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Semi-natural habitats mitigate the impact of food shortage on honey bees in farmlands

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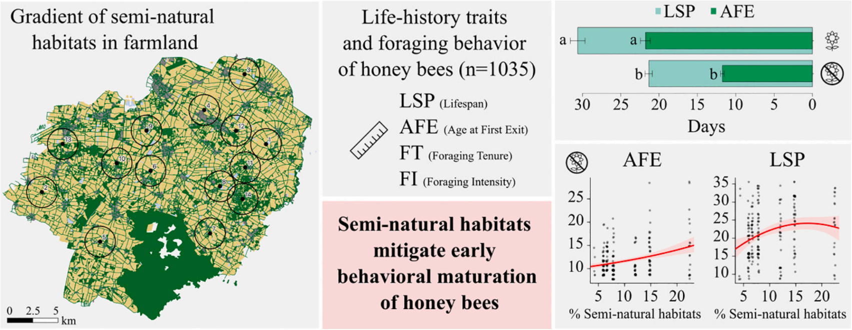
HIGHLIGHTS

- Simplified farmland landscapes lead to food shortages for pollinators.
- Food shortages accelerate behavioral maturation of honey bees.
- Food shortages reduce honey bee lifespan.
- A semi-natural habitat mitigates the impact of food shortages on honey bees.
- Maintaining semi-natural habitats in farmlands can support pollinator conservation.

GRAPHICAL ABSTRACT



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ABSTRACT

Landscape simplification and the loss of semi-natural habitats are identified as important drivers of insect pollinator decline in farmlands, by disrupting the availability of floral resources and facilitating the occurrence of food shortages. Food shortages can lead to accelerated behavioral maturation in honey bees, with potential consequences for colony survival. However, little is known about the magnitude of behavioral maturation mediated by to food shortage under real field conditions, and whether it could be mitigated by the presence of semi-natural habitats. Here, we monitored the lifespan (LSP), age at first exit (AFE), foraging tenure, and foraging intensity of 1035 honey bees along a landscape gradient of semi-natural habitats in farmlands. We found a clear acceleration of behavioral maturation of bees during the food shortage season, with precocity in AFE between 6 and 10 days earlier and reduced LSP by 5 to 9 days, with no effect on foraging tenure or foraging intensity. We also found that higher proportions of semi-natural habitats mitigated behavioral maturation of bees by up to 6 days. Beyond the direct effects on adult bees, we found no delayed effect of larval feeding status on

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adult life-history traits or foraging behavior. Nevertheless, our results strongly advocate the implementation of policies aimed at increasing the coverage of semi-natural environments (e.g., grasslands, forests, hedgerows) in intensive agricultural landscapes to support honey bee survival and pollinator conservation.

1. Introduction

The intensification of farming in Europe has simplified landscapes over the last century (Ridding et al., 2020), which has reduced farmland biodiversity and has been identified as an important driver of insect pollinator decline (Biesmeijer et al., 2006; Krebs et al., 1999; Parreño et al., 2022; Potts et al., 2010; Raven and Wagner, 2021; Robinson and Sutherland, 2002). Paradoxically, the decline of pollinators has led to pollination deficits and yield gaps and raising concerns about food security (Garibaldi et al., 2011; Potts et al., 2016), while 35 % of the world's volume of fruits and seeds produced directly for the human consumption come from pollinator-dependent crops (Klein et al., 2007). On the other hand, the use of managed pollinators, such as the Western honey bee *Apis mellifera*, to support crop pollination has increased (Aizen and Harder, 2009; Garibaldi et al., 2017). However, managed honey bee colonies have been experiencing significant mortalities for several decades in Europe and worldwide (Bruckner et al., 2023; Gray et al., 2019; Neumann and Carreck, 2010; Requier et al., 2020a).

Managed honey bee mortality is linked to a combination of factors, including pests and diseases, climate change and the agricultural intensification (Goulson et al., 2015; Potts et al., 2010). Landscape simplification is known to disrupt the spatio-temporal availability of floral resources, particularly due to the alternation of mass flowering seasons during crop blooming and food shortage seasons (Danner et al., 2017; Dolezal et al., 2019a; Requier et al., 2015; Timberlake et al., 2019). Such food shortages reduce pollen intakes and can lead to larval malnutrition, with carry over effects on population dynamics and colony survival (Requier et al., 2017). Indeed, larvae which suffered from food shortage are less likely to become adult foragers, start foraging earlier, and have reduced foraging tenure (the number of days as a forager) and lifespan (Perry et al., 2015; Scofield and Mattila, 2015). In addition to the effects of food shortage observed at colony level, some studies have shown negative effects on the physiology and behavior of individual bees (Di Pasquale et al., 2013; Wright et al., 2018).

Laboratory studies have shown that food shortage reduces the fat body mass and vitellogenin levels of individual honey bees (Alaux et al., 2010; Dolezal et al., 2019a). In addition, it has also been shown that a reduction of pollen availability may distribute the nursing capacity and the lifespan of honey bees (Di Pasquale et al., 2016). Honey bees are also able to adapt their foraging behavior during food shortage seasons by spending less time in the hive between flights and by increasing the frequency of foraging trips (Fewell and Winston, 1992). Furthermore, resource manipulation experiments have shown that food scarcity can lead to an accelerated maturation of foraging behavior (Schulz et al., 1998). Indeed, bee workers perform a division of labor in the colony, which is structured by temporal polyethism (Johnson, 2008; Robinson, 1992). Young bees (<20 days old) are dedicated to in-hive activities such as nest cleaning and nursing, while older bees perform flight activities outside the nest for guarding and foraging (Seeley, 1982).

