signal sent to the computer did not inform the directionality of the bee's movement (towards or away from the hive) which was then mitigated during data analysis. Moreover, guard bees staying by the colony entrance would have repeated readings over a short period of time. Hence, only signals that were at least 180 seconds apart were included in the analysis to resolve this issue.

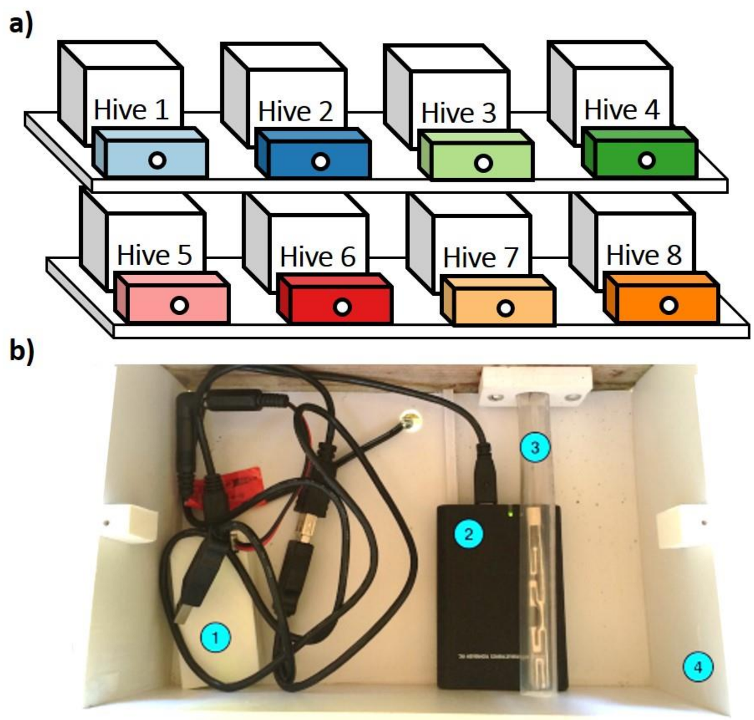

Figure 4. a) Experimental setup scheme not to scale with four hives placed in the top shelf and four in the bottom shelf. The RFID systems were placed in a plastic box at the hive entrances. **b)** Inside view of the entrance box containing the RFID system. 1. box containing the Intel Edison and Breakout Board; 2. RU-824 antenna; 3. tube connecting the hive to the entrance, and 4. protective plastic box.

Data analysis

All statistical analyses were carried out using the R software[64]. Data filtering and merging RFID and meteorological data was performed using a custom R script (available on data repository). Lifespan of foragers was calculated based on the difference between the last recorded data and the date the bees were tagged. First foraging trip was calculated with the difference between the first trip recorded and the tagging date and the density estimates were calculated based on the smoothed histogram using the "geom_density" function in the R package ggplot2. Likewise, the daily foraging activity were also calculated using the density function in the package ggplot2. To analyse the influence that both biotic and abiotic factors have on the observed drifting rates we used a model selection approach using the package glmulti to select the best set of explanatory variables based on the models Akaike's Information Criterion. The selected best model had drifting numbers coded as the dependent variable with lifespan, hive ID, number of days to begin foraging as well as several meteorological factors coded as covariates with a Poisson error distribution. We then used the same approach to select a model with the bees' lifespan coded as the dependent variable but used a *quasipoisson* error distribution do deal with overdispersion detected in this model. In addition, we tested whether the proportion of drifters present on the colonies was different before and after marking the colony entrances by fitting a binomial GLMM with the proportion of foragers that drifted to an unrelated colony as the dependent variable, colony marking (before or after) as a fixed factor and hive ID and an observation-level random effect variable to cope with overdispersion as random factors. Finally, we tested whether drifters had any preference on the direction they would drift. To this end, we ran a binomial GLM with the direction of the drifting event (i.e. horizontal and vertical) as the dependent variable, both the natal hives ID and the host hives ID as cofactors and individual IDs as a random factor. When appropriate, models were tested for temporal autocorrelation, which was not observed in the data. The R script used in the analyses as well as the original datasets are publicly available in the data repository[65] (temporary link https://data.mendeley.com/datasets/k9s83b9g4z/draft?a=f3bfc7d6-e9e8-4084-9694-e959a31c0be3).

