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1 **Long-term experimental drought alters floral scent and pollinator visits in a**  
2 **Mediterranean plant community despite overall limited impacts on plant phenotype**  
3 **and reproduction**

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7

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12

13 Running title: Pollination in a drier world.

14

15 **Abstract**

16 1. Pollinators are declining globally, with climate change implicated as an important driver.  
17 Climate change can induce phenological shifts and reduce floral resources for pollinators, but  
18 little is known about its effects on floral attractiveness and how this might cascade to affect  
19 pollinators, pollination functions and plant fitness.

20 2. We used an *in situ* long-term drought experiment to investigate multiple impacts of  
21 reduced precipitation in a natural Mediterranean shrubland, a habitat where climate change is  
22 predicted to increase the frequency and intensity of droughts. Focusing on three insect-  
23 pollinated plant species that provide abundant rewards and support a diversity of pollinators  
24 (*Cistus albidus*, *Salvia rosmarinus* and *Thymus vulgaris*), we investigated the effects of  
25 drought on a suite of floral traits including nectar production and floral scent. We also  
26 measured the impact of reduced rainfall on pollinator visits, fruit set and germination in  
27 *S. rosmarinus* and *C. albidus*.

28 3. Drought altered floral emissions of all three plant species qualitatively, and reduced nectar  
29 production in *T. vulgaris* only. *Apis mellifera* and *Bombus gr. terrestris* visited more flowers  
30 in control plots than drought plots, while small wild bees visited more flowers in drought  
31 plots than control plots. Pollinator species richness did not differ significantly between  
32 treatments. Fruit set and seed set in *S. rosmarinus* and *C. albidus* did not differ significantly  
33 between control and drought plots, but seeds from drought plots had slower germination for  
34 *S. rosmarinus* and marginally lower germination success in *C. albidus*.

35 5. *Synthesis*. Overall, we found limited but consistent impacts of a moderate experimental  
36 drought on floral phenotype, plant reproduction and pollinator visits. Increased aridity under  
37 climate change is predicted to be stronger than the level assessed in the present study.  
38 Drought impacts will likely be stronger and this could profoundly affect the structure and  
39 functioning of plant-pollinator networks in Mediterranean ecosystems.

40

41 **Keywords**

42 Climate change; Floral traits; Plant fitness; Pollination; Reduced rainfall; Volatile Organic

43 Compound (VOC); Water deficit; Water-limited.

44

45

46 **Second language abstract**

47 1. Le changement climatique est une des causes importantes du déclin des pollinisateurs. Il

48 peut notamment provoquer une réduction de la production de ressources florales et des

49 décalages phénologiques entre les périodes de floraison et d'activité des pollinisateurs.

50 Cependant les effets du changement climatique sur l'attractivité des fleurs, et les

51 conséquences sur les interactions plantes-pollinisateurs, les fonctions de pollinisation et la

52 reproduction des plantes restent peu connus.

53 2. Nous avons mené une expérimentation *in situ* simulant une intensification de la sécheresse

54 à long terme pour mesurer les multiples impacts de la réduction des précipitations dans une

55 communauté végétale Méditerranéenne caractéristique de la garrigue écorchée. Dans cet

56 habitat, les prédictions climatiques se caractérisent par une augmentation de la fréquence et

57 de l'intensité des épisodes de sécheresse. Nous avons centré nos mesures sur trois espèces

58 parmi les plus abondantes et fournissant la plus grande quantité de ressources florales pour

59 les pollinisateurs (*Cistus albidus*, *Salvia rosmarinus* et *Thymus vulgaris*). Nous avons mesuré

60 un ensemble de trait floraux, y compris la production de nectar et l'émission d'odeurs florales

61 sur les plantes en conditions de sécheresse ou sous précipitations naturelles (contrôle). Nous

62 avons également mesuré l'effet de la réduction des précipitations sur les visites des

63 pollinisateurs, la production de fruits et la germination chez *S. rosmarinus* et *C. albidus*.

64 3. La réduction des précipitations a provoqué une altération des odeurs florales des trois  
65 espèces de plantes, ainsi qu'une réduction de la production de nectar chez *T. vulgaris*. *Apis*  
66 *mellifera* et *Bombus gr. terrestris* ont visité plus de fleurs dans les parcelles contrôle que dans  
67 les parcelles en conditions de sécheresse, alors que les petites abeilles sauvages ont montré un  
68 comportement opposé. La richesse spécifique des pollinisateurs n'était pas significativement  
69 différente entre les deux traitements. Finalement, la production de fruits et de graines de  
70 *S. rosmarinus* et *C. albidus* n'étaient pas significativement modifiées par le traitement. Enfin,  
71 les graines issues de plantes en conditions de sécheresse ont germé légèrement plus lentement  
72 chez *S. rosmarinus*, et avec un taux de germination légèrement plus faible chez *C. albidus*.

73 5. *Synthèse*. Globalement, la réduction des précipitations, relativement modérée, a provoqué  
74 des effets limités mais consistants sur les traits floraux, ainsi que sur les visites des  
75 pollinisateurs et sur la reproduction des plantes. L'intensification prédite des épisodes de  
76 sécheresse dans cette région est plus importante que celle testée dans cette étude. Les impacts  
77 seront donc probablement plus forts, avec des conséquences possibles importantes sur la  
78 structure et le fonctionnement des réseaux de pollinisation dans les écosystèmes  
79 méditerranéens.

## 80 **1. Introduction**

81 Pollinators are essential to the reproduction of more than 90 % of angiosperm species  
82 (Ollerton et al., 2011) and pollinate 75 % of crop species, representing an annual market  
83 value of \$235 to 577 billion (IPBES, 2016; Christmann, 2020). Anthropogenic habitat  
84 destruction and land-use intensification (including insecticide use) are commonly thought to  
85 be the main drivers of pollinator population declines globally (Potts et al., 2016; IPBES,  
86 2016; Wagner, 2020; Dicks et al., 2021; Zattara & Aizen, 2021). The impacts of climate  
87 change on plant-pollinator interactions and pollinator populations have been considerably less  
88 studied, and could have been underestimated (Kammerer et al., 2021; Raven & Wagner,  
89 2021). There is an urgent need to document the causes and mechanisms of pollinator decline  
90 and especially the role of climate change to predict and prevent further disruption of  
91 pollination functions.

92

93 Climate change may negatively affect plant-pollinator interactions in many ways (Gérard et  
94 al., 2020), by causing phenological mismatches between the period of activity of pollinator  
95 species and the flowering period of their host plants (Memmott et al., 2007; Duchenne et al.,  
96 2020), shifts of their geographic range (Rasmont et al., 2015), and a change in floral  
97 resources (pollen and nectar; Waser & Price, 2016) which compose the bulk of pollinators'  
98 diet. Indeed, nectar production is sensitive to the quantity and seasonality of rainfall, and  
99 production is generally lower in drier conditions (Kuppler & Kotowska, 2021) especially in  
100 temperate regions (Waser & Price, 2016; Gallagher & Campbell, 2017; Phillips et al., 2018).  
101 Nectar production is also sensitive to temperature and many species reach maximum  
102 production at an optimal temperature (Jakobsen & Kritjansson, 1994; Petanidou & Smets,  
103 1996). Drought-induced reduction in the production and timing of floral resources available

104 to pollinators could therefore lead to declines in their abundance (Thomson, 2016; Forister et  
105 al., 2018; Timberlake et al., 2020).

106

107 Although much less studied, climate change can also disrupt plant-pollinator interactions in a  
108 more subtle way, by altering floral signalling and attractiveness (Walter, 2020). Pollinators  
109 use and learn visual and olfactory flower signals – including floral display (number of  
110 flowers), flower size and colour, and floral scent – to detect, recognize, and locate their  
111 preferred floral resources (Raguso, 2008; Giurfa & Sandoz, 2012; Burkle & Runyon, 2019).  
112 Floral scent is a blend of many different volatile organic compounds (VOCs) emitted by  
113 floral tissue that guide pollinators towards floral resources. The activation of plant defences  
114 also leads to the emission of specific VOCs from inflorescence tissue, which blend in  
115 pollinator-attractive floral scent plumes (Wright & Schiestl, 2009; Cunningham, 2012;  
116 Borghi et al., 2019). Therefore, floral scent is highly sensitive to increased temperature (Yuan  
117 et al., 2009; Farré-Armengol et al., 2014) and drought, with increased emissions under  
118 moderate stress (Burkle & Runyon, 2016; Campbell et al., 2019; Glenny et al., 2018). Altered  
119 floral attractiveness could therefore affect pollinators' foraging behaviour and resource  
120 choices (Flacher et al., 2017; 2020). For instance, herbivore-induced plant volatiles present in  
121 floral scent tend to deter pollinators from floral resources in attacked plants (Kessler et al.,  
122 2011; Hoffmeister & Junker, 2017). Similarly water-limited plants can be less visited by  
123 pollinators due to changes in flower attractiveness and floral rewards (Descamps et al., 2018;  
124 Rering et al., 2020).

125

126 More broadly, climate change and especially drought affects plant physiology and  
127 development. Drought reduces stomatal conductance and therefore carbon uptake, reducing  
128 photosynthesis and plant growth (Reddy et al., 2004; Prieto et al., 2009; Saunier et al., 2018),

129 and plant reproduction (Ogaya & Peñuelas, 2007). The emission of plant volatiles following  
130 the activation of plant defences is generally increased under moderate drought and reduced  
131 under severe or chronic drought (Blanch et al., 2007; Ormeño et al., 2007; Saunier et al.,  
132 2017), because of restricted carbon acquisition (Staudt et al., 2002) and down-regulation of  
133 carbon-consuming functions such as VOC emissions (Rennenberg et al., 2006). Plant species  
134 in semi-arid regions such as the Mediterranean Basin are generally drought-adapted and have  
135 developed drought escape, tolerance or avoidance resistance mechanisms, notably via  
136 increased carbon uptake efficiency (Nardini et al., 2014; Aslam et al., 2015). Yet, under  
137 climate change, the drought resistance threshold of Mediterranean plant species and  
138 communities may be exceeded, reducing ecosystem productivity and threatening plant  
139 diversity (Malone et al., 2016; Rodriguez-Ramirez et al., 2017).

140

141 Mediterranean regions within Europe are predicted to be particularly affected by climate  
142 change, with a predicted average reduction in rainfall of up to 30 % in summer and 10-20 %  
143 in spring by the end of this century (Giorgi & Lionello, 2008, Mariotti et al., 2015). In  
144 addition, this region is a biodiversity hotspot, especially for pollinators (Nieto et al., 2014:  
145 Orr et al., 2021), and may be more fragile than some other biomes. For example, Newbold et  
146 al. (2020) predicted a disproportionate reduction in species richness in regions with  
147 Mediterranean climate, which host more species closer to their temperature limit compared to  
148 other biomes. A more thorough evaluation of climate change impacts on plant-pollinator  
149 interactions and pollination functions in this region is therefore needed.

150

151 In this study we investigated the impacts of long-term drought (*in situ* experimentally-  
152 reduced rainfall) on plant-pollinator interactions in a natural Mediterranean shrubland  
153 community. We compared a suite of floral traits between plants growing under control and



154 amplified drought conditions including the number of flowers, flower size and colour, floral  
155 scent, and nectar production. We also quantified pollinator visits to these plants and measured  
156 plant fitness. We asked: (i) how does drought alter floral traits?; (ii) how do pollinators  
157 respond to drought-induced changes in floral traits?; and (iii) how do changes in visiting  
158 pollinator community coupled with drought affect plant maternal fitness? We expected  
159 drought to affect all three aspects, and in particular to cause increased floral scent emissions,  
160 reduced nectar production, reduced pollinator visits and reduced fruit and seed production.

