Estimates of nectar productivity through a simulation approach differ from the nectar produced in 24 h

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(Article begins on next page)

ABSTRACT

1. Nectar is a key resource for numerous insects. Despite its importance, nectar productivity has mainly been assessed using one sampling method, in which the volume of nectar produced by a flower is measured after 24 h of isolation from insects (‘measured 24 h volume’ hereafter). This method assumes that nectar removal by flower-visiting insects does not affect nectar productivity. Hence, a linearity in the nectar production dynamic is assumed. The effect of nectar removal could lead to an actual volume of nectar produced per flower over 24 h being higher or lower than the measured 24 h volume. Whether the nectar productivity is influenced by insect activity still therefore needs to be assessed.
2. In a field experiment, we estimated the nectar production dynamics of lavender (*Lavandula hybrida*) and fennel (*Foeniculum vulgare*) flowers and tested whether they met the linearity assumption. Then, we developed a simulation model to identify how different scenarios of insect foraging activity: nectar removal rate (average and maximum), and flower-selection strategies (random selection or rewarding flower selection) alter the estimated 24 h volume of nectar for both crops (‘estimated 24 h volume’ hereafter). Finally, we tested whether the estimated 24 h volume differed from the measured 24 h volume for both crops.
3. Lavender and fennel showed equal measured 24 h volume of nectar but the produced nectar volume over 6 h suggested that a flower of lavender was more productive than a flower of fennel. Both nectar production dynamics did not meet the assumption of linearity. The simulation models showed that the estimated 24 h volume increased with maximum nectar removal rate for lavender, and the opposite was found for fennel. Rewarding selection always increased the estimated 24 h volume for fennel while for lavender a positive effect was detected at average rate of nectar removal. We found that the estimated 24 h volume was always greater than the measured 24 h volume.
4. Our model demonstrated that the effect of insect foraging activity on flower’s nectar productivity should be considered while estimating the resources produced by plants. As an

alternative, measures of produced nectar volume in short time spans may be compared with the measured 24 h volume to check the reliability of this widespread method.

Key words: mass-flowering crops, floral resources, floral traits, nectar rewards, insect foraging, plant–insect interactions

1 INTRODUCTION

Pollinator richness and abundance are directly associated with the diversity, quality, and quantity of floral resources, specifically pollen and nectar (Donkersley et al., 2014; Goulson et al., 2015; Roulston & Goodell, 2011). Therefore, it is vital to develop pollinator conservation strategies that consider which natural and cultivated areas provide substantial nectar resources (Aronne et al., 2012; Baude et al., 2016; Quinlan et al., 2021). Several studies have evaluated the nutritional contribution of plants to pollinators by estimating the quantity of nectar produced under different environments, considering historical or seasonal variations (Baude et al., 2016; Guezen & Forrest, 2021; Hicks et al., 2016; Timberlake et al., 2019). These estimates are based on the measure of the nectar volume produced by flowers after a 24 h period isolated from flower-visiting insects, using a mesh bag, as proxy for plant species nectar productivity (Table 1). This method assumes that 1) the volume and frequency of nectar removal by flower-visiting insects (Table 1) do not affect the actual volume of nectar produced per flower over 24 h and 2) that there are no physiological or physical mechanisms (e.g., plant response to water availability, temperature, phenology) that might slow down or accelerate nectar production or lead to nectar re-absorption at daily scale. These two assumptions are in line with the expectation that the production of nectar by a flower over time is linear (Figure 1A).

Several empirical studies have provided line of evidences regarding the implausibility of a linear nectar production dynamic (Table 1): a) flowers visited by foraging animals several times have been found to produce either more or less nectar than flower visited a single time (Biella et al., 2021;

Castellanos et al., 2002; Luo et al., 2014; Ordano & Ornelas, 2004; Ornelas & Lara, 2009; Stahl et al., 2012; Ye et al., 2017); b) insect-pollinated plants have been found to fully fill their flowers of nectar within a few hours and then stop their nectar production (Castellanos et al., 2002; Luo et al., 2014); and c) some plants have displayed nectar reabsorption (Burquez & Corbet, 1991; Pacini & Nepi, 2007; Parachnowitsch et al., 2019).

When the conditions of linearity in the nectar production dynamic (Table 1) are not met, the use of the measured 24 h volume to compare nectar productivity between plant species faces two major issues: 1) the non-linear nectar production dynamics of the flowers of two plant species can intersect each other - thus, the comparison of nectar productivity between them may change depending on the time of the measurement (Figure 1B); 2) nectar removal by flower-visiting insects can restart the non-linear nectar production dynamic (Ordano & Ornelas, 2004; Pacini & Nepi, 2007). Therefore, a flower that had multiple nectar removals may show either higher or lower cumulative volume of nectar produced than a flower whose nectar was never removed (Figure 1C). For the same reason, equal nectar removal frequencies but under different time spans between consecutive removals may lead to different cumulative volume of nectar produced (Figure 1C).

