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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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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.

1. Introduction

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

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

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

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

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

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

2. Material and Methods

2.1. Study site: CLIMED long-term drought experiment

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

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

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

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

219

2.2. Floral traits involved in pollinator attraction

2.2.1. Floral scent

We randomly selected up to 14 plant individuals per species in each treatment (control vs. drought) with a maximum of two (four for *T. vulgaris*) plants in the same plot. A few samples were lost during laboratory analysis, hence final sample sizes were 23 (control: 11; drought: 12) for *S. rosmarinus*, 22 (control: 11; drought: 11) for *C. albidus*, and 19 (control: 6 female, 6 hermaphroditic; drought: 5 female, 2 hermaphroditic) for *T. vulgaris*. Floral scent sampling and data processing is described in detail in Supporting Information (1.1.). Briefly, the 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 (1st-3rd quantiles) were enclosed in 2 L bags and placed under a
231 constant flow of purified air (inlet 1000 mL.min⁻¹, outlet 200 mL.min⁻¹). 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 ± 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 $\mu\text{g.h}^{-1}.\text{gDM}^{-1}$) were calculated by subtracting the

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

2.2.2. Nectar production

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

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

When measuring plant-pollinator interactions, it is necessary to control for the flowering phenology of each species and the number of flowers at each sampling date, because pollinators are naturally attracted to patches with more flowers (Vrdoljak et al., 2016) and the flowering phenology of each species also influences the visitor community. To assess flowering phenology, the total number of flowers per plant was measured each week from March 9th to May 23rd, 2018 (12 weeks total), on two marked plant individuals per species (*S. rosmarinus*, *C. albidus*, and *T. vulgaris*) in each plot (20 individuals per treatment, except *T. vulgaris*: control: 11, drought: 8). On each individual, all flowers present in a volume delimited by the maximum height of the plant and a marked 40 × 40 cm quadrat were counted or estimated. For individuals smaller than the quadrat, their percent cover in the quadrat was measured, and all their flowers were counted, to obtain a number of flowers per m² for all plant individuals. When *S. rosmarinus* plants had many flowers around the flowering peak, flowers were counted by groups of ten, visually estimating the area covered by ten flowers.. For each individual, we calculated the date of its flowering peak as the week with the maximum number of flowers counted, and the total number of flowers as the sum of all flowers counted over all sampling dates. We also calculated a proxy for the flowering period as the number of weeks with at least half as many flowers as the maximum number of flowers recorded. Finally, we measured the impact of drought on flower colour and size on flowers collected for nectar production measures, and we have detailed the methods and results for these traits in [Supporting Information \(1.4.\)](#).

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 ($\sim 1.5 \text{ m}^2$) 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

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

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

2.4. Plant reproduction

As an estimate of plant female fitness we measured the fruit set of each marked plant individual of *C. albidus* and *S. rosmarinus* (two per plot). As a proxy for fruit set, we counted the total number of fruits per m² with the same method as for the total number of flowers (section 2.2.3) on May 31st for *C. albidus* and on four successive weeks (May 3rd to May 23rd) for *S. rosmarinus*. This was because first ripe fruits dehisced before the last ones were fully

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

2.5. Statistical analyses

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

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

2.5.1. Floral scent

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

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

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

2.5.2. Other floral traits

Nectar. We calculated the proportion of flowers with nectar present as the number of flowers with nectar volume >0 over the total number of flowers sampled per individual and analysed 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 m², 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

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

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

2.5.4. Plant reproduction

The drought impact on the number of fruits per m² was tested with a GLMM with a negative binomial error distribution for each species ([section 2.5.1](#)). For each species, the impact of

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

3. Results

3.1. Efficacy of the rainfall reduction in 2018

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

3.2. Floral traits involved in pollinator attraction

3.2.1. Floral scent

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

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

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

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

3.2.2. Nectar production and other floral traits

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

3.3. Plant-pollinator interactions

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

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

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

3.4. Plant reproduction

Drought did not affect the number of fruits per m² for either *S. rosmarinus* or *C. albidus*, nor did it affect the mean and variance in seed number per fruit or the mean seed mass (Table 4, Fig. 6). Finally, drought had a limited impact on seeds (Appendix section 2.; Table S15, Fig. S5). Seeds from *C. albidus* plants under drought had a marginally significant higher viability rate but a marginally significant lower germination rate. Seeds from *S. rosmarinus* plants under drought had a slower germination (Table S15, Fig. S5D).