161

162

## 163 **2. Material and Methods**

### 164 **2.1. Study site: CLIMED long-term drought experiment**

165 All field data were collected in February-June 2018. We used a subset of established plots  
166 that were part of the CLIMED (CLImate change effects on MEDiterranean biodiversity)  
167 long-term drought experiment situated at Massif de l'Étoile in Marseille, France (43° 22' N,  
168 5° 25' E). This site is under the management of Aix-Marseille University for research  
169 purposes only and therefore no fieldwork permit was required. This site has a typical woody  
170 shrub community dominated by three species: *Quercus coccifera* Linnaeus, 1753 (Fagaceae;  
171 anemophilous and a resource of very limited use to pollinators in the region; Ropars et al.,  
172 2020a), *Salvia rosmarinus* Spenn., 1835 (Lamiaceae; previously *Rosmarinus officinalis*;  
173 Drew et al., 2017), and *Cistus albidus* Linnaeus, 1753 (Cistaceae; Montès et al., 2008). Local  
174 cumulative precipitation between January and May 2018 (the flowering period surveyed)  
175 reached 291 mm, while the average precipitation between January and May for the period  
176 2008-2018 was 205 mm (Marseille-Marignane meteorological station; [www.infoclimat.fr](http://www.infoclimat.fr)).  
177 The site is equipped with 46 metallic control and 46 4 × 4 m rain-exclusion shelters  
178 established in October 2011, spaced by 1 to 30 m (Santonja et al., 2017). Plot locations were

179 chosen randomly at the time of establishment of the long-term experiment, and were assigned  
180 at random to control or drought treatment (Montès et al., 2008). Gutters from rain-exclusion  
181 shelters in drought plots were designed to exclude up to 30 % and excluded on average  
182 ( $\pm$  SE)  $12 \pm 2\%$  of precipitation between 2011 and 2018 at the centre of the plots; the  
183 intercepted water was carried away from the site with a pipe system. In control plots, the  
184 upside-down gutters intercepted a very small fraction of precipitation and rainfall reached the  
185 ground (Montès et al., 2008; Santonja et al., 2017). This water deficit attempts to mimic the  
186 mean predicted changes during the dry season in the Mediterranean area by the end of this  
187 century except in winter when rainfall is expected to increase (Giorgi & Lionello, 2008:  
188 averages for 2071-2100 relative to 1961-1990: December to February +0 to +10 %, March to  
189 May -10 to -20 %, June to August -20 to -30 %, September to November -0 to -10 %;  
190 Mariotti et al., 2015: averages for 2071-2098 relative to 1980-2005: December to February -  
191 0.1 to +0.2 mm/day, June to August -0.1 to -0.3 mm/day). The moderate but chronic  
192 experimental water deficit induced by the CLIMED experiment can alter plant physiology:  
193 carbon assimilation was reduced in *C. albidus*, and transpiration was reduced in *C. albidus*  
194 and *S. rosmarinus* but water use efficiency was not significantly changed in 2014 (Rodríguez-  
195 Ramirez, 2017). Between January and May 2018, permanent soil moisture probes (TDR100,  
196 Campbell Scientific Inc., Logan, Utah) measured soil moisture at 10, 20 and 40 cm in two  
197 control and two drought plots. For clarity we use the term *drought* to refer to the drought  
198 treatment in our study.

199

200 We selected 10 control plots and 10 drought plots out of the 92 plots, based on: (i) where  
201 *Thymus vulgaris* Linnaeus, 1753 (Lamiaceae) was present (four plots for each treatment only)  
202 because it is an important resource for pollinators (Ropars et al., 2020a); and (ii) a high and  
203 similar percentage cover of *C. albidus* and *S. rosmarinus* (Fig. 1). The chosen control and

204 drought plots were homogeneously distributed throughout the site (Fig. S1). We measured the  
205 percentage cover of each species in selected plots twice (February and June 2018). The  
206 percentage cover of *S. rosmarinus*, *C. albidus* and *Q. coccifera* and *T. vulgaris* was 21, 19, 15  
207 and 0.5 % on average respectively in the 20 plots selected, and the community composition  
208 did not differ significantly between treatments throughout the long-term experiment  
209 (Table S4). Despite such low diversity, this plant community is natural, and is representative  
210 of the site and of the type of dense, closed vegetation plant communities found in the region  
211 in areas where wildfires are ancient (> 10 years; Pimont et al., 2018). *Thymus vulgaris*,  
212 *C. albidus* and *S. rosmarinus* are all perennial, entomogamous shrub species; *T. vulgaris* is  
213 gynodioecious and obligate entomogamous (dichogamous; Arnan et al., 2014), while  
214 *S. rosmarinus* and *C. albidus* are self-compatible but with limited self-pollination (Blasco &  
215 Mateu, 1995; Hammer & Junghanns, 2020). A fourth shrub species, *Ulex parviflorus* Pourr.,  
216 1788, was also present but very rare (0.3 % percentage cover) with very few flowers during  
217 the study period, and other flowering species were even rarer (Table S3). We did not observe  
218 any insect visit to these very rare species and hence excluded them from our study.

219

## 220 **2.2. Floral traits involved in pollinator attraction**

### 221 *2.2.1. Floral scent*

222 We randomly selected up to 14 plant individuals per species in each treatment (control vs.  
223 drought) with a maximum of two (four for *T. vulgaris*) plants in the same plot. A few samples  
224 were lost during laboratory analysis, hence final sample sizes were 23 (control: 11; drought:  
225 12) for *S. rosmarinus*, 22 (control: 11; drought: 11) for *C. albidus*, and 19 (control: 6 female,  
226 6 hermaphroditic; drought: 5 female, 2 hermaphroditic) for *T. vulgaris*. Floral scent sampling  
227 and data processing is described in detail in [Supporting Information \(1.1.\)](#). Briefly, the  
228 collection of floral scent volatiles was performed via dynamic headspace sampling *in situ*.

229 Inflorescences from plant canopy bearing around 30-50 (*S. rosmarinus*), 2-3 (*C. albidus*) or  
230 100-400 (*T. vulgaris*) flowers (1<sup>st</sup>-3<sup>rd</sup> quantiles) were enclosed in 2 L bags and placed under a  
231 constant flow of purified air (inlet 1000 mL.min<sup>-1</sup>, outlet 200 mL.min<sup>-1</sup>). Two leaf-only scent  
232 samples in each plant species and treatment were also collected as a comparison, enclosing  
233 branches of comparable sizes than the inflorescences in floral samples ([Supporting](#)  
234 [Information 1.1. and 2.1.](#)). VOCs were adsorbed on a Carbotrap/Tenax cartridge (Sigma-  
235 Aldrich) placed at the bag outlet for 10 min for *S. rosmarinus* and *T. vulgaris*, and 15 min for  
236 *C. albidus*, so as to not exceed the breakthrough volume of each VOC (Ormeño et al., 2007).  
237 Ambient air (one sample every three plant scent sample) was also sampled as blank control  
238 and temperature recorded for emission rate normalization (see below).

239

240 Samples were analysed using gas chromatography coupled with mass spectrometry after  
241 thermodesorption (GC-MS). The methodology is detailed in [Supporting Information 1.1.](#)  
242 Briefly, peaks were extracted and peak area was automatically measured with *MZmine2*  
243 (version 2.18.1 developed for gas chromatography; Pluskal et al., 2010) after baseline  
244 correction. Peak retention indexes calculations and peak identification were performed in R  
245 (R Core Team 2020 version 3.6.3). Individual peak mass spectra were compared with that of  
246 21 pure standard molecules injected separately as well as reference spectra (libraries Adams,  
247 2007 and NIST, 2011) using the R function ‘SpectrumSimilarity’ (R library ‘OrgMassSpecR  
248 v0.5-3’; Stein & Scott, 1994) and with a tolerance in retention index of  $\pm 15$  between the  
249 analysed peak and the reference molecule. Despite these precautions the identification  
250 remains tentative. Only identified VOCs previously reported as plant volatiles, with an  
251 average similarity  $>0.8$  and whose area exceeded three times that of ambient air samples in  
252 average were retained for analysis (Campbell et al., 2019 and see [Supporting Information](#)  
253 [1.1.](#)). Emission rates of each VOC (in  $\mu\text{g}\cdot\text{h}^{-1}\cdot\text{gDM}^{-1}$ ) were calculated by subtracting the

254 quantities in their corresponding ambient air sample and normalized by the total dry mass of  
255 the bagged inflorescence and by temperature (Sabillón & Cremades, 2001; Ormeño et al.,  
256 2007).

257

### 258 2.2.2. Nectar production

259 For each plant individual on which we sampled floral scent we also selected five flowers  
260 (only 2.5 on average for *C. albidus*) to measure nectar production (as well as flower size and  
261 colour, [Supporting Information 1.4](#)). We measured nectar standing crop (otherwise referred  
262 to as nectar production for simplicity) in each flower using 0.5  $\mu\text{L}$  microcapillary tubes  
263 (Hirschmann Laborgeraete, Germany), placed in contact with nectaries. Flowers chosen were  
264 about to open for *S. rosmarinus* (any prior pollinator visit would have been prevented by the  
265 closed corolla) and sampled before 9:00 for *C. albidus* and *T. vulgaris*, to reduce variability  
266 due to flower ageing (3-4 days for *S. rosmarinus* and *T. vulgaris* and 1-2 days for *C. albidus*;  
267 authors pers. obs. and Flo et al., 2018) and nectar removal by pollinators (Flacher et al.,  
268 2020). Nectar volume was calculated (in  $\mu\text{L}/\text{flower}$ ) by measuring the amount of liquid in a  
269 microcapillary tube with a digital calliper (Digit-Cal MK IV, Brown & Sharpe, USA). Sugar  
270 concentration was measured immediately afterwards using a hand-held refractometer (Eclipse  
271 0-30°Brix, Bellingham & Stanley Ltd, UK) calibrated by the manufacturer. The whole  
272 volume of nectar collected was deposited on the measuring surface of the refractometer and  
273 diluted with 1  $\mu\text{L}$  of pure water (measured with a 1  $\mu\text{L}$  microcapillary tube) to increase the  
274 total volume and measure reproducibility. The sugar concentration (in  $\mu\text{g}/\mu\text{L}$ ) and total sugar  
275 content (in  $\mu\text{g}$ ) were calculated *a posteriori* using the conversion table from ° Brix to g/L by  
276 Kearns and Inouye (2003) and by applying the dilution factor and a temperature correction  
277 after the manufacturer's correction table (Flacher et al., 2020).