This behavioral maturation is highly variable in individual life histories (Requier et al., 2020b; Smith et al., 2022) and depends on the colony's food needs (Janmaat and Winston, 2000; Ribbands, 1952). Although earlier behavioral maturation increases the number of foragers (Schulz et al., 2002, 1998), it also leads to a shorter lifespan of foragers (Janmaat and Winston, 2000; Smith et al., 2022), with potentially detrimental effects on colony survival (Perry et al., 2015). Unfortunately, knowledge on behavioral maturation is mostly limited to laboratory experiments or controlled environments. For example, the effect of landscape simplification on the life history of individual bees in real field conditions is not yet understood, especially considering the foraging range of honey bees (Steffan-Dewenter and Kuhn, 2003), whereas a hypothesis of intermediate habitat quality is emerging in agricultural areas, where a moderate semi-natural habitat maximizes bee biodiversity (Desaegher et al., 2023).

In this study, we monitored the life history of many honey bee individuals in an intensive agricultural area in western France, consisting of temporally and spatially fluctuating floral resources, using radio-frequency identification (RFID) (Streit et al., 2003). We measured key life history traits including lifespan (LSP), age at first exit (AFE, in days), foraging tenure (FT, i.e. days spent as foragers) and foraging intensity (FI, i.e. hours spent outside the hive) of honey bees across the temporal variation in mass flowering and food shortage seasons (Prado et al., 2020; Requier et al., 2020b). First, we tested whether honey bee workers could accelerate their behavioral maturation by advancing their AFE in response to food shortage seasons, with potential negative consequences on LSP. We also tested the potential positive effects of food shortage on foraging investment (FT and FI) to compensate for limited resource availability. Next, we considered a trade-off between AFE and FT, with shorter FT for the earliest and latest AFE. In terms of spatial variation, we tested whether the presence of semi-natural habitats (SNH) could mitigate the intensity of food shortage effects for honey bees in farmland and thus potentially buffer the associated behavioral maturation effects on bee life history traits. Finally, we tested whether food shortage and SNH experienced as larvae can influence adult bee life history traits and foraging investment.

2. Material and methods

2.1. Study area and study sites

The study was conducted in the Long Term Social-Ecological Research 'Zone Atelier Plaine & Val de Sèvre' (LTSER ZA-PVS; Fig. 1A) in western France (46°23′N, 0°41′W) from April to September 2012. It is an intensive agricultural study area of 435km^2, consisting mainly of wheat, sunflower, maize and oilseed rape crops under predominantly conventional farming practices (Bretagnolle et al., 2018). In this study area, honey bees massively collect pollen and nectar from oilseed rape and sunflowers, but suffer from food shortage in absence of mass-flowering crops and forage in SNH (Bretagnolle and Gaba, 2015; Requier et al., 2015). SNH consist of grasslands, woodlands and hedgerows and make up 34 % of the total study area (Fig. 1A). Previous palynological analyses of honey bee diet (pollen and nectar) in our study area indicated that the semi-natural vegetation mainly foraged by honey bees was composed of herbaceous species such as poppy (*Papaver rhoeas*), *Sinapis* sp., annual mercurial (*Mercurialis annua*), yellow mignonette (*Reseda lutea*), or clover (*Trifolium* sp.), and woody species like hawthorn (*Crataegus* sp.), chestnut (*Castanea sativa*), blackthorn (*Prunus* sp.), bramble (*Rubus* sp.) or maple (*Acer* sp.) (Requier et al., 2015). We selected 14 sites along a gradient of SNH, ranging from 3.4 % to 28.2 % within a radius of 1.5 km around hives (the average foraging range of honey bees in farmland (Steffan-Dewenter and Kuhn, 2003; Fig. 1B). We categorized these proportions into three groups to ensure that roughly one-third of the monitored workers lived in each landscape type (low SNH < 6 %; medium 6 % to 12 %; high >12 %). It is noteworthy that although the proportion of urban habitat was calculated, it was excluded from the analyses due to its low variability between sites (an average of 8,9 % ± 1,4 % of urban area around the sites).

2.2. Monitoring honey bees

A total of 14 hives (Dadant-Blatt 5-frames type) of *A. mellifera mellifera* × *caucasica* (sister colonies from the INRAE Le Magneraud apiary, located 30 km west of the study area; 46°09′N, 0°41′W) were placed in the center of each study site in March 2012 (Fig. 1A). Due to logistic constraints, in each period, half of the colonies (i.e. seven colonies) were equipped with RFID (radio-frequency identification) devices to monitor tagged honey bee workers (mic3®-TAG 64-bit RO, iID2000, 13.56 MHz system, 1.0 mm × 1.6 mm × 0.5 mm; Microsensys GmbH). Note that, the colonies were not moved or changed between periods, only the RFID readers were alternated between sites. Each RFID tag had a unique identification number and weighed approximately 3 mg, or about 3 % of the honey bee worker's body mass. Considering that the jabot of bees (i.e., the stomach) can contain up to 70 mg of nectar (Ribbands, 1953), the tag is not expected to interfere with the life history of the honey bee (Streit et al., 2003). The entry and exit activities of each tagged bee were automatically registered by two continuous adjacent rows of RFID readers (iID2000, 2 k6 HEAD; Microsensys GmbH) placed at the entrance of the 14 hives. The readers recorded the identity, date and time (1 s accuracy) of each passage of a tagged bee within a range of 3 mm (Streit et al., 2003). We distinguished the entry and exit of bees by translating the collected hits to infer the directionality of events between the inner and outer rows of readers (Requier et al., 2020b). The full description of the device and the computational technique can be found in the method of Requier et al. (2020b).

