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

(Article begins on next page)

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1   **ABSTRACT**

2   1. Nectar is a key resource for numerous insects. Despite its importance, nectar productivity has

3   mainly been assessed using one sampling method, in which the volume of nectar produced by

4   a flower is measured after 24 h of isolation from insects ('measured 24 h volume' hereafter).

5   This method assumes that nectar removal by flower-visiting insects does not affect nectar

6   productivity. Hence, a linearity in the nectar production dynamic is assumed. The effect of

7   nectar removal could lead to an actual volume of nectar produced per flower over 24 h being

8   higher or lower than the measured 24 h volume. Whether the nectar productivity is influenced

9   by insect activity still therefore needs to be assessed.

10 2. In a field experiment, we estimated the nectar production dynamics of lavender (*Lavandula*

11   *hybrida*) and fennel (*Foeniculum vulgare*) flowers and tested whether they met the linearity

12   assumption. Then, we developed a simulation model to identify how different scenarios of

13   insect foraging activity: nectar removal rate (average and maximum), and flower-selection

14   strategies (random selection or rewarding flower selection) alter the estimated 24 h volume of

15   nectar for both crops ('estimated 24 h volume' hereafter). Finally, we tested whether the

16   estimated 24 h volume differed from the measured 24 h volume for both crops.

17 3. Lavender and fennel showed equal measured 24 h volume of nectar but the produced nectar

18   volume over 6 h suggested that a flower of lavender was more productive than a flower of

19   fennel. Both nectar production dynamics did not meet the assumption of linearity. The

20   simulation models showed that the estimated 24 h volume increased with maximum nectar

21   removal rate for lavender, and the opposite was found for fennel. Rewarding selection always

22   increased the estimated 24 h volume for fennel while for lavender a positive effect was

23   detected at average rate of nectar removal. We found that the estimated 24 h volume was

24   always greater than the measured 24 h volume.

25 4. Our model demonstrated that the effect of insect foraging activity on flower's nectar

26   productivity should be considered while estimating the resources produced by plants. As an

27   alternative, measures of produced nectar volume in short time spans may be compared with

28   the measured 24 h volume to check the reliability of this widespread method.

29

30   Key words: mass-flowering crops, floral resources, floral traits, nectar rewards, insect foraging,

31   plant–insect interactions

32   **1 INTRODUCTION**

33   Pollinator richness and abundance are directly associated with the diversity, quality, and quantity of

34   floral resources, specifically pollen and nectar (Donkersley et al., 2014; Goulson et al., 2015;

35   Roulston & Goodell, 2011). Therefore, it is vital to develop pollinator conservation strategies that

36   consider which natural and cultivated areas provide substantial nectar resources (Aronne et al., 2012;

37   Baude et al., 2016; Quinlan et al., 2021). Several studies have evaluated the nutritional contribution

38   of plants to pollinators by estimating the quantity of nectar produced under different environments,

39   considering historical or seasonal variations (Baude et al., 2016; Guezen & Forrest, 2021; Hicks et

40   al., 2016; Timberlake et al., 2019). These estimates are based on the measure of the nectar volume

41   produced by flowers after a 24 h period isolated from flower-visiting insects, using a mesh bag, as

42   proxy for plant species nectar productivity (Table 1). This method assumes that 1) the volume and

43   frequency of nectar removal by flower-visiting insects (Table 1) do not affect the actual volume of

44   nectar produced per flower over 24 h and 2) that there are no physiological or physical mechanisms

45   (e.g., plant response to water availability, temperature, phenology) that might slow down or accelerate

46   nectar production or lead to nectar re-absorption at daily scale. These two assumptions are in line

47   with the expectation that the production of nectar by a flower over time is linear (Figure 1A).

48   Several empirical studies have provided line of evidences regarding the implausibility of a linear

49   nectar production dynamic (Table 1): a) flowers visited by foraging animals several times have been

50   found to produce either more or less nectar than flower visited a single time (Biella et al., 2021;

51 Castellanos et al., 2002; Luo et al., 2014; Ordano & Ornelas, 2004; Ornelas & Lara, 2009; Stahl et

52 al., 2012; Ye et al., 2017); b) insect-pollinated plants have been found to fully fill their flowers of

53 nectar within a few hours and then stop their nectar production (Castellanos et al., 2002; Luo et al.,

54 2014); and c) some plants have displayed nectar reabsorption (Burquez & Corbet, 1991; Pacini &

55 Nepi, 2007; Parachnowitsch et al., 2019).

56 When the conditions of linearity in the nectar production dynamic (Table 1) are not met, the use of

57 the measured 24 h volume to compare nectar productivity between plant species faces two major

58 issues: 1) the non-linear nectar production dynamics of the flowers of two plant species can intersect

59 each other - thus, the comparison of nectar productivity between them may change depending on the

60 time of the measurement (Figure 1B); 2) nectar removal by flower-visiting insects can restart the non-

61 linear nectar production dynamic (Ordano & Ornelas, 2004; Pacini & Nepi, 2007). Therefore, a

62 flower that had multiple nectar removals may show either higher or lower cumulative volume of

63 nectar produced than a flower whose nectar was never removed (Figure 1C). For the same reason,

64 equal nectar removal frequencies but under different time spans between consecutive removals may

65 lead to different cumulative volume of nectar produced (Figure 1C).

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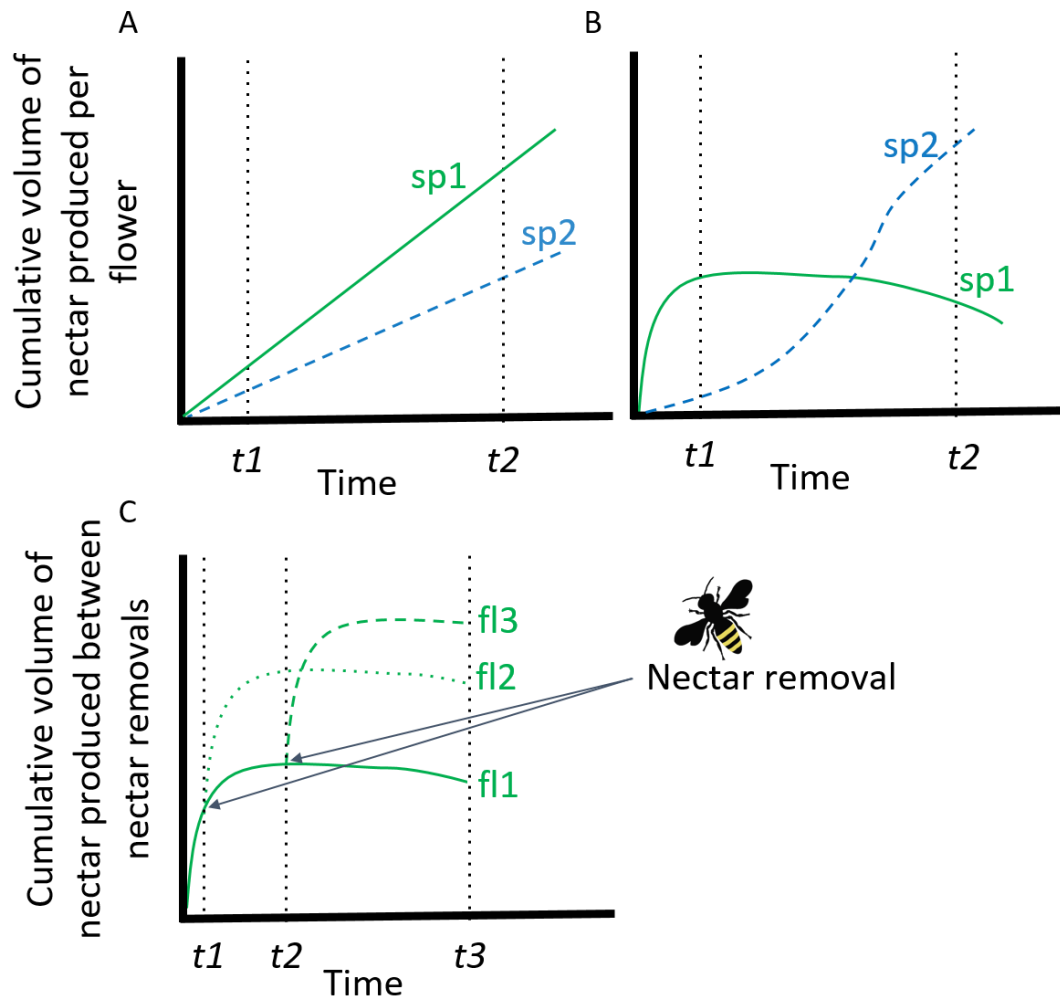
Figure 1. Cumulative volume of nectar produced by two flowers belonging to different plant species (A, B) and the cumulative volume of nectar produced between nectar removals for flowers of the same plant species (C). (A) Linear nectar production dynamics for two flowers belonging to two different species (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.

