




RESEARCH ARTICLE

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

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Abstract

1. Pollinators are declining globally, with climate change implicated as an important driver. Climate change can induce phenological shifts and reduce floral resources for pollinators, but little is known about its effects on floral attractiveness and how this might cascade to affect pollinators, pollination functions and plant fitness.
2. We used an *in situ* long-term drought experiment to investigate multiple impacts of reduced precipitation in a natural Mediterranean shrubland, a habitat where climate change is predicted to increase the frequency and intensity of droughts. Focusing on three insect-pollinated plant species that provide abundant rewards and support a diversity of pollinators (*Cistus albidus*, *Salvia rosmarinus* and *Thymus vulgaris*), we investigated the effects of drought on a suite of floral traits including nectar production and floral scent. We also measured the impact of reduced rainfall on pollinator visits, fruit set and germination in *S. rosmarinus* and *C. albidus*.
3. Drought altered floral emissions of all three plant species qualitatively, and reduced nectar production in *T. vulgaris* only. *Apis mellifera* and *Bombus gr. terrestris* visited more flowers in control plots than drought plots, while small wild bees visited more flowers in drought plots than control plots. Pollinator species richness did not differ significantly between treatments. Fruit set and seed set in *S. rosmarinus* and *C. albidus* did not differ significantly between control and drought plots, but seeds from drought plots had slower germination for *S. rosmarinus* and marginally lower germination success in *C. albidus*.
4. *Synthesis.* Overall, we found limited but consistent impacts of a moderate experimental drought on floral phenotype, plant reproduction and pollinator visits. Increased aridity under climate change is predicted to be stronger than the level assessed in the present study. Drought impacts will likely be stronger and this

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could profoundly affect the structure and functioning of plant–pollinator networks in Mediterranean ecosystems.

KEYWORDS

climate change, floral traits, plant fitness, pollination, reduced rainfall, volatile organic compound, water deficit, water-limited

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 (Christmann, 2020; IPBES, 2016). Anthropogenic habitat destruction and land-use intensification (including insecticide use) are commonly thought to be the main drivers of pollinator population declines globally (Dicks et al., 2021; IPBES, 2016; Potts et al., 2016; Powney et al., 2019; Wagner, 2020; 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 (Duchenne et al., 2020; Memmott et al., 2007), shifts of their geographical 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 (Gallagher & Campbell, 2017; Phillips et al., 2018; Waser & Price, 2016). Nectar production is also sensitive to temperature and many species reach maximum production at an optimal temperature (Jakobsen & Krijtjansson, 1994; Petanidou & Smets, 1996). Drought-induced reduction in the production and timing of floral resources available to pollinators could therefore lead to declines in their abundance (Forister et al., 2018; Thomson, 2016; Timberlake et al., 2020).

Although much less studied, climate change can also disrupt plant–pollinator interactions in a more subtle way, by altering floral signalling and attractiveness (Walter, 2020). Pollinators use and learn visual and olfactory flower signals—including floral display (number of flowers), flower size and colour, and floral scent—to detect, recognize, and locate their preferred floral resources (Bourke & Runyon, 2019; Giurfa & Sandoz, 2012; Raguso, 2008). Floral scent is a blend of many different volatile organic compounds (VOCs) emitted by floral tissue that guide pollinators towards floral resources. The activation of plant defences also leads to the emission of specific VOCs from inflorescence tissue, which blend in pollinator-attractive floral scent plumes

(Borghi et al., 2019; Cunningham, 2012; Wright & Schiestl, 2009). Therefore, floral scent is highly sensitive to increased temperature (Farré-Armengol et al., 2014; Yuan et al., 2009) and drought, with increased emissions under moderate stress (Bourke & Runyon, 2016; Campbell et al., 2019; Glenney et al., 2018). Altered floral attractiveness could therefore affect pollinators' foraging behaviour and resource choices (Flacher et al., 2017, 2020). For instance, herbivore-induced plant volatiles present in floral scent tend to deter pollinators from floral resources in attacked plants (Hoffmeister & Junker, 2017; Kessler et al., 2011). Similarly, water-limited plants can be less visited by pollinators due to changes in flower attractiveness and floral rewards (Descamps et al., 2018; Rering et al., 2020).

More broadly, climate change and especially drought affects plant physiology and development. Drought reduces stomatal conductance and therefore carbon uptake, reducing photosynthesis and plant growth (Prieto et al., 2009; Reddy et al., 2004; 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 (Aslam et al., 2015; Nardini et al., 2014). 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; Rodríguez-Ramírez 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 | MATERIALS 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, Affre, Aubert, et al., 2020), *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 1–30 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 (Rodríguez-Ramírez, 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, Affre, Aubert, et al., 2020); and (ii) a high and similar percentage cover of *C. albidus* and *S. rosmarinus* (Figure 1). The chosen control and drought plots were homogeneously distributed throughout the site (Figure 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%



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

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.