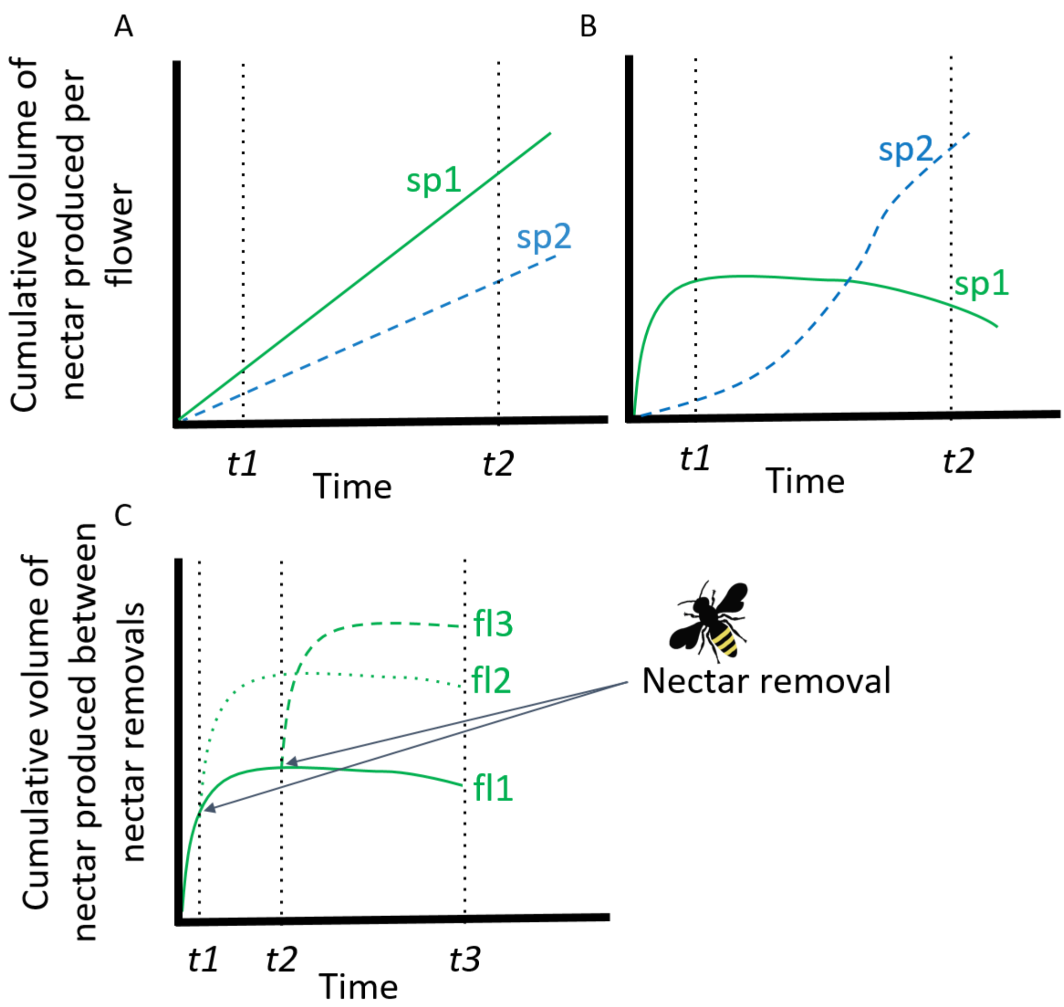

Figure 1. Cumulative volume of nectar produced by two flowers belonging to different plant species (A, B) and the cumulative volume of nectar produced between nectar removals for flowers of the same plant species (C). (A) Linear nectar production dynamics for two flowers belonging to two different species (sp1 and sp2), assuming for both empty flowers at t0. The comparison between nectar productivities does not change (s1 > sp2). (B) Non-linear nectar production dynamics for two flowers belonging to two different species. The comparison between nectar productivities depends on the time of measurement (at t1, sp1 > sp2; at t2, sp1 < sp2). (C) Cumulative volume of nectar produced by three flowers (fl1, fl2, and fl3) belonging to the same species. Nectar removals occur at t1 for fl2, at t2 for fl3. When nectar volume is measured at t3, the cumulative volume of nectar produced by fl2 and fl3 differs from that produced by fl1 because of different nectar removal frequencies, whereas the volume of nectar produced by fl2 and fl3 differs because of different time spans between nectar removals.

The nutritional contribution of plants to pollinators can also be estimated by measuring the standing nectar volume (Corbet, 2003; Parachnowitsch et al., 2019; Table 1). Standing nectar volume represents the nectar reward available to an insect visitor which randomly selects a flower (Parachnowitsch et al., 2019). Its volume is the result of both nectar production dynamics and nectar removal by flower visitors (Corbet, 2003; Parachnowitsch et al., 2019). But the process of flower selection can be different from random. Flower-visiting insects can adjust their behavior to select flowers that provide the largest nectar reward (Knauer et al., 2021). Flower selection is shaped by the memories of olfactory and visual cues associated with rewarding/non-rewarding flowers and by insect's perception (Lichtenberg et al., 2020). Cue perception is context dependent (Dötterl et al., 2014; Hill et al., 2001), affected by floral traits (Krishna & Keasar, 2018), and differs between insect species with some species exhibiting higher levels of perception (e.g. *Apis mellifera* and *Bombus terrestris*) than others (e.g. *Trigona fuscipennis*) (Corbet et al., 1984; Goulson et al., 2001). Theoretically, low perception can lead to random flower selection and to a higher variability in the nectar reward collected. Being opposite, high perception can lead to a better selection of rewarding flowers and a lower reward variability (Ohashi & Thomson, 2005; Pleasants & Zimmerman, 1983).

Table 1. Definition of the considered variables

Variable	**Definition**
Nectar productivity	Measure to compare nectar production between plant species. This can refer to the measured 24 h volume or to the measure of nectar produced over a different time period.
Produced nectar volume	Volume of nectar produced per isolated from insect flowers over a defined time period after draining.
Measured 24 h volume	Volume of nectar produced (μL) by one flower during 24 hours of isolation from pollinators. It is the most common measurement in studies assessing plant nectar productivity.
Nectar removal	Complete removal of nectar contained in a flower by a flower-visiting insect.

Nectar removal rate	Amount of nectar removals during a given period.
Nectar production dynamic	Curve describing the volume of nectar produced by a flower at a given time since the last nectar removal.
Estimated 24 h volume	Estimation of nectar volume produced (µL) by one flower for 24 hours taking into account the effect of nectar removal by insects. This is an alternative measure to assess plant nectar productivity proposed in this paper. This estimation is calculated through the simulation model as the sum of the estimated nectar volume collected by insects per flower.
Actual volume of nectar produced per flower over 24 h	Produced nectar volume (µL) in one flower exposed to open pollination for 24 hours. Nectar removal frequencies and the time span between nectar removals may influence this value. This variable cannot be measured in the field as the measurement would interfere with the variable itself. Estimated nectar volume and measured nectar volume are proxies of this variable.
Estimated nectar volumes collected by insects	Estimation of the nectar volume collected by an insect during a flower visit leading to nectar removal. This is one of the simulation outcomes.
Standing nectar volume	Volume of nectar available in a randomly selected flower. It gives an estimate of the nectar reward available to a visitor which randomly selects a flower.

The nectar production dynamics and the foraging activity (nectar removal rate and flower selection strategy of insects) have been assessed in different field studies (Burquez & Corbet, 1991; Castellanos et al., 2002; Chabert et al., 2018; Goulson et al., 2001) but have rarely been studied together aiming to assess nectar productivity (see Comba et al., 1999 and Corbet et al., 2001). Analyzing these variables together would allow a better estimation of the volume of nectar produced per flower over 24 h ('estimated 24 h volume', Table 1). The estimated 24 h volume per flower can be calculated as the sum of the nectar volume collected by insects during each nectar removal ('estimated volume collected by insects', Table 1) across the day and provides an alternative measure to assess the nectar productivity of flowers. Unlike the measured 24 h volume, the estimated 24 h volume and estimated volume collected by insects incorporate the stochastic effect of insect flower selection, which is driven by insect perception and floral cues. Furthermore, the reliability of the measured 24 h volume as a proxy of plant nectar productivity can be validated using the estimated 24 h volume. In fact, the estimated 24 h volume is expected to be equal to the measured 24 h volume when the nectar production dynamic is linear. Substantial differences between the two measurements would highlight 1) non-linear nectar production dynamics, 2) an effect of the insect foraging activity on plant productivity.

In this study, we investigated the nectar production dynamics and insect foraging activity of two mass-flowering crops (MFC), fennel (*Foeniculum vulgare*) and lavender (*Lavandula hybrida*). First, we tested whether the nectar production dynamics of the two crops met the assumption of linearity. Subsequently, we developed a stochastic simulation model that calculates the estimated 24 h volume of the two crops with respect to the nectar production dynamics and the insect foraging activity. The study was performed in an area where the density of insects and specifically the managed honeybee (*Apis mellifera*), is expected to be extremely high which imply that the insect foraging activity could be a major driver of the estimated 24 h volume of nectar. The field investigation addressed the following questions for the two crops: 1) Do the two crop species have different measured 24 h volume, nectar production dynamics, and nectar removal rates (Table 1)? 2) Are the nectar production dynamics linear? The simulation addressed the following questions: 1) does insect foraging activity affect the estimates of the simulated standing nectar volume, the volume of nectar collected by insects, and the estimated 24 h volume of nectar? 2) Does the estimated 24 h volume substantially differ from the measured 24 h volume? If a deviation from linearity in nectar production dynamic for the two crops is found, we expect a significant effect of insect foraging activity on the estimated variables leading to an estimated 24 h volume being greater than the measured 24 h volume.