References

1 Wallace, K. J. Classification of ecosystem services: problems and solutions. *Biol Conserv* **139**, 235-246 (2007).

2 Potts, S. G. *et al.* Safeguarding pollinators and their values to human well-being. *Nature* **540**, 220-229 (2016).

3 Klein, A. M. *et al.* Importance of pollinators in changing landscapes for world crops. *Proc Biol Sci* **274**, 303-313, doi:10.1098/rspb.2006.3721 (2007).

4 Ollerton, J., Winfree, R. & Tarrant, S. How many flowering plants are pollinated by animals? *Oikos* **120**, 321-326 (2011).

5 Kleijn, D. *et al.* Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature communications* **6**, 1-9 (2015).

6 Garibaldi, L. A. *et al.* Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *science* **339**, 1608-1611 (2013).

7 Heard, T. A. The role of stingless bees in crop pollination. *Annu Rev Entomol* **44**, 183-206, doi:10.1146/annurev.ento.44.1.183 (1999).

8 Michener, C. D. *The bees of the world*. 2nd edn, 972 (2007).

9 Nunes-Silva, P., Hrncir, M., da Silva, C. I., Roldão, Y. S. & Imperatriz-Fonseca, V. L. Stingless bees, *Melipona fasciculata*, as efficient pollinators of eggplant (*Solanum melongena*) in greenhouses. *Apidologie* **44**, 537-546 (2013).

10 Ramírez, V. M., Ayala, R. & González, H. D. in *Pot-pollen in stingless bee melittology* 139-153 (Springer, 2018).

11 Roubik, D., Heard, T. & Kwapong, P. Stingless bee colonies and pollination. *The pollination of cultivated plants: A compendium for practitioners* **2**, 39-64 (2018).

12 Roubik, D. W. *Pollination of cultivated plants in the tropics*. Vol. 118 (Food & Agriculture Org., 1995).

13 Cortopassi-Laurino, M. *et al.* Global meliponiculture: challenges and opportunities. *Apidologie* **37**, 275-292 (2006).

14 Quezada-Euán, J. J. G., Nates-Parra, G., Maués, M. M., Roubik, D. W. & Imperatriz-Fonseca, V. L. The economic and cultural values of stingless bees (Hymenoptera: Meliponini) among ethnic groups of tropical America. *Sociobiology* **65**, 534-557 (2018).

15 Orr, M. C. *et al.* Global Patterns and Drivers of Bee Distribution. *Curr Biol* (2020).

16 Eltz, T., Bruhl, C. A., van der Kaars, S. & Linsenmair, E. K. Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. *Oecologia* **131**, 27-34, doi:10.1007/s00442-001-0848-6 (2002).

17 Silva, M. D. & Ramalho, M. The influence of habitat and species attributes on the density and nest spacing of a stingless bee (Meliponini) in the Atlantic Rainforest. *Sociobiology* **63**, 991-997 (2016).

18 Pfeiffer, K. J. & Crailsheim, K. Drifting of honeybees. *Ins soc* **45**, 151-167, doi:10.1007/s000400050076 (1998).

19 Nolan, M. P. & Delaplane, K. S. Distance between honey bee *Apis mellifera* colonies regulates populations of *Varroa destructor* at a landscape scale. *Apidologie* **48**, 8-16 (2017).

20 Bordier, C., Pioz, M., Crauser, D., Le Conte, Y. & Alaux, C. Should I stay or should I go: honeybee drifting behaviour as a function of parasitism. *Apidologie* **48**, 286-297 (2017).

21 Plowright, C., O'Connell, C. E., Roberts, L. J. & Reid, S. L. The use of proximal and distal cues in nest entrance recognition by bumble bees. *J Apic Res* **34**, 57-64 (1995).

22 Mateus, S., Ferreira-Caliman, M., Menezes, C. & Grüter, C. Beyond temporal-polyethism: division of labor in the eusocial bee *Melipona marginata*. *Ins soc* **66**, 317-328 (2019).

23 Biesmeijer, J. & Tóth, E. Individual foraging, activity level and longevity in the stingless bee *Melipona beecheii* in Costa Rica (Hymenoptera, Apidae, Meliponinae). *Ins soc* **45**, 427-443 (1998).

24 Grüter, C. in *Stingless Bees* (ed Christoph Grüter) 1-42 (Springer, 2020).

25 Visscher, P. & Dukas, R. Survivorship of foraging honey bees. *Ins soc* **44**, 1-5 (1997).

26 Gomes, R. L. C., Menezes, C. & Contrera, F. A. L. Worker longevity in an Amazonian *Melipona* (Apidae, Meliponini) species: effects of season and age at foraging onset. *Apidologie* **46**, 133-143 (2015).