We collected one frame of capped brood from the hive the day before bee marking. This frame was kept in the incubator overnight at 34–35 °C without adult bees. Each newly emerged bee collected the following day was fitted with an RFID tag. The tags were glued to their upper thorax with a biocompatible dental cement (TempoSIL®2; Coltène/Whaledent sarl) without anesthetic. Four successive cohorts were tagged in April, May, June and July. Care was taken to homogenize the number of bees tagged between months (i.e., the period variable), with 150 to 300 1-day emerged bees tagged per cohort (Supporting information, Table S1). Once the entire cohort was marked, bees were grouped in a candy-coated queen introduction cage and transported to the experimental hives (cages were maintained at 34–35 °C during transport). In total, 2300 honey bees were marked (Table S1).

2.3. Individual life-history traits and foraging investment

We extracted honey bee life-history traits and foraging behavior from the hits recorded by the RFID reader at the hive entrance, after cleaning the raw dataset using the method of Requier et al. (2020b). Life span (LSP) was measured in days until the last recorded RFID hit for each bee. For the other traits, measurements were calculated after removing bee forays shorter than 4 s and forays longer than 2 h. The age of first exit (AFE) of bees was defined in days up to the first recorded RFID hit (i.e., first exit activity). We then calculated foraging tenure (FT) as the time from AFE to LSP. Finally, we measured foraging intensity (FI) as the sum of the time of all their flights (Prado et al., 2020). For our study we focused on bees whose AFE could be calculated, i.e. bees that made at least one flight trip. In total, 1035 adult bees were included in the analysis (Table S1).

2.4. Effect of larval nutrition on adult bees

In order to assess the possible impact of malnutrition during the larval stage on the life-history of the adult bees, the tagged bees could originate either from the colony itself (hereafter referred to as in situ colony/individuals) or from colonies of the INRAE Le Magneraud apiary where the colonies are fed ad libitum (hereafter referred to as control colony/individuals). Indeed, their diet is supplemented with syrup throughout the summer to ensure a constant supply of carbohydrates. In addition, flower strips (about one hectare in total) are planted around the hives each year to limit the pollen shortage. The INRAE Le Magneraud apiary is located 30 km west of the study area and presents a similar climate and agricultural landscape. The area around the apiary is dominated by crops (58 % in a radius of 1.7 km), including mainly maize, sunflower and oilseed rape, and a high proportion of SNH (26 %) (Odoux et al., 2012). During the tagging sessions, the emerging adults

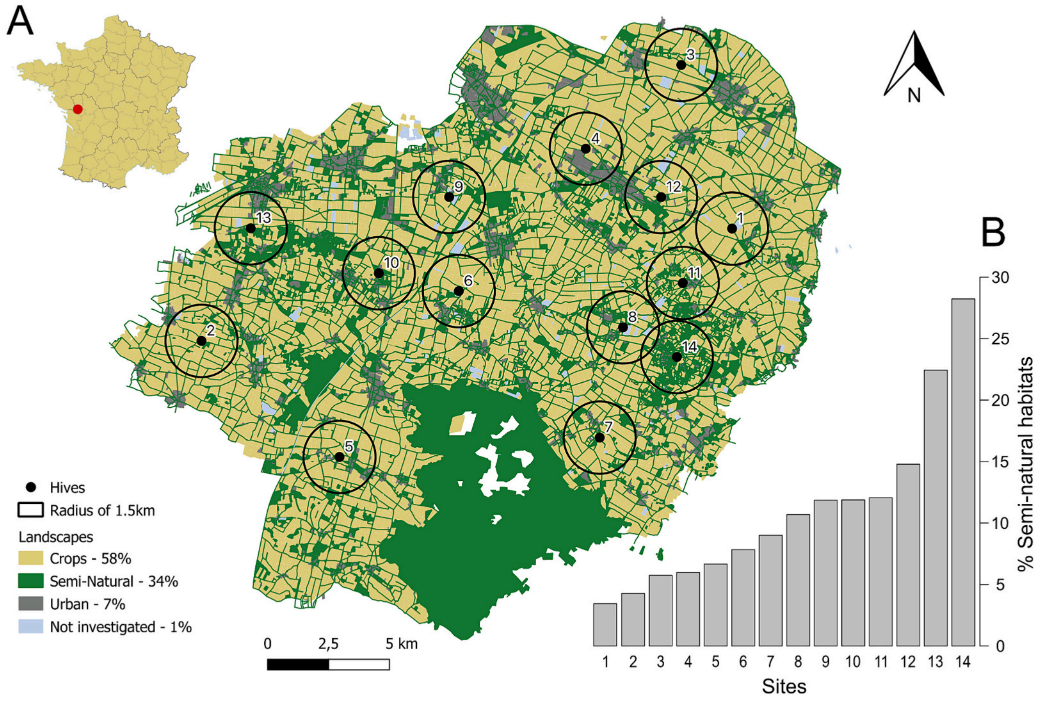

Fig. 1. Location of the study area and study sites along a gradient of semi-natural habitats. (A) The study area is located in the Long Term Social-Ecological Research 'Zone Atelier Plaine & Val de Sèvre' (LTSER ZA-PVS). (B) We placed 14 RFID-equipped hives along a gradient of semi-natural habitats (% of semi-natural habitats within a radius of 1.5 km around each colony).

from both colonies were tagged separately to determine their colony of origin (Table S1). All tagged worker bees were then collected in the same candy-coated queen introduction cage and introduced to the original experimental colony.

2.5. *Data analysis*

All statistical analyses were performed using the *R* software version 4.2.2 (R Core Team, 2023). The statistical unit used in the analysis is the individual honey bee. Bees from the same colony are pseudo-replicates, but all colonies are independent in terms of landscape, as we had one hive per study site.