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 are described in detail in Supporting Information (1.1). Briefly, the collection of floral scent volatiles was performed via dynamic headspace sampling *in situ*. Inflorescences from plant canopy bearing around 30–50 (*S. rosmarinus*), 2–3 (*C. albidus*) or 100–400 (*T. vulgaris*) flowers (1st–3rd quantiles) were enclosed in 2 L bags and placed under a constant flow of purified air (inlet 1000 ml min⁻¹, outlet 200 ml min⁻¹). Two leaf-only scent samples in each plant species and treatment were also collected as a comparison, enclosing branches of comparable sizes than the inflorescences in floral samples (Supporting Information 1.1 and 2.1). VOCs were adsorbed on a Carbotrap/Tenax cartridge (Sigma-Aldrich) placed at the bag outlet for 10 min for *S. rosmarinus* and *T. vulgaris*, and 15 min for *C. albidus*, so as to not exceed the breakthrough volume of each VOC (Ormeño et al., 2007). Ambient air (one sample every three plant scent sample) was also sampled as blank control and temperature recorded for emission rate normalization (see below).

Samples were analysed using gas chromatography (GC) coupled with mass spectrometry after thermodesorption. The methodology is detailed in Supporting Information 1.1. Briefly, peaks were extracted and peak area was automatically measured with MZmine2 (version 2.18.1 developed for GC; Pluskal et al., 2010) after baseline correction. Peak retention indexes calculations and peak identification were performed in R (R Core Team, 2020 version 3.6.3). Individual peak mass spectra were compared with that of 21 pure

standard molecules injected separately as well as reference spectra (libraries Adams, 2007 and NIST, 2011) using the R function 'SpectrumSimilarity' (R library 'OrgMassSpecR v0.5-3'; Stein & Scott, 1994) and with a tolerance in retention index of ± 15 between the analysed peak and the reference molecule. Despite these precautions, the identification remains tentative. Only identified VOCs previously reported as plant volatiles, with an average similarity >0.8 and whose area exceeded three times that of ambient air samples in average were retained for analysis (Campbell et al., 2019 and see Supporting Information 1.1). Emission rates of each VOC (in $\mu\text{g h}^{-1} \text{g}_{\text{DM}}^{-1}$) 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 (Ormeño et al., 2007; Sabillón & Cremades, 2001).

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 μL 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 $\mu\text{L}/\text{flower}$) by measuring the amount of liquid in a microcapillary tube with a digital caliper (Digit-Cal MK IV, Brown & Sharpe). Sugar concentration was measured immediately afterwards using a hand-held refractometer (Eclipse 0–30°Brix, Bellingham & Stanley Ltd) calibrated by the manufacturer. The whole volume of nectar collected was deposited on the measuring surface of the refractometer and diluted with 1 μL of pure water (measured with a 1 μL microcapillary tube) to increase the total volume and measure reproducibility. The sugar concentration (in $\mu\text{g}/\mu\text{L}$) and total sugar content (in μg) were calculated *a posteriori* using the conversion table from °Brix to g/L by Kearns and Inouye (1993) 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 10, visually estimating the area covered by 10 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

To quantify plant-pollinator interactions, pollinator visits were observed once a week for 12 weeks on the same days as flowering phenology, by monitoring for 5 min in each of the 20 plots: in each plot, we chose the three patches (~1.5 m²) with the highest flower density to increase the chance of observing interactions (Ropars, Affre, Schurr, et al., 2020). This represented a total of 20 h of observation. Each patch was assigned to one observer, and all observed flowers of each flowering species were counted using the same method as for flowering phenology (see Section 2.2.3) to control for plot attractiveness to pollinators (patches with higher flower density are often more attractive and receive more visits; Feldman, 2006; Vrdoljak et al., 2016). Similarly to the plant individual level, the total number of observed flowers per plot and the flowering phenology at the plot level were not significantly different between control and drought plots (data not shown).

We defined a single visit when the observed insect touched the reproductive parts of a flower. We recorded the number of visits, the functional group of the visiting insect and the plant species visited (*S. rosmarinus*, *C. albidus* or *T. vulgaris*). Functional groups recorded were as follows: (1) *Bombus gr. terrestris*, (2) the managed honeybee *Apis mellifera*, (3) small wild bees (smaller than *A. mellifera*), (4) large wild bees (larger than *A. mellifera*), (5) Coleoptera and (6) Diptera. *Bombus gr. terrestris* is by far the most abundant *Bombus* group species in the region and the other very rare species are functionally similar (Ropars, Affre, Aubert, et al., 2020). No wild *Apis mellifera* colony was recorded close to our study site and we assumed that 100 %

of *A. mellifera* we observed were managed (see also Herrera, 2020). For clarity, we refer to *Apis mellifera* as the managed honeybee in this study. The six pollinator groups defined above are easily identified *in situ*. Visits by non-Apoidea Hymenoptera and by Lepidoptera were extremely rare and therefore not considered. Observations were carried out under optimal weather conditions, that is, 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, Ceratinii 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 mixed model (LMM) or generalized linear mixed model (GLMM) 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 (Arnan et al., 2014; Thompson et al., 2002). 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 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 'cplpls' 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, that is, 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 three-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 'stat'; R Core Team, 2020). The response variable was implemented as a two-column matrix containing the number of flowers with and without nectar (Phillips et al., 2018). Using flowers with nectar only, we then analysed the drought impact on nectar volume (*100 and rounded, which corresponded to an estimated measure error of 2%) and sugar content (μg , rounded) using GLMMs with Poisson and negative binomial distributions, respectively (functions 'glmer' and 'glmer.nb', R library 'lme4'; Bates et al., 2015).