27 Roubik, D. W. Seasonality in colony food storage, brood production and adult survivorship: studies of *Melipona* in tropical forest (Hymenoptera: Apidae). *J Kans Entomol Soc*, 789-800 (1982).

28 Free, J. The drifting of honey-bees. *The Journal of Agricultural Science* **51**, 294-306 (1958).

29 Free, J. & Spencer-Booth, Y. Further experiments on the drifting of honey-bees. *The Journal of Agricultural Science* **57**, 153-158 (1961).

30 Chapman, N. C., Beekman, M. & Oldroyd, B. P. Worker reproductive parasitism and drift in the western honeybee *Apis mellifera*. *Behav Ecol Sociobiol* **64**, 419-427, doi:10.1007/s00265-009-0858-7 (2009).

31 Chapman, N. C., Higgs, J. S., Wattanachaiyingcharoen, W., Beekman, M. & Oldroyd, B. P. Worker reproductive parasitism in naturally orphaned colonies of the Asian red dwarf honey bee, *Apis florea*. *Ins soc* **57**, 163-167, doi:10.1007/s00040-009-0061-x (2009).

32 Chapman, N. C. *et al.* Queenless colonies of the Asian red dwarf honey bee (*Apis florea*) are infiltrated by workers from other queenless colonies. *Behav Ecol* **20**, 817-820, doi:10.1093/beheco/arp065 (2009).

33 Nanork, P. *et al.* Social parasitism by workers in queenless and queenright *Apis cerana* colonies. *Mol Ecol* **16**, 1107-1114, doi:10.1111/j.1365-294X.2006.03207.x (2007).

34 Nanork, P., Paar, J., Chapman, N. C., Wongsiri, S. & Oldroyd, B. P. Entomology: Asian honeybees parasitize the future dead. *Nature* **437**, 829, doi:10.1038/437829a (2005).

35 Birmingham, A. L., Hoover, S. E., Winston, M. L. & Ydenberg, R. C. Drifting bumble bee (Hymenoptera: Apidae) workers in commercial greenhouses may be social parasites. *Can J Zool* **82**, 1843-1853, doi:10.1139/z04-181 (2004).

36 Birmingham, A. L. & Winston, M. L. Orientation and drifting behaviour of bumblebees (Hymenoptera: Apidae) in commercial tomato greenhouses. *Can J Zool* **82**, 52-59, doi:10.1139/z03-201 (2004).

37 Zanette, L. R. S., Miller, S. D. L., Faria, C. M. A., Lopez-Vaamonde, C. & Bourke, A. F. G. Bumble bee workers drift to conspecific nests at field scales. *Ecol Entomol* **39**, 347-354, doi:10.1111/een.12109 (2014).

38 Takahashi, J.-i., Martin, S. J., Ono, M. & Shimizu, I. Male production by non-natal workers in the bumblebee, *Bombus deuteronymus* (Hymenoptera: Apidae). *J Ethol* **28**, 61-66, doi:10.1007/s10164-009-0155-y (2009).

39 Oliveira, R. C., Oi, C. A., Vollet-Neto, A. & Wenseleers, T. Intraspecific worker parasitism in the common wasp, *Vespula vulgaris*. *Anim Behav* **113**, 79-85, doi:10.1016/j.anbehav.2015.12.025 (2016).

40 Van Oystaeyen, A. *et al.* Sneaky queens in *Melipona* bees selectively detect and infiltrate queenless colonies. *Anim Behav* **86**, 603-609, doi:10.1016/j.anbehav.2013.07.001 (2013).

41 Wenseleers, T., Alves, D. A., Francoy, T. M., Billen, J. & Imperatriz-Fonseca, V. L. Intraspecific queen parasitism in a highly eusocial bee. *Biol Lett* **7**, 173-176, doi:10.1098/rsbl.2010.0819 (2011).

42 Sommeijer, M. J., de Bruijn, L. L. & Meeuwsen, F. Reproductive behaviour of stingless bees: solitary gynes of *Melipona favosa* (Hymenoptera: Apidae, Meliponini) can penetrate existing nests. *Entomologische Berichten-Nederlandse Entomogische Vereenigung* **63**, 31-35 (2003).

43 de Figueiredo-Mecca, G., Bego, L. R. & do Nascimento, F. S. Foraging behavior of Scaptotrigona depilis (Hymenoptera, Apidae, Meliponini) and its relationship with temporal and abiotic factors. *Sociobiology* **60**, 267-282 (2013).