2.5.1. *Effects of temporal fluctuation in flower resources*

The effects of the temporal fluctuation in mass-flowering (oilseed rape in April and sunflowers in July) and food shortage (in May and June) seasons (i.e., the period effect) on life history traits (AFE and LSP) and foraging investment traits (FT and FI) were assessed using Kruskal-Wallis tests (non-parametric test due to a non-homogeneity of variances). Pairwise comparisons between periods were performed using the Wilcoxon test with Bonferroni adjustment, and the corresponding graphs were plotted using the *pyramid.plot* function from the *plotrix* R package (Lemon, 2006).

2.5.2. *Links among life-history traits and foraging investment*

We examined the relationship between our life-history traits and foraging investment traits with the proportion of semi-natural habitat (SNH) as a covariate. We considered both linear and quadratic effects of the proportion of SNH in the models, based on previous evidence of a linear effect on honey bee colony survival (Smart et al., 2016) and on the effect of intermediate quality habitat on bee biodiversity in farmland (Desaegher et al., 2023). We used the Akaike Information Criterion to find the best compromise between model fit and complexity and to select the best model (i.e. the most parsimonious model with the smallest Akaike Information Criterion). We ran a linear model (LM) to test the relationship between LSP and AFE, three generalized linear models with gamma error distribution (GLM) to test the relationship between foraging investment traits (FT and FI), the quadratic relationship between FT and AFE, and between FI and AFE.

2.5.3. *Mitigation of temporal resource fluctuation through semi-natural habitats*

The mitigating effect of SNH during the food shortage on our response variables was tested. As seen in the Kruskal-Wallis test, we had an effect of the introduction period for most of our variables. To examine the effect of the food shortage (May and June vs. April and July), we split the dataset in terms of introduction period before running the models. For life-history traits, we considered both the linear and quadratic effect of SNH and selected the best model using Akaike Information Criterion criteria. For each period separately, we ran an LM to test the relationship between LSP and SNH, and three gamma GLMs to test the relationship of AFE, FT and FI with SNH.

2.5.4. *Effect of larval nutrition on adult bees*

To investigate the effect of larval food shortage on adult life history traits and foraging activities, we performed our analyses in two steps. First, we performed a LM to test the relationship between larval condition (i.e., the effect of colony of origin) and LSP, and three GLMs to test the relationship of colony of origin with AFE, FT and FI. In each model, we used the introduction period as a covariate, as we expected a one-month delay effect of larval feeding status on adult bees. In addition, as in previous analyses, we considered the linear or quadratic effect of SNH as a covariate and selected the best model using Akaike Information Criterion criteria. We then calculated the predictive values from these models for each colony of origin and introduction period. Finally, we calculated the differences between the predictive values of each colony of origin ($\Delta = \text{predict}_{\text{control colony}} - \text{predict}_{\text{in-situ colony}}$) as a function of the proportion of SNH and the introduction period.

The significant effects of the models were assessed using the anova function from the *car* R package (Fox and Weisberg, 2019). The confidence intervals of the model predictions were calculated using the *add_ci* function from the *ciTools* R package (Haman and Avery, 2020). The significance level for the statistical tests was set at 5 % for the probability of rejecting the true null hypothesis.

3. Results

3.1. *Effects of temporal fluctuation in flower resources*

We found a significant effect of the temporal fluctuation of the flower resource (period effect) on LSP (Kruskal-Wallis test, chi-squared = 76.792, $p < 0.001$; Fig. 2A), with shorter LSP during the food shortage season (May and June) compared to the oilseed rape flowering season in April (Wilcoxon test, $p < 0.001$ in May, $p < 0.001$ in June) and between the food shortage season in May and the sunflower flowering season in July ($p < 0.001$). We found no difference in LSP between June and July. We observed similar effects of temporal variation in flower resources on AFE (Kruskal-Wallis test, chi-squared = 170.901, $p < 0.001$; Fig. 2A). We observed a significant effect of temporal fluctuation of flower resource (period effects) on FI (Kruskal-Wallis test, chi-squared = 52.591, $p < 0.001$; Fig. 2B). Honey bees spent significantly less time outside the hive in April compared to the other periods (Wilcoxon test, $p < 0.001$, Fig. 2B). Although FI did not differ between May, June and July (Wilcoxon test, $p = 0.293$), our results showed a significantly longer time spent by individuals introduced in July compared to those introduced in June (Wilcoxon test, $p = 0.011$). We found no effect of temporal fluctuation in flower resources on FT (Wilcoxon test, chi-squared = 3.194, $p = 0.363$; Fig. 2B).

3.2. *Links among life-history traits and foraging investment*

We found a positive linear relationship between LSP and AFE. In addition, SNH had a quadratic effect on this relationship (LM, $F_{3,1031} = 215.153$, $p_{AFE} < 0.001$, $p^2_{SNH} < 0.001$, Supporting information, Fig. S1A). More specifically, SNH increased the LSP of bees at a given AFE, up to an age of first exit of 24 days, which accounted for approximately 92.65 % of our dataset. We also found a positive linear relationship between the two foraging investment traits, with significant effect of SNH (GLM, $F_{2,1032} = 183.178$, $p_{FT} < 0.001$, $p_{SNH} = 0.011$; Fig. 2C). SNH reduced FI for a given FT. Finally, we found a non-linear (quadratic) relationship between AFE and FT with a significant effect of SNH (GLM, $F_{4,1030} = 14.157$, $p^2_{AFE} < 0.001$, $p^2_{SN} < 0.001$; Fig. 2D). FT increased with AFE until 14 days and then decreased, and SNH reinforced this pattern. Specifically, in an environment with a low proportion of SNH, the highest predicted FT was 9.69 days for an AFE of 14.17 days, compared to a FT of 11.59 days for an AFE of 13.29 days in an environment with high proportion of SNH. A similar non-linear relationship was found between FI and AFE, which was also strengthened by SNH (GLM, $F_{3,1031} = 7.610$, $p^2_{AFE} < 0.001$, $p_{SN} < 0.01$; Fig. S1B).