80 The nutritional contribution of plants to pollinators can also be estimated by measuring the standing

81 nectar volume (Corbet, 2003; Parachnowitsch et al., 2019; Table 1). Standing nectar volume

82 represents the nectar reward available to an insect visitor which randomly selects a flower

83 (Parachnowitsch et al., 2019). Its volume is the result of both nectar production dynamics and nectar

84 removal by flower visitors (Corbet, 2003; Parachnowitsch et al., 2019). But the process of flower

85 selection can be different from random. Flower-visiting insects can adjust their behavior to select

86 flowers that provide the largest nectar reward (Knauer et al., 2021). Flower selection is shaped by the

87 memories of olfactory and visual cues associated with rewarding/non-rewarding flowers and by

88 insect's perception (Lichtenberg et al., 2020). Cue perception is context dependent (Dötterl et al.,

89 2014; Hill et al., 2001), affected by floral traits (Krishna & Keasar, 2018), and differs between insect

90 species with some species exhibiting higher levels of perception (e.g. *Apis mellifera* and *Bombus*

91 *terrestris*) than others (e.g. *Trigona fuscipennis*) (Corbet et al., 1984; Goulson et al., 2001).

92 Theoretically, low perception can lead to random flower selection and to a higher variability in the

93 nectar reward collected. Being opposite, high perception can lead to a better selection of rewarding

94 flowers and a lower reward variability (Ohashi & Thomson, 2005; Pleasants & Zimmerman, 1983).

95 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.

96

97 The nectar production dynamics and the foraging activity (nectar removal rate and flower selection

98 strategy of insects) have been assessed in different field studies (Burquez & Corbet, 1991; Castellanos

99 et al., 2002; Chabert et al., 2018; Goulson et al., 2001) but have rarely been studied together aiming

100 to assess nectar productivity (see Comba et al., 1999 and Corbet et al., 2001). Analyzing these

101 variables together would allow a better estimation of the volume of nectar produced per flower over

102 24 h ('estimated 24 h volume', Table 1). The estimated 24 h volume per flower can be calculated as

103 the sum of the nectar volume collected by insects during each nectar removal ('estimated volume

104 collected by insects', Table 1) across the day and provides an alternative measure to assess the nectar

105 productivity of flowers. Unlike the measured 24 h volume, the estimated 24 h volume and estimated

106 volume collected by insects incorporate the stochastic effect of insect flower selection, which is

107 driven by insect perception and floral cues. Furthermore, the reliability of the measured 24 h volume

108 as a proxy of plant nectar productivity can be validated using the estimated 24 h volume. In fact, the

109 estimated 24 h volume is expected to be equal to the measured 24 h volume when the nectar

110 production dynamic is linear. Substantial differences between the two measurements would highlight

111 1) non-linear nectar production dynamics, 2) an effect of the insect foraging activity on plant

112 productivity.

113 In this study, we investigated the nectar production dynamics and insect foraging activity of two

114 mass-flowering crops (MFC), fennel (*Foeniculum vulgare*) and lavender (*Lavandula hybrida*). First,

115 we tested whether the nectar production dynamics of the two crops met the assumption of linearity.

116 Subsequently, we developed a stochastic simulation model that calculates the estimated 24 h volume

117 of the two crops with respect to the nectar production dynamics and the insect foraging activity. The

118 study was performed in an area where the density of insects and specifically the managed honeybee

119 (*Apis mellifera*), is expected to be extremely high which imply that the insect foraging activity could

120 be a major driver of the estimated 24 h volume of nectar. The field investigation addressed the

121 following questions for the two crops: 1) Do the two crop species have different measured 24 h

122 volume, nectar production dynamics, and nectar removal rates (Table 1)? 2) Are the nectar production

123 dynamics linear? The simulation addressed the following questions: 1) does insect foraging activity

124 affect the estimates of the simulated standing nectar volume, the volume of nectar collected by insects,

125 and the estimated 24 h volume of nectar? 2) Does the estimated 24 h volume substantially differ from

126 the measured 24 h volume? If a deviation from linearity in nectar production dynamic for the two

127 crops is found, we expect a significant effect of insect foraging activity on the estimated variables

128 leading to an estimated 24 h volume being greater than the measured 24 h volume.

129

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)

158 (Schurr et al., 2021). Although lavender is known to be probed by various insects (Valchev et al.,

159 2022; Balfour et al., 2013; Benachour, 2017; Herrera, 1990), the range of visitors for lavender is

160 expected to be smaller than that of visitors for fennel due to the morphological differences between

161 the flowers (open vs tubular).

162 *2.2 Field measurements of nectar*

163 Nectar measurements were performed in 9 lavender crops and 14 fennel crops (Table S2.), between

164 the end of June and the end of July in the years 2019, 2020, and 2021, when the flowering periods of

165 fennel and lavender overlapped. All 652 measurements were performed under good weather

166 conditions (sunny days and light wind; Table S1, S2 and Figure S1). All nectar measurements were

167 made on one inflorescence in the active flowering stage. For both crops, we considered active

168 inflorescences as those having at least 50% of flowers opened without any browning indicating flower

169 senescence (Guitton et al., 2010). In addition, for fennel, we selected umbels with completely yellow

170 flowers and only peripheral flowers withered (Schurr et al., 2021, 2022). For lavender, we selected

171 inflorescences in the middle of the plant (approximately between 30 and 50 cm from the ground,

172 depending on the age of the plant), whereas for fennel, we selected inflorescences in secondary

173 branches at a standard height (approximately 1.6 ± 0.2 m from the ground) and with an average width

174 of 10 cm. To avoid pseudoreplication, only one inflorescence was selected for each sampled plant.

175 For the selected inflorescences, nectar was extracted from 11 flowers on average (range: 4–25) for

176 the standing nectar volume, and always 10 flowers for the produced nectar volume and the measured

177 24 h volume using a single 0.5 µl or 1 µl microcapillary (HIRSCHMANN®, minicaps). The volume

178 extracted by a single microcapillary was then measured and divided by the number of sample flowers

179 in the same inflorescence, resulting in an average nectar volume per flower. The following variables

180 were measured:

181 a) Standing nectar volume: volume of nectar available in randomly selected open flowers. The

182 standing nectar volume was measured from the flower of 81 and 48 plants of fennel and lavender,

183   respectively, from a single site where both crops were present (Table S1, S2 and Figure S1). Standing

184   nectar volumes were recorded between 09:30 and 14:30 for lavender and between 09:15 and 16:45

185   for fennel. There was a minimum distance of 20 m between each sampled plant, which were located

186   at least 5 m from the border of the field.

187   b) Produced nectar volume: volume of nectar produced by a flower over a defined time span. After

188   drainage, the sampled inflorescence was enclosed in a mesh bag to prevent insect visits for five

189   different time spans: 30, 60, 120, 210, and 360 min. Then, inflorescences were unbagged, the nectar

190   volume of 10 randomly selected flowers was measured, and the mean volume per flower was

191   calculated. To account for potential daily temporal variations, we distributed the treatments across

192   the day, except for the 360 min treatment due to time constraints. The produced nectar volume was

193   measured from the flowers of 249 and 176 plants from 10 and 7 crops of fennel and lavender,

194   respectively (Table S1, S2 and Figure S1). The produced nectar volumes were used to estimate the

195   nectar production dynamics per species.

196   c) The measured 24 h volume was assessed using a protocol similar to the one adopted for produced

197   nectar volume, but inflorescences were not drained prior to bagging and enclosed for a 24 h period in

198   a nylon mesh bag. This is the standard measurement method for nectar production which is widely

199   used in the literature (e.g., Baude et al., 2016; Hicks et al., 2016; Timberlake et al., 2019). The

200   measured 24 h volume was measured from the flowers of 77 and 21 plants from 7 and 2 crops of

201   fennel and lavender, respectively (Table S1, S2 and Figure 1). The sugar concentration of the

202   produced nectar and the measured 24 h volume was measured using a refractometer (Bellingham

203   Stanley; g sucrose per 100 g solution, expressed as brix %). Permission for the fieldworks was not

204   needed.

