


# Drought reduces floral resources for pollinators

Benjamin B. Phillips<sup>1#</sup>  | Rosalind F. Shaw<sup>1#</sup> | Matthew J. Holland<sup>1</sup> | Ellen L. Fry<sup>2</sup> | Richard D. Bardgett<sup>2</sup> | James M. Bullock<sup>3</sup> | Juliet L. Osborne<sup>1</sup>

<sup>1</sup>Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, UK

<sup>2</sup>School of Earth and Environmental Sciences, The University of Manchester, Manchester, UK

<sup>3</sup>NERC Centre for Ecology and Hydrology, Wallingford, Oxfordshire, UK

## Correspondence

Juliet L. Osborne, Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, UK.  
Email: j.l.osborne@exeter.ac.uk

## Funding information

Natural Environment Research Council, Grant/Award Number: NE/J014680/1

## Abstract

Climate change is predicted to result in increased occurrence and intensity of drought in many regions worldwide. By increasing plant physiological stress, drought is likely to affect the floral resources (flowers, nectar and pollen) that are available to pollinators. However, little is known about impacts of drought at the community level, nor whether plant community functional composition influences these impacts. To address these knowledge gaps, we investigated the impacts of drought on floral resources in calcareous grassland. Drought was simulated using rain shelters and the impacts were explored at multiple scales and on four different experimental plant communities varying in functional trait composition. First, we investigated the effects of drought on nectar production of three common wildflower species (*Lathyrus pratensis*, *Onobrychis viciifolia* and *Prunella vulgaris*). In the drought treatment, *L. pratensis* and *P. vulgaris* had a lower proportion of flowers containing nectar and *O. viciifolia* had fewer flowers per raceme. Second, we measured the effects of drought on the diversity and abundance of floral resources across plant communities. Drought reduced the abundance of floral units for all plant communities, irrespective of functional composition, and reduced floral species richness for two of the communities. Functional diversity did not confer greater resistance to drought in terms of maintaining floral resources, probably because the effects of drought were ubiquitous across component plant communities. The findings indicate that drought has a substantial impact on the availability of floral resources in calcareous grassland, which will have consequences for pollinator behaviour and populations.

## KEYWORDS

calcareous grassland, climate change, drought stress, functional traits, *Lathyrus pratensis*, nectar, *Onobrychis viciifolia*, pollination, *Prunella vulgaris*, water availability

## 1 | INTRODUCTION

Climate change is predicted to impact invertebrate groups worldwide, leading to changes in their physiology, phenology and distribution (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Prather

et al., 2013). Understanding how animal pollinators will be affected is of particular interest, given their importance in maintaining plant diversity (Ollerton, Winfree, & Tarrant, 2011) and in ensuring food security through crop pollination (Gallai, Salles, Settele, & Vaissière, 2009; Klein et al., 2007). Climate change is likely to have a range of implications for pollinators (Settele, Bishop, & Potts, 2016), for example by causing range shifts and spatial or phenological mismatch in plant–pollinator

<sup>#</sup>These authors contributed equally to the work and are joint first authors.

interactions (Hegland, Nielsen, Lázaro, Bjerknæs, & Totland, 2009; Memmott, Craze, Waser, & Price, 2007; Miller-Struttman et al., 2015). Climate change may also affect pollinators indirectly, if the quantity or quality of floral resources is affected.

One of the major aspects of climate change is predicted increases in the occurrence and intensity of drought (periods of abnormal precipitation deficit) across many regions worldwide (Dai, 2013; IPCC, 2014). Drought has been identified as a major threat to pollinators and pollination (Brown et al., 2016), and will act primarily through changes in the availability of floral resources upon which pollinators rely (Thomson, 2016). Broadly, a reduction in water availability will affect photosynthetic rate (Pinheiro & Chaves, 2011), leading to fewer resources available to plants for investment into reproduction and flowers. Drought has been shown to reduce flower size (Halpern, Adler, & Wink, 2010), the number of flowers per plant (Burkle & Runyon, 2016), result in flowers that produce less pollen (Waser & Price, 2016) and a lower proportion of viable pollen grains (Al-Ghazawi, Zaitoun, Gosheh, & Alqudah, 2009), and affect floral volatiles, which can influence the attractiveness of flowers to pollinators (Burkle & Runyon, 2016). In general, water availability has been found to affect nectar in terms of volume (Carroll, Pallardy, & Galen, 2001; Gallagher & Campbell, 2017; Halpern et al., 2010; Lee & Felker, 1992; Villarreal & Freeman, 1990) and sometimes also sugar concentration (Waser & Price, 2016; Wyatt, Broyles, & Derda, 1992; Zimmerman & Pyke, 1988).

Changes in nectar volume or sugar concentration are likely to affect pollinator foraging behaviour because flower selection can be influenced by subtle differences in these factors (Cnaani, Thomson, & Papaj, 2006). Furthermore, changes in nectar will affect the energy intake rate of pollinators (Schweiger et al., 2010), which is optimized at intermediate sugar concentrations (Borrell, 2007). Effects of drought on other floral traits have been shown to result in fewer visits by bees (Al-Ghazawi et al., 2009; Gallagher & Campbell, 2017), although Burkle and Runyon (2016) found that the response of other pollinator groups was both plant and pollinator species-specific, with visitation rate increasing in some circumstances. More broadly, changes in the overall availability of floral resources will affect pollinators at the population level (Baude et al., 2016; Carvell et al., 2006, 2017; Roulston & Goodell, 2011).

There is likely to be much variation in the responses of floral resources of different plant species to drought, depending on aspects of their life history. For example, long-lived species may be adapted to respond to drought by reducing their investment in floral resources, due to trade-offs between survival and reproduction (Galen, 2000), whereas short-lived species may maintain a high level of investment in floral resources during drought to ensure reproduction over their lifetime. The reproductive system of a plant is also likely to be important because plants with mixed mating systems can switch reproductive strategy in response to changes in environmental conditions (Goodwillie, Kalisz, & Eckert, 2005). For example, plants may move from outcrossing towards selfing when under environmental stress (Levin, 2010) such as drought (Kay & Picklum, 2013), although the opposite may also be true (Bishop, Jones, O'Sullivan, & Potts, 2017). Plants without a mixed reproductive strategy, or with a greater dependency

on outcrossing, are therefore expected to maintain greater investment in floral resources under adverse conditions. As a result, changes in the production of floral resources by a plant can be either an adaptive response or a negative consequence of drought stress.