278

279 2.2.3. Flowering phenology and number of flowers and other floral traits

280 When measuring plant-pollinator interactions, it is necessary to control for the flowering  
281 phenology of each species and the number of flowers at each sampling date, because  
282 pollinators are naturally attracted to patches with more flowers (Vrdoljak et al., 2016) and the  
283 flowering phenology of each species also influences the visitor community. To assess  
284 flowering phenology, the total number of flowers per plant was measured each week from  
285 March 9<sup>th</sup> to May 23<sup>rd</sup>, 2018 (12 weeks total), on two marked plant individuals per species  
286 (*S. rosmarinus*, *C. albidus*, and *T. vulgaris*) in each plot (20 individuals per treatment, except  
287 *T. vulgaris*: control: 11, drought: 8). On each individual, all flowers present in a volume  
288 delimited by the maximum height of the plant and a marked 40 × 40 cm quadrat were  
289 counted or estimated. For individuals smaller than the quadrat, their percent cover in the  
290 quadrat was measured, and all their flowers were counted, to obtain a number of flowers per  
291 m<sup>2</sup> for all plant individuals. When *S. rosmarinus* plants had many flowers around the  
292 flowering peak, flowers were counted by groups of ten, visually estimating the area covered  
293 by ten flowers.. For each individual, we calculated the date of its flowering peak as the week  
294 with the maximum number of flowers counted, and the total number of flowers as the sum of  
295 all flowers counted over all sampling dates. We also calculated a proxy for the flowering  
296 period as the number of weeks with at least half as many flowers as the maximum number of  
297 flowers recorded. Finally, we measured the impact of drought on flower colour and size on  
298 flowers collected for nectar production measures, and we have detailed the methods and  
299 results for these traits in [Supporting Information](#) (1.4.).

300

301

302 **2.3. Plant-pollinator interactions**

303 To quantify plant-pollinator interactions, pollinator visits were observed once a week for 12  
304 weeks on the same days as flowering phenology, by monitoring for 5 min in each of the 20  
305 plots: in each plot we chose the three patches (~1.5 m<sup>2</sup>) with the highest flower density to  
306 increase the chance of observing interactions (Ropars et al., 2020b). This represented a total  
307 of 20 hours of observation. Each patch was assigned to one observer, and all observed  
308 flowers of each flowering species were counted using the same method as for flowering  
309 phenology (see [section 2.2.3.](#)) to control for plot attractiveness to pollinators (patches with  
310 higher flower density are often more attractive and receive more visits; Feldman, 2006;  
311 Vrdoljak et al., 2016). Similarly to the plant individual level, the total number of observed  
312 flowers per plot and the flowering phenology at the plot level were not significantly different  
313 between control and drought plots (data not shown).

314

315 We defined a single visit when the observed insect touched the reproductive parts of a flower.  
316 We recorded the number of visits, the functional group of the visiting insect, and the plant  
317 species visited (*S. rosmarinus*, *C. albidus* or *T. vulgaris*). Functional groups recorded were:  
318 (1) *Bombus gr. terrestris*, (2) the managed honeybee *Apis mellifera*, (3) small wild bees  
319 (smaller than *A. mellifera*), (4) large wild bees (larger than *A. mellifera*), (5) Coleoptera, and  
320 (6) Diptera. *Bombus gr. terrestris* is by far the most abundant *Bombus* group species in the  
321 region and the other very rare species are functionally similar (Ropars et al., 2020a). No wild  
322 *Apis mellifera* colony was recorded close to our study site and we assumed that 100 % of  
323 *A. mellifera* we observed were managed (see also Herrera, 2020). For clarity we refer to *Apis*  
324 *mellifera* as the managed honeybee in this study. The six pollinator groups defined above are  
325 easily identified *in situ*. Visits by non-Apoidea Hymenoptera and by Lepidoptera were  
326 extremely rare and therefore not considered. Observations were carried out under optimal  
327 weather conditions, i.e., on sunny days with temperatures above 15° C and without strong

328 wind, between 10:00 and 16:00 from 9<sup>th</sup> March to 5<sup>th</sup> April and from 8:00 to 14:00 from 13<sup>th</sup>  
329 April to 23<sup>rd</sup> May. Observations were recorded in the 20 plots (grouped in four blocks)  
330 successively in a block-randomized order at each sampling date. Contrary to our expectations  
331 and because *T. vulgaris* was rare (but always selected in the observed most flower-dense  
332 patches when flowering), insect visits to *T. vulgaris* were rare. In particular, all 85 recorded  
333 visits by *A. mellifera* on *T. vulgaris* took place in a single plot on a single day. We therefore  
334 discarded these visits from our analyses.

335

336 Immediately after the 5 min observation round in each plot, visiting insects were caught with  
337 a sweep net during the following 5 min, adding 30 s to that duration for each insect caught to  
338 account for insect handling time and disturbance to the patch. Insects were then frozen  
339 overnight and prepared for identification in the laboratory. They were pinned and dried prior  
340 to identification by professional taxonomists: David Genoud for Andrenidae, Anthophorini,  
341 *Colletes* spp. and Halictidae, Matthieu Aubert for Megachilidae, Ceratini and *Hylaeus* spp.,  
342 Eric Dufrière for *Nomada* and *Mellecta* spp., Christophe Lauriaut for Bombyliidae, Gabriel  
343 Nève for Syrphidae and other Diptera, and Jean-Yves Meunier and Jean-Pierre Hebrard for  
344 Coleoptera.

345

346

#### 347 **2.4. Plant reproduction**

348 As an estimate of plant female fitness we measured the fruit set of each marked plant  
349 individual of *C. albidus* and *S. rosmarinus* (two per plot). As a proxy for fruit set, we counted  
350 the total number of fruits per m<sup>2</sup> with the same method as for the total number of flowers  
351 ([section 2.2.3](#)) on May 31<sup>st</sup> for *C. albidus* and on four successive weeks (May 3<sup>rd</sup> to May 23<sup>rd</sup>)  
352 for *S. rosmarinus*. This was because first ripe fruits dehisced before the last ones were fully



353 formed in *S. rosmarinus*; the maximum count was used as a proxy for fruit number. We also  
354 collected up to 40 and 13 fruits per individual for *S. rosmarinus* and *C. albidus*, respectively  
355 on May 31<sup>st</sup>. This was the maximum number of intact (non-parasitized) fruits in *C. albidus*.  
356 We counted the number of seeds per fruit, and we calculated the mean and variance in  
357 number of seeds per fruit for each plant individual. Finally, we measured the mean seed mass,  
358 by weighing all collected seeds of a plant individual together (Ohaus® Discovery semi-micro  
359 analytical balance; resolution 0.1 mg). We also conducted a seed germination experiment in  
360 Spring 2019 with *S. rosmarinus* and *C. albidus* seeds collected in Spring 2018 to assess seed  
361 viability, germination, and survival (detailed in [Supporting Information 3.1.](#)).

362

363

## 364 **2.5. Statistical analyses**

365 All statistics were performed using R version 3.6.3 (R Core Team 2020). We performed  
366 multivariate analyses of floral scent and pollinator community compositions (detailed below).  
367 Otherwise (unless specified), we used linear (LMMs) or generalised linear (GLMMs) mixed  
368 models with a poisson or a negative binomial error distribution function to account for data  
369 structure and overdispersion (frequent in count data), specified based on the distribution of  
370 model residuals. Random effects were the plot (repeated measures in the same plot), and the  
371 plant nested within the plot for plant traits (repeated measures on the same plant). The fixed  
372 effect was the treatment (control versus drought). For tests on plant traits involving  
373 *T. vulgaris*, the sex (female versus hermaphroditic) was also added as a cofactor to account  
374 for sexual dimorphism (Thompson et al., 2002; Arnan et al., 2014). The absence of residual  
375 heteroscedasticity and overdispersion was verified in the best model (functions  
376 ‘plot(simulateResiduals())’ and ‘testDispersion’; R library ‘DHARMA’; Hartig, 2019). The

377 significance of fixed effects was estimated through a stepwise regressive type-II model  
378 comparison with an ANOVA based on  $\chi^2$  tests.

379

380

381

### 382 *2.5.1. Floral scent*

383 First, we analysed how drought altered floral scent chemical profiles of the three species  
384 independently. We performed a multivariate analysis on  $^4\sqrt{\text{}}$ -transformed emission rates of all  
385 quantified volatile organic compounds (VOCs). Such transformation reduces variance  
386 heterogeneity across VOCs spanning several orders of magnitude in natural plant chemical  
387 profiles (Hervé et al., 2018). Typical metabolomic datasets often comprise many more  
388 molecules than samples, and these molecules or explanatory variables are often strongly  
389 inter-correlated, notably due to shared metabolic pathways (Junker et al., 2017). The  
390 canonical powered partial least squares discriminant analysis overcomes these biases by  
391 combining classification and regression and is commonly used for the analysis of chemical  
392 datasets (function ‘cppls’ with parameters ‘centre’ and ‘scale’ to true, R library ‘pls’; Mevik  
393 et al., 2019; Indahl et al., 2009; Hervé et al., 2018). We implemented the treatment as factor  
394 and three components (or latent variables; further components always captured less than 5 %  
395 of the variance). The three resulting synthetic components hence reflect the maximized  
396 covariance between the drought response variable and the VOC predictor variables. To  
397 remove noise, i.e. VOCs with little contribution to covariance and group differentiation, we  
398 performed one round of variable selection, retaining only VOCs contributing most to group  
399 separation based on their relative projection to the axis separating group barycenters in the 3-  
400 dimensional space, and up to 2/3 of total axis contribution. To assess drought impact, we then  
401 performed a cross-validation significance test on the matrix of selected VOCs (Westerhuis et

402 al., 2008), using the treatment as factor and three components (function ‘MVA.test’, R library  
403 ‘RVAideMemoire’; Hervé, 2019; model: “PLS-DA”, cmv=TRUE, and otherwise defaults  
404 parameters). In short and for each species separately, all samples were randomly divided into  
405 three sets of equal length and respecting the proportions of control and drought samples in the  
406 full dataset. The first was set aside as the test group (outer loop). The second and third sets  
407 were used for model training and validation (inner loop). The first set was then used to test  
408 the consensus model. Inner and outer loops were repeated in 999 permutations. The function  
409 outputs the classification error rate and a *P*-value computed using the Benjamini and  
410 Hochberg (1995) correction for multiple testing. For *T. vulgaris* flower dimorphism is also  
411 likely to be reflected in floral scent, so we added the sex (female or hermaphroditic) as an  
412 additional response in both the multivariate analysis and the cross-validation test (parameter  
413 ‘Y.add’).

414

415 Second, we analysed how drought affected the total emission rate (all VOCs summed per  
416 sample), and the total emission rates per chemical class for each plant species using two-  
417 sample *t*-tests on  $\sqrt[4]{}$ -transformed data. Similarly, we looked at how drought affected the  
418 diversity of VOCs quantified in emissions, using *t*-tests on the number of VOCs quantified in  
419 each sample. Finally, we analysed the impact of the sample type (flowers and leaves vs.  
420 leaves only) on the chemical profile to identify typically floral versus leafy VOCs in our  
421 experimental conditions ([Supporting Information 2.1.](#)).

422

### 423 2.5.2. Other floral traits

424 *Nectar*. We calculated the proportion of flowers with nectar present as the number of flowers  
425 with nectar volume >0 over the total number of flowers sampled per individual and analysed  
426 it with a GLM with a binomial distribution (link function ‘logit’; function ‘glm’; R library

427 ‘stat’; R Core Team, 2020). The response variable was implemented as a two-column matrix  
428 containing the number of flowers with and without nectar (Phillips et al., 2018). Using  
429 flowers with nectar only, we then analysed the drought impact on nectar volume (\*100 and  
430 rounded, which corresponded to an estimated measure error of 2 %) and sugar content (µg,  
431 rounded) using GLMMs with poisson and negative binomial distributions, respectively  
432 (functions ‘glmer’ and ‘glmer.nb’, R library ‘lme4’; Bates et al., 2015).