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

2.5.3 | Pollinator observations

We first analysed the drought impact on the total number of visits per plot throughout the season for each plant species using a GLMM with a Poisson distribution (function 'glmer') and the treatment in interaction with the plant species (*S. rosmarinus* or *C. albidus*; $N = 20$ for each species, 10 per treatment) as fixed effects. Then, we analysed the impact of drought on the weekly number of visits by each pollinator functional group in each plot and to each plant species, using a two-step Hurdle modelling approach (Geslin et al., 2020). The first test worked on the presence or absence of visits of each group, assessing the attractiveness of a plot (how likely is each plant species in a plot

likely to be visited by each functional group). We used a GLMM with a binomial distribution (function 'glmer'), implementing the treatment in interaction with the plant species (*S. rosmarinus* versus *C. albidus*) and the 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 covariables 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 *Glyptotendipes* sp., Table S12), and such data were 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 h 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; Tables S5–S7; Figure 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

TABLE 1 Drought impact on floral scent emissions: results of the multivariate analysis (cppls) of scent composition showing group separations (variance explained by treatment and samples, classification error rate [CER], and number of misclassified samples; see Figure 2), and analysis of total emission rates and diversity of volatile organic compounds (VOCs) emitted (t-tests). Significant effects of drought are shown in bold. 'C > D': emitted at higher rates in control plants compared to plants under drought; 'C < D': emitted at lower rates in control plants compared to plants under drought.

Species	Number of VOCs selected	Multivariate analysis (cppls)					Number of VOCs	
		Variance explained (% axes 1,2,3 = total)		CER (%)	Number of misclassified samples	p	C > D	C < D
		Y (treatment)	X (samples)					
<i>S. rosmarinus</i>	11	74,7,6 = 87	19,27,13 = 58	16.4	4 of 23	0.0025**	3	8
<i>C. albidus</i>	7	37,26,5 = 67	10,65,11 = 85	22.2	5 of 22	0.013*	4	3
<i>T. vulgaris</i>	8	51,29,3 = 82	4,35,10 = 51	23.0	4 of 19	0.034*	3	5

* $p < 0.05$; ** $p < 0.01$.

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 and S5–S7; Figure 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; Figure 3).

Total number of flowers was not affected by drought in either of the three species, and neither was flowering phenology (Table S9; Figure 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 and S11; Figure S3).

3.3 | Plant–pollinator interactions

We recorded a total of 6576 flower visits, including 6064 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: $\chi^2 = 1.24$, $df = 1$, $p = 0.26$; Figure 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: $74.7 \pm 13.0/40.6 \pm 7.3$; bumblebees: control/drought: $22.4 \pm 14.7/4.4 \pm 1.3$; small wild bees: control/drought: $1.8 \pm 0.4/11.4 \pm 7.3$; Table 3; Figure 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%–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 ($t = 1.04$, $df = 17.3$, $p = 0.31$; Figure 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 m^2 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; Figure 6). Finally, drought had a limited impact on seeds (Appendix Section 2; Table S15; Figure S5). Seeds from *C. albidus* plants under drought had a marginally significant higher viability rate but a marginally

Total emissions (t-test)					VOC diversity (t-test)				
t	df	p	Mean \pm SE ($\mu\text{g g}_{\text{DM}}^{-1} \text{h}^{-1}$)		t	df	p	Mean number \pm SE	
			C	D				C	D
−0.214	20.6	0.83	32.4 \pm 5.0	33.4 \pm 4.4	−0.615	20.5	0.54	18 \pm 1	20 \pm 2
0.527	20.0	0.60	18.9 \pm 9.7	13.5 \pm 6.3	1.76	19.7	0.093	10 \pm 2	6 \pm 2
−1.01	7.53	0.34	627 \pm 122	1659 \pm 850	0.880	8.88	0.40	16 \pm 1	14 \pm 2

significant lower germination rate. Seeds from *S. rosmarinus* plants under drought had a slower germination (Table S15; Figure 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