4. Discussion

Our study assesses the impacts of an induced long-term experimental drought on floral traits, plant-pollinator interactions and plant reproduction in a natural Mediterranean community. Overall, we found a limited impact of amplified drought: floral scent was consistently altered by drought in all three species tested, but the other floral traits (flower colour and size and flowering phenology) were not affected, except nectar production in *T. vulgaris*, which was

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

4.1. Limited impact of drought

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

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

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

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

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 (Borghi 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 α -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 α -
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

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

4.4. Limitations of the study and next steps

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

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

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

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

Our study was similar to an *in situ* choice experiment, since foraging bees could freely choose between control and drought plots (Nordström et al., 2017). In reality, climate change is likely to affect entire plant communities and up to a regional scale, leaving no such choice 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

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

5. Acknowledgments

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6. Conflict of interests

All authors have declared to have no conflict of interest.

7. Authors' contributions

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

8. Data availability

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

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1314

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)			number of mis- classified samples	<i>P</i>	number of VOCs		<i>t</i>	df	<i>P</i>	mean ± SE (µg.g _{DM} ⁻¹ .h ⁻¹)		<i>t</i>	df	<i>P</i>	mean number ± SE	
		Y (treatment)	X (samples)	CER (%)			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	0.0025 **	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	0.013 *	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	0.034 *	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	χ^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	0.059
Volume of nectar per flower		1	1.13	0.29
Sugar content per flower		1	6.19	0.013 *

* $P < 0.05$.

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	χ^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 (>0)</u> <i>S. rosmarinus</i> : 90 / 92; <i>C. albidus</i> : 83 / 60				
Drought treatment : Plant species :		4†	10.3	0.035 *
Pollinator group				
Comparison of means across pollinator groups:	Ratio control / drought ($\pm$ SE)			P
<i>C. albidus</i> :				
<i>A. mellifera</i>	1.08 $\pm$ 0.54			0.88
Large wild bees	1.14 $\pm$ 0.79			0.85
Bumblebees	1.07 $\pm$ 0.44			0.87
Coleoptera	0.987 $\pm$ 0.36			0/97
Diptera	NA†			NA†
Small wild bees	1.00 $\pm$ 0.39			0.99
<i>S. rosmarinus</i> :				
<i>A. mellifera</i>	1.72 $\pm$ 0.36			0.011 *
Large wild bees	1.12 $\pm$ 0.35			0.72
Bumblebees	4.84 $\pm$ 3.12			0.016 *
Coleoptera	1.00 $\pm$ 1.56			0.99
Diptera	0.392 $\pm$ 0.312			0.24
Small wild bees	0.220 $\pm$ 0.105			0.0015 **