Given that responses to drought are often plant species-specific, the impacts on plant communities are likely to depend on species composition (Grime et al., 2000). For example, a greater diversity of plant strategies may provide greater community resilience to drought events (Zwicke, Picon-Cochard, Morvan-Bertrand, Prud'homme, & Volaire, 2015), including in the provision of floral resources. Although the overall provision of floral resources by a plant community may not change if some drought-resistant species replace drought-sensitive ones, changes to the diversity and quality of floral resources may affect individual pollinators (Kaluza et al., 2017; Vaudo, Tooker, Grozinger, & Patch, 2015) and the diversity of the pollinator community (Ghazoul, 2006). Differences in the functional traits of a plant community may also influence the resilience of that community and of its ecosystem functions to drought (Isbell et al., 2015; Oliver, Isaac et al., 2015). In particular, functional traits that relate to water uptake, water use and water retention, such as deep rooting structures, are likely to enable drought tolerance and therefore affect the overall performance of plants that are subjected to drought. This is likely to result in a broad range of benefits, including in terms of a greater production of floral resources. Similarly, greater diversity of functional traits may provide benefits to the plant, in terms of overall performance and resistance to drought, due to niche complementarity (Gross, Sudings, Lavorel, & Roumet, 2007; Gubsch et al., 2011), for example if different root types are collectively able to utilize a greater proportion of available water.

Existing studies of the response of floral resources and pollinators to drought have commonly been conducted on plants of arid and semi-arid regions (Al-Ghazawi et al., 2009; Takkis, Tscheulin, Tsalkatis, & Petanidou, 2015), where drought events are relatively common, or in the laboratory (Villarreal & Freeman, 1990). There are few such experiments in temperate regions where drought is expected to increase in frequency and severity due to climate change (Dai, 2013; IPCC, 2014). Ecosystems in these regions may be more severely affected because drought has not previously been an important environmental factor (Chen, van der Werf, de Jeu, Wang, & Dolman, 2013). To develop a more complete understanding of the potential impacts of drought over the coming decades, it is essential to investigate these impacts on a variety of plant communities in more temperate regions.

In this study, we investigated the impacts of an experimental summer drought event on floral resources in calcareous grassland in order to better understand potential effects of climate change on insect pollinators. Specifically, we tested: (1) how drought affects the availability of floral resources at the flower and community level; and (2) whether responses to drought vary among communities of different plant functional composition. To do so, we used four different experimentally sown plant communities of calcareous grassland. The plant communities were derived from three sets of species grouped using database-derived information on their functional traits, particularly root traits and specific leaf area, which are likely

to affect resistance to drought (Buckland, Grime, Hodgson, & Thompson, 1997; Cantarel, Bloor, & Soussana, 2013; Comas, Becker, Cruz, Byrne, & Dierig, 2013). In this way, we were able to explore how responses to drought varied across plant communities based on their functional trait composition, and control for the effects of species composition to ensure the general applicability of the results. We hypothesized that:

1. Drought (reduction in water availability) leads to lower photosynthetic rate, resulting in reduced sugar concentration in nectar.
2. Drought leads to less water available in the plant, resulting in reduced nectar volume;
3. Drought leads to fewer resources available to plants and therefore lower investment in reproduction, resulting in a reduction in the number of flowers produced;
4. Plant communities with functional traits that relate to efficient uptake and use of water are more resistant to the impacts of drought, resulting in greater maintenance of floral resources; and
5. Plant communities with a greater functional diversity of traits that relate to uptake and use of water have greater niche complementarity between species in terms of their ability to exploit available water resources, resulting in a greater maintenance of floral resources.

## 2 | MATERIALS AND METHODS

### 2.1 | Experimental design

The experiment was conducted in Wiltshire, UK (50.991207°N, -2.069834°W) using sown plant communities in ex-arable calcareous grassland (Fry et al., 2018). The plant communities consisted of typical calcareous grassland species (from UK National Vegetation Classification Community CG3a *Bromus erectus* grassland; Rodwell, 1992) and represented realistic community structures for the region. Four plant communities with contrasting functional trait compositions were sown onto bare soil in May 2013. The traits used to differentiate species were hypothesized to exert differing effects on soil carbon and nitrogen cycling, but are also likely to be related to water acquisition, water use and resistance to drought (Buckland et al., 1997; Cantarel et al., 2013; Comas et al., 2013). Functional group 1 (FG1; 16 species) consisted of species with variable longevity, deep tap or stoloniferous roots, and large, thin leaves, which we hypothesized to exhibit low nutrient cycling and poor resistance to drought (Buckland et al., 1997; Gould, Quinton, Weigelt, De Deyn, & Bardgett, 2016). Functional group 2 (FG2; 15 species) consisted of long-lived species with a shallow tap root and small rosettes, which we hypothesized to exhibit low nutrient cycling but with fairly good resistance to drought. Functional group 3 (FG3; 20 species) consisted of long-lived species with shallow, fibrous roots and thick, fleshy leaves, consistent with high nutrient cycling and fairly good resistance to drought. The fourth plant community contained all three functional groups (FG123; 51 species). The plant species within each functional group are listed in Table S1. Plant communities were sown into 8 × 8 m plots, separated by 2 m

guard rows. The site was divided into six rows, forming experimental blocks, and each plant community was randomly allocated to a single plot in each block ( $n = 24$ ), in order to control for spatial, edge and neighbouring effects (Figure S1). The number of seeds applied to each plot was determined by the mean seedbank density for each species (from the LEDA Traitbase; Kleyer et al., 2008), the mean seed weight for each species (from the Kew SID; Royal Botanic Gardens Kew, 2016), and scaled for number of functional groups per plot.