3.3. *Mitigation of temporal resource fluctuation through semi-natural habitats*

The proportion of SNH affected the core life-history traits, but not systematically across periods (Fig. S2). We found SNH effects on all the core life-history traits during the food shortage season (May and June). However, we found no effect of SNH on AFE (Fig. S2A), LSP (Fig. S2E) and FI (Fig. S2M) during the oilseed rape flowering season (April), contrarily to FT (Fig. S2I). During the first food shortage season (May), SNH delayed AFE (GLM, $F_{1,233} = 25.337$, $p_{SN} < 0.001$; Fig. 3A) and LSP to a maximum of 17.2 % of SNH (LM, $F_{2,232} = 7.715$, $p^2_{SN} < 0.001$; Fig. 3B). SNH also quadratically affected FT (GLM, $F_{2,232} = 4.448$, p^2_{SNH}

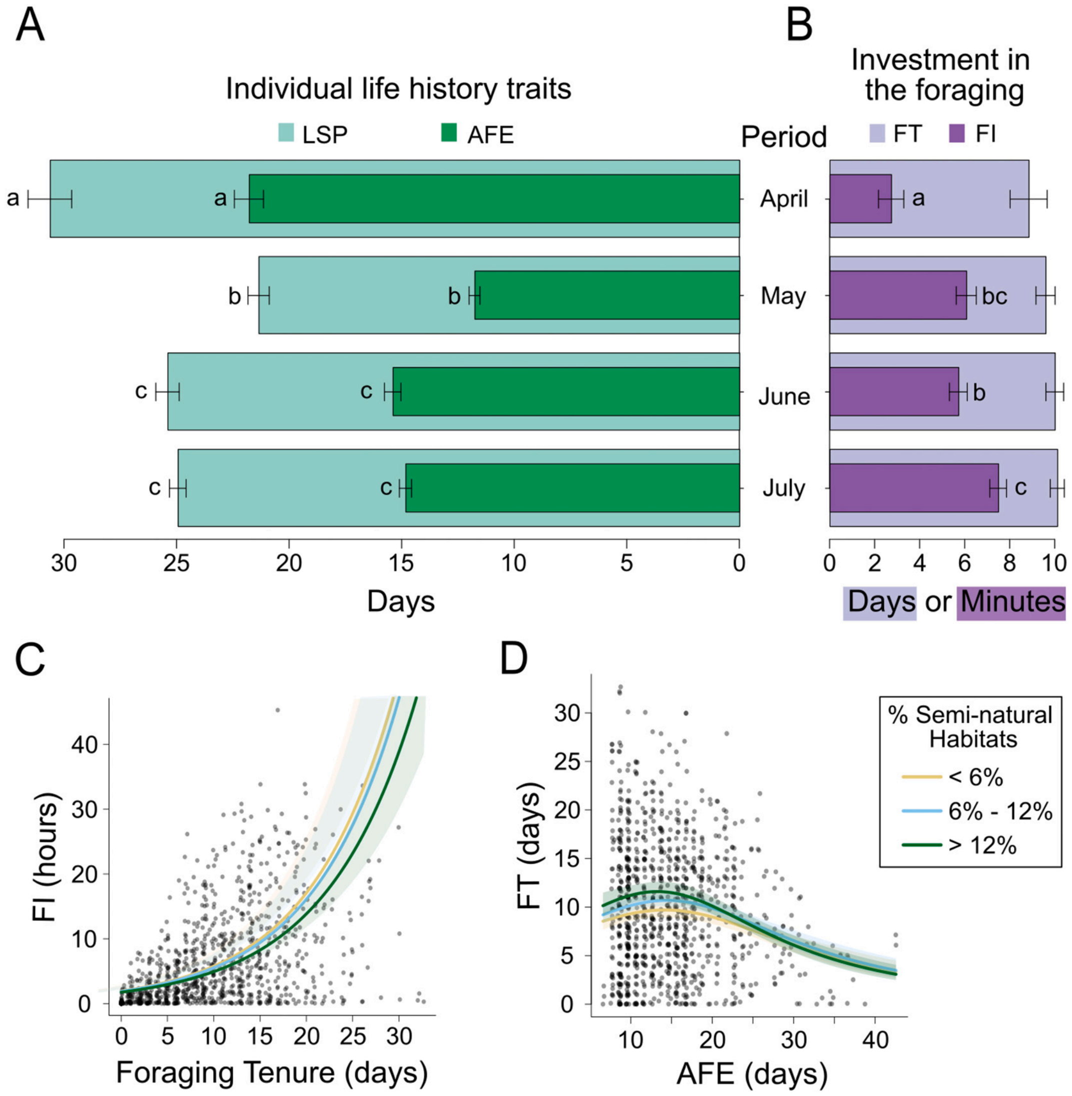

Fig. 2. Relationships between life history traits, foraging investments and their response to temporal fluctuation in resource availability. Effect of period introduction on (A) LSP and AFE, and (B) FT and FI of individual honey bees. The green colors represent individual life history traits (LSP in light green and AFE in dark green) and the purple colors represent foraging investment (FT in light purple and FI in dark purple). The letters show a significant difference between each period at a 5 % risk. The linear relationship between FI and FT (C) and the quadratic relationship between FT and AFE (D). The colored lines correspond to the prediction of the GLM with its 95 % confidence interval for each category of semi-natural habitat (less than % in yellow, between 6 % and 11.86 % in blue, >11.87 % in green).