2 MATERIALS AND METHODS

2.1 Study area and species

The experiment was carried out in the Mediterranean area of "Plateau de Valensole" (Alpes-de-Haute-Provence, South of France, Figure S1 and Table S1). The region has a sub-Mediterranean-type climate (hot summers and mild and rainy winters). The area presents an agricultural landscape resulting in a mosaic of truffle oak groves, grain crops (durum and soft wheat or barley), and mass-flowering-crops (MFC; especially *Lavandula hybrida*, *Salvia sclarea*, *Foeniculum vulgare*, and *Helichrysum italicum*). These MFC are cultivated for essential oils that are used in the pharmaceutical, cosmetic, and beverage industries. Among them, we studied lavender (*L. hybrida,* Lamiaceae), which is important for both economic reasons (medicinal, cosmetic, and honey production) and tourism (Provence's emblematic plant), and fennel (*F. vulgare,* Apiaceae*)*, which is used to flavor aniseed drinks. *Lavandula hybrida*, also called lavandin, is a hybrid of *L. angustifolia* and *L. latifolia*. Like many hybrids, lavender is sterile and does not produce any functional pollen. This species is nevertheless known to be a good nectar producer (Dussaubat et al., 2021; Escriche et al., 2017). *Lavandula hybrida* grows up to 1 m high and produces numerous blue flowers organized in dense spikes. The floral morphology is tubular (7 mm long and 1–2 mm wide) with nectaries located deep at the bottom of the flower. The fennel variety used was 'Jupiter' (developed by Pernod-Ricard® Company), whose potential for nectar and pollen production is unknown. This plant can grow up to 2.5 m in height and forms numerous small, yellow flowers organized in large, flat inflorescences called umbels (Piccaglia & Marotti, 2001). Each flower contains five stamens. Fennel nectaries are located on the stigma surfaces and are easily accessible to flower-visiting insects. The flowering period of lavender in the Valensole area extends from mid-June to the end of July. Fennel crops can be sown in two separate periods of the year, resulting in two distinct flowering periods that extend from mid-June to mid-September. Fennel crops and lavender can have a bloom overlap between three to five weeks.

The study area harbors an intense beekeeping industry, which means that honeybees (*Apis mellifera*) are the most abundant flower-visiting insects by far (Schurr et al., 2021). In the study area, fennel flowers are visited by a wide range of insects (Hymenoptera, Lepidoptera, Coleoptera, and Diptera)

(Schurr et al., 2021). Although lavender is known to be probed by various insects (Valchev et al., 2022; Balfour et al., 2013; Benachour, 2017; Herrera, 1990), the range of visitors for lavender is expected to be smaller than that of visitors for fennel due to the morphological differences between the flowers (open vs tubular).

2.2 Field measurements of nectar

Nectar measurements were performed in 9 lavender crops and 14 fennel crops (Table S2.), between the end of June and the end of July in the years 2019, 2020, and 2021, when the flowering periods of fennel and lavender overlapped. All 652 measurements were performed under good weather conditions (sunny days and light wind; Table S1, S2 and Figure S1). All nectar measurements were made on one inflorescence in the active flowering stage. For both crops, we considered active inflorescences as those having at least 50% of flowers opened without any browning indicating flower senescence (Guitton et al., 2010). In addition, for fennel, we selected umbels with completely yellow flowers and only peripheral flowers withered (Schurr et al., 2021, 2022). For lavender, we selected inflorescences in the middle of the plant (approximately between 30 and 50 cm from the ground, depending on the age of the plant), whereas for fennel, we selected inflorescences in secondary branches at a standard height (approximately 1.6 ± 0.2 m from the ground) and with an average width of 10 cm. To avoid pseudoreplication, only one inflorescence was selected for each sampled plant. For the selected inflorescences, nectar was extracted from 11 flowers on average (range: 4–25) for the standing nectar volume, and always 10 flowers for the produced nectar volume and the measured 24 h volume using a single 0.5 µl or 1 µl microcapillary (HIRSCHMANN®, minicaps). The volume extracted by a single microcapillary was then measured and divided by the number of sample flowers in the same inflorescence, resulting in an average nectar volume per flower. The following variables were measured:

a) Standing nectar volume: volume of nectar available in randomly selected open flowers. The standing nectar volume was measured from the flower of 81 and 48 plants of fennel and lavender, respectively, from a single site where both crops were present (Table S1, S2 and Figure S1). Standing nectar volumes were recorded between 09:30 and 14:30 for lavender and between 09:15 and 16:45 for fennel. There was a minimum distance of 20 m between each sampled plant, which were located at least 5 m from the border of the field.

b) Produced nectar volume: volume of nectar produced by a flower over a defined time span. After drainage, the sampled inflorescence was enclosed in a mesh bag to prevent insect visits for five different time spans: 30, 60, 120, 210, and 360 min. Then, inflorescences were unbagged, the nectar volume of 10 randomly selected flowers was measured, and the mean volume per flower was calculated. To account for potential daily temporal variations, we distributed the treatments across the day, except for the 360 min treatment due to time constraints. The produced nectar volume was measured from the flowers of 249 and 176 plants from 10 and 7 crops of fennel and lavender, respectively (Table S1, S2 and Figure S1). The produced nectar volumes were used to estimate the nectar production dynamics per species.

c) The measured 24 h volume was assessed using a protocol similar to the one adopted for produced nectar volume, but inflorescences were not drained prior to bagging and enclosed for a 24 h period in a nylon mesh bag. This is the standard measurement method for nectar production which is widely used in the literature (e.g., Baude et al., 2016; Hicks et al., 2016; Timberlake et al., 2019). The measured 24 h volume was measured from the flowers of 77 and 21 plants from 7 and 2 crops of fennel and lavender, respectively (Table S1, S2 and Figure 1). The sugar concentration of the produced nectar and the measured 24 h volume was measured using a refractometer (Bellingham Stanley; g sucrose per 100 g solution, expressed as brix %). Permission for the fieldworks was not needed.

2.3 Nectar removal rate

The nectar removal rate by insects in a 5 min period was measured in a 0.36 m^2 plot. Plots were delimited by a quadrat measuring 0.6 × 0.6 m. We chose this size of quadrats based on the number of flowers that could be observed at the same time by a single experimenter. Plots were distributed randomly across 9 different fields (see number of observations per field in Table S2) and were surveyed once. Nectar removal was recorded when an insect stayed for more than 1 s on the reproductive parts of a flower to gather resources (simple landings were not counted as a visit). A single insect could remove the nectar from multiple flowers during the same observation (personal observation). Each insect was identified as one of the two following categories: *Apis mellifera* or other insects. The number of flowers in the plot was also systematically estimated following the methods described by Schurr et al. (2022), excluding inflorescences having immature or senescent flowers that do not produce nectar.

2.4 Simulation

2.4.1 Overview of the simulation model

We developed a simulation model of the estimated nectar volumes collected by insects across the day, the estimated 24 h volume, and the simulated standing nectar volume. The simulation is a stochastic process in which the insect’s flower selection is driven by a probability distribution that defines the likelihood of a flower being selected. The simulation was developed using plant and insect variables extracted from field measurements following the steps described in Figure 2.