44 Giannini, T. C. *et al.* Unveiling the contribution of bee pollinators to Brazilian crops with implications for bee management. *Apidologie*, 1-16 (2020).

45 Slaa, E. J., Chaves, L. A. S., Malagodi-Braga, K. S. & Hofstede, F. E. Stingless bees in applied pollination: practice and perspectives. *Apidologie* **37**, 293-315 (2006).

46 Silva-Neto, C. d. M. e. *et al.* The stingless bee mandaçaia (*Melipona quadrifasciata* Lepeletier) increases the quality of greenhouse tomatoes. *J Apic Res* **58**, 9-15 (2019).

47 Hikawa, M. & Miyanaga, R. Effects of pollination by *Melipona quadrifasciata* (Hymenoptera: Apidae) on tomatoes in protected culture. *Appl Entomol Zool* **44**, 301-307 (2009).

48 Del Sarto, M. C. L., Peruquetti, R. C. & Campos, L. A. O. Evaluation of the neotropical stingless bee *Melipona quadrifasciata* (Hymenoptera: Apidae) as pollinator of greenhouse tomatoes. *J Econ Entomol* **98**, 260-266 (2005).

49 Bispo dos Santos, S. A., Roselino, A. C., Hrncir, M. & Bego, L. R. Pollination of tomatoes by the stingless bee *Melipona quadrifasciata* and the honey bee *Apis mellifera* (Hymenoptera, Apidae). *Gen Mol Res* **8**, 751 (2009).

50 Cruz, D. O., Freitas, B. M., Silva, L. A., Silva, E. M. S. & Bomfim, I. G. A. Pollination efficiency of the stingless bee *Melipona subnitida* on greenhouse sweet pepper. *Pesqu Agropecu Bras* **40**, 1197-1201 (2005).

51 Caro, A., Moo-Valle, H., Alfaro, R. & Javier, Q. E. Pollination services of Africanized honey bees and native *Melipona beecheii* to buzz-pollinated annatto (*Bixa orellana* L.) in the neotropics. *Agricultural and forest entomology* (2017).

52 Nunes-Silva, P. *et al.* Radiofrequency identification (RFID) reveals long-distance flight and homing abilities of the stingless bee *Melipona fasciculata*. *Apidologie*, 1-14 (2019).

53 Giannini, T. C. *et al.* Safeguarding Ecosystem Services: A Methodological Framework to Buffer the Joint Effect of Habitat Configuration and Climate Change. *PLoS One* **10**, e0129225, doi:10.1371/journal.pone.0129225 (2015).

54 Ramalho, M., Kleinert-Giovannini, A. & Imperatriz-Fonseca, V. L. Important bee plants for stingless bees (*Melipona* and Trigonini) and Africanized honeybees (*Apis mellifera*) in neotropical habitats: a review. *Apidologie* **21**, 469-488 (1990).

55 Ramalho, M. Stingless bees and mass flowering trees in the canopy of Atlantic Forest: a tight relationship. *Acta Botanica Brasilica* **18**, 37-47 (2004).

56 Nagamitsu, T., Momose, K., Inoue, T. & Roubik, D. W. Preference in flower visits and partitioning in pollen diets of stingless bees in an Asian tropical rain forest. *Researches on Population Ecology* **41**, 195-202 (1999).

57 Viana, B. F., Kleinert, A. d. M. P. & Imperatriz-Fonseca, V. L. Abundance and flower visits of bees in a cerrado of Bahia, Tropical Brazil. *Stud Neotrop Fauna Environ* **32**, 212-219 (1997).

58 Pedro, S. R. M. The Stingless Bee Fauna In Brazil (Hymenoptera: Apidae). *Sociobiology* **61**, 348-354 (2014).

59 Kuhn-Neto, B., Contrera, F. A., Castro, M. S. & Nieh, J. C. Long distance foraging and recruitment by a stingless bee, Melipona mandacaia. *Apidologie* **40**, 472-480 (2009).

60 Araujo, E. D., Costa, M., Chaud-Netto, J. & Fowler, H. G. Body size and flight distance in stingless bees (Hymenoptera: Meliponini): inference of flight range and possible ecological implications. *Braz J Biol* **64**, 563-568, doi:10.1590/s1519-69842004000400003 (2004).