205   *2.3 Nectar removal rate*

206   The nectar removal rate by insects in a 5 min period was measured in a 0.36 m^2 plot. Plots were

207   delimited by a quadrat measuring 0.6 × 0.6 m. We chose this size of quadrats based on the number of

208 flowers that could be observed at the same time by a single experimenter. Plots were distributed

209 randomly across 9 different fields (see number of observations per field in Table S2) and were

210 surveyed once. Nectar removal was recorded when an insect stayed for more than 1 s on the

211 reproductive parts of a flower to gather resources (simple landings were not counted as a visit). A

212 single insect could remove the nectar from multiple flowers during the same observation (personal

213 observation). Each insect was identified as one of the two following categories: *Apis mellifera* or

214 other insects. The number of flowers in the plot was also systematically estimated following the

215 methods described by Schurr et al. (2022), excluding inflorescences having immature or senescent

216 flowers that do not produce nectar.

217 *2.4 Simulation*

218 <u>2.4.1 Overview of the simulation model</u>

219 We developed a simulation model of the estimated nectar volumes collected by insects across the

220 day, the estimated 24 h volume, and the simulated standing nectar volume. The simulation is a

221 stochastic process in which the insect's flower selection is driven by a probability distribution that

222 defines the likelihood of a flower being selected. The simulation was developed using plant and insect

223 variables extracted from field measurements following the steps described in Figure 2.
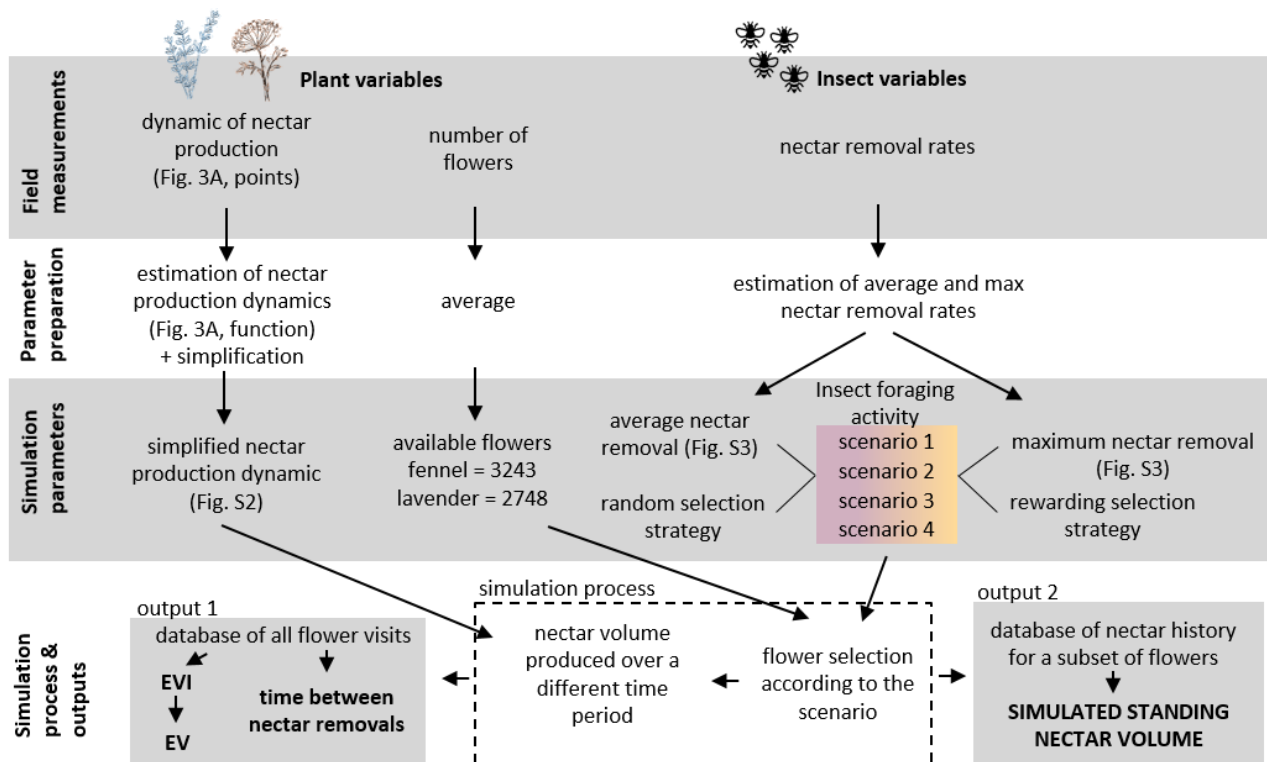
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Figure 2. Flowchart of the simulation of estimated 24 h volume (EV), estimated volume collected by insects (EVI), the time between consecutive nectar removals, and simulated standing nectar volume for fennel and lavender.

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

240 dynamics after an insect visit, without changes in the nectar production rate due to the potential

241 stimulation/depression effects linked to insect visits.

242 The "number of available flowers" was estimated by calculating the average number of flowers

243 present in all the observation plots for determining the nectar removal rate (see Section 2.3 Nectar

244 Removal Rate). The effect of different numbers of available flowers that could be selected by flower-

245 visiting insects was not the focus of this study, and it was therefore kept constant in all simulations.

246 Insect foraging activity parameters were organized into four scenarios with a full factorial design.

247 Each scenario is a combination of two levels of nectar removal rate (average and maximum) and two

248 types of flower selection strategies (random and rewarding). Nectar removal rates were measured in

249 the field (see Section 2.3 Nectar Removal Rate). The average nectar removal rate (Figure S3) was

250 estimated between 06:00 and 20:00, when flower-visiting insects were active (see Section 2.5

251 Statistical analysis). For feasibility reasons (time to reach the crops), we could not perform nectar

252 removal observations earlier than 08:30 or later than 18:30. Therefore, for earlier than 8.30 and later

253 than 18:30 estimates, we assigned the first and last actual estimates, respectively. The maximum

254 nectar removal rate was also considered and was set to be constant across all simulations and equal

255 to the maximum nectar removal rate value recorded for each plant species (Figure S3). Although a

256 constant nectar removal rate is unlikely under field conditions, the maximum level allows the

257 simulation of the highest nectar demands. In the simulation, insects that did not select between

258 rewarding and non-rewarding flowers had a random selection strategy (random level), insects that

259 could select between rewarding and non-rewarding flowers adopted a rewarding strategy (rewarding

260 level). Under the random selection strategy, all flowers had the same probability of having the nectar

261 removed (probability functions in Figure S4). With the rewarding strategy, the probability of a flower

262 having the nectar removed by an insect was set to increase proportionally as the time since the last

263 nectar removal (Figure S4). We did not assign different probabilities among insect groups or species,

264 despite different perception capacities among insects of a community is common, as the aim was to

265 test extreme levels (random vs rewarding).

266 2.4.3 Simulation process and outputs

267 The simulation process reproduced plant–insect interactions over an area of 0.36 m^2. The simulation

268 was modeled for 14 h, starting at 06:00, when flower-visiting insects generally begin their foraging

269 activity, and ending at 20:00. We divided the 14 h of the simulation into units of 5 min and assigned

270 an identification to each available flower. Every 5 min, the simulation process defined which of the

271 available flowers was selected for nectar removal according to the scenario. Then, from the nectar

272 production dynamic parameter, the nectar volume of each flower was extrapolated at each time unit,

273 according to the time elapsed since the last nectar removal. To calculate the estimated nectar volumes,

274 we assumed that insects collected all available nectar at each visit. This assumption was validated in

275 the field prior to data collection because we tested whether visiting insects collected all nectar using

276 a microcap immediately after visits (10 observations for lavender after honeybee removals and 10 for

277 fennel after the removals of different insects).

278 The process produced two outputs. The first one is the quantification of the estimated nectar volume

279 collected by insects for each nectar removal and the time passed between two consecutive nectar

280 removal for the same flower. The output of the estimated nectar volume collected by insects was used

281 to determine the estimated 24 h volume as the sum of the estimated nectar volume collected by insects

282 per flower throughout the day. The second simulation output is the simulated standing nectar volume,

283 which was calculated using the complete flower history, which is a measure of the nectar volume

284 across time considering insect visits (see the example in Figure S4). The flower history was recorded

285 for a random subset of 50 flowers per simulation. The simulation was repeated 10 times per plant

286 species for each scenario (2 species × 4 scenarios × 10 simulations), producing 80 simulations in

287 total. All simulation data were aggregated to assess the differences in the estimated nectar volumes

288 collected by insects, estimated 24 h volume of nectar, simulated standing nectar volume, and time

289 between consecutive visits among scenarios. The parameters used for the simulation could be of

290 course influenced by different seasonal or climatic factors; however, this was not accounted for as it

291 was beyond the scope of this study. The simulations were performed with R 4.0.2 (see data

292 availability statement for the simulation code).