Each of the 24 plots contained three subplots ( $1 \times 1.5$  m) which were at least 1 m from each other and from the edge of the plot. Each subplot was given one of three treatments: (1) Drought (D), covered with a transparent roof to exclude rain, simulating drought; (2) Control (C), not covered with a roof; and (3) Roofed control (R), covered with a transparent roof with 5 cm holes, allowing rain to pass through, but controlling for possible roof effects such as increased temperature and decreased light intensity (Vogel et al., 2013). Control and roofed subplots received ambient rainfall during the 6-week period. Drought shelters were in place for 6 weeks, in two successive years, between 28th May and 11th July in 2015 between 6th June and 13th July in 2016. The 6-week period represents a one in one hundred year drought event, and was simulated using a Gumbel distribution (VGAM package; Yee, 2010), based on a decade long (2004–2014) daily rainfall dataset from a local weather station (51.010277°N, -2.641915°W, Yeovilton Air Base). This study was carried out in 2016, following the second drought. Soil moisture content (SMC) was measured at the end of the drought period and it was significantly lower in the drought treatment (mean SMC  $\pm$  SE: control  $33.05 \pm 0.50$ , roofed control  $31.09 \pm 0.77$ , drought  $23.55 \pm 0.93$ ). All data were collected at least 2 days after drought shelters had been removed and within 7 days following this. During this time, there was little rainfall.

### 2.2 | Flower and raceme scale

Three plant species, which were sown as part of the experimental study, *Lathyrus pratensis* (from FG2), *Onobrychis viciifolia* (from FG3), *Prunella vulgaris* (from FG2), were selected based on their abundance, cover, floral traits, flowering period and ease of nectar extraction. *L. pratensis* is hermaphrodite and normally cross-pollinated though has some capacity for selfing (Fitter & Peat, 1994). *O. viciifolia* is hermaphrodite (Fitter & Peat, 1994) and considered to be obligate cross-pollinated (Hanley, Franco, Pichon, Darvill, & Goulson, 2008); self-pollination is possible but results in lack of vigour and few if any viable seeds (Hayot Carbonero, Mueller-Harvey, Brown, & Smith, 2011). *P. vulgaris* is gymnomonoecious and either cross- or self-pollinated (Fitter & Peat, 1994), with a high capacity for autonomous selfing (Ling et al., 2017). Whilst it would have been preferable to have one plant species from each functional group, none of the plant species in FG1 met these criteria at the time of the study. Subplots which contained only FG1 were therefore only used for the community-scale studies (see below). Racemes of these species were randomly selected from all available flowering racemes across subplots. The number of racemes tested per subplot varied according to their

availability. Racemes were selected from different individual plants if possible, but this was not always clear, due to the vegetative spread of some species. Racemes were covered with a fine mesh bag for 24 hr to prevent flower visitation by invertebrates and labelled to ensure they were only used once. After 24 hr, bags were removed and the number of flowers on the raceme was recorded. Up to three flowers per raceme (if available) were randomly selected to measure nectar volume and sugar concentration, following standard protocols (Corbet, 2003). As nectar was not removed from flowers before applying bags, the amount of nectar in flowers after 24 hr represented a combination of standing crop and 24 hr accumulation. Nectar volume ( $\mu\text{l}$ ) was measured using glass microcapillary tubes (sizes 0.5, 1, 2, and 5  $\mu\text{l}$  microcaps, Drummond Scientific, Broomall PA, USA). Nectar sugar concentration (mg/mg) was measured using a hand-held refractometer modified for small volumes (Eclipse, Bellingham & Stanley, Tunbridge Wells, UK). When the volume of nectar per individual flower was insufficient to provide a reading on the refractometer, nectar was pooled from multiple flowers on the same raceme to provide an average value. Despite this, it was not always possible to obtain a reading (144 out of 703 cases). Nectar sugar concentration as measured by the refractometer, i.e. weight of solute per weight of solution ( $C$ ; mg/mg), was converted to nectar sugar concentration in terms of weight of solute per volume of solution ( $c$ ; mg/ $\mu\text{l}$ ) using  $c = (0.0037291C + 0.0000178C^2 + 0.9988603)C/100$  (from Prŷs-Jones & Corbet, 1991). The weight of sugar produced per flower over 24 hr ( $w$ ) (mg) was then calculated using  $w = vc$ , where  $v$  is volume of nectar ( $\mu\text{l}$ ) and  $c$  is sugar concentration of nectar (mg/ $\mu\text{l}$ ). When a concentration reading was absent because nectar volume was too small, a value was used that was the mean of measurements from flowers of the same plant species and in the same treatment.

### 2.3 | Community scale

Surveys were carried out in 1 m<sup>2</sup> quadrats in the centre of each subplot of all treatment plots. All flowering plants were identified to species level and the number of floral units was recorded for each species. A floral unit was defined as one or multiple flowers that can be visited by an insect without having to fly between them (following Baldock et al., 2015). Surveys were completed at each subplot on two occasions, on different days, between 18th and 22nd July. The survey order of plots was randomized. Subplots within each plot were surveyed consecutively but in a randomized order.

### 2.4 | Statistical analyses

All statistical analyses were carried out in R 3.3.1 (R Core Team, 2015). For flower and raceme scale analyses (nectar volume per flower, sugar concentration per flower, weight of sugar in nectar per flower and number of flowers per raceme), linear mixed effects (LMM) models were used ('nlme' package; Pinheiro, Bates, DebRoy, & Sarkar, 2016). Explanatory variables were plant species and drought treatment and their interaction, with a priori pairwise contrasts used to examine differences between control, roofed control

and drought treatments within each plant species ('lsmmeans' package; Lenth, 2016). Plot and raceme identity were included as a random effect for flower scale measurements. Response variables were transformed where required in order to meet model assumptions (see Table S2). The proportion of flowers containing nectar was analysed as above, but using a generalized linear mixed effects model (GLMM) with binomial error structure ('lme4' package; Bates, Mächler, Bolker, & Walker, 2015). Likelihood ratio tests (LRT) were used to assess if the main effects improved the GLMM fit.