433

434 *Flowering phenology and number of flowers.* We analysed the impact of drought on  
435 flowering peak and the duration of the flowering period using two-sample Wilcoxon tests,  
436 because of the very small variance due to the per-week count. To analyse the total number of  
437 flowers counted throughout the season per plant per m<sup>2</sup>, we used a GLMM with a negative  
438 binomial distribution.

439

#### 440 2.5.3. Pollinator observations

441 We first analysed the drought impact on the total number of visits per plot throughout the  
442 season for each plant species using a GLMM with a poisson distribution (function ‘glmer’)  
443 and the treatment in interaction with the plant species (*S. rosmarinus* or *C. albidus*; N = 20  
444 for each species, 10 per treatment) as fixed effects. Then, we analysed the impact of drought  
445 on the weekly number of visits by each pollinator functional group in each plot and to each  
446 plant species, using a two-step Hurdle modelling approach (Geslin et al., 2020). The first test  
447 worked on the presence or absence of visits of each group, assessing the attractiveness of a  
448 plot (how likely is each plant species in a plot likely to be visited by each functional group).  
449 We used a GLMM with a binomial distribution (function ‘glmer’), implementing the  
450 treatment in interaction with the plant species (*S. rosmarinus* versus *C. albidus*) and the  
451 functional group (*A. mellifera*, bumble bee, large wild bees, small wild bees, Coleoptera and

452 Diptera) as fixed effects, along with the scaled observation duration and the scaled counted  
453 number of flowers as co-variables to control for differences in the number of flowers per plot.  
454 The second test worked on the number of visits, assessing the interaction strength between  
455 each plant species and each visitor functional group (how intensely are each plant species  
456 expected to be visited?). We selected data with visits only (removing all zeros), and we used  
457 the same fixed and random effects as in the first test, but with a negative binomial  
458 distribution (function 'glmer.nb'). Since the interaction term was significant in this second  
459 test, we performed a *post hoc* comparison of means within functional groups and plant  
460 species and between treatments (function 'emmeans': 'specs = pairwise ~ treatment |  
461 pollinator functional group \* plant species'; R library 'emmeans'; Lenth, 2019).

462

463 Finally, we analysed the drought impact on the pollinator community composition at a  
464 species level. We calculated the abundance and species richness of the total number of insect  
465 visitors caught in each plot through the season. Species identified to genus only were not  
466 counted in species richness (except one single specimen of *Glyphipterix* sp., [Table S12](#)), and  
467 such data was also used to estimate sampling completeness (methods in [Table S13](#)). Drought  
468 impact on the abundance and species richness were analysed using *t*-tests. We also performed  
469 a constrained correspondence analysis to test whether drought affected community  
470 composition, using a permutation test with 999 permutations and a Fisher test (functions 'cca'  
471 and 'anova.cca', R library 'vegan'; Oksanen et al., 2019) on the same species used for species  
472 richness, but removing singletons.

473

#### 474 2.5.4. Plant reproduction

475 The drought impact on the number of fruits per m<sup>2</sup> was tested with a GLMM with a negative  
476 binomial error distribution for each species ([section 2.5.1](#)). For each species, the impact of

477 drought on the mean number of seeds per fruit, the variance in seed number per fruit  
478 (multiplied by ten and rounded), and the mean seed mass was tested using a LMM, a GLMM  
479 with a negative binomial error distribution, and a LMM, respectively.

480

481

## 482 **3. Results**

### 483 **3.1. Efficacy of the rainfall reduction in 2018**

484 Between January and May 2018, soil moisture was lower in drought plots than in control  
485 plots by 1.2 % [-0.6; 2.6], 6.1 % [4.7; 7.6] and 6.1 % [-0.4; 7.5] on average [1<sup>st</sup> quantile; 3<sup>rd</sup>  
486 quantile] at 10, 20 and 40 cm depth, respectively. Monthly soil moisture variability did not  
487 differ between control and drought plots, and soil moisture was overall always lower in  
488 drought plots except during and in the 2-3 hours after rainfall events.

489

### 490 **3.2. Floral traits involved in pollinator attraction**

#### 491 *3.2.1. Floral scent*

492 A total of 37, 29 and 28 floral scent VOCs were present and quantified in *S. rosmarinus*,  
493 *C. albidus* and *T. vulgaris* respectively, belonging to the fatty acid derivatives (FADs),  
494 monoterpenoids, benzenoid and sesquiterpenoid chemical families (Tables S5-S7). After  
495 removing those present in two or fewer samples for each species, 31, 21 and 21 VOCs were  
496 included in analyses.

497

498 Drought strongly altered floral scent profiles in all three species, with clear separation  
499 between the chemical profiles from plants in each treatment (Tables 1, S5-S7, Fig. 2). Eight  
500 and five VOCs were emitted at greater rates in *S. rosmarinus* and *T. vulgaris* plants under  
501 drought respectively, and three VOCs were emitted at lower rates in each species in plants

502 under drought, compared with control plants. Also floral emissions of *T. vulgaris* tended to  
503 be greater in drought conditions, although not significantly so due to high variability. An  
504 opposite pattern was found for *C. albidus* with three VOCs emitted at greater rates and four at  
505 lower rates in plants under drought compared to control plants. Floral emissions of *C. albidus*  
506 also tended to be less diverse in drought conditions (six VOCs in average) compared to  
507 control conditions (10 VOCs in average), likely because of minor VOCs emitted below the  
508 quantification threshold (Table 1). Among VOCs emitted at higher rates under drought, we  
509 found typical green-leaf volatiles (GLVs) including 3Z-Hexenol in all three species, although  
510 3Z-Hexenyl acetate was emitted at a lower rate in drought conditions for *T. vulgaris*. The  
511 other discriminating molecules were more species-specific and included some of the major  
512 VOCs in floral blends: Camphor and E-Caryophyllene emitted at greater rates and Borneol  
513 emitted at a lower rate in *S. rosmarinus* plants under drought; ar-Curcumene and  $\alpha$ -  
514 Zingiberene emitted at lower rates in *C. albidus* plants under drought; and p-Cymene and p-  
515 Thymol emitted at higher rates in *T. vulgaris* plants under drought (Tables S5-S7). Both  
516 typically floral and leafy VOCs were found among discriminating molecules under drought in  
517 all three species, and leaf-only scent profiles were significantly different from flower plus  
518 leaf scent profiles (Supporting Information 2.1.; Tables S3, S5-S7, Fig. 2).

519

520 Finally, total emissions of oxygenated FADs (including the GLVs) were significantly greater  
521 in drought conditions in *S. rosmarinus*, but the difference was not significant for the other  
522 two species (Table S8). Total emissions of other chemical families did not differ significantly  
523 between treatments in any species.

524

525 3.2.2. Nectar production and other floral traits

526 In *T. vulgaris*, drought caused a marginally significant 38 % reduction in the proportion of  
527 flowers producing nectar, and a reduction of 49 % in sugar content per flower. No significant  
528 effects on nectar production were observed in *S. rosmarinus* and *C. albidus* (Table 2, Fig. 3).  
529 Total number of flowers was not affected by drought in either of the three species, and  
530 neither was flowering phenology (Table S9, Fig. S2). Drought did not affect flower size or  
531 flower colour significantly in any of the species, although the yellow centre of *C. albidus*  
532 flowers was marginally brighter in plants under drought (Tables S10, S11, Figs. S3).

533

534

### 535 3.3. Plant-pollinator interactions

536 We recorded a total of 6,576 flower visits, including 6,064 on *S. rosmarinus*, 400 on  
537 *C. albidus* and 112 on *T. vulgaris* (visits on *T. vulgaris* were not included in analyses, see  
538 section 2.3.). Drought did not affect the total number of visits by pollinators to either  
539 *S. rosmarinus* or *C. albidus* flowers ( treatment \* plant species interaction:  $\chi^2 = 0.668$ ,  $df = 2$ ,  
540  $P = 0.41$ ; treatment:  $\chi^2 = 1.24$ ,  $df = 1$ ,  $P = 0.26$ ; Fig. 4).

541

542 Drought affected the number of visits by some pollinator functional groups to *S. rosmarinus*  
543 flowers, but not the presence or absence of visits: honeybees and bumblebees visited  
544 *S. rosmarinus* flowers at a higher rate in control plots than in drought plots, while the group  
545 of small wild bees visited *S. rosmarinus* flowers at a higher rate in drought plots (mean  $\pm$  SE  
546 number of visits per 5 min per plot when at least one visit was recorded: honeybees: control /  
547 drought:  $74.7 \pm 13.0$  /  $40.6 \pm 7.3$ ; bumblebees: control / drought:  $22.4 \pm 14.7$  /  $4.4 \pm 1.3$ ;  
548 small wild bees: control / drought:  $1.8 \pm 0.4$  /  $11.4 \pm 7.3$ ; Table 3, Fig. 5).

549



550 A total of 327 flower visiting insects were caught throughout the experiment in both  
551 treatments (including 125 *A. mellifera* individuals), representing 22 Hymenoptera species, six  
552 Coleoptera species, one Lepidoptera species and three Diptera species (Table S12). This  
553 represented 62 to 74 % of the total species richness at this site (Table S13). Drought did not  
554 impact the abundance ( $t = 0.738$ ,  $df = 17.7$ ,  $P = 0.47$ ) nor the species richness ( $t = 1.04$ ,  
555  $df = 17.3$ ,  $P = 0.31$ ; Fig. S4) of insects caught. The composition of the visiting community  
556 after removing singletons (12 of 33 species) was also not significantly affected by drought  
557 ( $F_{1,18} = 0.670$ ;  $P = 0.91$ ; Table S12).

558

559

### 560 3.4. Plant reproduction

561 Drought did not affect the number of fruits per m<sup>2</sup> for either *S. rosmarinus* or *C. albidus*, nor  
562 did it affect the mean and variance in seed number per fruit or the mean seed mass (Table 4,  
563 Fig. 6). Finally, drought had a limited impact on seeds (Appendix section 2.; Table S15,  
564 Fig. S5). Seeds from *C. albidus* plants under drought had a marginally significant higher  
565 viability rate but a marginally significant lower germination rate. Seeds from *S. rosmarinus*  
566 plants under drought had a slower germination (Table S15, Fig. S5D).

567

568

## 569 4. Discussion

570 Our study assesses the impacts of an induced long-term experimental drought on floral traits,  
571 plant-pollinator interactions and plant reproduction in a natural Mediterranean community.

572 Overall, we found a limited impact of amplified drought: floral scent was consistently altered  
573 by drought in all three species tested, but the other floral traits (flower colour and size and  
574 flowering phenology) were not affected, except nectar production in *T. vulgaris*, which was

575 drastically reduced. Pollinator responses were limited with no impact on total number of  
576 visits nor species richness. However, the relative contribution of *Apis mellifera* and small  
577 wild bees to total visits differed between drought and control plots. Finally, consequences for  
578 plant reproduction were also limited: fruit and seed sets were similar in control and drought  
579 plots, although seeds from drought plots had slower germination for *S. rosmarinus* and  
580 marginally reduced germination success in *C. albidus*. In interpreting these somewhat  
581 surprising results, we consider three main questions: (4.1.) Why are there only limited effects  
582 of drought on plant floral traits and reproduction? (4.2.) Why are there significant differences  
583 in floral scent composition, despite limited differences in other floral traits? And (4.3.) Can  
584 the observed differences in flower visitor community composition be attributed to the  
585 observed differences in floral scent?