293 2.4.4 Nectar resources at landscape level

294 For each crop, we calculated the daily sugar production per flower (g) using the formula described

295 by Baude et al. (2016): S= 10d × V × C where V is the nectar volume produced per flower (µl), C is

296 the sugar concentration and d is density calculated at a concentration C (g sucrose per 100 g solution)

297 by the formula $d = 0.0037921C + 0.0000178C^2 + 0.9988603$. Daily sugar production was calculated

298 first using the average estimated 24 h volume for V between scenarios and the average sugar

299 concentration recorded from produced nectar measurements for d and C and then using the measured

300 24 h nectar volume for V and its average sugar concentration for d and C. We then estimated the daily

301 nectar production at the landscape level (g ha^{-2} day^{-1}) by multiplying the sugar production by the

302 average estimated number of flowers per hectare. The number of flowers per hectare was estimated

303 from the average number of flowers counted in the plots employed for the nectar removal

304 measurements. These calculations allow a comparison between the daily sugar production at the

305 landscape level measured with the estimated 24 h volume or with the measured 24 h volume.

306 *2.5 Statistical analysis*

307 We used generalized additive mixed models (GAMM) (Wood, 2017) to test the difference between

308 fennel and lavender in terms of 1) nectar production dynamics, 2) sugar concentration of the produced

309 nectar volume, 3) measured 24 h nectar volume, 4) sugar concentration of the measured 24 h volume,

310 5) nectar removal rate, and 6) proportion of honeybees compared to other flower-visiting insects. In

311 all six models, the plant species was considered a fixed factor. For the first and second models, the

312 time since nectar draining was modeled with cubic spline smoothing. The third and fourth model

313 included the field and date and hour of sampling as fixed factors, the fifth model included the field as

314 random factor and the number of flowers, and the sixth model included the date. The error

315 distributions were gamma (model 1 and 3), binomial (model 2, 4 and 6), and gaussian with a log link

316 (model 5) (model structure and error distribution in Supplementary Table 1). These are considered

317 the most suitable error distributions for right skewed continuous data, proportions, and count data,

318 respectively (Faraway, 2016; Zuur et al., 2009).

319 The estimate of the GAMM for produced nectar volume corresponds to the species' nectar production

320 dynamics. We validated the consistency of nectar production dynamic peaks by running the model

321 100 times on a random subset of 80% data on the produced nectar volumes. From these models, we

322 extracted the ranges between the minimum and maximum peak across the models. A GAMM model

323 was also implemented to estimate the average nectar removal rate across the day using plant species,

324 number of flowers, and time of day as fixed factors. The latter two variables were modeled using

325 cubic spline smoothers. The predictions of GAMMs for the produced nectar volume and nectar

326 removal rates were used to implement the simulation parameters.

327 To draw the curve of the linear nectar production dynamic, we connected the volume of an empty

328 flower (0 μl) to the average measured 24 h volume. The residuals (difference between produced nectar

329 volume of field data and model estimates) of the linear dynamics vs the residuals of the nectar

330 production dynamics estimated using the GAMM model were compared through a GAMM model

331 having model approach (linear vs GAMM), plant species and the time since nectar draining modeled

332 with cubic spline smoothing.

333 GAMMs were also used to estimate the nectar volume collected by insects and the simulated standing

334 nectar volume over the simulation time. The time was modeled with cubic spline smoothing. The

335 most accurate scenario was identified by calculating the mean error (Hyndman & Athanasopoulos,

336 2018). Low values for mean error indicate better simulation predictions. In addition, we visually

337 inspected the residuals between the models of the simulated standing nectar volume and field standing

338 nectar volume (Figure S12 and S13). The respect of model assumption was routinely checked using

339 the DARMHA package (Figure S6). Model statistics are reposted in Supplementary Table 1. All

340 analyses were carried out with R 4.0.2 (R Core Team, 2000), using the mgcv package for GAMM

341 (Wood & Wood, 2015).

342

343 **3 RESULTS**

344 *3.1 Field experiment results*

345 *3.1.1 Measured 24 h nectar volume*

346 The measured 24 h nectar volume and the corresponding sugar concentration over 24 h were not

347 different between the two crops (Figure 3B, non-predictive GAMM; volume per flower: $0.061 \pm$

348 0.042 µl and 0.062 ± 0.036 µl; concentration per flower: 66.09 ± 13.33 % and 67.48 ± 6.75 %,

349 respectively, for fennel and lavender; mean $\pm$ SD).
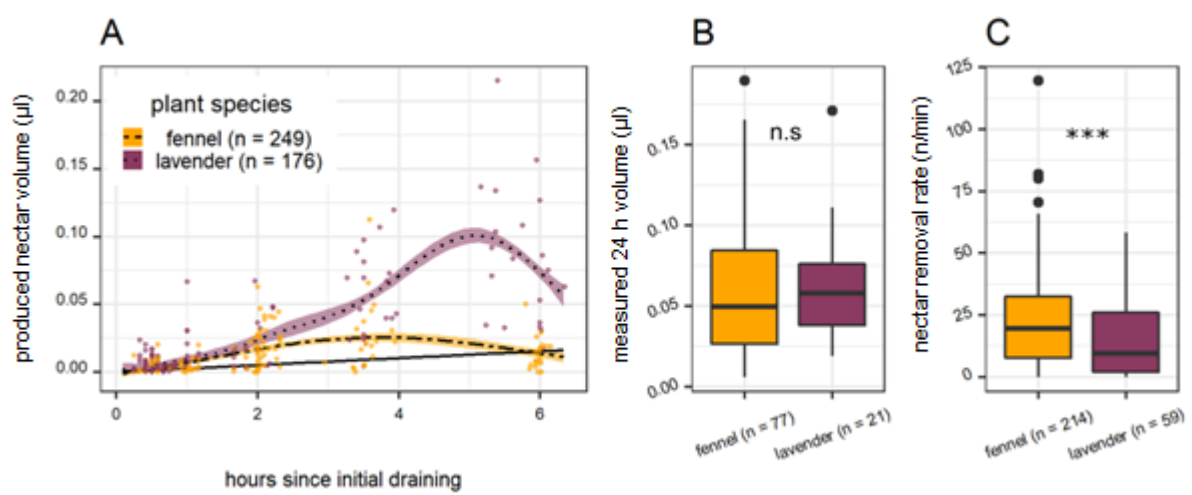
350 *3.1.2 Nectar production dynamic*

351 The nectar production dynamics of the fennel and lavender flowers were better estimated by a non-

352 linear function (Figure 3A): the residual variance was larger for linear models than for non-linear

353 across both species (Figure S7, P < 0.001 for model approach). The fennel and lavender flowers

354 showed different non-linear nectar production dynamics across time (P < 0.001 for plant species, time

355 and plant species $\times$ time since draining, R–sq (adj) = 62 %). Two hours after draining, the model

356 estimates indicated that lavender flowers had a greater produced nectar volume than fennel flowers

357 (Figure 3A). The estimates of lavender nectar production dynamics showed a steady increase of the

358 produced nectar up to 5 h (peak range: 4.8–5.5 h; Figure S8), when the produced nectar started

359 decreasing unexpectedly. Model estimates indicated a slow production and a peak of nectar

360 production for fennel at 3.75 h since draining (peak range: 3.3–3.9 h; Figure S8). The sugar

361 concentration of the produced nectar (between 0–6 h) was not correlated with time for either fennel

362   or lavender (non-predictive GAMM, R–sq (adj) = 6 %; Figure S9). The average sugar concentration

363   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

365   The nectar removal rate was significantly higher for fennel than for lavender (P < 0.001 for plant

366   species) (Figure 3C), and the nectar removal in 24 h pattern changed between fields (Figure S11). For

367   both crops, the most abundant flower-visiting insect was the honeybee; this was especially

368   pronounced for lavender (P < 0.003) (Figure S10). The proportion of honeybees to other insects was

369   0.86 ± 0.30 for lavender and 0.62 ± 0.36 for fennel (mean ± SD).