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	χ^2	<i>P</i>
<i>S. rosmarinus</i>	20 [4-53] / 20 [4-43]			
Number of fruits per m ²			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
<i>C. albidus</i>	20 [2-13] / 20 [2-11]			
Number of fruits per m ²			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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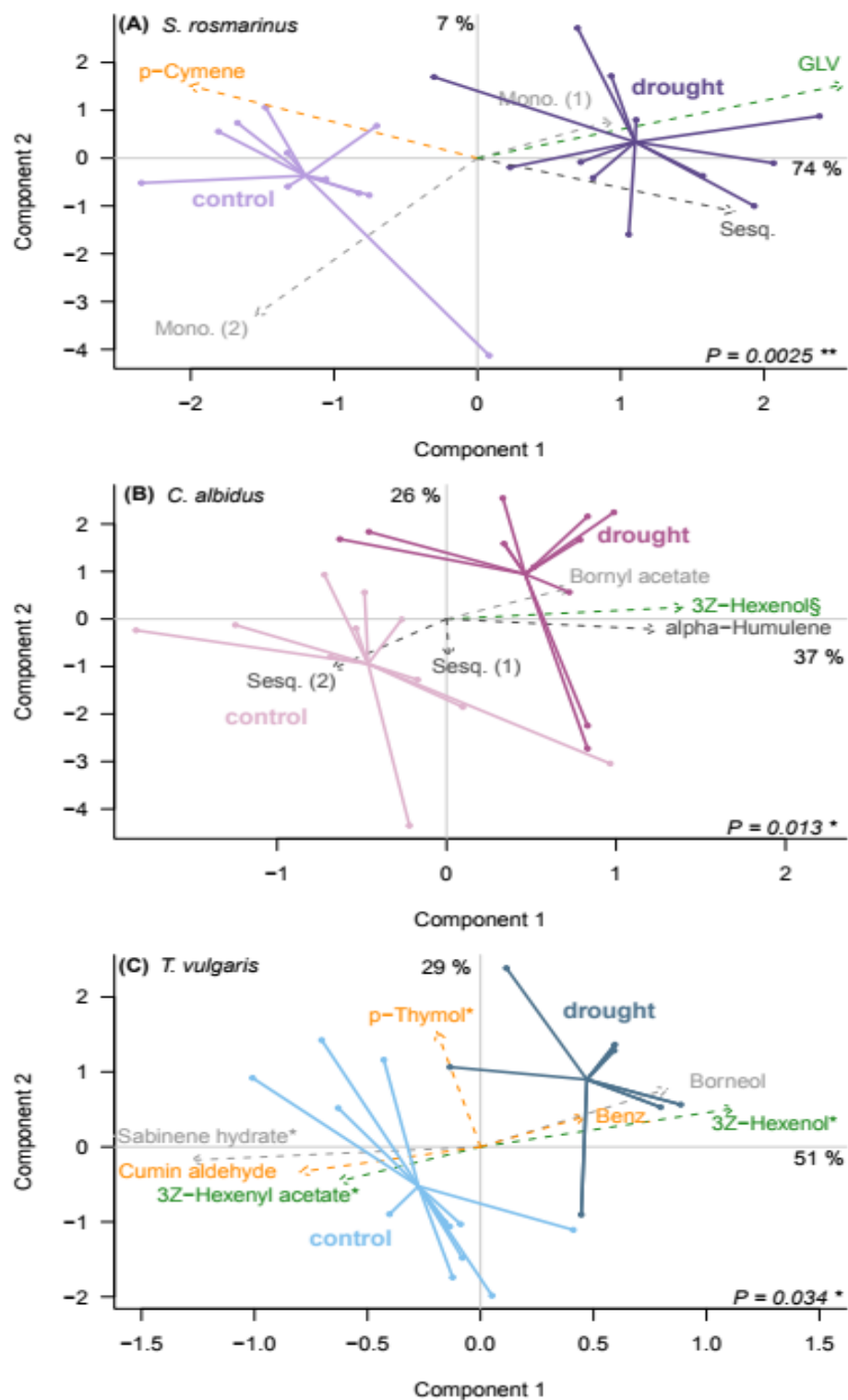


Figure 2. Multivariate analysis separating floral scent emissions across treatments (control, drought) on floral scent of (A) *S. rosmarinus*, (B) *C. albidus*, and (C) *T. vulgaris*. The position of