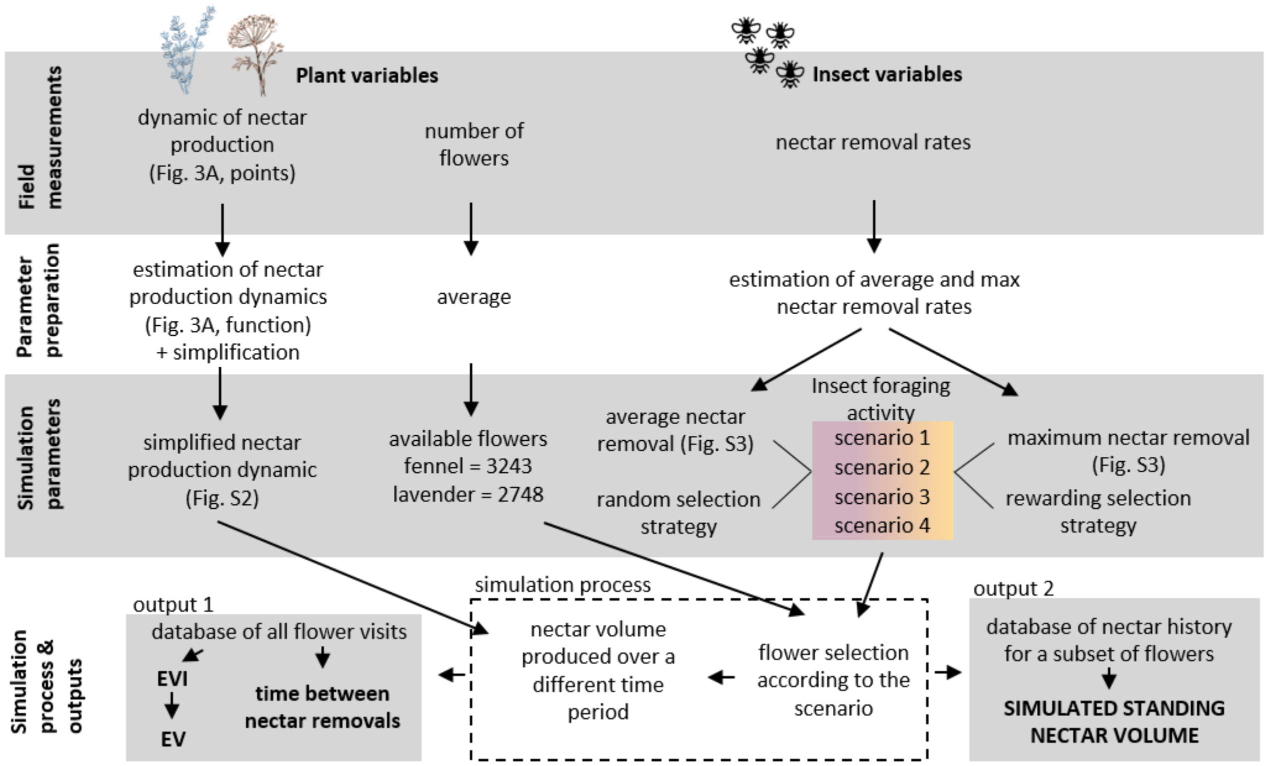

Figure 2. Flowchart of the simulation of estimated 24 h volume (EV), estimated volume collected by insects (EVI), the time between consecutive nectar removals, and simulated standing nectar volume for fennel and lavender.

2.4.2 Simulation parameters

To obtain the simulation parameters, preparation steps were performed, which involved the estimation and simplification of the field measurements. The simulation parameters were as follows: 1) nectar production dynamics, 2) available number of flowers and 3) insect foraging activity scenarios.

The nectar production dynamics is the function indicating the volume of nectar produced by a flower between two consecutive nectar removals. Because the nectar production dynamics were unknown for observations longer than six hours (see Figure 3A and Discussion), nectar production dynamics as a parameter were simplified by maintaining a constant nectar volume when the estimation reached a peak (Figure S2). At the peak, the flowers were considered full, i.e. nectar was neither produced nor re-absorbed/evaporated. The simulation assumed that flowers repeat the same nectar production dynamics after an insect visit, without changes in the nectar production rate due to the potential stimulation/depression effects linked to insect visits.

The "number of available flowers" was estimated by calculating the average number of flowers present in all the observation plots for determining the nectar removal rate (see Section 2.3 Nectar Removal Rate). The effect of different numbers of available flowers that could be selected by flower-visiting insects was not the focus of this study, and it was therefore kept constant in all simulations.

Insect foraging activity parameters were organized into four scenarios with a full factorial design. Each scenario is a combination of two levels of nectar removal rate (average and maximum) and two types of flower selection strategies (random and rewarding). Nectar removal rates were measured in the field (see Section 2.3 Nectar Removal Rate). The average nectar removal rate (Figure S3) was estimated between 06:00 and 20:00, when flower-visiting insects were active (see Section 2.5 Statistical analysis). For feasibility reasons (time to reach the crops), we could not perform nectar removal observations earlier than 08:30 or later than 18:30. Therefore, for earlier than 8.30 and later than 18:30 estimates, we assigned the first and last actual estimates, respectively. The maximum nectar removal rate was also considered and was set to be constant across all simulations and equal to the maximum nectar removal rate value recorded for each plant species (Figure S3). Although a constant nectar removal rate is unlikely under field conditions, the maximum level allows the simulation of the highest nectar demands. In the simulation, insects that did not select between rewarding and non-rewarding flowers had a random selection strategy (random level), insects that could select between rewarding and non-rewarding flowers adopted a rewarding strategy (rewarding level). Under the random selection strategy, all flowers had the same probability of having the nectar removed (probability functions in Figure S4). With the rewarding strategy, the probability of a flower having the nectar removed by an insect was set to increase proportionally as the time since the last nectar removal (Figure S4). We did not assign different probabilities among insect groups or species, despite different perception capacities among insects of a community is common, as the aim was to test extreme levels (random vs rewarding).

2.4.3 Simulation process and outputs

The simulation process reproduced plant–insect interactions over an area of 0.36 m^2. The simulation was modeled for 14 h, starting at 06:00, when flower-visiting insects generally begin their foraging activity, and ending at 20:00. We divided the 14 h of the simulation into units of 5 min and assigned an identification to each available flower. Every 5 min, the simulation process defined which of the available flowers was selected for nectar removal according to the scenario. Then, from the nectar production dynamic parameter, the nectar volume of each flower was extrapolated at each time unit, according to the time elapsed since the last nectar removal. To calculate the estimated nectar volumes, we assumed that insects collected all available nectar at each visit. This assumption was validated in the field prior to data collection because we tested whether visiting insects collected all nectar using a microcap immediately after visits (10 observations for lavender after honeybee removals and 10 for fennel after the removals of different insects).

The process produced two outputs. The first one is the quantification of the estimated nectar volume collected by insects for each nectar removal and the time passed between two consecutive nectar removal for the same flower. The output of the estimated nectar volume collected by insects was used to determine the estimated 24 h volume as the sum of the estimated nectar volume collected by insects per flower throughout the day. The second simulation output is the simulated standing nectar volume, which was calculated using the complete flower history, which is a measure of the nectar volume across time considering insect visits (see the example in Figure S4). The flower history was recorded for a random subset of 50 flowers per simulation. The simulation was repeated 10 times per plant species for each scenario (2 species × 4 scenarios × 10 simulations), producing 80 simulations in total. All simulation data were aggregated to assess the differences in the estimated nectar volumes collected by insects, estimated 24 h volume of nectar, simulated standing nectar volume, and time between consecutive visits among scenarios. The parameters used for the simulation could be of course influenced by different seasonal or climatic factors; however, this was not accounted for as it was beyond the scope of this study. The simulations were performed with R 4.0.2 (see data availability statement for the simulation code).