586

#### 587 **4.1. Limited impact of drought**

588 The overall limited impact of drought on floral traits and plant reproduction was unexpected,  
589 since many studies have reported changes in nectar production, flowering phenology, flower  
590 size and number, and fruit or seed set under possibly more intense drought (reviewed in  
591 Borghi et al., 2019 and Descamps et al., 2021) including in Mediterranean, drought-adapted  
592 shrub species (del Cacho et al., 2013). A possible explanation for the lack of response in our  
593 system is that Mediterranean plant species have evolved drought-resistance mechanisms that  
594 could mitigate drought impacts (Nardini et al., 2014; Aslam et al., 2015). These mechanisms  
595 or traits may have been further selected for in our experimental drought plots over six years,  
596 through differential mortality, increasing drought resistance in the plant community  
597 (Rodriguez-Ramirez, 2017; Rodriguez-Ramirez et al., 2017). An alternative, or perhaps  
598 complementary explanation is that our study was conducted during a period of unusually high  
599 rainfall (42 % higher than the long-term average; [section 2.1](#)), resulting in only modest

600 differences in soil moisture between treatments (section 3.1). Heavy rainfall events  
601 ( $\geq 5 \text{ mm.h}^{-1}$ ) could have caused water run-off on the ground into drought plots and causing  
602 the especially low difference in soil moisture at shallow depths. The small difference in soil  
603 moisture possibly led to high enough water availability to not affect plant performance in  
604 drought plots, reducing overall differences in floral traits between experimental and control  
605 plots during our study year (Pérez-Llorca et al., 2019; Abbaszadeh et al., 2020).

606

607 Only *T. vulgaris* had a drastically reduced nectar standing crop under drought (total sugar  
608 reduced by  $\sim 75\%$  when combining sugar per flower and flowers with nectar). This suggests  
609 a lower drought resistance than *S. rosmarinus* and *C. albidus*. *Thymus vulgaris* is widely  
610 characterized as drought-sensitive, compared to congeneric species (Ashrafi et al., 2018) and  
611 has also shallower roots than *S. rosmarinus* and *C. albidus*. Drought sensitivity however may  
612 also have been increased by competition for light and the dominance of the three shrub  
613 species (*Q. coccifera*, *S. rosmarinus*, and *C. albidus*) in this ungrazed site (Millan et al.,  
614 2019), also causing low abundance of *T. vulgaris*. An alternative factor explaining nectar  
615 standing crops in drought and control plots in *S. rosmarinus* and *C. albidus* is the  
616 composition of the flower-visiting community. Large, social bee species such as *Apis*  
617 *mellifera* and *Bombus gr. terrestris* visited more flowers in control than in drought plots,  
618 while small bees visited more flowers in drought plots. Larger, social bees collect nectar at a  
619 higher rate, so they could have depleted nectar resources in control plots faster than in  
620 drought plots, thereby reducing undetected differences in nectar standing crops between  
621 control and drought plots. This however is unlikely in *S. rosmarinus* since we chose closed,  
622 not yet visited flowers for nectar measures.

623

624 In animal-pollinated plants, drought could reduce plant reproduction via two main  
625 mechanisms: reduced resource allocation to reproduction, and reduced pollination as a result  
626 of lower floral resource provision or reduced attractiveness in water-limited plants  
627 (Descamps et al., 2021; Rering et al., 2020; Walter, 2020; Raderschall et al., 2021). Our  
628 experiment did not make possible to disentangle these two mechanisms since no hand  
629 pollination or pollinator exclusion treatments were included. We did find a limited impact of  
630 maternal drought (drought during production of seeds by maternal plants) on seed  
631 germination. Similar visit frequencies in control and drought plots could ensure pollination  
632 success and seed set production in the generalist plant species (or at least, species visited by a  
633 range of pollinators), although changes in the visitor community composition may have led to  
634 slight changes in the pollination efficiency (Burkle & Alarcón, 2011). Self-pollination is  
635 limited in the species studied (Blasco & Mateu, 1995; Hammer & Junghanns, 2020), but how  
636 drought may affect self-pollination rate is unknown. Alternatively, the minor changes  
637 measured in seed germination may be due to a physiological plant response to drought.  
638 Slower germination of seeds from drought-stressed *S. rosmarinus* plants suggests more  
639 poorly resourced seeds. It could make them more vulnerable to adverse environmental  
640 conditions, which are more likely under climate change (Quintana et al., 2004), so it is  
641 difficult to see how this is adaptive. However, the marginally lower germination rate in  
642 *C. albidus* seeds from drought-stressed plants could suggest increased seed dormancy, as  
643 found by Siles et al. (2017) for *C. albidus* seeds germinating in a harsher environment.  
644 Increased seed dormancy can be a bet-hedging strategy maximizing fitness in the long term  
645 and under more variable climatic conditions (Tavşanoğlu & Çatav, 2012).

646

#### 647 **4.2. Altered floral scent despite limited impacts on other floral traits**

648 Despite the moderate drought and its limited impacts on other floral traits, floral scent was  
649 consistently altered in all three of our study species. Like other plant volatile emissions, floral  
650 scent is particularly sensitive to environmental stress (Theis et al., 2007; Yuan et al., 2009;  
651 Glenny et al., 2018), notably because the activation of plant defences as a response to abiotic  
652 and biotic stress results in the emissions of volatile stress molecules (Harborne, 1991;  
653 Holopainen & Gershenzon, 2010; Loreto & Schnitzer, 2010; El-Esawi et al., 2017). Hence,  
654 even moderate drought could result in the higher emission, in floral scent, of typical green  
655 leaf volatiles such as 3Z-Hexenol and defensive terpenoids (Borghini et al., 2019). We did find  
656 increased emissions of 3Z-Hexenol in the floral scent of all three species under drought,  
657 consistent with other studies (Burkle & Runyon, 2016; Glenny et al., 2018; Rering et al.,  
658 2020). Also, the reduced emissions of  $\alpha$ -Zingiberene and ar-Curcumene found in *C. albidus*  
659 floral scent under drought here were also shown in *C. albidus* leaves under drought (Ormeño  
660 et al., 2007). In contrast, in *S. rosmarinus*, the sesquiterpenes E-Caryophyllene and  $\alpha$ -  
661 Humulene, emitted at higher rate in floral scent under drought and characterized as typical  
662 floral VOCs here (Table S5) were absent in *S. rosmarinus* leaf samples in a previous study  
663 (Ormeño et al., 2007). This may be because these sesquiterpenes have a dual function  
664 (defence and pollinator attraction; Schiestl, 2010), and the plant increases investment in bee-  
665 attractive molecules (Leonhardt et al., 2014; Abraham et al., 2018) to counterbalance other  
666 negative effects of drought (Kuppler & Kotowska, 2021). Drought stress also often increases  
667 the variability of floral scent emissions (Glenny et al., 2018), a trend we found in *T. vulgaris*;  
668 moderate stress increases total emissions (Glenny et al., 2018) but intense stress can reduce  
669 emissions (Cna'ani et al., 2015).

670

#### 671 **4.3. Can altered floral scent explain differences in pollinator visits?**

672 We found that drought altered the relative number of visits by different pollinator functional  
673 groups. Workers of *A. mellifera* and *B. gr. terrestris* visited more *S. rosmarinus* flowers in  
674 control than in drought plots, while the species-rich group of small wild bees visited more  
675 *S. rosmarinus* flowers in drought than control plots. The same trend, although not significant,  
676 was found in *C. albidus*. Other studies have found that a variety of bee species prefer non-  
677 water limited plants (Al-Ghzawi et al., 2009; Descamps et al., 2018; Rering et al., 2020;  
678 Höfer et al., 2021).

679

680 The measured floral scent alterations may partially explain such changes in pollinator visits.  
681 Altered emissions could negatively affect flower attractiveness to pollinators and may cause  
682 the rewiring of pollination networks, i.e. the modification of the relative intensity of plant-  
683 pollinator interactions within the community (Larue et al., 2016). The attractiveness of most  
684 VOCs to most pollinator species remains unknown, yet among the VOCs altered by drought  
685 in our three species, some are described as attractive to *A. mellifera* and other bee species  
686 (Table S14). Conversely the stress marker 3Z-Hexenol acetate was found to be slightly  
687 repellent to *B. terrestris* (Ceuppens et al., 2015). The stress-induced increased emission rate  
688 of VOCs with a defensive primary function (rather than pollinator attraction) could deter  
689 pollinators (Theis, 2006; Schiestl et al., 2014). Avoiding drought-stressed plants based on  
690 floral scent signals may be positively selected, or based on associative learning (Jaworski et  
691 al., 2015), if altered floral scent is a cue for reduced quality or quantity of floral resources  
692 (Wilson Rankin et al., 2020).

693

694 While a change in pollinator behaviour is unlikely to be motivated by altered floral scent  
695 alone especially in generalist pollination systems, pollinators may use it as evidence for  
696 altered floral resources in resource-limited plants (Flacher et al., 2020). We did not detect

697 changes in nectar standing crop in either *S. rosmarinus* or *C. albidus*, but we did not measure  
698 flower refill rate, nectar composition (ratio of different sugars and nutrients content), or  
699 pollen production and quality, which could have been affected by drought, potentially  
700 influencing bee choice (Petanidou, 2005). Wilson Rankin et al. (2020) showed that drought  
701 reduced nectar quality and quantity as well as pollen nutritional quality in *Trifolium*  
702 *willdenovii*, reducing colony fitness in *A. mellifera* and *B. impatiens*. The increased visitation  
703 rate towards plants experiencing drought by small wild bees (including some *Andrena*, *Osmia*  
704 and *Lasioglossum* species, [Table S12](#)) is more difficult to interpret, partly because of the  
705 diversity of insect species within this group. One speculative hypothesis is that, rather than  
706 being a response to floral scent, it is a signal of resource partitioning due to interspecific  
707 competition. *Apis mellifera* dominates the flower visitor community (81 % of all visits) in our  
708 study and throughout the Mediterranean Basin (Herrera, 2020). A study with the same  
709 observation methods and in a similar habitat 20 km away from our field site in 2017-2018  
710 found that the abundance and species richness of large wild bees was negatively affected by  
711 increased honeybee hive density on wild pollinators (Ropars et al., 2020b). The social  
712 structure of *A. mellifera* hives (all managed in the region), and their ability to communicate  
713 the location of resources, enables workers to exploit the most rewarding floral resources and  
714 to track resource availability much more efficiently than wild pollinator species (Hung et al.,  
715 2019; Hasenjager et al., 2020). The higher number of visits by *A. mellifera* to control plots  
716 suggests that they evaluated floral resources to be more abundant or of higher quality in  
717 control plots. If so, resources in the control plots would be more rapidly depleted, leaving  
718 resources in drought plots to other pollinator species and causing resource partitioning  
719 (Kuppler et al., 2017; Thomson & Page, 2020). We observed some *A. mellifera* workers  
720 visiting more than 70 flowers in 5 min, and we caught on average eight (and up to 44)  
721 workers per day during the 20 × 5 min of weekly observations. Such a workforce could

722 theoretically visit and empty all flowers on site (in a  $200 \times 200$  m radius), assuming they  
723 never revisit a flower – which is true over short time periods and more likely in mass-  
724 flowering species such as *S. rosmarinus* (Giurfa & Nuñez, 1992; Aizen et al., 2014).