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*, α -Humulene*,
 1387 Humulene epoxide II; "GLV": 3Z-Hexenol, Dodecanoic acid*. *C. albidus*: "Sesq. (1)": β -
 1388 Bourbonene, γ -Muurolene; "Sesq. (2)": ar-Curcumene, α -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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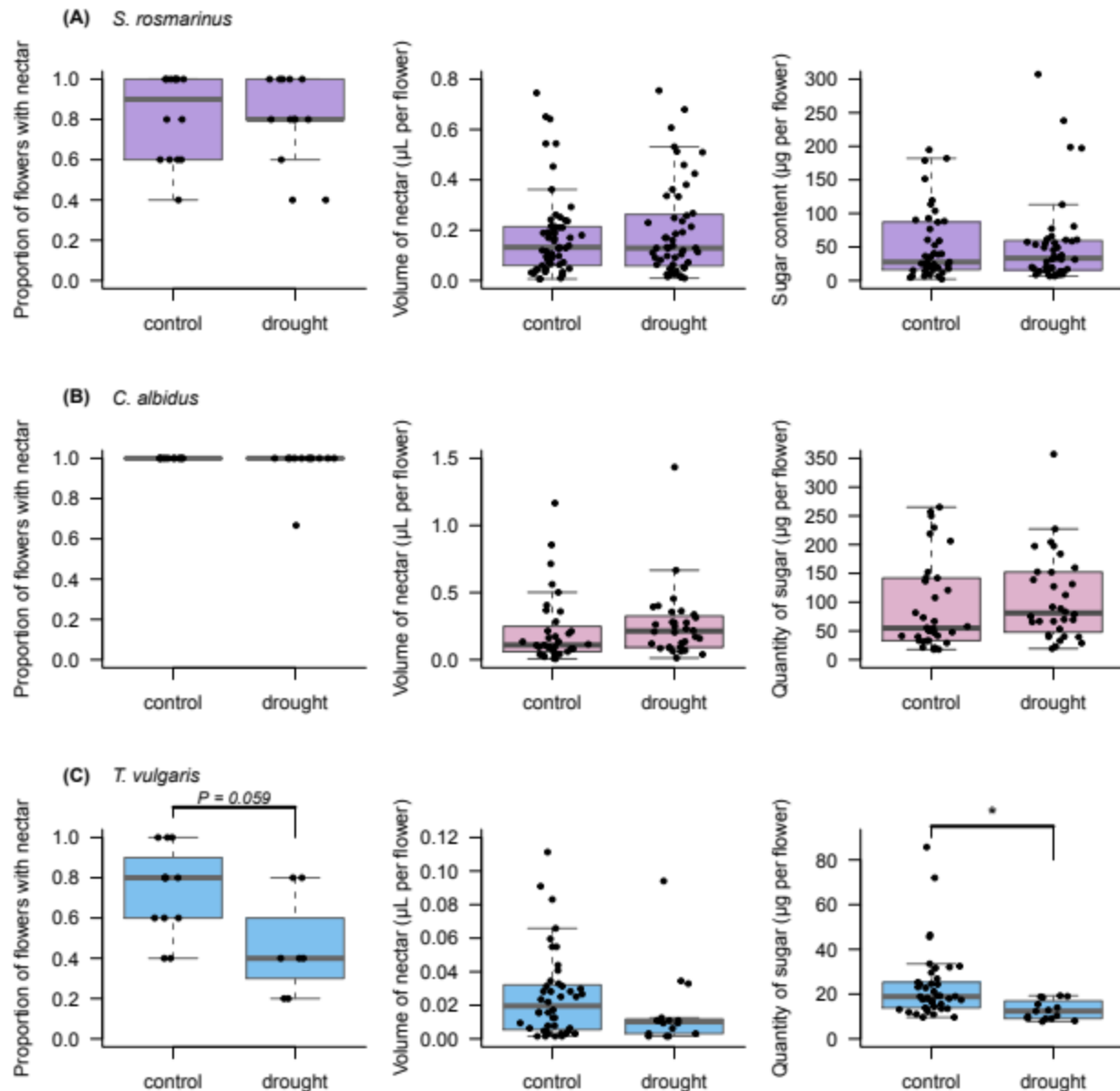


Figure 3. Impact of treatment (control, drought) on nectar production of (A) *S. rosmarinus*, (B) *C. albidus*, and (C) *T. vulgaris*. Proportion of flowers producing nectar (left column), and for flowers producing nectar volume of nectar per flower (middle column) and sugar content per flower (right column). Sample sizes are provided in Table 2. * indicates a significant difference at $P < 0.05$ (Table 2).