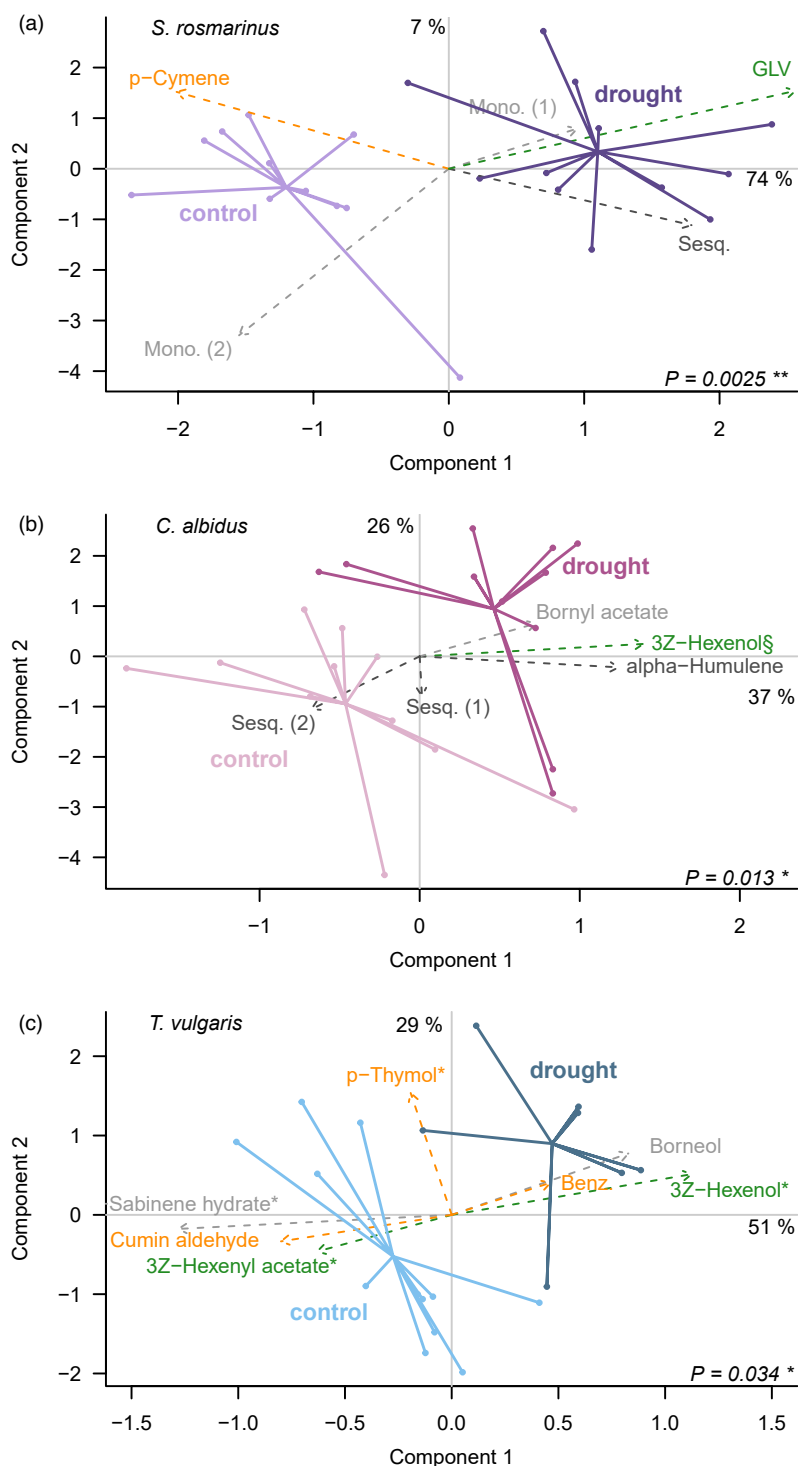
The overall limited impact of drought on floral traits and plant reproduction was unexpected, since many studies have reported changes in nectar production, flowering phenology, flower size and number, and fruit or seed set under possibly more intense drought (reviewed in Borghi et al., 2019 and Descamps 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 (Aslam et al., 2015; Nardini et al., 2014). These mechanisms or traits may have been further selected for in our experimental drought plots over 6 years, through differential mortality, increasing drought resistance in the plant community (Rodríguez-Ramírez, 2017; Rodríguez-Ramírez 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 (Abbaszadeh et al., 2020; Pérez-Llorca et al., 2019).

Only *T. vulgaris* had a drastically reduced nectar standing crop under drought (total sugar reduced by ~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; Raderschall et al., 2021; Rering et al., 2020; Walter, 2020). 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 (Bourke & 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).

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 the floral scent samples in the two-dimensional space is shown with dots connected to their group's barycentre with solid arrows. The contribution of volatile organic compounds (VOCs) to components 1 and 2 (most discriminating groups, Table 1) are shown with proportional dashed arrows, in which strongly correlated VOCs of the same family have been averaged in a single arrow ('Mono.'—light grey: monoterpenoids; 'Sesq.'—dark grey: sesquiterpenoids; 'GLV'—green: green-leaf volatiles; 'Benz.'—orange: benzenoids). *S. rosmarinus*: 'Mono. (1)': Camphor, Fenchone[§], Isopiperitenone*; 'Mono. (2)': Borneol, Camphene; 'Sesq.': E-Caryophyllene*, α -Humulene*, Humulene epoxide II; 'GLV': 3Z-Hexenol, Dodecanoic acid*. *C. albidus*: 'Sesq. (1)': β -Bourbonene, γ -Murolene; 'Sesq. (2)': ar-Curcumen, α -Zingiberene. *T. vulgaris*: 'Benz.': p-Cymene, Thymol acetate. *VOCs found at higher emission rates in floral samples; [§]VOCs found at higher emission rates in leaf-only samples (see Tables S5–S7). Significant differences between control and drought treatments are indicated with p-values (* $p < 0.05$; ** $p < 0.01$; Table 1).