371   Figure 3. Nectar productivity of fennel and lavender, and the results of nectar removal rate by flower-visiting

372   insects. (A) Nectar production dynamics over 6 h post flower draining; dotted and dashed lines indicate the

373   GAMM estimates, the solid line indicates the estimate for the linear nectar production dynamics of nectar for

374   both species assumed using the measured 24 h volume, shaded areas are confidence intervals, and points are

375   the produced nectar volumes; (B) Measured 24 h nectar volume; (C) Insect nectar removal rate. Orange and

376   purple points, smooth lines and boxplots refer to fennel and lavender, respectively. The asterisks indicate

377   significant differences according to GAMM (n.s. = no significant difference, *** = P < 0.0001).
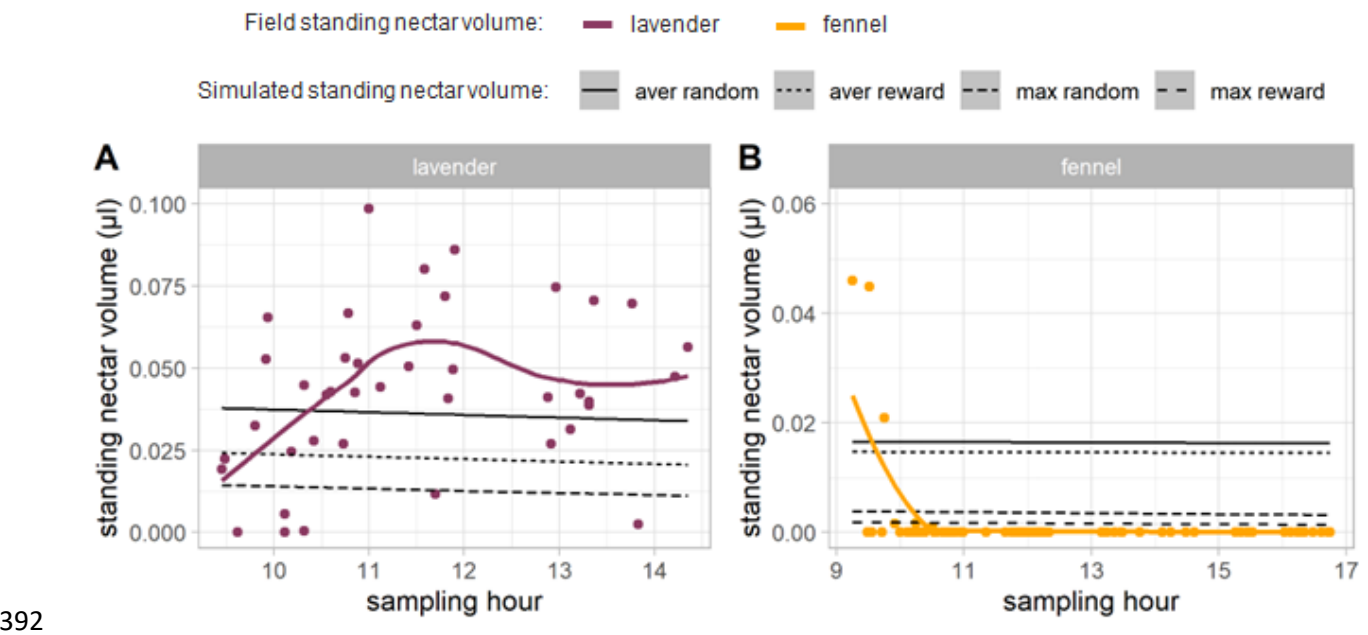
380   *3.1.4 Field standing nectar volume*

381   Fennel flowers were always found empty throughout the day except in the morning (field standing

382   nectar volume: 0.001 ± 0.007 μl, n = 81; [mean ± SD]; Figure 4B). Lavender flowers provided

383   standing nectar volume that fluctuated throughout the day (mean = 0.06 ± 0.05 μl, n = 48; Figure 4A).

384   *3.2 Simulation results*

385   *3.2.1 Simulated standing nectar volume*

386   The simulated estimate of standing nectar volume differed between species and scenarios (Figure 4,

387   S12 and S13). The scenario with the average nectar removal rate and random insect selection was the

388   most similar to the field standing nectar volume of lavender (mean error = -0.022, Table S4, Figure

389   4, and Figure S12). For fennel, the maximum nectar removal rate scenarios, either with random or

390   rewarding selection, were the most similar to the field standing nectar volume (mean error = -0.015

391   and -0.013 for random and rewarding respectively, Table S3, Figure 4 and S13).

392

393   Figure 4. Field standing nectar volumes across time and simulated standing nectar volume using four different

394   flower insect foraging scenarios: nectar removal rate average (aver) / maximum (max) × insect selection of

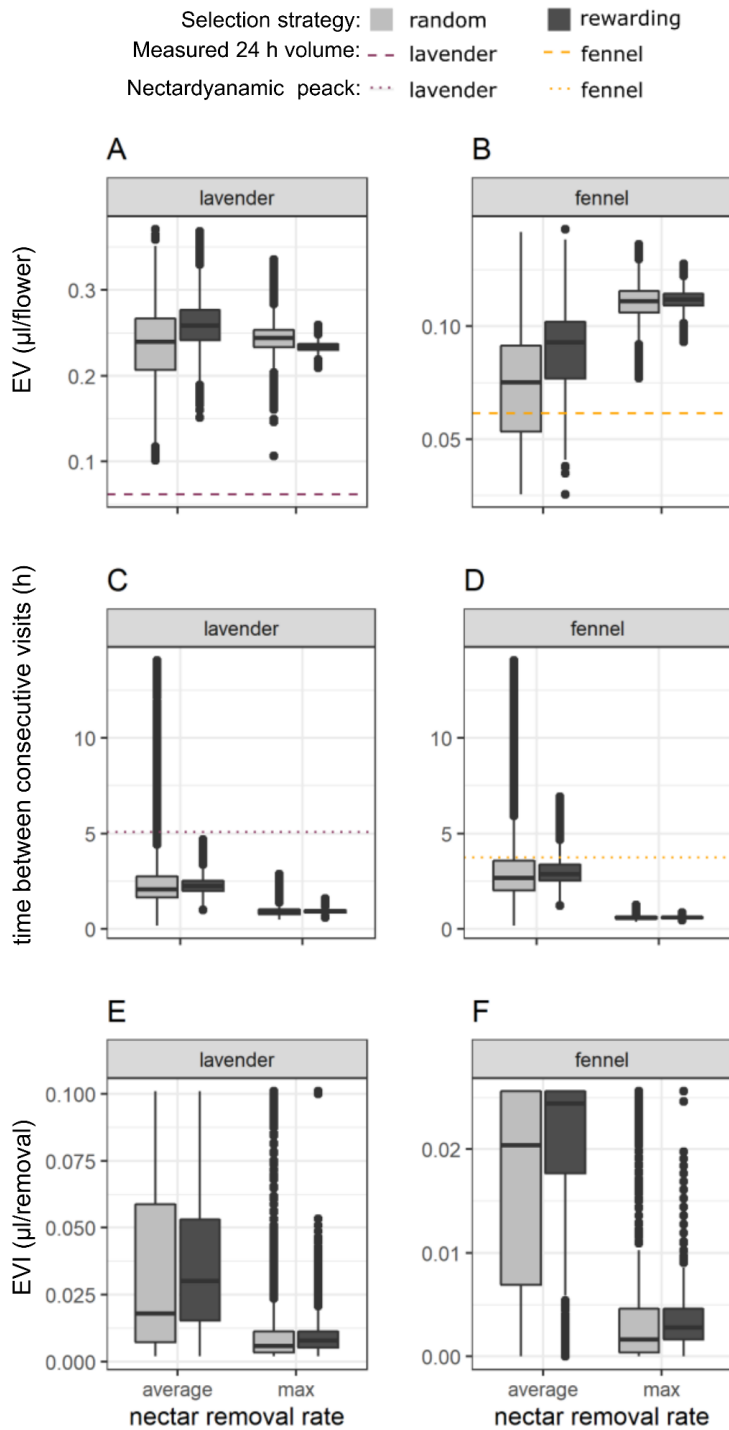395   flower random / rewarding (reward). For (A) lavender between 09:30 and 14:30 and (B) fennel between 09:15

396 and 16:45. Standing nectar scale is different between the two crops (max 0.1 µl for lavender and 0.06 for

397 fennel). Black lines show the simulated standing nectar volume, while solid lines show estimates for the

398 simulated standing nectar (orange for fennel and purple for lavender). Points show field measurements of

399 standing nectar. Field standing nectar was measured in a single field where both crops were present.

400 *3.2.2 Estimated 24 h nectar volume*

401 The estimated 24 h nectar volume varied between scenarios, with lavender having the highest

402 estimated 24 h volume under the average nectar removal rate and rewarding selection scenario (0.260

403 ± 0.003 µl) and the lowest estimated 24 h volume under the maximum nectar removal rate and

404 rewarding selection scenario (0.233 ± 0.006 µl; Figure 5A). Fennel estimated 24 h volume was the

405 highest in the maximum nectar removal rate and rewarding selection scenario (0.111 ± 0.004 µl) and

406 the lowest in the average nectar removal rate and random selection scenario (0.073 ± 0.025 µl) (mean

407 ± SD) (Figure 5B). Under all scenarios and for both species, the average estimated 24 h volumes were

408 higher than the average measured 24 h volumes (Figure 5A and 5B, mean values and 95% confidence

409 intervals are included in Table S4).