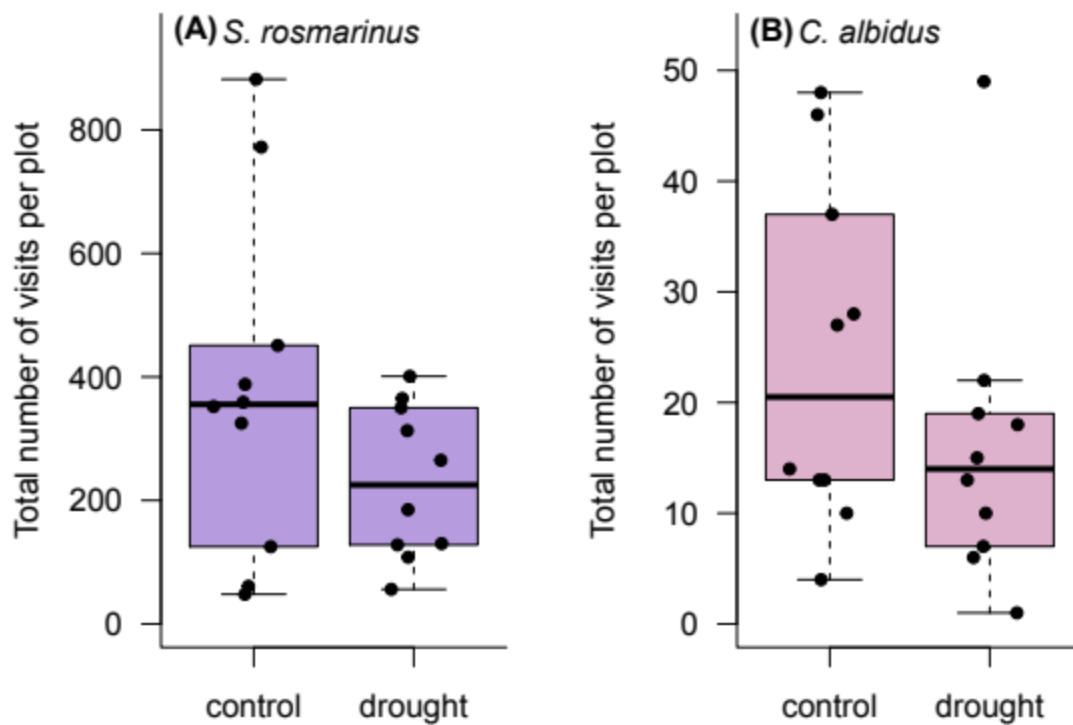


Figure 4. Drought impact on the total number of pollinator visits observed along the season to (A) *S. rosmarinus* and (B) *C. albidus*. N = 20 per treatment.