For community-scale analyses, LMMs or GLMMs were used as above. The data from the two survey periods were summed, because the time between survey periods was short. For the species richness of floral units, a LMM was used with the number of insect-pollinated plant species present in the plot, plant community, drought treatment, and the interaction between plant community and drought treatment as explanatory variables. For the number of floral units, a negative binomial GLMM was used (Bates et al., 2015), due to overdispersion of count data. Explanatory variables were plant community, drought treatment and their interaction, with a priori pairwise contrasts used to examine differences between control, roofed control and drought treatments within each plant community. In all cases, random variables were plot, nested within row, and the significance of main effects tested using LRTs. Full details of the statistical analyses can be found in Table S2.

## 3 | RESULTS

### 3.1 | Flower and raceme scale

Across the three plant species, 437 racemes were selected; of these, 372 had flowers remaining after 24 hr. Nectar was collected from the flowers of between 37 and 44 racemes per plant species per drought treatment. There were large differences between plant species in terms of nectar volume per flower ( $F_{2,274} = 225.07$ ,  $p < .001$ ), nectar sugar concentration per flower ( $F_{2,216} = 6.86$ ,  $p = .001$ ) and weight of sugar in nectar per flower ( $F_{2,274} = 184.80$ ,  $p < .001$ ) (Table 1). Flowers of *L. pratensis* had by far the greatest volume of nectar, followed by *P. vulgaris*, and then *O. viciifolia* (Table 1). There was no interaction between drought treatment and plant species (Table S2), and no significant overall effect of the drought treatment on nectar volume ( $F_{2,274} = 0.782$ ,  $p = .459$ ), nectar sugar concentration ( $F_{2,216} = 0.251$ ,  $p = .778$ ) or weight of sugar in nectar ( $F_{2,274} = 1.17$ ,  $p = .312$ ) (Table 1).

Including plant species and drought treatment improved the fit of the model examining the proportion of flowers with nectar present (Plant species LRT  $\chi^2(1) = 9.154$ ,  $p = .010$ ; drought treatment LRT  $\chi^2(1) = 16.026$ ,  $p < .001$ , Figure 1). The strength of the effect of drought varied with species: the proportion of flowers containing nectar was significantly lower in the drought than the control treatment for *L. pratensis* (contrast estimate  $-0.82 \pm 0.307$  SE,  $Z = -2.67$ ,  $p = .021$ ) and *P. vulgaris* (contrast estimate  $-1.15 \pm 0.315$  SE,  $Z = -3.67$ ,  $p = .001$ ), but *O. viciifolia* was not significantly affected (contrast estimate  $-0.74 \pm 0.347$  SE,  $Z = -2.12$ ,

**TABLE 1** The effect of drought treatment at the flower scale in terms of nectar volume, sugar concentration and weight of sugar in nectar, 24 hr after bagging, for each plant species (*Lathyrus pratensis*, *Onobrychis viciifolia* and *Prunella vulgaris*)

Species	Treatment	Nectar volume ( $\mu\text{l}$ ) (mean $\pm$ SE) (n flowers, n racemes)	Nectar sugar concentration (mg/ $\mu\text{l}$ ) (mean $\pm$ SE) (n flowers, n racemes)	Weight of sugar in nectar (mg) (mean $\pm$ SE) (n flowers, n racemes)
<i>L. pratensis</i>	Control	2.04 $\pm$ 0.177 (84, 37)	0.39 $\pm$ 0.015 (82, 36)	0.74 $\pm$ 0.064 (84, 37)
	Roofed	1.90 $\pm$ 0.214 (61, 28)	0.36 $\pm$ 0.019 (55, 27)	0.70 $\pm$ 0.086 (61, 28)
	Drought	1.85 $\pm$ 0.217 (52, 35)	0.36 $\pm$ 0.023 (46, 32)	0.65 $\pm$ 0.078 (52, 35)
<i>O. viciifolia</i>	Control	0.16 $\pm$ 0.016 (94, 39)	0.47 $\pm$ 0.017 (76, 30)	0.07 $\pm$ 0.007 (94, 39)
	Roofed	0.19 $\pm$ 0.024 (84, 33)	0.44 $\pm$ 0.016 (63, 20)	0.08 $\pm$ 0.010 (84, 33)
	Drought	0.18 $\pm$ 0.022 (65, 35)	0.48 $\pm$ 0.020 (39, 27)	0.08 $\pm$ 0.010 (65, 35)
<i>P. vulgaris</i>	Control	0.41 $\pm$ 0.036 (100, 41)	0.41 $\pm$ 0.017 (79, 33)	0.15 $\pm$ 0.013 (100, 41)
	Roofed	0.33 $\pm$ 0.025 (90, 35)	0.42 $\pm$ 0.021 (70, 26)	0.13 $\pm$ 0.010 (90, 35)
	Drought	0.31 $\pm$ 0.028 (73, 37)	0.39 $\pm$ 0.024 (48, 31)	0.11 $\pm$ 0.010 (73, 37)

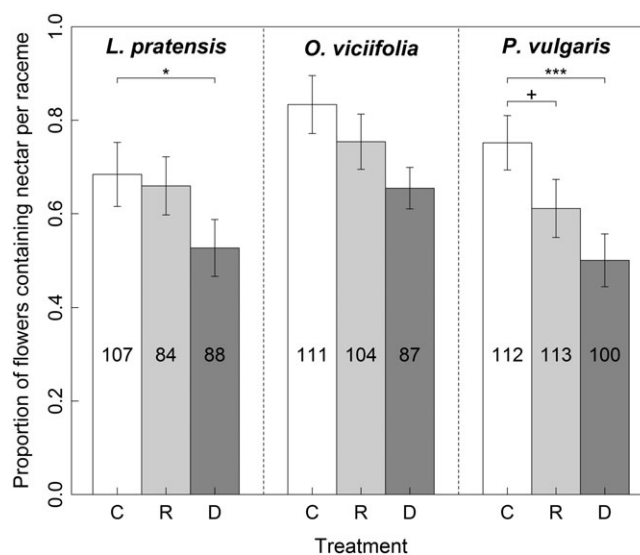
Sample size (n) refers to the number of individual flowers tested and the number of racemes tested.