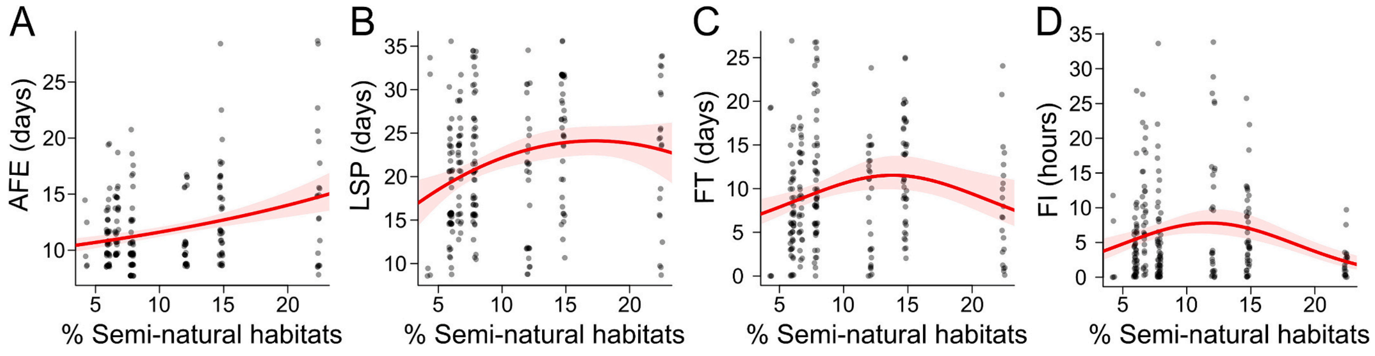

Fig. 3. Effects of the proportion of semi-natural habitats on the life history traits and foraging behavior of individual honey bees introduced during a food shortage season. AFE (A), LSP (B), FT (C) and FI (D) of individual honey bee workers introduced in May as a function of the proportion of semi-natural habitats around the hive. The red straight line with shading represents the trend curve with the 95 % confidence interval obtained with a model (i.e. an LM for LSP and a GLM for AFE, FT and FI) when the effect of semi-natural habitat is significant. We tested a linear relationship for AFE and a quadratic relationship for LSP, FT and FI.

< 0.05, max. at 13.8 % SNH; Fig. 3C) and FI (GLM, $F_{2,232} = 8.878$, $p^{2}_{SNH} < 0.001$, max. at 11.7 % SNH; Fig. 3D). Very similar effects of SNH on all the core life-history traits were found for the second food shortage season (in June; Fig. S2C, F). Then, SNH had less effect during sunflower flowering (in July), with a significant positive effect on AFE (Fig. S2D), but not on LSP (Fig. S2H), and negative effects on foraging investment (Fig. S2I, K).

3.4. *Effect of larval nutrition on adult bees*

Based on the difference between the predicted values, we found that the AFE of bees originated from the in-situ colonies was delayed by one to five days compared to the individuals of bees originated from the control colonies, depending on period and SNH (GLM, $F_{6,1028} = 44.868$, $p_{colony\ of\ origin} < 0.001$, $p_{period} < 0.001$, $p^{2}_{SNH} < 0.001$; Fig. 4A). This difference is most pronounced at intermediate SNH values and in April, when neither the bees nor larvae experienced food shortage. However, this maximum difference was reduced to 1.29 days when the adult bees experienced a food shortage in May. When the larvae experienced food shortage and emerged as adults in June and July, the AFE of bees from the in-situ colonies was delayed by 2–2.5 days compared to the bees from the control colonies at intermediate SNH levels. We also observed that the LSP of individuals from in-situ colonies was 4.05 days longer than that of bees from control colonies. This difference remained consistent across all SNH values and periods, although their effects on LSP were also significant (LM, $F_{6,1028} = 35.169$, $p_{colony\ of\ origin} < 0.001$, $p_{period} < 0.001$, $p^{2}_{SN} < 0.001$; Fig. 4B). Furthermore, our results also showed that bees from in-situ colonies foraged for an additional 1–2.5 days longer than bees originated from the control colonies, depending on SNH but not on the period (GLM, $F_{6,1028} = 7.727$, $p_{colony\ of\ origin} < 0.001$, $p_{period} = 0.319$, $p^{2}_{SNH} < 0.001$; Fig. 4C). The most pronounced difference was observed at intermediate SNH values, specifically when SNH reached 12.84 %. We did not find any effect of the colony origin or SNH on FI, but the previously identified effect of time period remained visible. (GLM, $F_{6,1028} = 9.156$, $p_{colony\ of\ origin} = 0.684$, $p_{period} < 0.001$, $p_{SNH} = 0.078$; Fig. 4D).

4. Discussion

Landscape simplification has led to a reduction of semi-natural habitats (SNH) in farmlands and to an important temporal fluctuation in the availability of floral resources with the occurrence of food shortage seasons for bees (Danner et al., 2017; Dolezal et al., 2019b; Requier et al., 2015; Timberlake et al., 2019). In this study, we found that bees had an earlier age at first exit (AFE) and a shorter lifespan (LSP) during food shortage season, while investment in foraging activities (FI and FT) remained stable. This may indicate an acceleration of behavioral maturation of honey bee workers in response to food shortage, and support previous experimental studies based on resource manipulation, by limiting the pollen gathering (Janmaat and Winston, 2000) or by exchanging a frame of honey for an empty one (Schulz et al., 1998). In addition, we observed a trade-off between the age of behavioral maturation (here AFE) and foraging duration, independently of the period. Workers with early or late behavioral maturation have a shorter foraging lifetime. However, for bees with the same pattern of behavioral maturation, an increase in the proportion of semi-natural habitats is associated with an increase in foraging tenure and worker lifespan. The presence of SNH also appears to buffer the effect of food shortage on the behavioral maturation of workers by delaying their age of first exit and increasing their lifespan, supporting previous studies at the colony level (Requier et al., 2015; Smart et al., 2016). Finally, in contrast to previous work, we did not observe a delay effect on adult performance in honey bees suffering from food shortage as larvae (Perry et al., 2015; Scofield and Mattila, 2015).