725

#### 726 **4.4. Limitations of the study and next steps**

727 Our study is based on just one year of data collection, and this prevents an understanding of  
728 how the abnormal rainy conditions might have affected our findings. Replicating the  
729 observations over successive years would help disentangle the effects of long-term,  
730 experimentally-induced drought trends from the effects of shorter-term extreme climatic  
731 events. Also, the CLIMED long-term experiment induces drought throughout the year,  
732 whereas climate change is predicted to cause more frequent and intense summer droughts, but  
733 wetter winters (Giorgi & Lionello, 2008; Mariotti et al., 2015). A more realistic drought  
734 simulation (more intense, but shorter) could more strongly affect flower attractiveness and  
735 the production of flower resources, with negative consequences for pollinator interactions  
736 (Walter, 2018; 2020).

737

738 Another limiting peculiarity of our study is the relatively low plant species richness at the  
739 study site (Table S4), resulting in flower resources dominated by just a handful of species.  
740 Despite consistent floral scent alteration in the three species tested, the low plant diversity  
741 prevents us from making generalisations about potential plant community changes and  
742 community-level resource changes under long-term drought. The most drought-sensitive  
743 species, *T. vulgaris*, was too rare in our system to quantify pollinator visits and therefore to  
744 assess the impact of reduced nectar production under drought on pollinator communities. If a  
745 similar impact of drought on *T. vulgaris* was confirmed in a more open habitat where this  
746 species is abundant (eg, in a similar shrubland 20 km away; Ropars et al., 2020a), this could



747 negatively affect pollinator populations (Weiner et al., 2014). In a nearby site, *T. vulgaris* was  
748 shown to support 14 flower-visiting species, including two with a potentially high  
749 dependence on *T. vulgaris* (Ropars et al., 2020a). Sustained nectar production in *C. albidus*  
750 and *S. rosmarinus* under drought could help support pollinator biodiversity, since these two  
751 plant species play a central role in the pollination network, supporting 37 and 35 pollinator  
752 species, respectively (Ropars et al., 2020a).

753

754 Finally, it is difficult to highlight cascading consequences of altered floral scent on pollinator  
755 visits, or changes in pollinator visits on plant reproduction, from our study. Inferences about  
756 the wider impacts of altered floral scent are prevented by a poor knowledge of the  
757 attractiveness of drought-induced changes in floral VOC emission rates. Laboratory  
758 experiments investigating the attractiveness of such VOCs singly or in mixtures, as well as  
759 preferences of naïve and experienced in a controlled environment between plants under  
760 control and drought conditions, would help make this connection (Jaworski et al., 2015;  
761 Burkle & Runyon, 2017; Proffit et al., 2020). Our experiment was not designed to disentangle  
762 the relative contributions of indirect drought, pollinator-induced and direct drought-induced  
763 impacts on plant reproduction, and for this reason the minor changes measured in plant  
764 reproduction cannot be unambiguously attributed to either observed changes in the flower  
765 visitor community (Kevan & Eisikowitch, 1990) or to plant physiology (Karimmojeni et al.,  
766 2014).

767

768 Our study was similar to an *in situ* choice experiment, since foraging bees could freely  
769 choose between control and drought plots (Nordström et al., 2017). In reality, climate change  
770 is likely to affect entire plant communities and up to a regional scale, leaving no such choice  
771 to pollinators. It would be useful – but logistically challenging – to further investigate climate

772 changes impacts at a community scale. For example, this could be attempted by choosing  
773 pairs of comparable large-scale communities such as entire valleys in different climatic  
774 conditions to assess the impact on pollinator foraging behaviour and population dynamics.  
775 Despite climate change, any habitat remains a mosaic of micro-climatic conditions (Maclean,  
776 2020) and our experiment therefore captures some of the realistic climate change predictions.  
777 Also, climate change may have direct impacts on pollinator behaviour, phenology and  
778 population dynamics (Burkle et al., 2013; Becher et al., 2014; Woodard, 2017), which were  
779 not considered here, and which would deserve further attention in integrative approaches.

780

#### 781 **4.6. Concluding remarks**

782 Our study showed that reduced rainfall altered floral scent in the three species studied,  
783 reduced nectar production in *T. vulgaris* only, and caused a shift in the flower visitor  
784 community in a Mediterranean system. Drought impacts were otherwise limited on floral  
785 traits and rewards, pollinator visits or reproductive success. Pollinators may adapt to altered  
786 floral olfactory and visual signals (Jaworski et al., 2015) but qualitative and quantitative  
787 changes in floral resources and therefore potentially in pollinator diet breadth (Schweiger et  
788 al., 2010) will affect pollinator fitness and this would deserve further attention. As next steps,  
789 we recommend investigating drought impacts in communities where *T. vulgaris* is more  
790 abundant, since this species did show a reduction in floral nectar reward in our experiment, in  
791 more diverse Mediterranean plant communities, and in communities with clearly identified  
792 specialized and generalist plant and pollinator species. Reduced floral resources and altered  
793 pollination functions may result in population declines in both pollinator and plant  
794 communities (Wagner, 2020), reducing the effectiveness of pollination functions and  
795 ecosystem productivity in biodiversity-rich but also already fragile Mediterranean  
796 ecosystems. Under predicted climate change, those ecosystems will also likely endure a

797 combination of extreme events such as intense drought episodes and heat waves of higher  
798 frequency and intensity. This is likely to exacerbate the effects we observed on flower  
799 attractiveness, plant-pollinator interactions and plant reproduction. Quantifying these impacts  
800 would help estimate the resilience of Mediterranean ecosystems under ever-increasing  
801 anthropogenic pressures.

802

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816

## 817 **6. Conflict of interests**

818 All authors have declared to have no conflict of interest.

819

## 820 **7. Authors' contributions**

821 CCJ, BG and CF designed the study; CCJ, BG, MZ, PC, GN and JYM conducted the  
822 pollinator observations and identification and plant phenology data collection; CCJ, MZ, PC  
823 and SD measured floral traits; CCJ and CL performed the chemical analysis; CCJ, MZ and  
824 ACTS conducted the seed germination experiment; CCJ, BG, MZ, PC and CF performed the  
825 data analysis; CCJ and BG wrote the manuscript, and CF, OTL and LVD provided critical  
826 comments and helped writing the manuscript. All authors approved the submission of the  
827 manuscript, and have declared no conflict of interest.

828

## 829 **8. Data availability**

830 Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.h70rxwdmz>  
831 (Jaworski et al., 2022a)). The repository contains all data sets as well as a metafile and a  
832 readme file. R code used for data analyses available from the Zenodo repository:  
833 <https://doi.org/10.5281/zenodo.6914377> (Jaworski et al., 2022b).

834

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## 1315 **10. Content of Appendix S1**

1316 1. Supplementary material and for main text

1317 1.1. Floral scent sampling and GC-MS analysis

1318 1.2. *MZMine2* batch parameters

1319 1.3. External calibrations and calculation of response coefficients  $k$

1320 **Table S1.** Dilutions used for external calibration of VOCs

1321 **Table S2.** Response coefficients  $K$  and intercepts  $B$  for VOC quantification.

1322 1.4. Measure of flower colour and size, and statistical analysis

1323 2. Supplementary results for main text

1324 2.1. Impact of the sample type (inflorescence vs. leaves) on scent emissions

1325 **Table S3.** Impact of the sample type (inflorescence vs. leaves) on scent emissions

1326 2.2. Supplementary tables – Results

1327 **Table S4.** Relative plant community composition in plots at the CLIMED site

1328 **Tables S5-S7.** List of VOCs identified and quantified in the three study species

1329 **Table S8.** Drought impact on total emission rates by chemical family.

1330 **Table S9.** Drought impact on the flowering phenology and flower number.

1331 **Table S10.** Drought impact on flower size.

1332 **Table S11.** Drought impact on flower colour.

1333 **Table S12.** Number of specimens of flower visitor species caught per treatment.

1334 **Table S13.** Estimation of sampled pollinator species richness

1335 **Table S14.** Detection and attraction or repellence of VOCs differentially expressed in the

1336 three studied species in response to drought by pollinator species.

1337 2.3. Supplementary figures – Results

1338 **Figure S1.** Aerial view of the CLIMED experimental site

1339 **Figure S2.** Drought impact on flowering phenology.



1340 **Figure S3.** Drought impact on flower colour represented in the *Apis mellifera* hexagon  
1341 colour space

1342 **Figure S4.** Drought impact on the total number of insect visitors caught along the season  
1343 and on species richness.

1344 3. Germination experiment

1345 3.1. Material and Methods

1346 3.2. Results and discussion

1347 **Table S15.** Impact of maternal drought and seed treatment on seed viability, germination  
1348 and survival.

1349 **Figure S5.** Impact of maternal drought and seed treatment on seed viability, germination  
1350 and survival.

1351 **11. Tables**

1352

1353 **Table 1.** Drought impact on floral scent emissions: results of the multivariate analysis (cppls) of scent composition showing group separations  
 1354 (variance explained by treatment and samples, classification error rate CER, and number of misclassified samples; see Fig. 2), and analysis of total  
 1355 emission rates and diversity of VOCs emitted (*t*-tests). Significant effects of drought are shown in bold. ‘C > D’: emitted at higher rates in control  
 1356 plants compared to plants under drought; ‘C < D’: emitted at lower rates in control plants compared to plants under drought.

Species	multivariate analysis (cppls)					total emissions ( <i>t</i> -test)					VOC diversity ( <i>t</i> -test)							
	number of VOCs selected	Variance explained (% axes 1,2,3 = total)		CER (%)	number of misclassified samples	<i>P</i>	number of VOCs		<i>t</i>	df	<i>P</i>	mean ± SE (µg.g <sub>DM</sub> <sup>-1</sup> .h <sup>-1</sup> )		<i>t</i>	df	<i>P</i>	mean number ± SE	
		Y (treatment)	X (samples)				C > D	C < D				C	D				C	D
<i>S. rosmarinus</i>	11	74,7,6 = 87	19,27,13 = 58	16.4	4 of 23	<b>0.0025</b> **	3	8	-0.214	20.6	0.83	32.4 ± 5.0	33.4 ± 4.4	-0.615	20.5	0.54	18 ± 1	20 ± 2
<i>C. albidus</i>	7	37,26,5 = 67	10,65,11 = 85	22.2	5 of 22	<b>0.013</b> *	4	3	0.527	20.0	0.60	18.9 ± 9.7	13.5 ± 6.3	1.76	19.7	0.093	10 ± 2	6 ± 2
<i>T. vulgaris</i>	8	51,29,3 = 82	4,35,10 = 51	23.0	4 of 19	<b>0.034</b> *	3	5	-1.01	7.53	0.34	627 ± 122	1,659 ± 850	0.880	8.88	0.40	16 ± 1	14 ± 2

1357 **Table 2.** Drought impact on nectar production. Significant effects ( $P < 0.05$ ) and marginally  
 1358 significant effects ( $P < 0.07$ ) of drought are shown in bold.

	Sample size plants:flowers per plant control / drought	df	$\chi^2$	$P$
<i>S. rosmarinus</i>				
	14:5 / 13:5			
Proportion of flowers producing nectar		1	0.0442	0.83
Volume of nectar per flower		1	0.171	0.68
Sugar content per flower		1	0.0431	0.84
<i>C. albidus</i>				
	12:3 / 12:1 to 3			
Proportion of flowers producing nectar		1	1.49	0.22
Volume of nectar per flower		1	0.804	0.37
Sugar content per flower		1	0.730	0.39
<i>T. vulgaris</i>				
	12:5 / 7:5			
Proportion of flowers producing nectar		1	3.58	<b>0.059</b>
Volume of nectar per flower		1	1.13	0.29
Sugar content per flower		1	6.19	<b>0.013 *</b>

1359 \*  $P < 0.05$ .