4.2 | Altered floral scent despite limited impacts on other floral traits

Despite the moderate drought and its limited impacts on other floral traits, floral scent was consistently altered in all three of our study species. Like other plant volatile emissions, floral scent is particularly sensitive to environmental stress (Glenny et al., 2018; Theis et al., 2007; Yuan et al., 2009), notably because the activation of plant defences as a response to abiotic and biotic stress

results in the emissions of volatile stress molecules (El-Esawi et al., 2017; Harborne, 1991; Holopainen & Gershenzon, 2010; Loreto & Schnitzler, 2010). Hence, even moderate drought could result in the higher emission, in floral scent, of typical GLVs such as 3Z-Hexenol and defensive terpenoids (Borghi et al., 2019). We did find increased emissions of 3Z-Hexenol in the floral scent of all three species under drought, consistent with other studies (Bürkle & Runyon, 2016; Glenny et al., 2018; Rering et al., 2020). Also, the reduced emissions of α -Zingiberene and ar-Curcumen found in *C.*

TABLE 2 Drought impact on nectar production. Significant effects ($p < 0.05$) and marginally significant effects ($p < 0.07$) of drought are shown in bold.

	Sample size plants:flowers per plant control/drought	df	χ^2	<i>p</i>
<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*

* $p < 0.05$.

albidus floral scent under drought here were also shown in *C. albidus* leaves under drought (Ormeño et al., 2007). In contrast, in *S. rosmarinus*, the sesquiterpenes E-Caryophyllene and α -Humulene, emitted at higher rate in floral scent under drought and characterized as typical floral VOCs here (Table S5) were absent in *S. rosmarinus* leaf samples in a previous study (Ormeño et al., 2007). This may be because these sesquiterpenes have a dual function (defence and pollinator attraction; Schiestl, 2010), and the plant increases investment in bee-attractive molecules (Abraham et al., 2018; Leonhardt et al., 2014) to counterbalance other negative effects of drought (Kuppler & Kotowska, 2021). Drought stress also often increases the variability of floral scent emissions (Glenny et al., 2018), a trend we found in *T. vulgaris*; moderate stress increases total emissions (Glenny et al., 2018) but intense stress can reduce emissions (Cna'ani et al., 2015).

4.3 | Can altered floral scent explain differences in pollinator visits?

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

The measured floral scent alterations may partially explain such changes in pollinator visits. Altered emissions could negatively affect flower attractiveness to pollinators and may cause the rewiring of pollination networks, that is, the modification of the relative

intensity of plant–pollinator interactions within the community (Larue et al., 2016). The attractiveness of most VOCs to most pollinator species remains unknown, yet among the VOCs altered by drought in our three species, some are described as attractive to *A. mellifera* and other bee species (Table S14). Conversely, the stress marker 3Z-Hexenol acetate was found to be slightly repellent to *B. terrestris* (Ceuppens et al., 2015). The stress-induced increased emission rate of VOCs with a defensive primary function (rather than pollinator attraction) could deter pollinators (Schiestl et al., 2014; Theis, 2006). Avoiding drought-stressed plants based on floral scent signals may be positively selected, or based on associative learning (Jaworski et al., 2015), if altered floral scent is a cue for reduced quality or quantity of floral resources (Wilson Rankin et al., 2020).

While a change in pollinator behaviour is unlikely to be motivated by altered floral scent alone especially in generalist pollination systems, pollinators may use it as evidence for altered floral resources in resource-limited plants (Flacher et al., 2020). We did not detect changes in nectar standing crop in either *S. rosmarinus* or *C. albidus*, but we did not measure flower refill rate, nectar composition (ratio of different sugars and nutrients content), or pollen production and quality, which could have been affected by drought, potentially influencing bee choice (Petanidou, 2005). Wilson Rankin et al. (2020) showed that drought reduced nectar quality and quantity as well as pollen nutritional quality in *Trifolium willdenovii*, reducing colony fitness in *A. mellifera* and *B. impatiens*. The increased visitation rate towards plants experiencing drought by small wild bees (including some *Andrena*, *Osmia* and *Lasioglossum* species, Table S12) is more difficult to interpret, partly because of the diversity of insect species within this group. One speculative hypothesis is that, rather than being a response to floral scent, it is a signal of resource partitioning due to interspecific competition. *Apis mellifera* dominates the flower visitor community (81% of all visits) in our study and throughout the Mediterranean Basin (Herrera, 2020). A study