$p = .085$ ) (Figure 1). The proportion of flowers containing nectar was also marginally significantly lower in the roofed control than the control treatment for *P. vulgaris* (contrast estimate  $-0.74 \pm 0.319$  SE,  $Z = -2.34$ ,  $p = .051$ ), but otherwise there were no significant differences between treatments of the same plant species. There were significantly different numbers of flowers per raceme for each species ( $F_{2,376} = 7.07$ ,  $p = .001$ , Figure 2) and overall there significantly fewer flowers per raceme in droughted treatments ( $F_{2,376} = 4.52$ ,  $p = .011$ , Figure 2). There were significantly fewer flowers on racemes of *O. viciifolia* in the drought than the control treatment (contrast estimate  $0.57 \pm 0.190$ ,  $T = 3.01$ ,  $p = .008$ ), but no other significant differences between treatments for the other plant species were detected (Figure 2; Table S2).

### 3.2 | Community scale

Across all surveys, flowers of 46 plant species were identified. The three study plant species constituted 40% of all floral units. Species richness of flowering plants was positively related to the number of insect-pollinated plant species sown in plots (estimate  $0.25 \pm 0.102$  SE,  $T = 5.24$ ,  $p = .019$ ). Floral species richness was significantly reduced by the drought treatment relative to the control for the FG1 (contrast estimate  $2.67 \pm 0.836$  SE,  $T = 3.19$ ,  $p = .008$ ) and FG123 plant communities (contrast estimate  $2.24 \pm 0.836$  SE,  $T = 2.69$ ,  $p = .028$ ) (Figure 3a; Table S2). The roofed control treatment also had a significant negative effect on floral diversity, but only in FG123 (contrast estimate  $2.37 \pm 0.819$  SE,  $T = 2.90$ ,  $p = .017$ ).

Including plant community and drought treatment significantly improved the fit of the model examining the number of floral units (Plant community LRT  $\chi^2(1) = 22.22$ ,  $p = .008$ , drought treatment LRT  $\chi^2(1) = 32.45$ ,  $p < .001$ ). The number of floral units was significantly reduced by the drought treatment relative to the control in the FG2 (contrast estimate  $2.14 \pm 0.647$  SE,  $Z = 2.50$ ,  $p = .033$ ), FG3 (contrast estimate  $3.64 \pm 1.087$  SE,  $Z = 4.34$ ,  $p < .001$ ) and FG123 (contrast estimate  $2.10 \pm 0.633$  SE,  $Z = 2.46$ ,  $p = .037$ ) plant communities, but no effect was detected for FG1 (contrast estimate



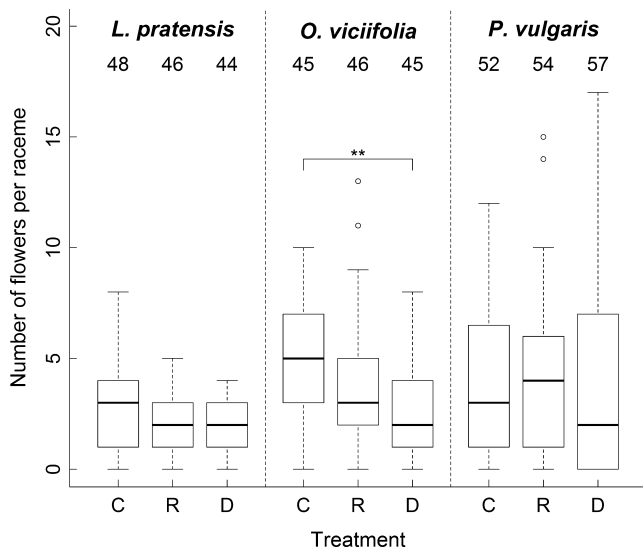
**FIGURE 1** The effect of drought treatment on the mean proportion of flowers per raceme that were found to contain nectar  $\pm$  SE, 24 hr after bagging, for each plant species (*Lathyrus pratensis*, *Onobrychis viciifolia* and *Prunella vulgaris*). Treatment refers to Control (C), Roofed control (R) and Drought (D). Sample sizes (n) are indicated by numbers within bars. Levels of significance between a priori contrasts are indicated by symbols (\* $p < .06$ , \* $p < .05$ , \*\* $p < .01$ , \*\*\* $p < .001$ )

$1.91 \pm 0.573$  SE,  $Z = 2.15$ ,  $p = .080$ ) (Figure 3b; Table S2). The roofed control treatment had significantly fewer floral units than the control for FG3 (contrast estimate  $2.26 \pm 0.682$  SE,  $Z = 2.71$ ,  $p = .019$ ), and there were significantly fewer floral units in the drought treatment than the roofed control treatment for FG1 (contrast estimate  $0.43 \pm 0.130$  SE,  $Z = -2.80$ ,  $p = .014$ ) and FG123 (contrast estimate  $0.48 \pm 0.143$  SE,  $Z = -2.47$ ,  $p = .036$ ).