61 Van Nieuwstadt, M. & Iraheta, C. R. Relation between size and foraging range in stingless bees (Apidae, Meliponinae). *Apidologie* **27**, 219-228 (1996).

62 Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes Gonçalves, J. L. & Sparovek, G. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* **22**, 711-728 (2013).

63 Endou, T., Ishizaka, Hironori, Oota, Masahiko, Tasaki, Kouji, Hosoi, Hiroyuki. RFID tag and automatic recognition system. United States patent (2014).

64 R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria, 2020).

65 Oliveira, R. C. (Mendeley Data, 2021).

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Author contributions

VLIF, FALC, RJ and had the original idea. FALC, HA, RJ, LC, GP and GCV performed the experiments. PS provided the RFID system for the experiments. RCO analysed the data and wrote the first draft of the manuscript. All authors revised and approved the final version of the manuscript.

Competing interests

We declare we have no competing interests.

Data availability

The original dataset as well as the R script used to analyse the data are publicly available Mendeley Data[65] (temporary link https://data.mendeley.com/datasets/k9s83b9g4z/draft?a=f3bfc7d6-e9e8-4084-9694-e959a31c0be3).

Figures

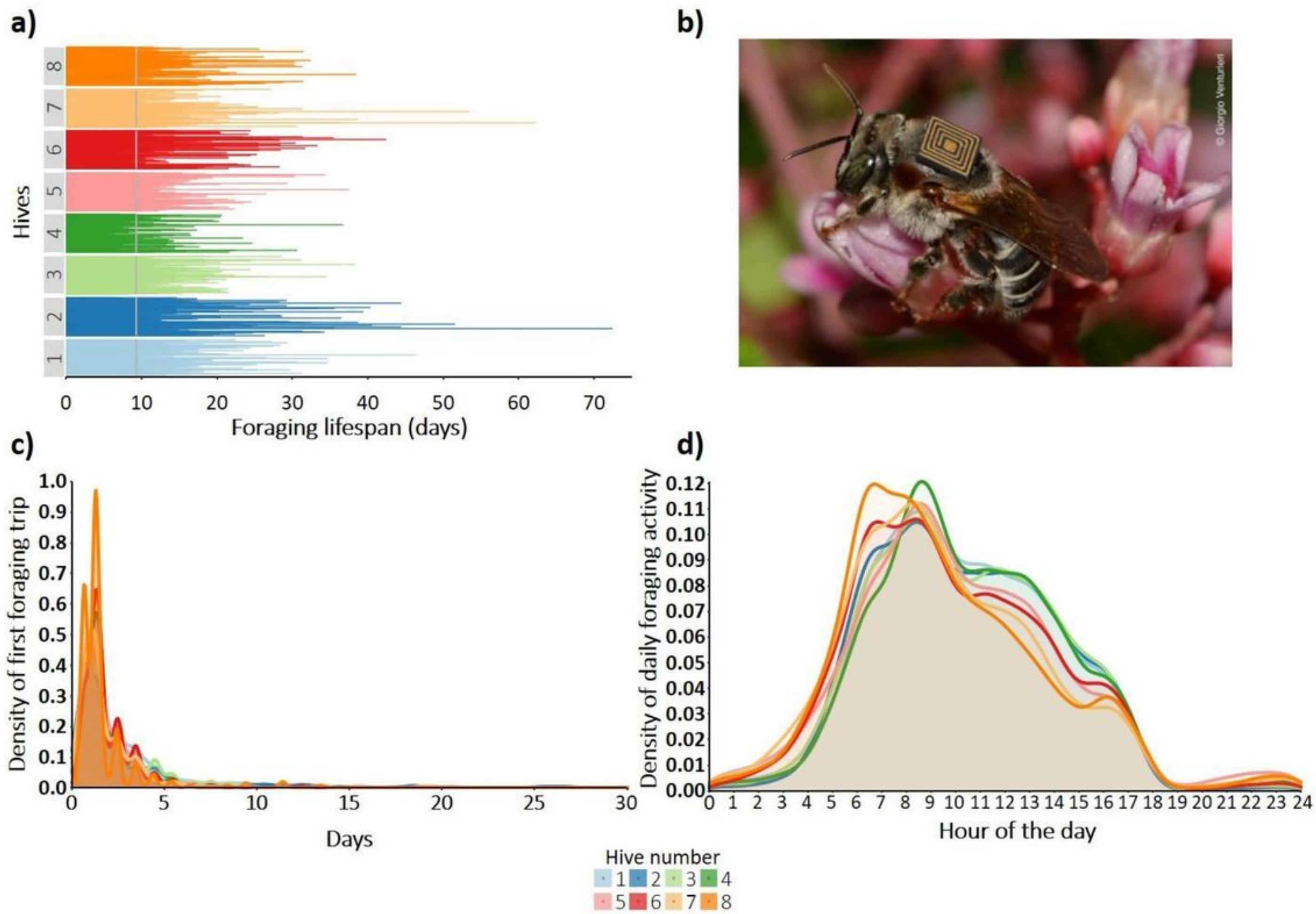

Figure 1

a) Worker bees' lifespan based on the difference between the last reading on the RFID system and the day they were tagged. Different colonies are plotted on the y axis with every row corresponding to an individual bee. The vertical grey line represents the mean lifespan of 9.3 days. b) Picture of a M. fasciculata forager with a RFID tag on her thorax. Photo by Giorgio Cristino Venturieri. c) Density plot of the bees' first foraging trip calculated as the difference between the tagging data and the first record on the reader. d) Density plot displaying the foragers activity throughout the day. Peak activity was recorded between 5:00 to 10:00 in all colonies.

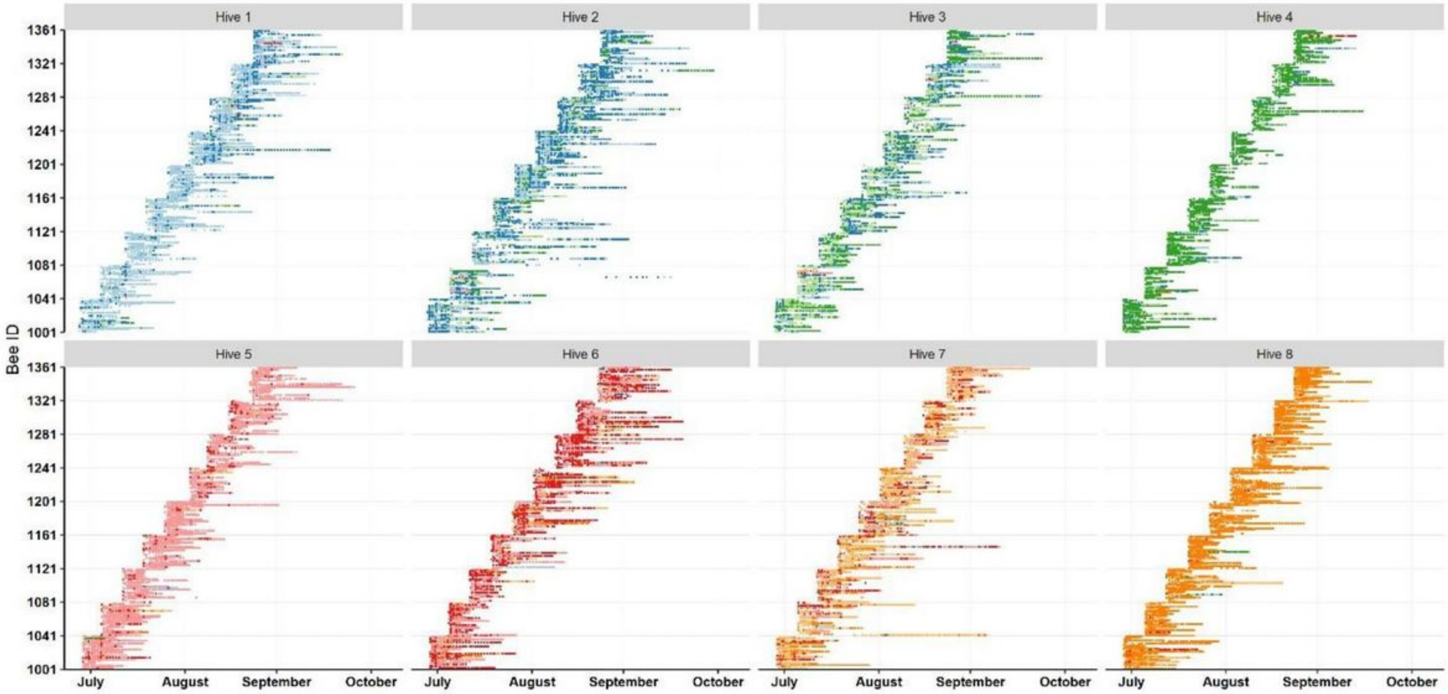

Figure 2

Foraging activity of all bees during experimental period. Each row represents the RFID scans of an individual bee, with the colours corresponding to their respective natal hives. In total 2880 bees were tagged in nine separate sessions demonstrated by the ladder-like appearance along the y axis. That is, at every session 40 tagged bees were introduced per colony.