2.4.4 Nectar resources at landscape level

For each crop, we calculated the daily sugar production per flower (g) using the formula described by Baude et al. (2016): $S = 10d \times V \times C$ where V is the nectar volume produced per flower (μl), C is the sugar concentration and d is density calculated at a concentration C (g sucrose per 100 g solution) by the formula $d = 0.0037921C + 0.0000178C^2 + 0.9988603$. Daily sugar production was calculated first using the average estimated 24 h volume for V between scenarios and the average sugar concentration recorded from produced nectar measurements for d and C and then using the measured 24 h nectar volume for V and its average sugar concentration for d and C. We then estimated the daily nectar production at the landscape level (g ha^{-2} day^{-1}) by multiplying the sugar production by the average estimated number of flowers per hectare. The number of flowers per hectare was estimated from the average number of flowers counted in the plots employed for the nectar removal measurements. These calculations allow a comparison between the daily sugar production at the landscape level measured with the estimated 24 h volume or with the measured 24 h volume.

2.5 Statistical analysis

We used generalized additive mixed models (GAMM) (Wood, 2017) to test the difference between fennel and lavender in terms of 1) nectar production dynamics, 2) sugar concentration of the produced nectar volume, 3) measured 24 h nectar volume, 4) sugar concentration of the measured 24 h volume, 5) nectar removal rate, and 6) proportion of honeybees compared to other flower-visiting insects. In all six models, the plant species was considered a fixed factor. For the first and second models, the time since nectar draining was modeled with cubic spline smoothing. The third and fourth model included the field and date and hour of sampling as fixed factors, the fifth model included the field as random factor and the number of flowers, and the sixth model included the date. The error distributions were gamma (model 1 and 3), binomial (model 2, 4 and 6), and gaussian with a log link (model 5) (model structure and error distribution in Supplementary Table 1). These are considered the most suitable error distributions for right skewed continuous data, proportions, and count data, respectively (Faraway, 2016; Zuur et al., 2009).

The estimate of the GAMM for produced nectar volume corresponds to the species' nectar production dynamics. We validated the consistency of nectar production dynamic peaks by running the model 100 times on a random subset of 80% data on the produced nectar volumes. From these models, we extracted the ranges between the minimum and maximum peak across the models. A GAMM model was also implemented to estimate the average nectar removal rate across the day using plant species, number of flowers, and time of day as fixed factors. The latter two variables were modeled using cubic spline smoothers. The predictions of GAMMs for the produced nectar volume and nectar removal rates were used to implement the simulation parameters.

To draw the curve of the linear nectar production dynamic, we connected the volume of an empty flower (0 μl) to the average measured 24 h volume. The residuals (difference between produced nectar volume of field data and model estimates) of the linear dynamics vs the residuals of the nectar production dynamics estimated using the GAMM model were compared through a GAMM model having model approach (linear vs GAMM), plant species and the time since nectar draining modeled with cubic spline smoothing.

GAMMs were also used to estimate the nectar volume collected by insects and the simulated standing nectar volume over the simulation time. The time was modeled with cubic spline smoothing. The most accurate scenario was identified by calculating the mean error (Hyndman & Athanasopoulos, 2018). Low values for mean error indicate better simulation predictions. In addition, we visually inspected the residuals between the models of the simulated standing nectar volume and field standing nectar volume (Figure S12 and S13). The respect of model assumption was routinely checked using the DARMHA package (Figure S6). Model statistics are reposted in Supplementary Table 1. All analyses were carried out with R 4.0.2 (R Core Team, 2000), using the mgcv package for GAMM (Wood & Wood, 2015).

3 RESULTS

3.1 Field experiment results

3.1.1 Measured 24 h nectar volume

The measured 24 h nectar volume and the corresponding sugar concentration over 24 h were not different between the two crops (Figure 3B, non-predictive GAMM; volume per flower: 0.061 ± 0.042 µl and 0.062 ± 0.036 µl; concentration per flower: 66.09 ± 13.33 % and 67.48 ± 6.75 %, respectively, for fennel and lavender; mean ± SD).

3.1.2 Nectar production dynamic

The nectar production dynamics of the fennel and lavender flowers were better estimated by a non-linear function (Figure 3A): the residual variance was larger for linear models than for non-linear across both species (Figure S7, $P < 0.001$ for model approach). The fennel and lavender flowers showed different non-linear nectar production dynamics across time ($P < 0.001$ for plant species, time and plant species × time since draining, R–sq (adj) = 62 %). Two hours after draining, the model estimates indicated that lavender flowers had a greater produced nectar volume than fennel flowers (Figure 3A). The estimates of lavender nectar production dynamics showed a steady increase of the produced nectar up to 5 h (peak range: 4.8–5.5 h; Figure S8), when the produced nectar started decreasing unexpectedly. Model estimates indicated a slow production and a peak of nectar production for fennel at 3.75 h since draining (peak range: 3.3–3.9 h; Figure S8). The sugar concentration of the produced nectar (between 0–6 h) was not correlated with time for either fennel or lavender (non-predictive GAMM, R–sq (adj) = 6 %; Figure S9). The average sugar concentration was 56.25 ± 7.45% for fennel (n = 48) and 53.39 ± 14.01% for lavender (n = 56) (mean ± SD).

3.1.3 Flower-visiting insects

The nectar removal rate was significantly higher for fennel than for lavender (P < 0.001 for plant species) (Figure 3C), and the nectar removal in 24 h pattern changed between fields (Figure S11). For both crops, the most abundant flower-visiting insect was the honeybee; this was especially pronounced for lavender (P < 0.003) (Figure S10). The proportion of honeybees to other insects was 0.86 ± 0.30 for lavender and 0.62 ± 0.36 for fennel (mean ± SD).

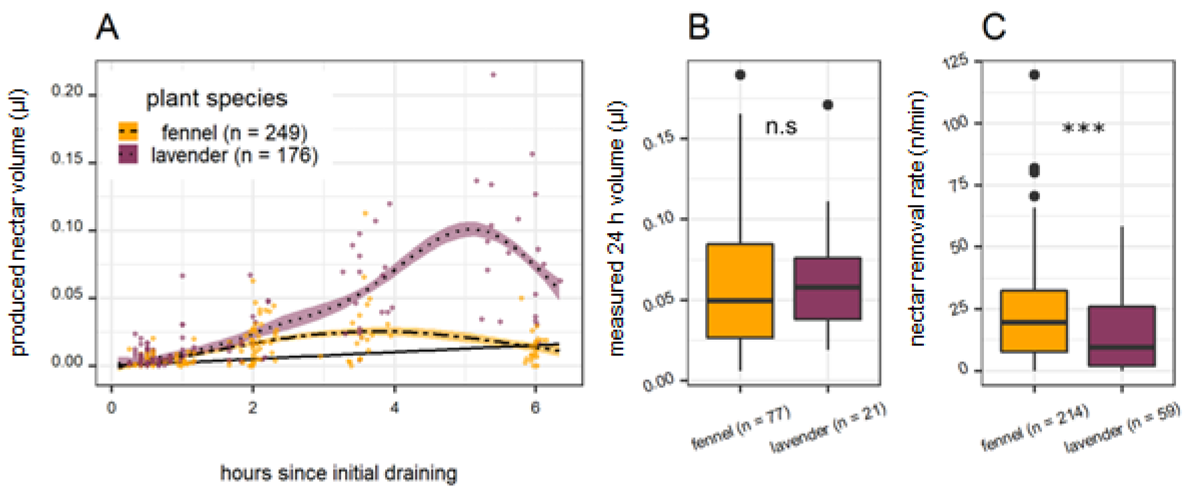

Figure 3. Nectar productivity of fennel and lavender, and the results of nectar removal rate by flower-visiting insects. (A) Nectar production dynamics over 6 h post flower draining; dotted and dashed lines indicate the GAMM estimates, the solid line indicates the estimate for the linear nectar production dynamics of nectar for both species assumed using the measured 24 h volume, shaded areas are confidence intervals, and points are the produced nectar volumes; (B) Measured 24 h nectar volume; (C) Insect nectar removal rate. Orange and purple points, smooth lines and boxplots refer to fennel and lavender, respectively. The asterisks indicate significant differences according to GAMM (n.s. = no significant difference, *** = $P < 0.0001$).