## 4 | DISCUSSION

Experimental drought treatments resulted in fewer resources available to pollinators and this was an accumulation of effects at multiple





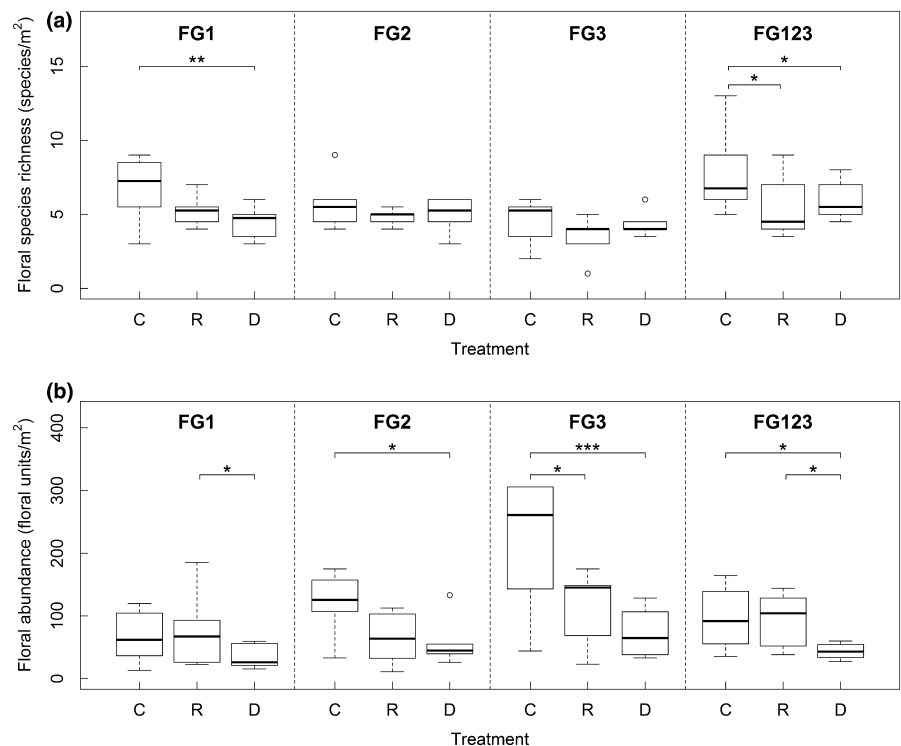
**FIGURE 2** The effect of drought treatment on the number of flowers per raceme, 24 hr after bagging, for each plant species (*Lathyrus pratensis*, *Onobrychis viciifolia* and *Prunella vulgaris*). Treatment refers to Control (C), Roofed control (R) and Drought (D). Sample sizes ( $n$ ) are indicated by numbers above boxplots. Levels of significance between a priori contrasts are indicated by symbols ( $^+p < .06$ ,  $*p < .05$ ,  $**p < .01$ ,  $***p < .001$ )

scales. Primarily, there were fewer flowers overall, and fewer of those flowers contained nectar. However, the mechanisms by which this occurred differed among both plant species and plant communities.

Among plant species, *L. pratensis* and *P. vulgaris* responded by reducing the proportion of flowers that contained nectar on each raceme, whilst *O. viciifolia* responded with a reduction in the number

of flowers per raceme. The roofed control treatment appeared to have a similar, but lesser effect to the drought treatment on all three plant species, suggesting that some of this response was due to other microclimatic effects of the roof such as increased temperature and decreased light intensity. Producing a greater proportion of nectarless flowers could be a mechanism for conserving resources without reducing reproductive potential, because it may be less costly for pollinators to visit these flowers than to discriminate between those that are secreting and nonsecreting (Bell, 1986). Similarly, a previous study showed that nectarless flowers can be produced in response to environmental stress (Petanidou & Smets, 1996; but see Takis et al., 2015). Alternatively, diverting resources into fewer flowers may allow nectar volume and sugar concentration to be maintained in those flowers, as we observed for *O. viciifolia*. The difference in response of *O. viciifolia*, compared to the other two species, may be due to differences in breeding system. *O. viciifolia* is obligate cross-pollinated (Hanley et al., 2008), so maintaining nectar in fewer flowers may be important in ensuring pollinator visitation. In contrast, *L. pratensis* has the capacity to self-pollinate (Fitter & Peat, 1994) and *P. vulgaris* has a high capacity for autonomous selfing (Ling et al., 2017). *P. vulgaris* and *L. pratensis* may therefore have a lower reproductive cost of stopping nectar production in some flowers as those flowers may still be able to self-fertilize without pollinator visitation.

For flowers that did contain nectar, drought had no effect on the volume or sugar concentration of that nectar. This is contrary to our first and second hypotheses and contrasts with many previous studies that have demonstrated changes in nectar volume in response to water availability (Carroll et al., 2001; Gallagher & Campbell, 2017; Lee & Felker, 1992; Villarreal & Freeman, 1990; Wyatt et al., 1992; Zimmerman & Pyke, 1988). It is possible that the reduction in soil



**FIGURE 3** The effect of drought treatment on the four experimental plant communities (FG1, FG2, FG3, FG123) in terms of (a) floral species richness, and (b) floral abundance. Each box represents the six subplots of that treatment type for each plant community. Treatment refers to Control (C), Roofed control (R) and Drought (D). Levels of significance between a priori contrasts are indicated by symbols ( $^+p < .06$ ,  $*p < .05$ ,  $**p < .01$ ,  $***p < .001$ )

moisture content in this experiment (approximately 10% reduction in soil moisture content immediately after drought period) was not great enough to induce nectar volume changes. This may have been partly due to plants accessing moisture through root systems that extended beyond the subplot or because some rain was reaching the subplots as runoff. Additionally, calcareous grasslands are relatively resistant to drought (Grime et al., 2008). Sugar production per flower was lower in our study than in other habitats for *L. pratensis* and *P. vulgaris*, the two plant species for which other data are available (Baude et al., 2016), suggesting that plants are already exhibiting a conservative physiological strategy. For these reasons, other habitats may exhibit an even greater reduction in floral resources in response to drought than calcareous grasslands. This should be considered when interpreting the results of this study compared to other regions, and highlights the need to carry out such experiments across a range of habitats.

As the three study plant species constituted 40% of all floral units, the effects of drought at the flower and raceme scale will have affected nectar availability at the community scale, even if other plant species did not respond in the same way. In agreement with our third hypothesis, the drought treatment reduced the number of floral units in all four plant communities, despite no change in vegetative cover. This will affect the overall availability of nectar and pollen in the community.