410 *3.2.3 Time between nectar removals and the estimated nectar volumes collected by insects*

411 Both for fennel and lavender, the average time between two consecutive flower nectar removals was

412 always shorter than the time required for the flower to reach the peak of nectar production dynamics

413 (highest average time span between visits 2.33 ± 1.22 h and 3.12 ± 1.82 h for lavender and fennel,

414 respectively; Figure 5C and Figure 5D). In the maximum nectar removal scenario, flowers were

415 always visited before the nectar production dynamic peak was reached. The estimated nectar volumes

416 collected by insects were highest in the average nectar removal rate and rewarding selection scenario

417 (0.022 ± 0.003 µl for fennel and 0.046 ± 0.003 µl for lavender) and the lowest in the maximum nectar

418 removal rate and random selection scenario for both plant species (0.004 ± 0.001 for fennel and 0.014

419 ± 0.002 µl for lavender) (mean ± SD) (Fig 5E and 5F, mean values and 95% confidence intervals are

420 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).

427 The daily sugar production at the landscape level calculated with the estimated 24 h volume was 5797

428 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

429 g ha^{-2} day^{-1} for fennel and lavender, respectively when estimated with the measured 24 h volume.

430

431 **4 DISCUSSION**

432 In this study we tested if the widespread measure of the nectar production of a flower, i.e. after 24 h

433 of isolation from insects ("measured 24 h" volume; e.g. Baude et al., 2016; Hicks et al., 2016;

434 Timberlake et al., 2019) accurately represents the nectar productivity of two common mass-flowering

435 crops, fennel and lavender. This measure assumes a linearity in the dynamic of nectar production and

436 consequently no effects of insect foraging activity on plant nectar productivity. Here, we found non-

437 linear nectar production dynamics for the two crops. Hence, the assumption of linearity was not met.

438 We then developed a simulation model of the estimated 24 h volume of nectar taking into account

439 the non-linear dynamic of nectar production and the insect foraging activity. The estimated 24 h

440 nectar volumes generated by our simulation were affected by the insect foraging activity. The

441 estimated 24 h volume was greater than the measured 24 h volume, substantially for lavender and

442 slightly for fennel.

443 *4.1 Nectar resources produced by lavender and fennel for flower visitors*

444 We found that lavender flowers produced nectar more quickly than fennel flowers (median speed

445 1.31×10^{-4} and 0.52×10^{-4} µl/min). While their production appears similar on a 24-hour scale, our

446 results on smaller time intervals (6 hours) showed that lavender actually produced more nectar than

447 fennel. Therefore, we believe that in order to correctly assess the nectar production of plants and by

448 extension of plant communities and landscapes, we must take into account the dynamics of nectar

449 production which will ultimately allow us to better assess the availability of resources offered to

450 flower visiting-insects.

451 In a time span of 3.75 h after draining, lavender flowers had a nectar production dynamic that

452 exceeded the average measured 24 h volume. This result suggests that lavender flowers may reabsorb

453 nectar when it is not exploited for long periods. As hypothesized for other plants, a re-absorption

454 mechanism might reduce the energy costs to attract pollinators required to ensure seed sets (Burquez

455 & Corbet, 1991; Nepi & Stpiczyńska, 2008; Pacini & Nepi, 2007). Signs of nectar reabsorption have

456 previously been observed in *Lavandula pubescens* (Nuru et al., 2015), but have never been studied

457 for *Lavandula hybrida*; therefore, this finding must be confirmed through dedicated analyses.

458 Regarding fennel, the nectar production dynamic peaked before 4 h, but the peak was lower than the

459 measured 24 h volume. This difference suggests that the nectar production between 6 and 24 h after

460 draining continues. Peaks of the dynamic of nectar production varied considerably probably because

461 of the individual flower and plant phenotypic variations (Castellanos et al., 2002; Luo et al., 2014;

462 Nicolson & Nepi, 2005), as well as by exogenous factors (e.g. temperature) (Chabert et al., 2018).

463 For example, *Carum carvi* (Apiaceae) plants of the same variety grown under the same controlled

464 conditions showed fourfold differences in the produced nectar between anthesis and fertilization

465 (Langenberger & Davis, 2002). Therefore, the nectar production dynamics of lavender and fennel

466 should be considered as rough estimates of the average produced nectar, which may considerably

467 change during their flowering period. Despite these limitations our results showed that the nectar

468 production dynamic of both crops is more likely non-linear than linear.

469 For both plants, the measured 24 h volume was quantified in flowers that were not drained before

470 flower isolation, following the protocol adopted by previous studies (e.g., Baude et al., 2016; Hicks

471 et al., 2016; Timberlake et al., 2019). This may have led to imprecise estimation of the measured 24

472 h volume, given the time of the last insect visit was not known. We therefore cannot exclude the

473 possibility that flowers have produced nectar for more than 24 h. However, we found this unlikely as

474 fennel flowers in the area were usually empty, given the high nectar removal rate, hence the bias

475 should have been limited and not influential. For lavender, even if we cannot totally exclude that the

476 production might continue after 24 h, the peak in nectar production occurs a few hours after draining,

477 hence the bias could also be minimal here.

478 *4.2 Field standing nectar and flower-visiting insect foraging*

479 We found that the rate of nectar removal by insects was higher in fennel than in lavender. Honeybees

480 were the dominant flower visitors for both crops, although its dominance was less pronounced in

481 fennel. Honeybee dominance was likely due to the numerous managed honeybee colonies placed in

482 the study area for honey production. When measured in the same area, the standing nectar volume

483 was high for lavender, whereas it was close to zero from the first hour onwards for fennel. These

484 results suggest that the nectar produced by fennel is immediately consumed by insects.

485 Simultaneously, flower visitors' nectar removal rate seemed to be lower for the lavender flowers,

486 despite their larger nectar rewards. This outcome may be explained by the difference in the floral

487 traits of the two crops. Fennel presents open and easily accessible flowers grouped in inflorescences

488 which allow flower-visiting insects to rapidly detect and gather resources, and also to switch between

489 flowers. In contrast, in lavender, flower handling is more complicated because of the narrow

490 morphology of the flower (Balfour et al., 2013). This was reflected by the diversity of pollinators

491 observed on fennel flowers suggesting that fennel flower traits do not constrain insect visits (Schurr

492 et al., 2022; Smith-Ramírez et al., 2005; Thompson, 2001). On the other hand, we only observed few

493 species of flower-visiting insects foraging on lavender (Schurr, unpubl.), and this was also reported

494 in previous studies (Balfour et al., 2013; Benachour, 2017; Valchev et al., 2022). This could also be

495 explained by the fact that lavender does not produce pollen contrary to fennel and thus may attract

496 fewer flower-visiting species. These results suggest that future research should focus on quantifying

497 insect species-specific nectar resource availability.

498 *4.3 Simulation model results*

499 This study simulated the estimated 24 h nectar volume, the standing nectar volume, and the nectar

500 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).

526 Nevertheless, we found a general pattern for both crops: the estimated 24 h volume was always greater

527 than the measured 24 h volume. This pattern implies an underestimation of the daily sugar production

528 at the plant and at the landscape scale when the measured 24 h volume is used for its estimation. The

529 difference between the estimated and measured 24 h volume is probably due to the short time between

530 two nectar removals. In fact, the simulation showed that the time between consecutive removals was

531 often shorter than the time required for the flower to produce nectar up to the peak of the nectar

532 production dynamics. Therefore, flowers were pushed to continue nectar production constantly.

533 *4.4 Conclusion*

534 A short time for flowers to reach the peak of nectar production dynamic is consistent with previous

535 studies showing that flowers can fully produce nectar within a few hours, rather than requiring a

536 whole day (Castellanos et al., 2002; Luo et al., 2014). Despite this, most studies focusing on nectar

537 use the 24 h volume as a proxy of plant nectar productivity, probably because of feasibility, time and

538 money constraints. Our results clearly highlight that the measured 24 h volume underestimates the

539 plant nectar productivity. We showed that the activity of pollinators seems to favor the production of

540 nectar. This underestimation may be particularly prominent in environments where pollinators are

541 abundant, such as in intense beekeeping areas or in mass-flowering crops where nectar removal rates

542 are particularly high, given the high attractiveness of these crops to pollinators.

543 Our field and simulated results on nectar production provide a new method to assess the production

544 of resources among flowers that should be seen as complementary to more common methods.

545 However, this method may be practically difficult to set up in large studies on many plant species

546 because much time is needed to collect field variables. A first pragmatic step aiming to a better

547 understanding of plant nectar production and its effect on flower-visiting insects can be to measure

548 the nectar production of different plant species in a short time (e.g. six hours). This would highlight

549 whether the nectar productivity is in line with the measured 24 h volume of nectar. When this is not

550 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.