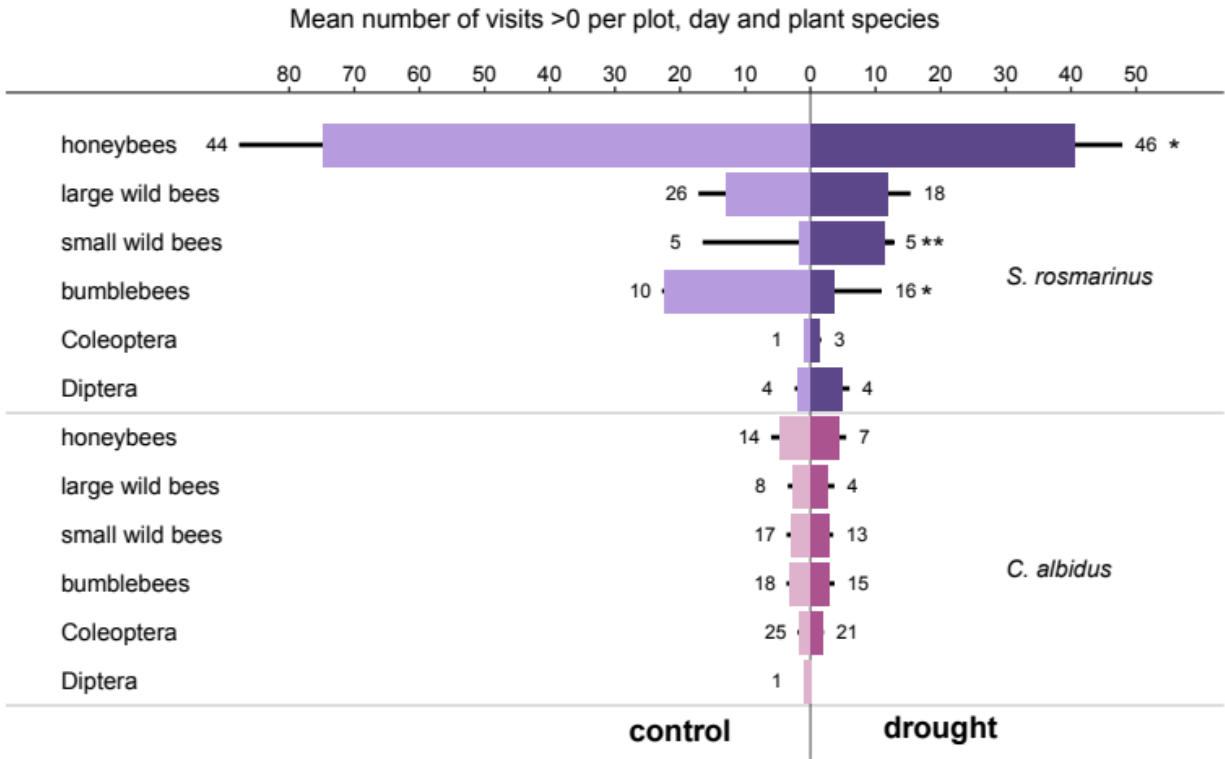


Figure 5. Drought impact on the mean number of visits ($\pm$ SE) per 5 min per plot by each pollinator functional group on *S. rosmarinus* (top, purple) and *C. albidus* (bottom, pink), after removing zeros. Sample sizes are shown adjacent to bars, and show the number of observations with visits (i.e.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

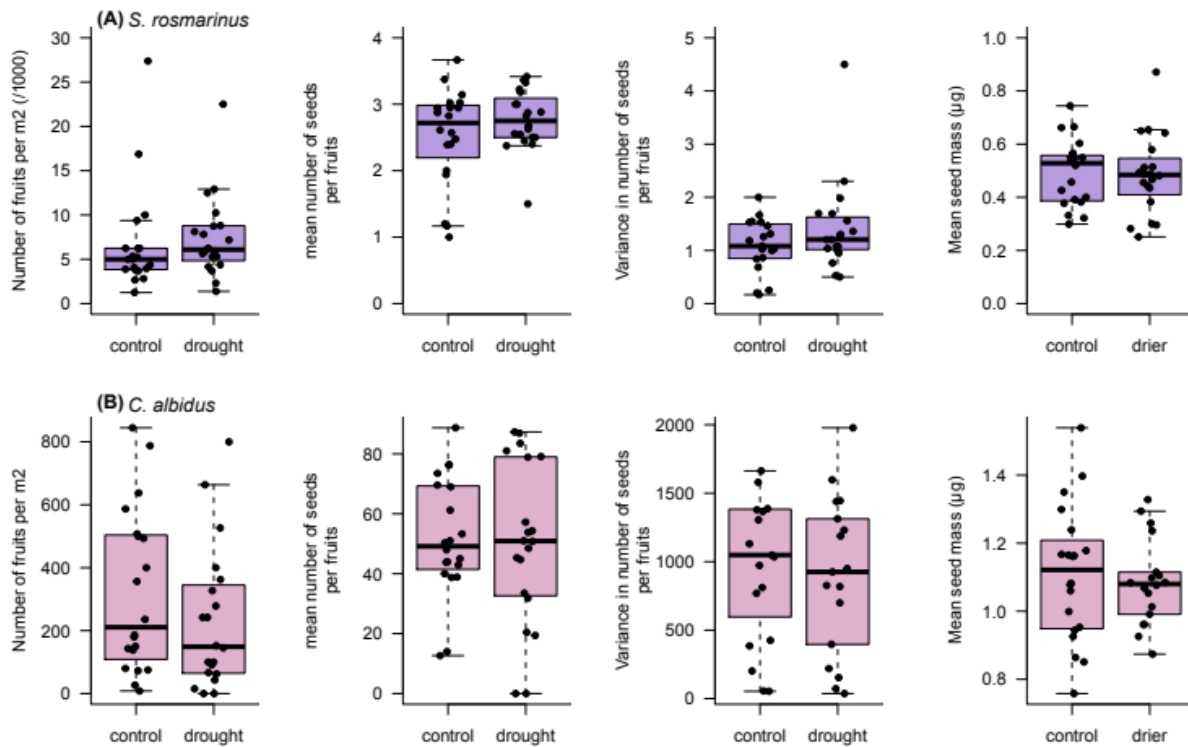


Figure 6. Drought impact on the number of fruits per m² (left), the mean seed number and variance in seed number per fruit (middle), and the mean seed mass (right) in *S. rosmarinus* (top row) and *C. albidus* (bottom row). Sample sizes are provided in [Table 4](#).