3.1.4 Field standing nectar volume

Fennel flowers were always found empty throughout the day except in the morning (field standing nectar volume: 0.001 ± 0.007 µl, n = 81; [mean ± SD]; Figure 4B). Lavender flowers provided standing nectar volume that fluctuated throughout the day (mean = 0.06 ± 0.05 µl, n = 48; Figure 4A).

3.2 Simulation results

3.2.1 Simulated standing nectar volume

The simulated estimate of standing nectar volume differed between species and scenarios (Figure 4, S12 and S13). The scenario with the average nectar removal rate and random insect selection was the most similar to the field standing nectar volume of lavender (mean error = -0.022, Table S4, Figure 4, and Figure S12). For fennel, the maximum nectar removal rate scenarios, either with random or rewarding selection, were the most similar to the field standing nectar volume (mean error = -0.015 and -0.013 for random and rewarding respectively, Table S3, Figure 4 and S13).

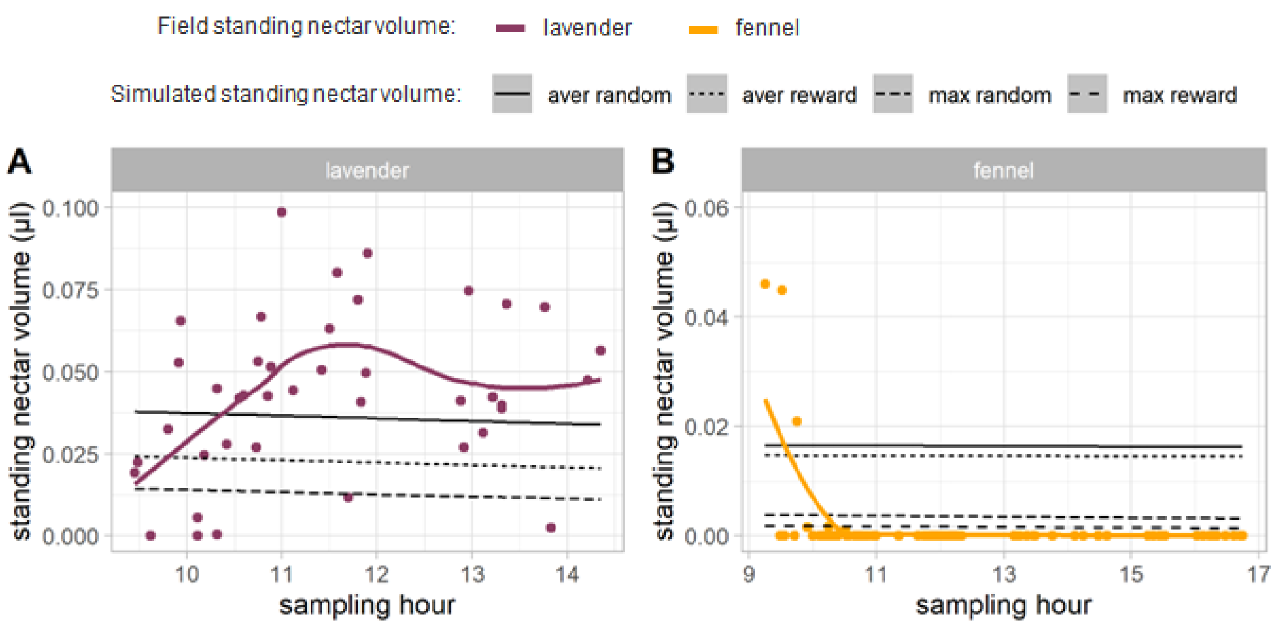

Figure 4. Field standing nectar volumes across time and simulated standing nectar volume using four different flower insect foraging scenarios: nectar removal rate average (aver) / maximum (max) × insect selection of flower random / rewarding (reward). For (A) lavender between 09:30 and 14:30 and (B) fennel between 09:15

and 16:45. Standing nectar scale is different between the two crops (max 0.1 µl for lavender and 0.06 for fennel). Black lines show the simulated standing nectar volume, while solid lines show estimates for the simulated standing nectar (orange for fennel and purple for lavender). Points show field measurements of standing nectar. Field standing nectar was measured in a single field where both crops were present.

3.2.2 Estimated 24 h nectar volume

The estimated 24 h nectar volume varied between scenarios, with lavender having the highest estimated 24 h volume under the average nectar removal rate and rewarding selection scenario (0.260 ± 0.003 µl) and the lowest estimated 24 h volume under the maximum nectar removal rate and rewarding selection scenario (0.233 ± 0.006 µl; Figure 5A). Fennel estimated 24 h volume was the highest in the maximum nectar removal rate and rewarding selection scenario (0.111 ± 0.004 µl) and the lowest in the average nectar removal rate and random selection scenario (0.073 ± 0.025 µl) (mean ± SD) (Figure 5B). Under all scenarios and for both species, the average estimated 24 h volumes were higher than the average measured 24 h volumes (Figure 5A and 5B, mean values and 95% confidence intervals are included in Table S4).

3.2.3 Time between nectar removals and the estimated nectar volumes collected by insects

Both for fennel and lavender, the average time between two consecutive flower nectar removals was always shorter than the time required for the flower to reach the peak of nectar production dynamics (highest average time span between visits 2.33 ± 1.22 h and 3.12 ± 1.82 h for lavender and fennel, respectively; Figure 5C and Figure 5D). In the maximum nectar removal scenario, flowers were always visited before the nectar production dynamic peak was reached. The estimated nectar volumes collected by insects were highest in the average nectar removal rate and rewarding selection scenario (0.022 ± 0.003 µl for fennel and 0.046 ± 0.003 µl for lavender) and the lowest in the maximum nectar removal rate and random selection scenario for both plant species (0.004 ± 0.001 for fennel and 0.014 ± 0.002 µl for lavender) (mean ± SD) (Fig 5E and 5F, mean values and 95% confidence intervals are included in Tab S4).