Our study suggests that food shortage seasons accelerate behavioral maturation and reduce the lifespan of honey bees. A possible explanation could be that honey bees become foragers earlier to meet the needs of the colony during food shortages, occasionally increasing the size of the forager population (Schulz et al., 1998). At the cost of a shorter lifespan, this early age of first foraging can be seen as a self-sacrifice that provides a benefit at the community level but is detrimental to the individual. While this strategy may pay off in the short term when foraging conditions deteriorate, it may also threaten colony survival if food shortages persist, possibly leading to colony collapse (Perry et al., 2015). Furthermore, our study confirms a positive correlation between the age of behavioral maturity and lifespan (Prado et al., 2020), but also suggests an influence of the habitat quality. Indeed, for the same age of behavioral maturity, honey bees live longer in environments with a higher proportion of SNH, which is consistent with previous findings on the colony survival (Smart et al., 2016).

Our results support that SNH, as a quality habitat, mitigates the effects of food shortage by allowing longer lifespan and late behavioral maturation in environments with a high proportion of semi-natural habitats. Although studies have highlighted the importance of semi-natural habitats for honey bee colonies (Requier et al., 2015) and bee health (Alaux et al., 2017; Dolezal et al., 2019b; Smart et al., 2016), to

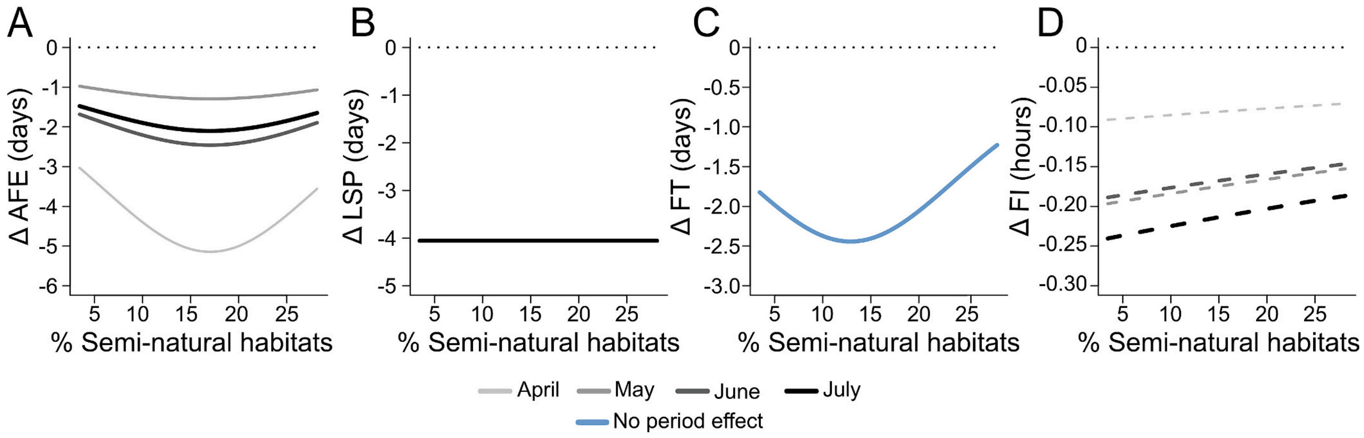

Fig. 4. Delayed effect of food shortage on life history traits and foraging behavior of honey bees. The difference between the predicted values of AFE (A), LSP (B), FT (C), FI (D) of bees that completed their larval stage in the control colony and those in the experimental colonies. The grey gradient refers to the period of introduction when it had a significant effect (from April in light grey to July in black), otherwise the line is in blue. The dashed lines show a non-significant effect of the amount of semi-natural habitat. The dotted line represents zero difference between the predicted value of the two colony origins. When the difference is negative, the control individuals have a lower value of their life history traits compared to the in situ individuals.

our knowledge this is the first evidence of semi-natural habitat effects on worker life history traits during food shortage seasons. While our study included a large number of bees and study sites, our results would benefit from validation by replication in other study areas, wider farming practices or different crops.

In contrast to previous work that found a negative linear correlation (Rueppell et al., 2007), our results highlighted a trade-off between behavioral maturation and foraging tenure with the longest lifespan as forager for an AFE of 14 days. We suggest that this trade-off is related to the physiological state of honey bee workers. On the one hand an incomplete physiological maturation of the needed to the transition to foraging activities such as reduction of body weight (Amdam and Omholt, 2002) and increasing flight capacity (Vance et al., 2009) may reduce the workers lifespan. On the other hand, honey bees with late behavioral maturation could theoretically have their foraging life limited by the ageing process. Note that the increase in foraging time observed with increasing proportion of SNH may be the consequence of a longer total lifespan in these habitats. However, considering that, to our knowledge, this is the first time that a trade-off between behavioral maturity and foraging tenure has been described, further research may be required to validate and understand the mechanisms.

Interestingly, we did not find a general pattern of impact of the food shortage season on foraging intensity compare to the mass-flowering season, contrary to expectations derived from laboratory work (Fewell and Winston, 1992). This difference may be explained by the variables analyzed in the study by Fewell and Winston (1992), which found a strong effect on the amount of pollen brought back to the colony per bee, as a measure of foraging intensity. In addition, Fewell and Winston (1992) found that colonies with low pollen storage collected less nitrogen-rich pollen and speculated that honeybee workers collected pollen from plants that provided ample amounts of pollen rather than selecting a higher nitrogen-rich pollen. The combination of automatic video monitoring (Rodriguez et al., 2022) and pollen analysis could confirm our results on the time spend outside of the hive and those of Fewell and Winston (1992) on the quality and quantity of pollen collected. Moreover, the observed increase in foraging intensity after April is more likely due to higher temperatures and longer daylight hours than to food shortage, since honeybee activity is mainly influenced by meteorological elements (Burrill and Dietz, 1981).