There was a significant reduction in floral abundance in the drought treatment compared to the roofed control in the plant community dominated by deep rooted, thin leaved species (FG1) and in the functionally diverse plant community (FG123), indicating that reduced water availability was having a negative effect on floral abundance in these two communities. For the other two plant communities, characterized by small rosettes (FG2) and shallow rooted, fleshy leaved species (FG3), there was a decline in floral abundance between the open control and drought treatment. The roofed control appeared to have an intermediate effect (statistically significant only for FG3), suggesting that the reductions in floral abundance were in part due to an increase in temperature or reduction in light intensity under the rooves. The roofed control treatment allowed us to partially distinguish between the effects of water availability and possible experimental impacts on floral abundance, which were clear for three out of the four functional groups (FG1, FG2 and FG123). FG1 and FG123 also showed a reduction in floral diversity in response to treatments, although it was not clear whether this was due to the experimental effects of drought. However, as the recorded soil moisture content was also slightly lower in the roofed control treatment, intermediate responses may also be partly explained by a reduction in water availability.

Contrary to our fourth hypothesis, the differences in functional traits of plant communities did not appear to confer any differential resistance to drought. The community which showed the greatest magnitude of response to drought was FG3, with shallow rooted, fleshy leaved species, which is partly explained by the additional impacts of the experimental rooves on this community. The magnitude of reduction between the other plant communities was similar,

suggesting that none of the selected functional traits were able to provide greater resistance to drought. As calcareous grassland plant communities are relatively resistant to drought (Grime et al., 2008), the main strategy across plant communities may be to conserve root biomass and leaf biomass at the expense of reproductive structures.

Contrary to our fifth hypothesis, the functionally diverse plant community (FG123) did not exhibit greater productivity or resistance to drought in terms of floral resources. Greater overall functional diversity of a particular set of traits is expected to result in greater resistance of related functions (Isbell et al., 2015; Oliver, Isaac et al., 2015), for example due to niche complementarity between species (Gross et al., 2007; Gubsch et al., 2011), which may reduce the competition for limited resources. In this case, greater diversity of root traits was expected to result in greater overall availability of water to communities, resulting in more water resources available for floral displays. Our results suggest that the impacts of drought were too ubiquitous across component plant communities for there to have been a benefit in the functionally diverse community. However, functional diversity may still provide longer term benefits that were not measured in this study, for example in terms of recovery.

Given these findings, we can infer multiple impacts on both pollinators and pollination. Firstly, impacts at the flower scale are likely to affect pollinator foraging behaviour due to changes in the reliability of nectar reward. Secondly and most importantly, changes in the overall availability of floral resources, which affects the amount of food that is available to pollinators, will certainly have consequences at the population level (Baude et al., 2016; Carvell et al., 2006, 2017; Roulston & Goodell, 2011). However, determining population level effects on mobile species such as pollinators is difficult. To do so, it would be necessary to simulate drought across the foraging range of pollinator species, and to follow this through multiple years. In reality, this is only plausible by using real drought events (Oliver, Marshall et al., 2015; Thomson, 2016), or through modelling of population dynamics in response to landscape scale alteration in resources (Becher et al., 2014; Horn, Becher, Kennedy, Osborne, & Grimm, 2015).

Other studies have assessed the impacts of drought on floral resources using laboratory experiments (Villarreal & Freeman, 1990) and field experiments in arid or semiarid regions (Al-Ghazawi et al., 2009; Takkis et al., 2015). The advantages of our study are that it involves intact experimental plant communities based in situ in a temperate region. However, this does come with disadvantages, for example difficulties in differentiating between the effects of drought and other effects of the experimental roof. An additional limitation of our experiment is the use of only a single level of drought. Future research would benefit from assessing multiple levels of water availability, which would elucidate possible critical limits for different plant species and plant communities, and would help to isolate the effects of water availability from other roof effects.

To our knowledge, this is one of the first studies to assess the impacts of drought on floral resources for pollinators at the community level, particularly in a temperate region where the risk of drought is projected to increase under climate change. Drought was

found to affect the availability of floral resources in calcareous grassland, despite this being a relatively drought-resistant habitat (Grime et al., 2008). Importantly, effects were consistently observed across a range of plant species and across a range of plant communities with different functional trait compositions. Given that species-rich calcareous grasslands are an important refuge habitat for pollinator species in the United Kingdom (Baude et al., 2016), which provide ecosystem services in nearby farmland (Woodcock et al., 2013), this result suggests that they may support lower pollinator populations in the future under current climate change scenarios.

## ACKNOWLEDGEMENTS

We would like to thank Nigel Follett for use of the site, and Victoria Mallott, Rachel McDonald and Joanna Savage for assistance with fieldwork. BP would like to thank The Access & Achievement Foundation and The Haberdashers' Educational Foundation for personal financial support. An earlier draft was greatly improved by comments from two anonymous reviewers. This study was part of the Wessex Biodiversity and Ecosystem Service Sustainability (BESS) project, funded under the BESS programme, and supported by the Natural Environment Research Council (Wessex BESS, ref. NE/J014680/1). The research materials supporting this publication can be accessed at <https://doi.org/10.5285/eb2bc7a2-4bd8-455d-8f0d-7d379540e967>