REFERENCES

Aronne, G., Giovanetti, M., Guarracino, M. R., & de Micco, V. (2012). Foraging rules of flower selection applied by colonies of *Apis mellifera*: Ranking and associations of floral sources. *Functional Ecology*, *26*(5), 1186–1196. https://doi.org/10.1111/j.1365-2435.2012.02017.x

Balfour, N. J., Garbuzov, M., & Ratnieks, F. L. W. (2013). Longer tongues and swifter handling: Why do more bumble bees (*Bombus spp.*) than honey bees (*Apis mellifera*) forage on lavender (*Lavandula spp.*)? *Ecological Entomology*, *38*(4), 323–329. https://doi.org/10.1111/een.12019

Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., … Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, *530*(7588), 85–88. https://doi.org/10.1038/nature16532

Benachour, K. (2017). Insect visitors of lavender (*Lavandula officinalis* L.): comparison of quantitative and qualitative interactions of the plant with its main pollinators. *African Entomology*, *25*(2), 435–444. https://doi.org/10.4001/003.025.0435

Biella, P., Akter, A., Muñoz-Pajares, A. J., Federici, G., Galimberti, A., Jersáková, J., … Mangili, L. (2021). Investigating pollination strategies in disturbed habitats: The case of the narrow-endemic toadflax *Linaria tonzigii* (Plantaginaceae) on mountain screes. *Plant

Ecology, *222*(4), 511–523. https://doi.org/10.1007/s11258-021-01123-7

Burquez, A., & Corbet, S. A. (1991). Do flowers reabsorb nectar? *Functional Ecology*, *5*(3), 369–379.

Carisio, L., Schurr, L., Masotti, V., Porporato, M., Nève, G., Affre, L., Gachet, S., Geslin, B (2022). Data from: Estimates of nectar productivity through a simulation approach differ from the nectar produced in 24 h. *OSF repository*. https://doi.org/10.17605/OSF.IO/AHGVU

Chabert, S., Lemoine, T., Raimond Cagnato, M., Morison, N., & Vaissière, B. E. (2018). Flower age expressed in thermal time: is nectar secretion synchronous with pistil receptivity in oilseed rape (*Brassica napus* L.)? *Environmental and Experimental Botany*, *155*(November), 628–640. https://doi.org/10.1016/j.envexpbot.2018.08.004

Corbet, S. A. (2003). Nectar sugar content: Estimating crop and secretion rate in the field. *Apidologie*, *34*, 1–10. https://doi.org/10.1051/apido

Corbet, S. A., Bee, J., Dasmahapatra, K., Gale, S., Gorringe, E., La Ferla, B., … Vorontsova, M. (2001). Native or exotic? Double or single? Evaluating plants for pollinator-friendly Gardens. *Annals of Botany*, *87*(2), 219–232. https://doi.org/10.1006/anbo.2000.1322

Corbet, S. A., Kerslake, C. J. C., Brown, D., & Morland, N. E. (1984). Can Bees Select Nectar-Rich Flowers in a Patch? *Journal of Apicultural Research*, *23*(4), 234–242. https://doi.org/10.1080/00218839.1984.11100638

Donkersley, P., Rhodes, G., Pickup, R. W., Jones, K. C., & Wilson, K. (2014). Honeybee nutrition is linked to landscape composition. *Ecology and Evolution*, *4*(21), 4195–4206. https://doi.org/10.1002/ece3.1293

596   Dötterl, S., Glück, U., Jürgens, A., Woodring, J., & Aas, G. (2014). Floral reward,

597   advertisement and attractiveness to honey bees in dioecious Salix caprea. *PLoS ONE*,

598   *9*(3), 1–11. doi: 10.1371/journal.pone.0093421

599   Duffield, G. E., Gibson, R. C., Gilhooly, P. M., Hesse, A. J., Inkley, C. R., Gilbert, F. S., &

600   Barnard, C. J. (1993). Choice of flowers by foraging honey bees (*Apis mellifera*): Possible

601   morphological cues. *Ecological Entomology*, *18*(3), 191–197.

602   https://doi.org/10.1111/j.1365-2311.1993.tb01089.x

603   Dussaubat, C., Maisonnasse, A., Belzunces, L. P., Brunet, J. L., & Kretzschmar, A. (2021).

604   Preliminary report of honeybee physiological changes pre- and post-hybrid lavender

605   season in high and low weight gain colonies. *Apidologie*, *52*(2), 463–472.

606   https://doi.org/10.1007/s13592-020-00835-5

607   Escriche, I., Sobrino-Gregorio, L., Conchado, A., & Juan-Borrás, M. (2017). Volatile profile in

608   the accurate labelling of monofloral honey. The case of lavender and thyme honey. *Food*

609   *Chemistry*, *226*, 61–68. https://doi.org/10.1016/j.foodchem.2017.01.051

610   Faraway, J. J. (2016). *Extending the linear model with R: generalized linear, mixed effects and*

611   *nonparametric regression models*. Chapman and Hall/CRC.

612   Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., … Vereecken, N. J.

613   (2017). Massively introduced managed species and their consequences for plant–

614   pollinator interactions. *Advances in Ecological Research*, *57*, 147–199.

615   https://doi.org/10.1016/bs.aecr.2016.10.007

616   Goulson, D., Chapman, J. W., & Hughes, W. O. H. (2001). Discrimination of unrewarding

617   flowers by bees; direct detection of rewards and use of repellent scent marks. *Journal of*

618   *Insect Behavior*, *14*(5), 669–678. https://doi.org/10.1023/A:1012231419067

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined Stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957. https://doi.org/10.1126/science.1255957

Guezen, J. M., & Forrest, J. R. K. (2021). Seasonality of floral resources in relation to bee activity in agroecosystems. *Ecology and Evolution*, *11*(7), 3130–3147. https://doi.org/10.1002/ece3.7260

Guitton, Y., Nicolè, F., Moja, S., Benabdelkader, T., Valot, N., Legrand, S., … Legendre, L. (2010). Lavender inflorescence: A model to study regulation of terpenes synthesis. *Plant Signaling and Behavior*, *5*(6), 749–751. https://doi.org/10.4161/psb.5.6.11704

Herrera, C. M. (1990). Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. *Oikos*, *58*(3), 277–288. Retrieved from https://www.jstor.org/stable/3545218

Hicks, D. M., Ouvrard, P., Baldock, K. C. R., Baude, M., Goddard, M. A., Kunin, W. E., … Stone, G. N. (2016). Food for pollinators: Quantifying the nectar and pollen resources of urban flower meadows. *PLOS ONE*, *11*(6), e0158117. https://doi.org/10.1371/journal.pone.0158117

Hill, P. S. M., Hollis, J., & Wells, H. (2001). Foraging decisions in nectarivores: Unexpected interactions between flower constancy and energetic rewards. *Animal Behaviour*, *62*(4), 729–737. doi: 10.1006/anbe.2001.1775

Hyndman, R. J., & Athanasopoulos, G. (2018). *Forecasting: principles and practice.*

Iwasaki, J. M., & Hogendoorn, K. (2022). Mounting evidence that managed and introduced bees have negative impacts on wild bees: an updated review. *Current research in insect science*, 100043.

642   Knauer, A. C., Kokko, H., & Schiestl, F. P. (2021). Pollinator behaviour and resource

643   limitation maintain honest floral signaling. *Functional Ecology*, *35*(11), 2536–2549.

644   https://doi.org/10.1111/1365-2435.13905

645   Krishna, S., & Keasar, T. (2018). Morphological complexity as a floral signal: From

646   perception by insect pollinators to co-evolutionary implications. *International Journal of*

647   *Molecular Sciences*, *19*(6), 1–15. doi: 10.3390/ijms19061681

648   Langenberger, M. W., & Davis, A. R. (2002). Temporal changes in floral nectar production,

649   reabsorption, and composition associated with dichogamy in annual caraway (*Carum*

650   *carvi*; Apiaceae). *American Journal of Botany*, *89*(10), 1588–1598.

651   https://doi.org/10.3732/ajb.89.10.1588

652   Lichtenberg, E. M., Heiling, J. M., Bronstein, J. L., & Barker, J. L. (2020). Noisy communities

653   and signal detection: Why do foragers visit rewardless flowers?: Signal detection in floral

654   communities. *Philosophical Transactions of the Royal Society B: Biological Sciences*,

655   *375*(1802). doi: 10.1098/rstb.2019.0486

656   Luo, E. Y., Ogilvie, J. E., & Thomson, J. D. (2014). Stimulation of flower nectar

657   replenishment by removal: a survey of eleven animal-pollinated plant species. *Journal of*

658   *Pollination Ecology*, *12*(7), 52–62. https://doi.org/10.26786/1920-7603(2014)2

659   Nepi, M., & Stpiczyńska, M. (2008). The complexity of nectar: secretion and resorption

660   dynamically regulate nectar features. *Naturwissenschaften*, *95*(3), 177–184.