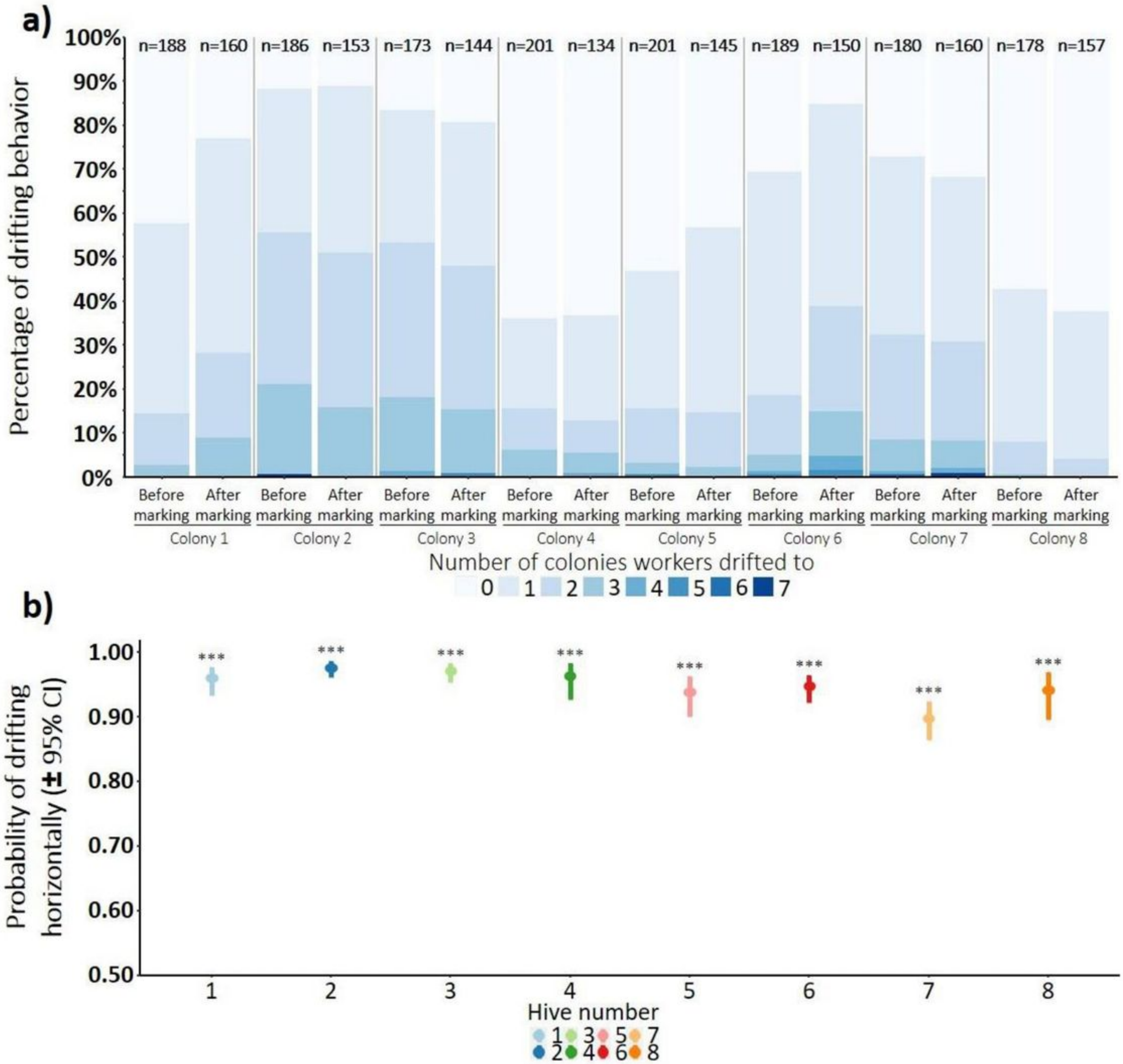

Figure 3

a) Percentages of drifting events to different foreign colonies during the experimental period before and after marking the colony entrances. Hives placed in the middle sections of the shelves presented higher rates of drifting behaviour with some drifters visiting all seven non-natal hives. n shows the number of tagged worker drifters per colony per period. b) Drifting events were most horizontal, with on average 96% of the drifting events being to colonies placed on the same shelf than the natal hives.