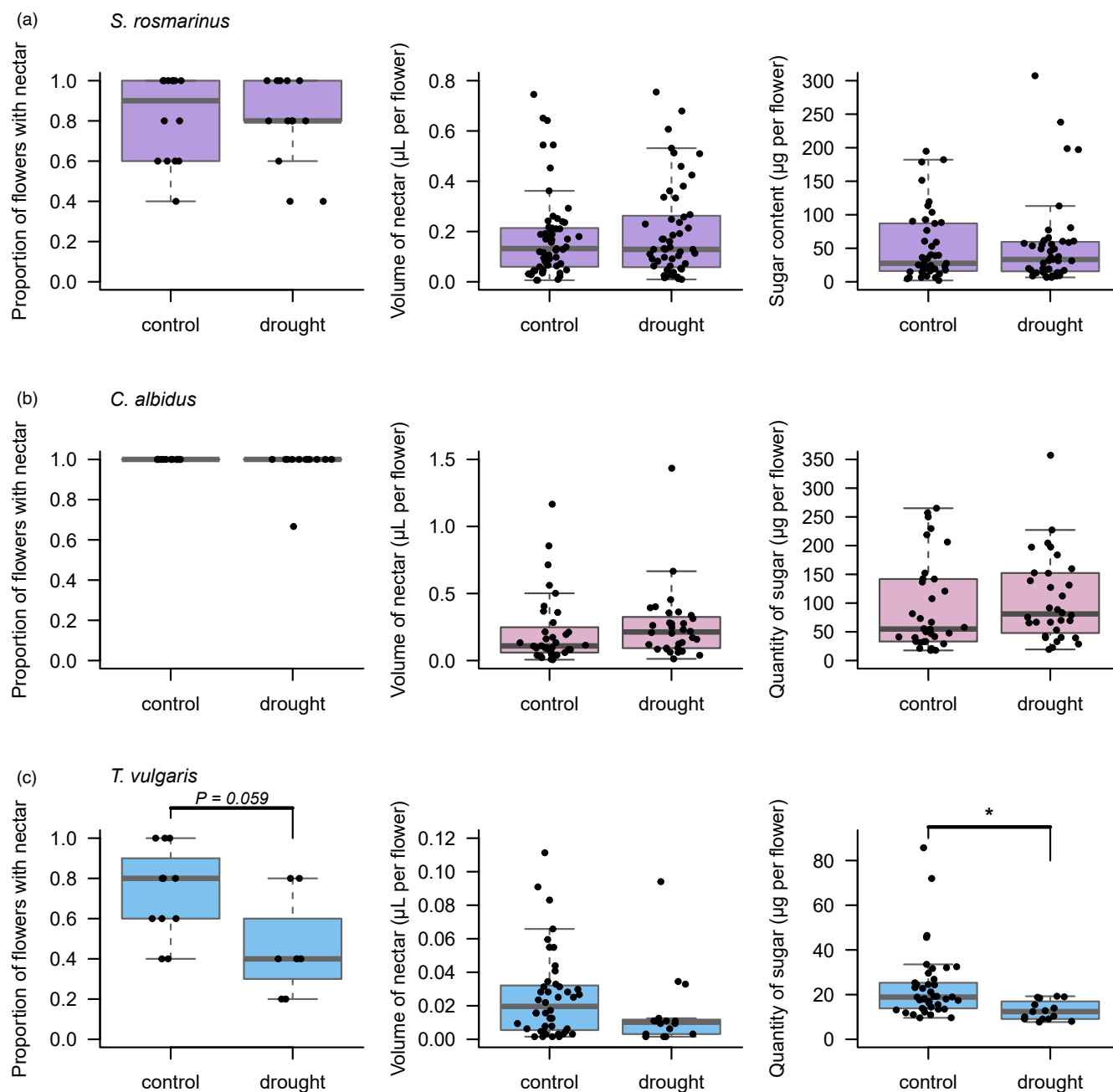


FIGURE 3 Impact of treatment (control, drought) on nectar production of (a) *S. rosmarinus*, (b) *C. albidus* and (c) *T. vulgaris*. Proportion of flowers producing nectar (left column), and for flowers producing nectar volume of nectar per flower (middle column) and sugar content per flower (right column).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

with the same observation methods and in a similar habitat 20 km away from our field site in 2017–2018 found that the abundance and species richness of large wild bees was negatively affected by increased honeybee hive density on wild pollinators (Ropars, Affre, Schurr, et al., 2020). The social structure of *A. mellifera* hives (all managed in the region), and their ability to communicate the location of resources, enables workers to exploit the most rewarding floral resources and to track resource availability much more efficiently than wild pollinator species (Hasenjager et al., 2020; Hung et al., 2019). The higher number of visits by *A. mellifera* to control plots suggests that they evaluated floral resources to be more abundant or of higher

quality in control plots. If so, resources in the control plots would be more rapidly depleted, leaving resources in drought plots to other pollinator species and causing resource partitioning (Kuppler et al., 2017; Thomson & Page, 2020). We observed some *A. mellifera* workers visiting more than 70 flowers in 5 min, and we caught on average eight (and up to 44) 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* (Aizen et al., 2014; Giurfa & Nuñez, 1992).