1360

1361 **Table 3.** Drought impact on pollinator visits (Hurdle model). Significant effects ( $P < 0.05$ ) of  
 1362 drought are shown in bold.

	Sample size control / drought (number of observations)	df	$\chi^2$	$P$
<u>Presence/absence of visits</u> <i>S. rosmarinus</i> : 558 / 570; <i>C. albidus</i> : 348 / 348				
Treatment:Plant species:Pollinator group		5	1.83	0.87
Treatment:Pollinator group		5	5.43	0.37
Treatment:Plant species		1	2.39	0.12
Plant species:Pollinator group		5	156	< 0.001 ***
Treatment		1	1.11	0.29
<u>Number of visits (&gt;0)</u> <i>S. rosmarinus</i> : 90 / 92; <i>C. albidus</i> : 83 / 60				
Drought treatment : Plant species :		4†	10.3	<b>0.035 *</b>
Pollinator group				
<u>Comparison of means across pollinator groups:</u>				
<i>C. albidus</i> :				
<i>A. mellifera</i>	1.08 ± 0.54			0.88
Large wild bees	1.14 ± 0.79			0.85
Bumblebees	1.07 ± 0.44			0.87
Coleoptera	0.987 ± 0.36			0/97
Diptera	NA†			NA†
Small wild bees	1.00 ± 0.39			0.99
<i>S. rosmarinus</i> :				
<i>A. mellifera</i>	1.72 ± 0.36			<b>0.011 *</b>
Large wild bees	1.12 ± 0.35			0.72
Bumblebees	4.84 ± 3.12			<b>0.016 *</b>
Coleoptera	1.00 ± 1.56			0.99
Diptera	0.392 ± 0.312			0.24
Small wild bees	0.220 ± 0.105			<b>0.0015 **</b>

1363 \*  $P < 0.05$ ; \*\*\*  $P < 0.001$ . † No visits by Diptera on *C. albidus*.

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1367 **Table 4.** Drought impact on fruit set and seed set.

	Sample size control / drought [range in number of fruits]	df	$\chi^2$	<i>P</i>
<u><i>S. rosmarinus</i></u>				
	20 [4-53] / 20 [4-43]			
Number of fruits per m <sup>2</sup>			0.369	0.54
Average seed number per fruit		1	1.54	0.22
Variance in seed number per fruit		1	1.84	0.17
Seed mass per plant individual		1	0.0423	0.84
<u><i>C. albidus</i></u>				
	20 [2-13] / 20 [2-11]			
Number of fruits per m <sup>2</sup>			0.902	0.34
Average seed number per fruit		1	0.0408	0.84
Variance in seed number per fruit		1	1.23	0.27
Seed mass per plant individual		1	0.194	0.66

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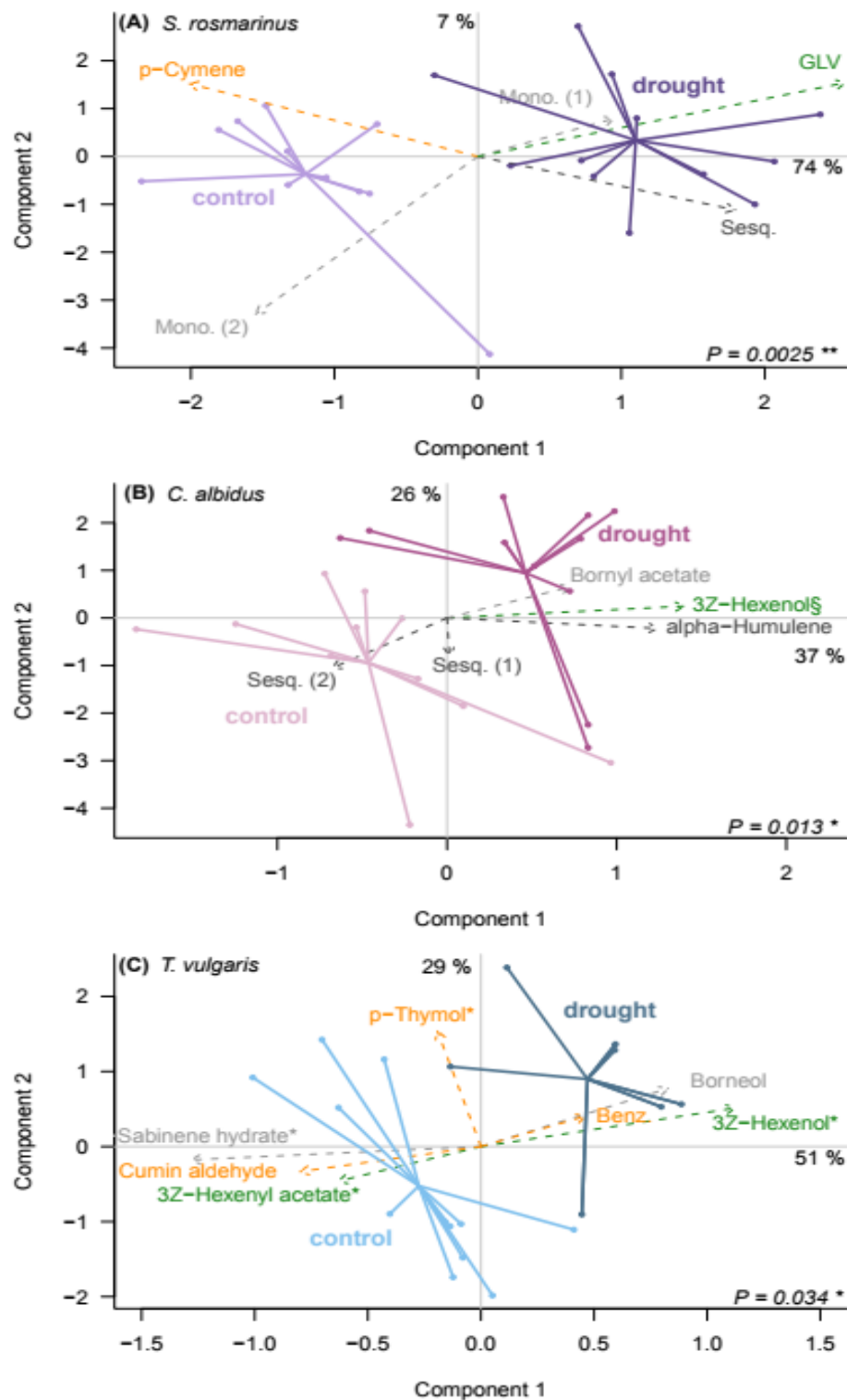
1370 **12. Figures**



1371

1372 **Figure 1.** The CLIMED facility in the Massif de l'Étoile north of Marseille, France (43° 22' N,  
1373 5° 25' E; June 2018). Foreground, left: drought plot, where gutters exclude up to 30 % of rainfall  
1374 and the water is carried away. Foreground, right: control plot, in which gutters are placed upside  
1375 down and rainfall reaches vegetation or the ground.

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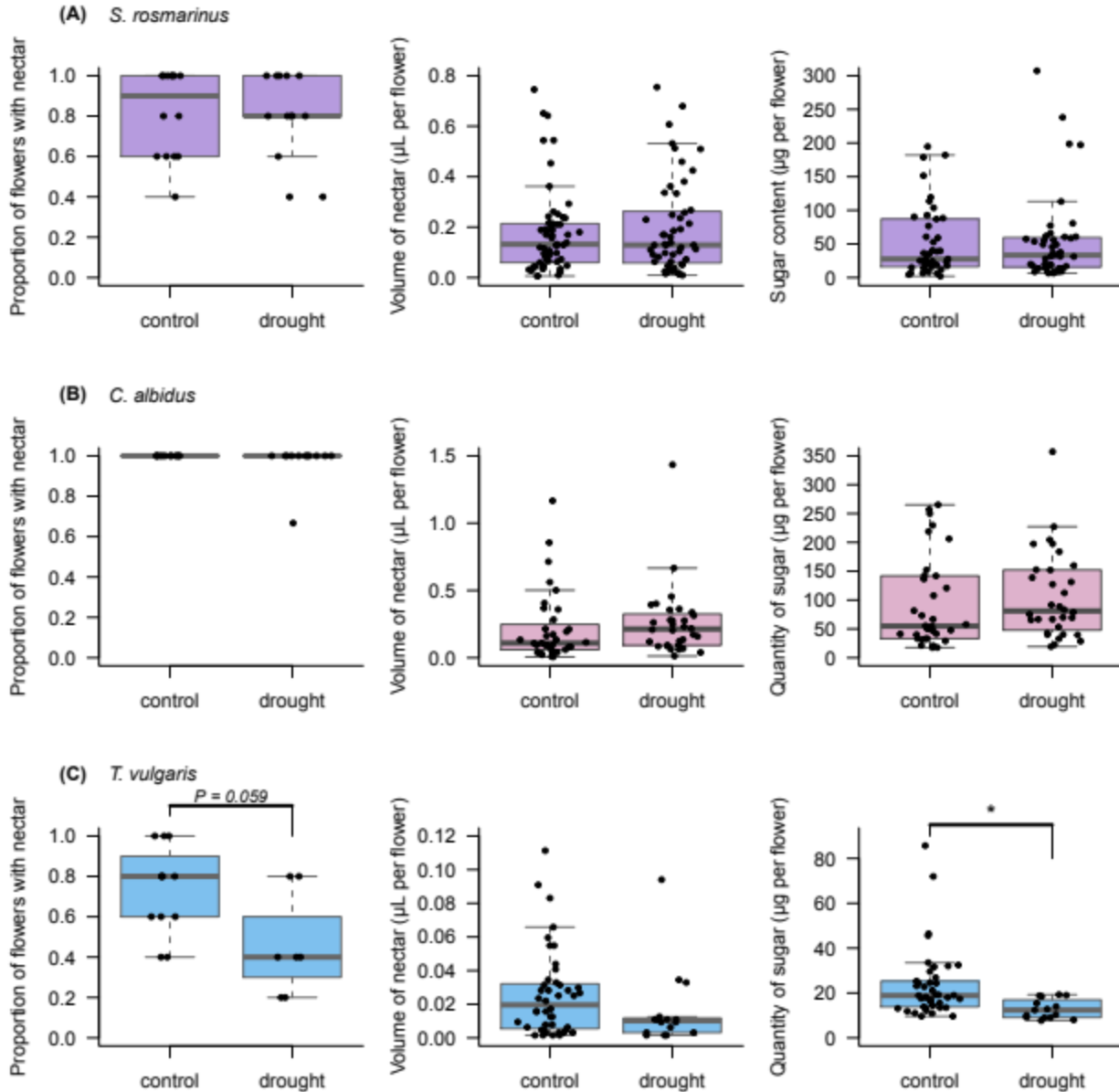
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1378 **Figure 2.** Multivariate analysis separating floral scent emissions across treatments (control,  
 1379 drought) on floral scent of (A) *S. rosmarinus*, (B) *C. albidus*, and (C) *T. vulgaris*. The position of

1380 the floral scent samples in the two-dimensional space is shown with dots connected to their  
1381 group's barycentre with solid arrows. The contribution of VOCs to components 1 and 2 (most  
1382 discriminating groups, [Table 1](#)) are shown with proportional dashed arrows, in which strongly  
1383 correlated VOCs of the same family have been averaged in a single arrow ("Mono." – light grey:  
1384 monoterpenoids; "Sesq." – dark grey: sesquiterpenoids; "GLV" – green: green-leaf volatiles;  
1385 "Benz." – orange: benzenoids). *S. rosmarinus*: "Mono. (1)": Camphor, Fenchone§,  
1386 Isopiperitenone\*; "Mono. (2)": Borneol, Camphene; "Sesq.": E-Caryophyllene\*,  $\alpha$ -Humulene\*,  
1387 Humulene epoxide II; "GLV": 3Z-Hexenol, Dodecanoic acid\*. *C. albidus*: "Sesq. (1)":  $\beta$ -  
1388 Bourbonene,  $\gamma$ -Muurolene; "Sesq. (2)": ar-Curcumene,  $\alpha$ -Zingiberene. *T. vulgaris*: "Benz.": p-  
1389 Cymene, Thymol acetate. \* VOCs found at higher emission rates in floral samples; §VOCs  
1390 found at higher emission rates in leaf-only samples (see [Tables S5-S7](#)). Significant differences  
1391 between control and drought treatments are indicated with *P*-values (\*:  $P < 0.05$ ; \*\*:  $P < 0.01$ ;  
1392 [Table 1](#)).