661   https://doi.org/10.1007/s00114-007-0307-2

662   Nicolson, S. W., & Nepi, M. (2005). Dilute nectar in dry atmospheres: nectar secretion

663   patterns in *Aloe castanea* (Asphodelaceae). *International Journal of Plant Sciences*,

664   *166*(2), 227–233. https://doi.org/10.1086/427616

Nuru, A., Al-Ghamdi, A. A., Tena, Y. T., Shenkut, A. G., Ansari, M. J., et al. (2015) Floral
Phenology, Nectar Secretion Dynamics, and Honey Production Potential, of Two
Lavender Species (*Lavandula Dentata*, and *L. Pubescens*) in Southwestern Saudi Arabia.
Journal of Apicultural Science, *59*(2), 135–144. https://doi.org/10.1515/jas-2015-0028

Ohashi, K., & Thomson, J. D. (2005). Efficient harvesting of renewing resources. *Behavioral
Ecology*, 16(3), 592–605. doi: 10.1093/beheco/ari031

Ordano, M., & Ornelas, J. F. (2004). Generous-like flowers: nectar production in two epiphytic
bromeliads and a meta-analysis of removal effects. *Oecologia*, *140*(3), 495–505.
https://doi.org/10.1007/s00442-004-1597-0

Ornelas, J. F., & Lara, C. (2009). Nectar replenishment and pollen receipt interact in their
effects on seed production of Penstemon roseus. *Oecologia*, *160*(4), 675–685.
https://doi.org/10.1007/s00442-009-1337-6

Pacini, E., & Nepi, M. (2007). *Nectar production and presentation*. In nectaries and nectar (pp.
167–214). Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-5937-7_4

Parachnowitsch, A. L., Manson, J. S., & Sletvold, N. (2019). Evolutionary ecology of nectar.
Annals of Botany, *123*(2), 247–261. https://doi.org/10.1093/aob/mcy132

Pleasants, John, M., & Zimmerman, M. (1983). The distribution of standing crop of nectar:
what does it really tell us? Oecologia, 57, 412–414.

Piccaglia, R., & Marotti, M. (2001). Characterization of some Italian types of wild fennel
(*Foeniculum vulgare* mill.). *Journal of Agricultural and Food Chemistry*, *49*(1), 239–244.
https://doi.org/10.1021/jf000636+

Quinlan, G., Milbrath, M., Otto, C., Smart, A., Iwanowicz, D., Cornman, R. S., & Isaacs, R.
(2021). Honey bee foraged pollen reveals temporal changes in pollen protein content and

changes in forager choice for abundant versus high protein flowers. *Agriculture, Ecosystems and Environment*, *322*(August). https://doi.org/10.1016/j.agee.2021.107645, 107645

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Roulston, T. H., & Goodell, K. (2011). The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, *56*, 293–312. https://doi.org/10.1146/annurev-ento-120709-144802

Sáez, A., Morales, C. L., Garibaldi, L. A., & Aizen, M. A. (2017). Invasive bumble bees reduce nectar availability for honey bees by robbing raspberry flower buds. *Basic and Applied Ecology*, *19*, 26–35. https://doi.org/10.1016/j.baae.2017.01.001

Schurr, L., Geslin, B., Affre, L., Gachet, S., Delobeau, M., Brugger, M., … Masotti, V. (2021). Landscape and local drivers affecting flying insects along fennel crops (*Foeniculum vulgare*, Apiaceae) and implications for its yield. *Insects*, *12*(5), 1–16. https://doi.org/10.3390/insects12050404

Schurr, L., Masotti, V., Geslin, B., Gachet, S., Mahé, P., Jeannerod, L., & Affre, L. (2022). To what extent is fennel crop dependent on insect pollination? *Agriculture, Ecosystems and Environment*, *338*(October 2021). doi: 10.1016/j.agee.2022.108047

Smith-Ramírez, C., Martinez, P., Nuñez, M., González, C., & Armesto, J. J. (2005). Diversity, flower visitation frequency and generalism of pollinators in temperate rain forests of Chiloé Island, Chile. *Botanical Journal of the Linnean Society*, *147*(4), 399–416. https://doi.org/10.1111/j.1095-8339.2005.00388.x

Stahl, J. M., Nepi, M., Galetto, L., Guimarães, E., & Machado, S. R. (2012). Functional

aspects of floral nectar secretion of *Ananas ananassoides*, an ornithophilous bromeliad

from the Brazilian savanna. *Annals of Botany*, *109*(7), 1243–1252.

https://doi.org/10.1093/aob/mcs053

Thompson, J. D. (2001). How do visitation patterns vary among pollinators in relation to floral

display and floral design in a generalist pollination system? *Oecologia*, *126*(3), 386–394.

https://doi.org/10.1007/s004420000531

Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral

resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied

Ecology*, *56*(7), 1585–1596. https://doi.org/10.1111/1365-2664.13403

Torné-Noguera, A., Rodrigo, A., Osorio, S., & Bosch, J. (2016). Collateral effects of

beekeeping: Impacts on pollen-nectar resources and wild bee communities. *Basic and

Applied Ecology*, *17*(3), 199–209. https://doi.org/10.1016/j.baae.2015.11.004

Valchev, H., Kolev, Z., Stoykova, B., & Kozuharova, E. (2022). Pollinators of *Lavandula

angustifolia* Mill., an important factor for optimal production of lavender essential oil.

BioRisk, *17*, 297–307. doi: 10.3897/biorisk.17.77364

Zimmerman, M. (1988). Pollination Biology of Montane Plants: Relationship Between Rate of

Nectar Production and Standing Crop. *The American Midland Naturalist*, *120*(1), 50–57.

Retrieved from https://www.jstor.org/stable/2425886

Wignall, V. R., Campbell Harry, I., Davies, N. L., Kenny, S. D., McMinn, J. K., & Ratnieks,

F. L. W. (2020). Seasonal variation in exploitative competition between honeybees and

bumblebees. *Oecologia*, *192*(2), 351–361. https://doi.org/10.1007/s00442-019-04576-w

Wood, S. N. (2017). Generalized additive models: An introduction with *R*. CRC Press

733   Wood, S., & Wood, M. S. (2015). Package 'mgcv.' *R package Version*, *1*, 29

734   Ye, Z. M., Jin, X. F., Wang, Q. F., Yang, C. F., & Inouye, D. W. (2017). Nectar replenishment

735   maintains the neutral effects of nectar robbing on female reproductive success of *Salvia*

736   *przewalskii* (Lamiaceae), a plant pollinated and robbed by bumble bees. *Annals of Botany*,

737   *119*(6), 1053–1059. https://doi.org/10.1093/aob/mcw285

738

739   **ABSTRACT**

740   Le nectar est une ressource alimentaire indispensable à de nombreux insectes. Une méthode est

741   communément utilisée pour estimer la production de nectar: elle consiste à échantillonner une fleur

742   après 24h d'isolement aux insectes (la fleur est ensachée). Cette méthode postule que toutes les fleurs

743   produisent du nectar à vitesse constante, indépendamment des prélèvements par les insectes.

744   Toutefois, toutes les plantes ne sont pas égales en termes de vitesse de production de nectar, et il a

745   aussi été prouvé que selon les espèces de plantes, le butinage a un effet (positif ou négatif) sur la

746   production de nectar. Il est donc important de connaître les rythmes de production nectarifères plus

747   précisément   avant   d'évaluer   la   productivité   des   plantes.

748   Dans une étude en plein champs, nous avons suivi la production de nectar de 2 plantes aromatiques

749   largement cultivées, le lavandin (*Lavandula hybrida*) et le fenouil (*Foeniculum vulgare*), en mesurant

750   la production de nectar sur différents pas de temps (inférieurs à 24h), et observé les comportements

751   de butinage afin de simuler des scénarios de visites d'insectes floricoles sur chaque culture.

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

753   Toutefois, le lavandin reconstitue les stocks de nectar beaucoup plus rapidement que le fenouil. En

754   simulant différents comportements de visite des insectes floricoles, nous avons mis en évidence que

755   la production quotidienne de nectar varie grandement, et que cette valeur est toujours très supérieure

756   à la mesure réalisée après 24h d'isolement, pour le lavandin comme pour le fenouil.

757   Ces travaux démontrent qu'une prise en compte des insectes floricoles et de la dynamique de

758   production est indispensable à l'estimation précise des quantités de nectar.