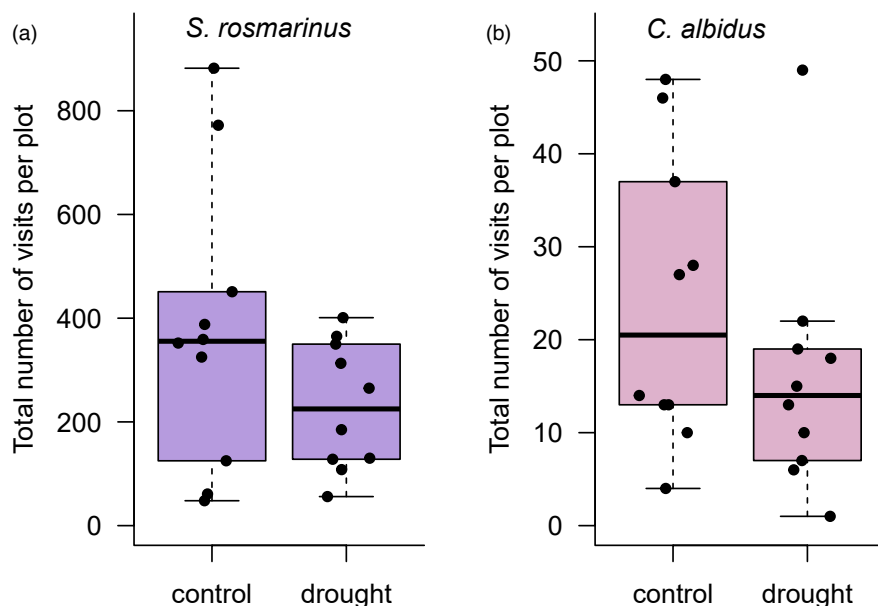


FIGURE 4 Drought impact on the total number of pollinator visits observed along the season to (a) *S. rosmarinus* and (b) *C. albidus*. $N = 20$ per treatment.

TABLE 3 Drought impact on pollinator visits (Hurdle model). Significant effects ($p < 0.05$) of drought are shown in bold.

	Sample size control/drought (number of observations)	df	χ^2	p
Presence/absence of visits	<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		0.37
Treatment:Plant species		1	5.43	
Plant species:Pollinator group		5	2.39	0.12
Treatment		1	156	<0.001***
Number of visits (>0)			1.11	0.29
Drought treatment: Plant species: Pollinator group	<i>S. rosmarinus</i> : 90/92; <i>C. albidus</i> : 83/60	4 ^a	10.3	0.035*
Comparison of means across pollinator groups:		Ratio control/drought (±SE)		p
<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 ^a		NA ^a
Small wild bees		1.00 ± 0.39		0.99
<i>S. rosmarinus</i> :				
<i>A. mellifera</i>		1.72 ± 0.36		0.011*
Large wild bees		1.12 ± 0.35		0.72
Bumblebees		4.84 ± 3.12		0.016*
Coleoptera		1.00 ± 1.56		0.99
Diptera		0.392 ± 0.312		0.24
Small wild bees		0.220 ± 0.105		0.0015***

^aNo visits by Diptera on *C. albidus*.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

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.

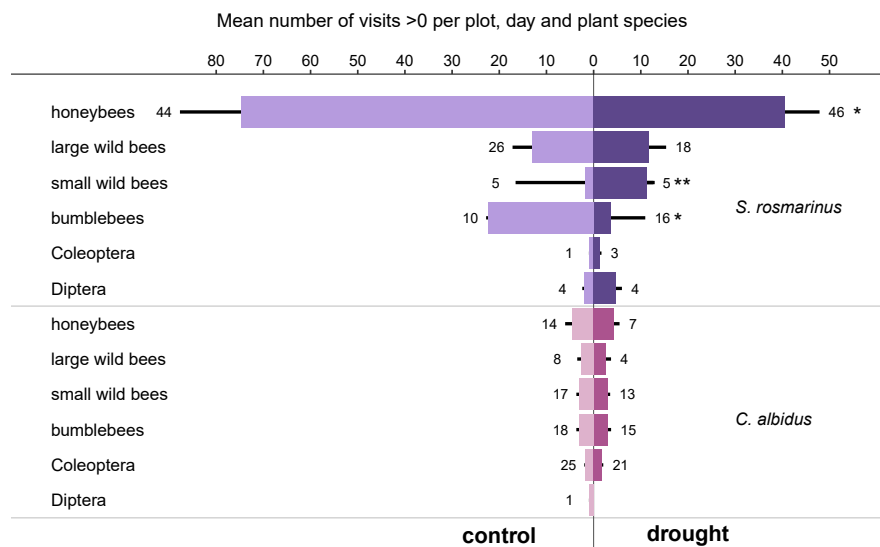


TABLE 4 Drought impact on fruit set and seed set.

	Sample size control/drought [range in number of fruits]	df	χ^2	p
<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

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 generalizations 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 (e.g. in a similar shrubland 20 km away; Ropars, Affre, Aubert, et al., 2020), 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, Affre, Aubert, et al., 2020). 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, Affre, Aubert, et al., 2020).