Given the limited available research on foragers' lifespan, and given the findings on foraging intensity, we expected to see an increase in foraging tenure in response to food shortages. However, we did not find such a difference between periods, despite earlier behavioral maturation and shorter lifespan during food shortages. Previous work suggests that the main driver of age polyethism is the combination of workers' expected lifespans (in relation to their health status) and the extrinsic mortality associated with the tasks (Woyciechowski and Moroń, 2009). Translated to our study, workers with the shortest expected lifespan (due to the impact of food shortage on colony resource storage) would have earlier behavioral maturation, and would move earlier to risker outdoor tasks such as foraging (Rueppell et al., 2007). Our results suggest that the foragers' lifespan is similar regardless of resource availability, despite earlier behavioral maturation and shorter total lifespan, tend to support Woyciechowski and Moroń's (2009) hypothesis. To further investigate the latter hypothesis, it would be interesting to test whether foraging tenure is stable under any circumstances (i.e. health status, resource availability, climate, etc.) and to investigate the possibility that foraging lifespan is a conservative trait in *Apis mellifera*.

Our study also failed to detect any effect of larval food shortage on the life history traits or foraging behavior of the bees. Although there were significant differences in behavioral maturation between control and in situ colonies, as well as variations across periods, we were unable to attribute these differences to food availability at the larval stage, due to the lack of a clear pattern linking the food shortage at the larval stage to adult performance. Instead, the results drew attention to two important points that warrant further investigation. First, regardless of resource availability or the environment surrounding the hive, honey bee workers from control colonies exhibited earlier behavioral maturation, shorter total and foragers' lifespans. Second, although the control colonies had shorter foragers' lifespan, they did not have lower foraging intensities, indicating that they spent proportionately more time outside the hive. Previous studies have shown that genetic strain can, to some extent, shape the behavioral maturation of honey bee workers (Calderone and Page, 1988; Kolmes et al., 1989). In our study, although all queens were sisters, the genetic variability remains as their mating was not controlled. An alternative hypothesis could be that honey bee workers from the control colony face kin discrimination in their adoptive colonies, which may reduce their social interactions and accelerates their behavioral maturation. Indeed, previous work has shown that the age at which foraging starts can be delayed by trophallaxis (Leoncini et al., 2004a, 2004b). On the other hand, some studies suggested that kinship may influence social interactions, with honey bees tending to be more involved in foraging interactions with their more related workers (Breed et al., 1985; Moritz and Hillesheim, 1990). However, our results and interpretations must be treated with caution and should be reinforced by a larger number of control sites.

Overall, our study shows that food shortage in agricultural areas is associated with accelerated behavioral maturation of honey bees, which can lead to colony collapse (Perry et al., 2015). However, this effect can be mitigated by the presence of SNH. Given the current decline of pollinators and the potential risk of food insecurity for humans (Potts et al., 2016), we strongly advocate the implementation of policies aimed at increasing the coverage of semi-natural environments within farmland to reduce honey bee mortality. Bee-friendly management practices such as planting hedgerows (Kremen and M'Gonigle, 2015; Ricketts et al., 2008), establishing flowering or non-flowering meadows (Ricketts et al., 2008; Smith et al., 2016) or designating fallow land (Carvell et al., 2007; Steffan-Dewenter and Tscharntke, 2001) can restore semi-natural habitats and protect pollinators (Ortego et al., 2024; Requier and Leonhardt, 2020). Although these actions have been encouraged since the 1990s by the Common Agricultural Policy through the Agri-Environment Schemes program, which seems to be paying off for pollinators (Albrecht et al., 2007; Scheper et al., 2013) despite debated results on the overall biodiversity (Kleijn and Sutherland, 2003), the new CAP (2023–2027) has gone further by conditioning the payment on the dedication of at least 3 % of arable land to those non-productive areas and features (EC, 2022). These directives can also be supplemented with more local fundings, such as the French government's program to plant 50,000 km of hedges by 2030 (French Ministry of Agriculture, 2023). Nevertheless, as the farmers are adjusting their practices with the political, social and economic contexts, policies are not enough and an individual support for farmers from advisors is needed to facilitate the transition to a more sustainable agriculture (Chantre and Cardona, 2014).

5. Conclusion

The results of our study suggest that honey bees accelerate their behavioral maturation due to the presence of food shortage seasons in intensive agricultural landscapes, leading to a reduction in their lifespan. Furthermore, we showed that semi-natural habitats mitigate the effects of food shortage on honey bees by reducing behavioral maturation of bees. These results, obtained under real field conditions, suggest that maintaining semi-natural habitats in farmlands can support honey bee survival and pollinator conservation. Therefore, we advocate the implementation of policies aimed at increasing the coverage of semi-natural environments in intensive agricultural landscapes to support pollinator conservation.

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CRediT authorship contribution statement

Elise Verrier: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation. **Vincent Bretagnolle:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **Pierrick Aupinel:** Writing – review & editing. **Axel Decourtye:** Writing – review & editing. **Mickaël Henry:** Writing – review & editing. **François Rebaudo:** Writing – review & editing, Visualization. **Fabrice Requier:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no competing interest.

Data availability

Data are openly available through the figshare repository (Requier et al., 2024); https://doi.org/10.6084/M9.FIGSHARE.24936831.V1.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175309.

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