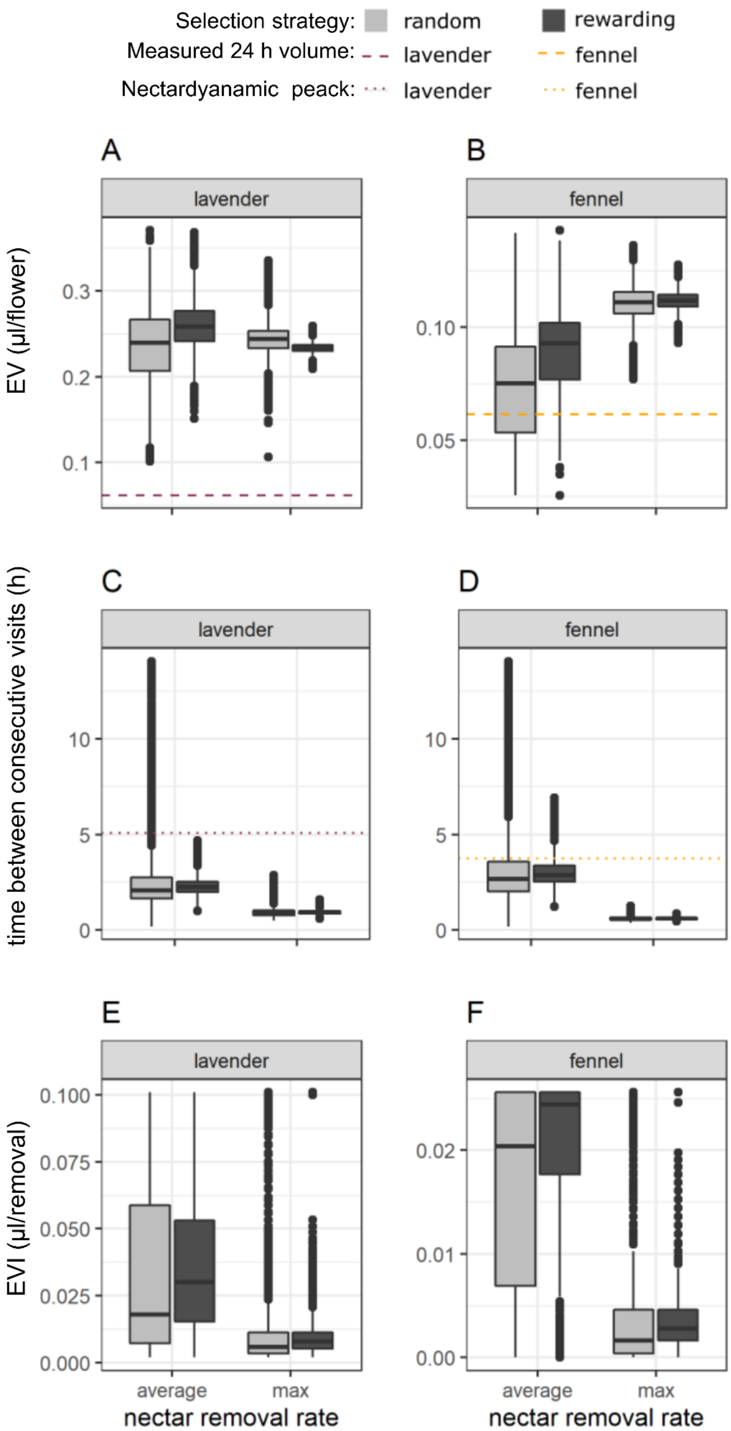

Figure 5. Estimated 24 h nectar volume (EV) according to different simulation scenarios (insect nectar removal rate average/maximum × insect selection of flower random/rewarding) for lavender (A) and for fennel (B). Simulation predictions of the time between two consecutive nectar removals from the same flower according to the simulation scenarios for fennel (B) and lavender (C). Simulation estimates of the nectar volumes collected by insects (EVI) at each nectar removal for lavender (E) and for fennel (F).

The daily sugar production at the landscape level calculated with the estimated 24 h volume was 5797 g ha^{-2} day^{-1} for fennel and 14501 g ha^{-2} day^{-1} for lavender, whereas it was 4839 g ha^{-2} day^{-1} and 4231 g ha^{-2} day^{-1} for fennel and lavender, respectively when estimated with the measured 24 h volume.

4 DISCUSSION

In this study we tested if the widespread measure of the nectar production of a flower, i.e. after 24 h of isolation from insects ("measured 24 h" volume; e.g. Baude et al., 2016; Hicks et al., 2016; Timberlake et al., 2019) accurately represents the nectar productivity of two common mass-flowering crops, fennel and lavender. This measure assumes a linearity in the dynamic of nectar production and consequently no effects of insect foraging activity on plant nectar productivity. Here, we found non-linear nectar production dynamics for the two crops. Hence, the assumption of linearity was not met. We then developed a simulation model of the estimated 24 h volume of nectar taking into account the non-linear dynamic of nectar production and the insect foraging activity. The estimated 24 h nectar volumes generated by our simulation were affected by the insect foraging activity. The estimated 24 h volume was greater than the measured 24 h volume, substantially for lavender and slightly for fennel.

4.1 Nectar resources produced by lavender and fennel for flower visitors

We found that lavender flowers produced nectar more quickly than fennel flowers (median speed 1.31×10^{-4} and 0.52×10^{-4} µl/min). While their production appears similar on a 24-hour scale, our results on smaller time intervals (6 hours) showed that lavender actually produced more nectar than fennel. Therefore, we believe that in order to correctly assess the nectar production of plants and by extension of plant communities and landscapes, we must take into account the dynamics of nectar production which will ultimately allow us to better assess the availability of resources offered to flower visiting-insects.

In a time span of 3.75 h after draining, lavender flowers had a nectar production dynamic that exceeded the average measured 24 h volume. This result suggests that lavender flowers may reabsorb nectar when it is not exploited for long periods. As hypothesized for other plants, a re-absorption mechanism might reduce the energy costs to attract pollinators required to ensure seed sets (Burquez & Corbet, 1991; Nepi & Stpiczyńska, 2008; Pacini & Nepi, 2007). Signs of nectar reabsorption have previously been observed in *Lavandula pubescens* (Nuru et al., 2015), but have never been studied for *Lavandula hybrida*; therefore, this finding must be confirmed through dedicated analyses. Regarding fennel, the nectar production dynamic peaked before 4 h, but the peak was lower than the measured 24 h volume. This difference suggests that the nectar production between 6 and 24 h after draining continues. Peaks of the dynamic of nectar production varied considerably probably because of the individual flower and plant phenotypic variations (Castellanos et al., 2002; Luo et al., 2014; Nicolson & Nepi, 2005), as well as by exogenous factors (e.g. temperature) (Chabert et al., 2018). For example, *Carum carvi* (Apiaceae) plants of the same variety grown under the same controlled conditions showed fourfold differences in the produced nectar between anthesis and fertilization (Langenberger & Davis, 2002). Therefore, the nectar production dynamics of lavender and fennel should be considered as rough estimates of the average produced nectar, which may considerably change during their flowering period. Despite these limitations our results showed that the nectar production dynamic of both crops is more likely non-linear than linear.

For both plants, the measured 24 h volume was quantified in flowers that were not drained before flower isolation, following the protocol adopted by previous studies (e.g., Baude et al., 2016; Hicks et al., 2016; Timberlake et al., 2019). This may have led to imprecise estimation of the measured 24 h volume, given the time of the last insect visit was not known. We therefore cannot exclude the possibility that flowers have produced nectar for more than 24 h. However, we found this unlikely as fennel flowers in the area were usually empty, given the high nectar removal rate, hence the bias should have been limited and not influential. For lavender, even if we cannot totally exclude that the production might continue after 24 h, the peak in nectar production occurs a few hours after draining, hence the bias could also be minimal here.