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

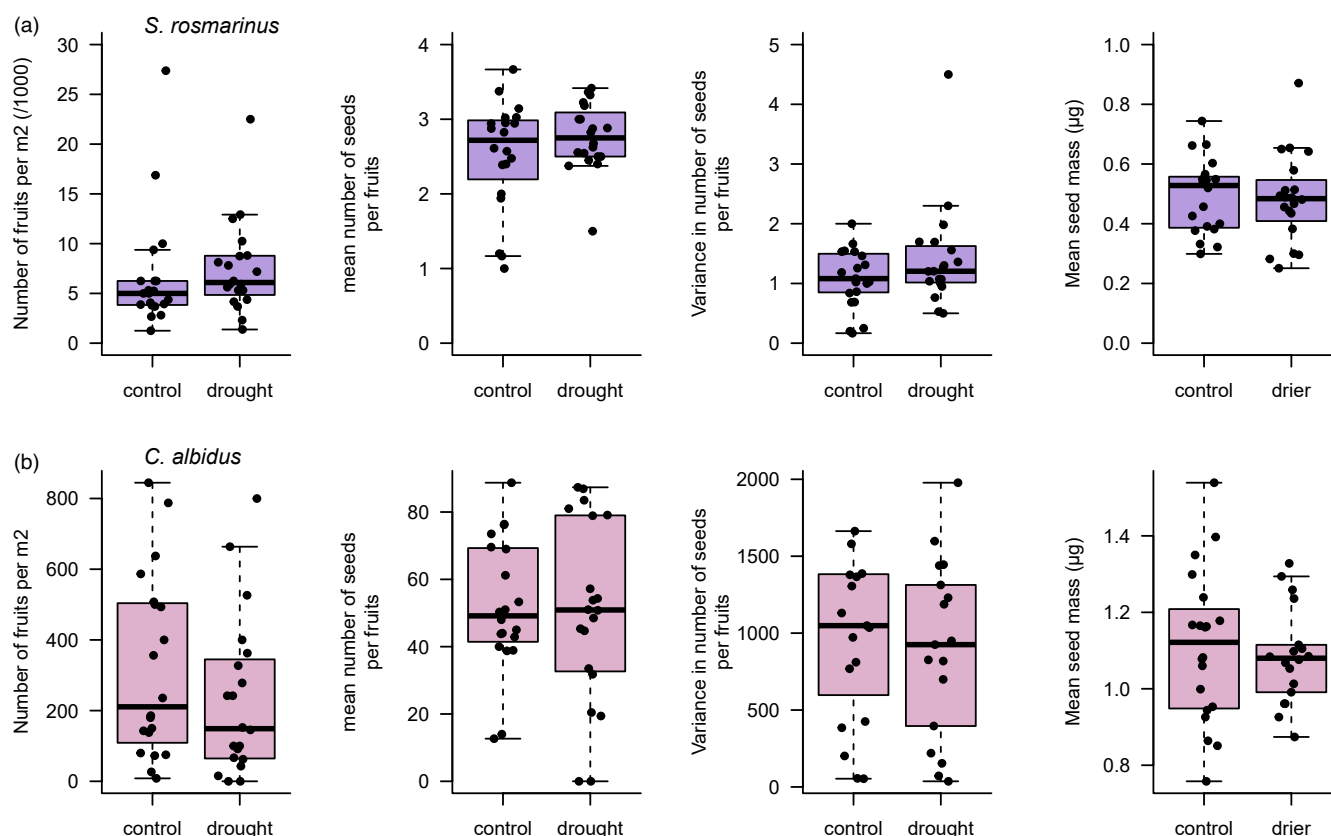


FIGURE 6 Drought impact on the number of fruits per m^2 (left), the mean seed number and variance in seed number per fruit (middle), and the mean seed mass (right) in *S. rosmarinus* (top row) and *C. albidus* (bottom row). Sample sizes are provided in Table 4.

of such VOCs singly or in mixtures, as well as preferences of naïve and experimented in a controlled environment between plants under control and drought conditions, would help make this connection (Burkle & Runyon, 2017; Jaworski et al., 2015; 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 changes impacts at a community scale. For example, this could be attempted by choosing pairs of comparable large-scale communities such as entire valleys in different climatic conditions to assess the impact on pollinator foraging behaviour and population dynamics. Despite climate change, any habitat remains a mosaic of micro-climatic conditions (Maclean, 2020) and our experiment therefore captures some of the realistic climate change predictions. Also, climate change may have direct impacts on pollinator behaviour, phenology and population dynamics (Becher

et al., 2014; Burkle et al., 2013; Woodard, 2017), which were not considered here, and which would deserve further attention in integrative approaches.

5 | CONCLUSIONS

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

in biodiversity-rich but also already fragile Mediterranean 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 will be essential to estimate the resilience of Mediterranean ecosystems under ever-increasing anthropogenic pressures.

AUTHOR CONTRIBUTIONS

Coline C. Jaworski, Benoît Geslin and Catherine Fernandez designed the study; Coline C. Jaworski, Benoît Geslin, Marie Zakardjian, Pauline Caillault, Gabriel Nève and Jean-Yves Meunier conducted the pollinator observations and identification and plant phenology data collection; Coline C. Jaworski, Marie Zakardjian, Pauline Caillault and Sylvie Dupouyet measured floral traits; Coline C. Jaworski and Caroline Lecareux performed the chemical analysis; Coline C. Jaworski, Marie Zakardjian and Aoife C. T. Sweeney conducted the seed germination experiment; Coline C. Jaworski, Benoît Geslin, Marie Zakardjian, Pauline Caillault and Catherine Fernandez performed the data analysis; Coline C. Jaworski and Benoît Geslin wrote the manuscript, and Catherine Fernandez, Owen T. Lewis and Lynn V. Dicks provided critical comments and helped writing the manuscript. All authors approved the submission of the manuscript, and have declared no conflict of interest.

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CONFLICT OF INTEREST

All authors have declared to have no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13974>.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.h70rxwdmz> (Jaworski et al., 2022a). The repository contains all datasets as well as a metafile and 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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