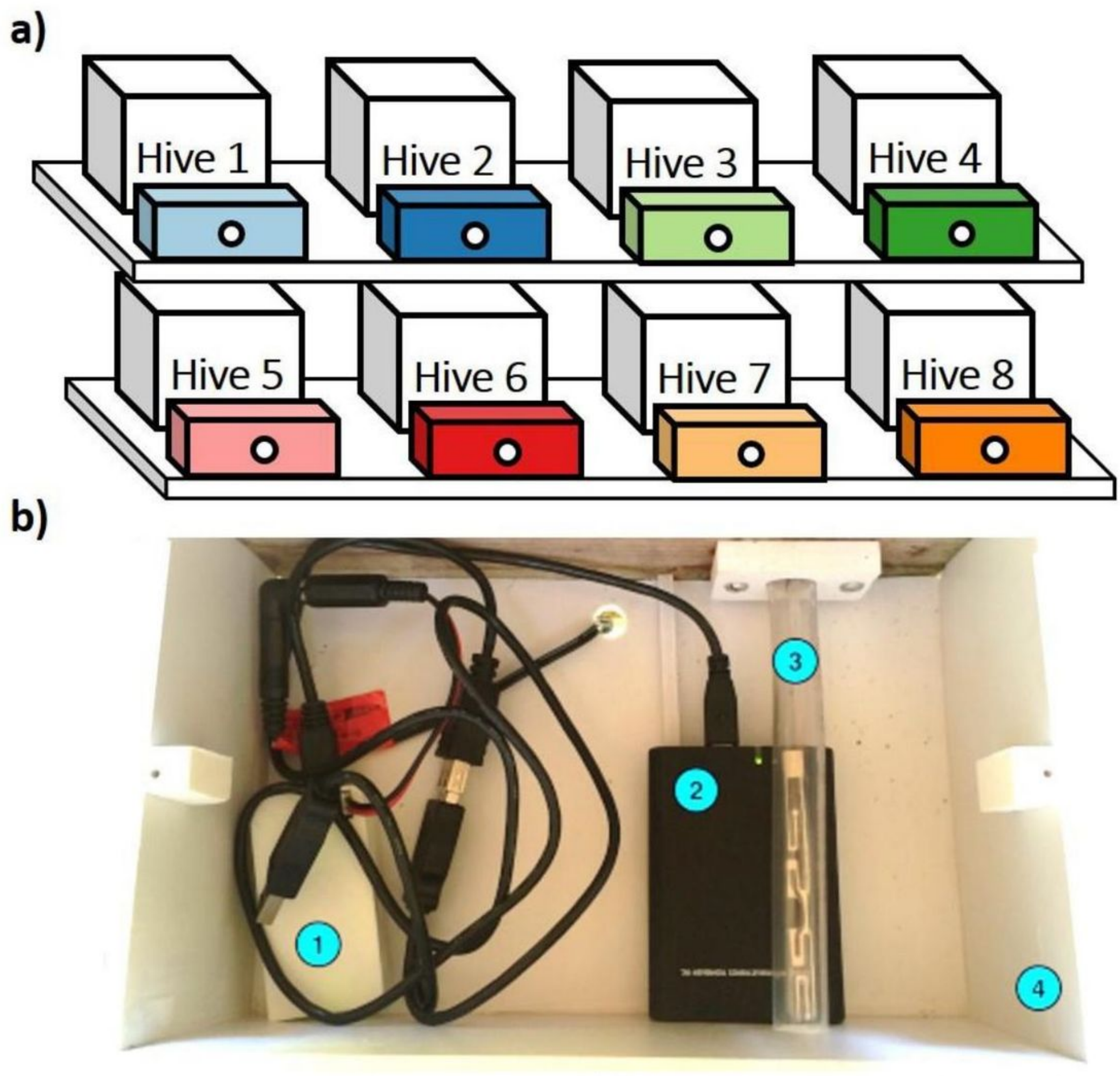

Figure 4

a) Experimental setup scheme not to scale with four hives placed in the top shelf and four in the bottom shelf. The RFID systems were placed in a plastic box at the hive entrances. b) Inside view of the entrance box containing the RFID system. 1. box containing the Intel Edison and Breakout Board; 2. RU-824 antenna; 3. tube connecting the hive to the entrance, and 4. protective plastic box.