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1395 **Figure 3.** Impact of treatment (control, drought) on nectar production of (A) *S. rosmarinus*, (B)

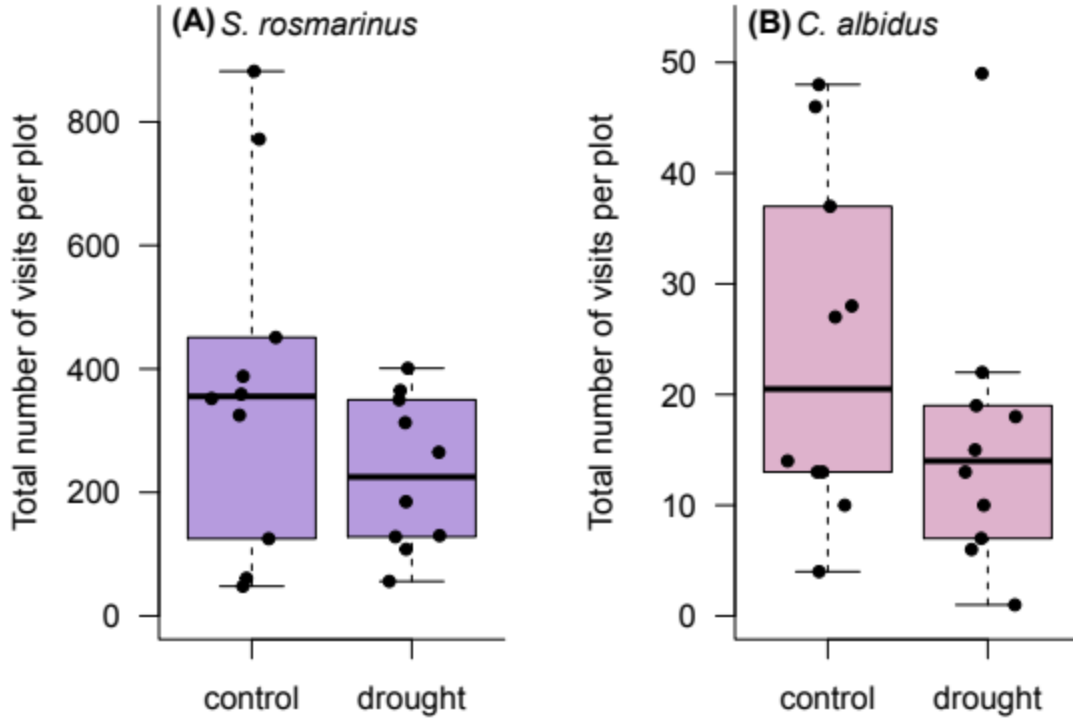
1396 *C. albidus*, and (C) *T. vulgaris*. Proportion of flowers producing nectar (left column), and for

1397 flowers producing nectar volume of nectar per flower (middle column) and sugar content per

1398 flower (right column). Sample sizes are provided in Table 2. \* indicates a significant difference

1399 at  $P < 0.05$  (Table 2).

1400



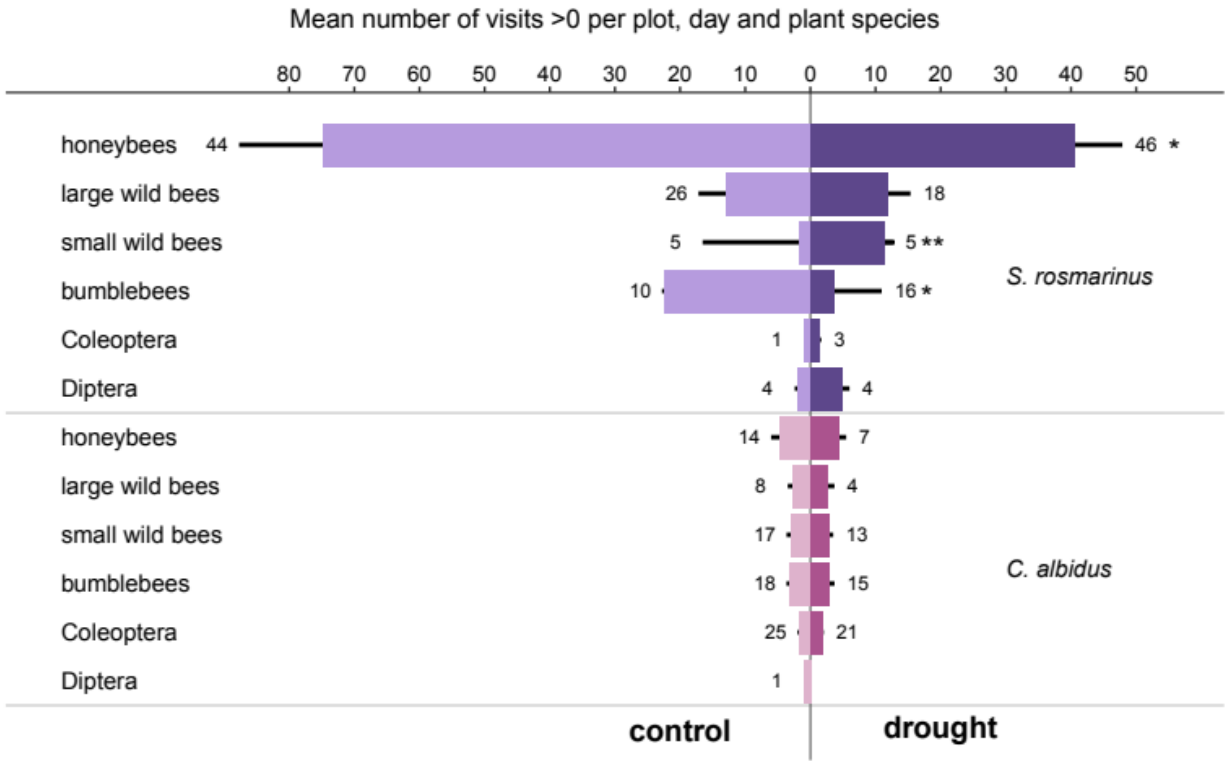
1401

1402 **Figure 4.** Drought impact on the total number of pollinator visits observed along the season to

1403 (A) *S. rosmarinus* and (B) *C. albidus*. N = 20 per treatment.

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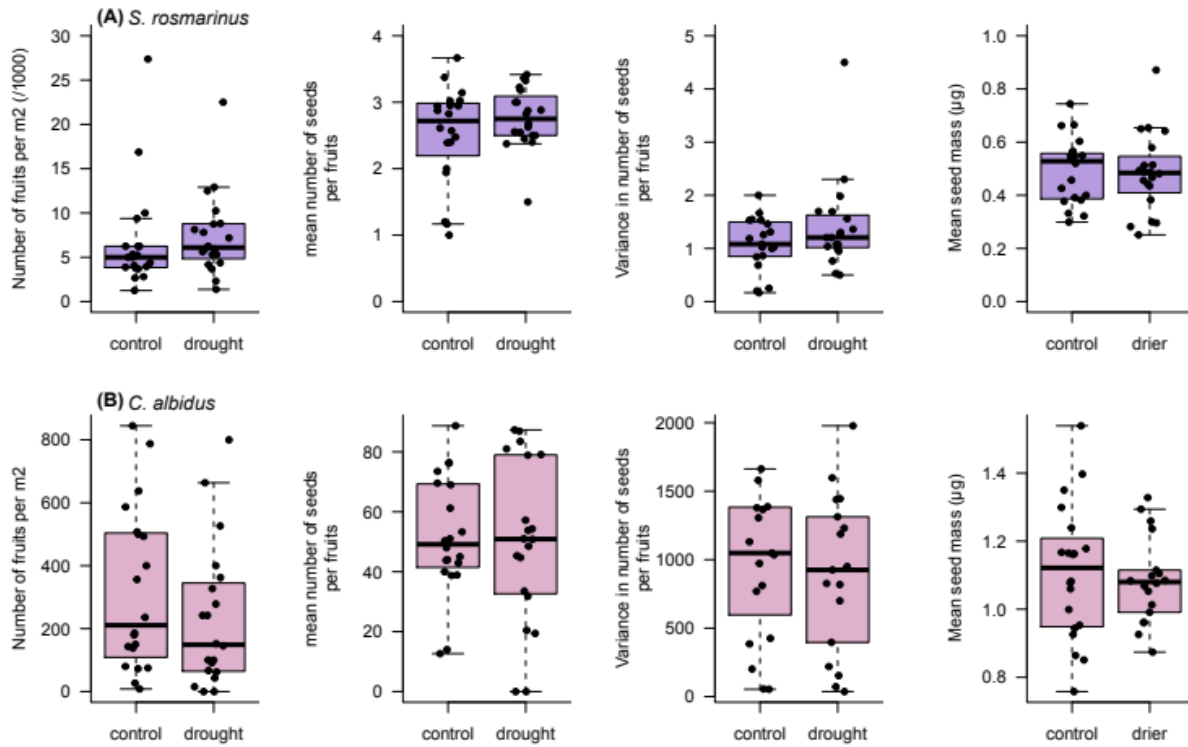
1406

1407 **Figure 5.** Drought impact on the mean number of visits ( $\pm$  SE) per 5 min per plot by each  
 1408 pollinator functional group on *S. rosmarinus* (top, purple) and *C. albidus* (bottom, pink), after  
 1409 removing zeros. Sample sizes are shown adjacent to bars, and show the number of observations  
 1410 with visits (i.e. sessions when at least one visit was observed for each plant species, treatment  
 1411 and pollinator group). Significant differences are highlighted with \* ( $P < 0.005$ ) and \*\* ( $P <$   
 1412  $0.001$ ; see [Table 3](#)).

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1416  
 1417 **Figure 6.** Drought impact on the number of fruits per m<sup>2</sup> (left), the mean seed number and  
 1418 variance in seed number per fruit (middle), and the mean seed mass (right) in *S. rosmarinus* (top  
 1419 row) and *C. albidus* (bottom row). Sample sizes are provided in [Table 4](#).

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1421