4.2 Field standing nectar and flower-visiting insect foraging

We found that the rate of nectar removal by insects was higher in fennel than in lavender. Honeybees were the dominant flower visitors for both crops, although its dominance was less pronounced in fennel. Honeybee dominance was likely due to the numerous managed honeybee colonies placed in the study area for honey production. When measured in the same area, the standing nectar volume was high for lavender, whereas it was close to zero from the first hour onwards for fennel. These results suggest that the nectar produced by fennel is immediately consumed by insects. Simultaneously, flower visitors' nectar removal rate seemed to be lower for the lavender flowers, despite their larger nectar rewards. This outcome may be explained by the difference in the floral traits of the two crops. Fennel presents open and easily accessible flowers grouped in inflorescences which allow flower-visiting insects to rapidly detect and gather resources, and also to switch between flowers. In contrast, in lavender, flower handling is more complicated because of the narrow morphology of the flower (Balfour et al., 2013). This was reflected by the diversity of pollinators observed on fennel flowers suggesting that fennel flower traits do not constrain insect visits (Schurr et al., 2022; Smith-Ramírez et al., 2005; Thompson, 2001). On the other hand, we only observed few species of flower-visiting insects foraging on lavender (Schurr, unpubl.), and this was also reported in previous studies (Balfour et al., 2013; Benachour, 2017; Valchev et al., 2022). This could also be explained by the fact that lavender does not produce pollen contrary to fennel and thus may attract fewer flower-visiting species. These results suggest that future research should focus on quantifying insect species-specific nectar resource availability.

4.3 Simulation model results

This study simulated the estimated 24 h nectar volume, the standing nectar volume, and the nectar volume collected by flower-visiting insects across a daily period, considering the effects of non-linear nectar production dynamics, nectar removal rate, and insect selection strategy. Some of the simulation scenarios produced standing nectar volume trends that were similar to those observed from the field data, suggesting that the model can provide reliable estimates.

For lavender, the average nectar removal rate and random selection scenario produced simulated standing nectar volume consistent with the field standing nectar volume. This suggests that flower-visiting insects select lavender flowers randomly because they are not capable of detecting olfactory cues associated with the presence of nectar in lavender or because of the lack of such cues. The result is in agreement with Duffield et al. (1993) findings that have shown that most lavender-visiting insects, such as honeybees, choose a flower on the basis of their dimension rather than their nectar content.

For fennel, the maximum nectar removal rate scenarios produced simulated standing nectar volumes that were the most consistent with the field one. This result supports the hypothesis that fennel flowers were highly exploited by flower-visiting insects, especially honeybees which were the most abundant visitor. This hypothesis is in accordance with previous findings of low-standing nectar volume due to high insect exploitation in other plant species (Corbet et al., 2001; Geslin et al., 2017; Sáez et al., 2017; Torné-Noguera et al., 2016; Wignall et al., 2020).

Our simulation showed that the estimated 24 h volume varied among the scenarios, and identical scenarios showed either increasing or decreasing volume for the two investigated crops. For example, the estimated 24 h volume produced under the maximum nectar removal rate and rewarding selection scenario was the greatest in fennel and the lowest in lavender. Therefore, a generalizable effect of insects on nectar productivity among plants is missing. The lack of a general pattern is due to the effects of flower-visiting insects on nectar productivity that are not 'a priori' predictable. Previous studies have shown that insect visits can either increase, decrease, or elicit no effect on nectar productivity (Castellanos et al., 2002; Luo et al., 2014; Ordano & Ornelas, 2004; Ornelas & Lara, 2009; Ye et al., 2017).

Nevertheless, we found a general pattern for both crops: the estimated 24 h volume was always greater than the measured 24 h volume. This pattern implies an underestimation of the daily sugar production at the plant and at the landscape scale when the measured 24 h volume is used for its estimation. The difference between the estimated and measured 24 h volume is probably due to the short time between two nectar removals. In fact, the simulation showed that the time between consecutive removals was often shorter than the time required for the flower to produce nectar up to the peak of the nectar production dynamics. Therefore, flowers were pushed to continue nectar production constantly.

4.4 Conclusion

A short time for flowers to reach the peak of nectar production dynamic is consistent with previous studies showing that flowers can fully produce nectar within a few hours, rather than requiring a whole day (Castellanos et al., 2002; Luo et al., 2014). Despite this, most studies focusing on nectar use the 24 h volume as a proxy of plant nectar productivity, probably because of feasibility, time and money constraints. Our results clearly highlight that the measured 24 h volume underestimates the plant nectar productivity. We showed that the activity of pollinators seems to favor the production of nectar. This underestimation may be particularly prominent in environments where pollinators are abundant, such as in intense beekeeping areas or in mass-flowering crops where nectar removal rates are particularly high, given the high attractiveness of these crops to pollinators.

Our field and simulated results on nectar production provide a new method to assess the production of resources among flowers that should be seen as complementary to more common methods. However, this method may be practically difficult to set up in large studies on many plant species because much time is needed to collect field variables. A first pragmatic step aiming to a better understanding of plant nectar production and its effect on flower-visiting insects can be to measure the nectar production of different plant species in a short time (e.g. six hours). This would highlight whether the nectar productivity is in line with the measured 24 h volume of nectar. When this is not the case, some corrections of nectar productivity estimates should be adopted.

Finally, our results bring new insights to accurately estimate the flower visitor's abundance that can be supported by landscapes. In the current debate about the competition between wild and domestic pollinators in many ecosystems (e.g., Iwasaki & Hogendoorn, 2022), an accurate estimation of the amount of resources produced by flowering plants could, for example, help to better assess the beehive load that can be installed in the landscape while preserving the native flower-visiting fauna.

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ABSTRACT

Le nectar est une ressource alimentaire indispensable à de nombreux insectes. Une méthode est communément utilisée pour estimer la production de nectar: elle consiste à échantillonner une fleur après 24h d'isolement aux insectes (la fleur est ensachée). Cette méthode postule que toutes les fleurs produisent du nectar à vitesse constante, indépendamment des prélèvements par les insectes. Toutefois, toutes les plantes ne sont pas égales en termes de vitesse de production de nectar, et il a aussi été prouvé que selon les espèces de plantes, le butinage a un effet (positif ou négatif) sur la production de nectar. Il est donc important de connaître les rythmes de production nectarifères plus précisément avant d'évaluer la productivité des plantes.

Dans une étude en plein champs, nous avons suivi la production de nectar de 2 plantes aromatiques largement cultivées, le lavandin (*Lavandula hybrida*) et le fenouil (*Foeniculum vulgare*), en mesurant la production de nectar sur différents pas de temps (inférieurs à 24h), et observé les comportements de butinage afin de simuler des scénarios de visites d'insectes floricoles sur chaque culture.

Il n'y avait pas de différences entre les deux cultures pour la production de nectar au bout de 24h.

Toutefois, le lavandin reconstitue les stocks de nectar beaucoup plus rapidement que le fenouil. En simulant différents comportements de visite des insectes floricoles, nous avons mis en évidence que la production quotidienne de nectar varie grandement, et que cette valeur est toujours très supérieure à la mesure réalisée après 24h d'isolement, pour le lavandin comme pour le fenouil.

Ces travaux démontrent qu'une prise en compte des insectes floricoles et de la dynamique de production est indispensable à l'estimation précise des quantités de nectar.