## ORCID

Benjamin B. Phillips  <http://orcid.org/0000-0003-4597-029X>

## REFERENCES

- Al-Ghazawi, A. A., Zaitoun, S., Gosheh, H., & Alqudah, A. (2009). Impacts of drought on pollination of *Trigonella moabitica* (Fabaceae) via bee visitations. *Archives of Agronomy and Soil Science*, *55*, 683–692. <https://doi.org/10.1080/03650340902821666>
- Baldock, K. C., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Osgathorpe, L. M., ... Vaughan, I. P. (2015). Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B*, *282*, 20142849. <https://doi.org/10.1098/rspb.2014.2849>
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.
- Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A., ... Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, *530*, 85–88. <https://doi.org/10.1038/nature16532>
- Becher, M. A., Grimm, V., Thorbek, P., Horn, J., Kennedy, P. J., & Osborne, J. L. (2014). BEEHAVE: A systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure. *Journal of Applied Ecology*, *51*, 470–472. <https://doi.org/10.1111/1365-2664.12222>
- Bell, G. (1986). The evolution of empty flowers. *Journal of Theoretical Biology*, *118*, 253–258. [https://doi.org/10.1016/S0022-5193\(86\)80057-1](https://doi.org/10.1016/S0022-5193(86)80057-1)
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*, 365–377. <https://doi.org/10.1111/j.1461-0248.2011.01736.x>
- Bishop, J., Jones, H. E., O'Sullivan, D. M., & Potts, S. G. (2017). Elevated temperature drives a shift from selfing to outcrossing in the insect-pollinated legume, faba bean (*Vicia faba*). *Journal of Experimental Botany*, *68*, 2055–2063.
- Borrell, B. J. (2007). Scaling of nectar foraging in orchid bees. *The American Naturalist*, *169*, 569–580. <https://doi.org/10.1086/512689>
- Brown, M. J., Dicks, L. V., Paxton, R. J., Baldock, K. C., Barron, A. B., Chauzat, M. P., ... Li, J. (2016). A horizon scan of future threats and opportunities for pollinators and pollination. *PeerJ*, *4*, e2249. <https://doi.org/10.7717/peerj.2249>
- Buckland, S. M., Grime, J. P., Hodgson, J. G., & Thompson, K. (1997). A comparison of plant responses to the extreme drought of 1995 in northern England. *Journal of Ecology*, *85*, 895–909.
- Burkle, L. A., & Runyon, J. B. (2016). Drought and leaf herbivory influence floral volatiles and pollinator attraction. *Global Change Biology*, *22*, 1644–1654. <https://doi.org/10.1111/gcb.13149>
- Cantarel, A. A. M., Bloor, J. M. G., & Soussana, J. F. (2013). Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. *Journal of Vegetation Science*, *24*, 113–126. <https://doi.org/10.1111/j.1654-1103.2012.01452.x>
- Carroll, A. B., Pallardy, S. G., & Galen, C. (2001). Drought stress, plant water status, and floral trait expression in fireweed *Epilobium angustifolium* (Onagraceae). *American Journal of Botany*, *88*, 438–446. <https://doi.org/10.2307/2657108>
- Carvell, C., Bourke, A. F., Dreier, S., Freeman, S. N., Hulmes, S., Jordan, W. C., ... Heard, M. S. (2017). Bumblebee family lineage survival is enhanced in high-quality landscapes. *Nature*, *543*, 547–549. <https://doi.org/10.1038/nature21709>
- Carvell, C., Roy, D. B., Smart, S. M., Pywell, R. F., Preston, C. D., & Goulson, D. (2006). Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, *132*, 481–489. <https://doi.org/10.1016/j.biocon.2006.05.008>
- Chen, T., van der Werf, G. R., de Jeu, R. A. M., Wang, G., & Dolman, A. J. (2013). A global analysis of the impact of drought on net primary productivity. *Hydrology and Earth System Sciences*, *17*, 3885–3894. <https://doi.org/10.5194/hess-17-3885-2013>
- Cnaani, J., Thomson, J. D., & Papaj, D. R. (2006). Flower choice and learning in foraging bumblebees: Effects of variation in nectar volume and concentration. *Ethology*, *112*, 278–285. <https://doi.org/10.1111/j.1439-0310.2006.01174.x>
- Comas, L. H., Becker, S. R., Cruz, V. M. V., Byrne, P. F., & Dierig, D. A. (2013). Root traits contributing to plant productivity under drought. *Frontiers in Plant Science*, *4*, 442.
- Corbet, S. A. (2003). Nectar sugar content: Estimating standing crop and secretion rate in the field. *Apidologie*, *34*, 1–10. <https://doi.org/10.1051/apido:2002049>
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, *3*, 52–58. <https://doi.org/10.1038/nclimate1633>
- Fitter, A. H., & Peat, H. J. (1994). The ecological flora database. *Journal of Ecology*, *82*, 415–425. <https://doi.org/10.2307/2261309>
- Fry, E. L., Hall, A. L., Savage, J., Bardgett, R. D., Ostle, N., Pywell, R. F., ... Iardi, M. (2018). Ecosystem functions and vegetation data for Winklesbury Hill, Salisbury Plain, UK 2016. NERC Environmental Information Data Centre. <https://doi.org/10.5285/e8a1bf2d-bc6b-452f-ab9d-40fa2288fce6>
- Galen, C. (2000). High and dry: Drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum* (Polemoniaceae). *American Naturalist*, *156*, 72–83.
- Gallagher, K. M., & Campbell, D. R. (2017). Shifts in water availability mediate plant-pollinator interactions. *New Phytologist*, *215*, 792–802. <https://doi.org/10.1111/nph.14602>
- Gallai, N., Salles, J. M., Settele, J., & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with



- pollinator decline. *Ecological Economics*, 68, 810–821. <https://doi.org/10.1016/j.ecolecon.2008.06.014>
- Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *Journal of Ecology*, 94, 295–304. <https://doi.org/10.1111/j.1365-2745.2006.01098.x>
- Goodwillie, C., Kalisz, S., & Eckert, C. G. (2005). The evolutionary enigma of mixed mating systems in plants: Occurrence, theoretical explanations and empirical evidence. *Annual Review of Ecology, Evolution, and Systematics*, 36, 47–79. <https://doi.org/10.1146/annurev.ecolsys.36.091704.175539>
- Gould, I. J., Quinton, J. N., Weigelt, A., De Deyn, G. B., & Bardgett, R. D. (2016). Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecology Letters*, 19, 1140–1149. <https://doi.org/10.1111/ele.12652>
- Grime, J. P., Brown, V. K., Thompson, K., Masters, G. J., Hillier, S. H., Clarke, I. P., ... Kieley, J. P. (2000). The response of two contrasting limestone grasslands to simulated climate change. *Science*, 289, 762–765. <https://doi.org/10.1126/science.289.5480.762>
- Grime, J. P., Fridley, J. D., Askew, A. P., Thompson, K., Hodgson, J. G., & Bennett, C. R. (2008). Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences*, 105, 10028–10032. <https://doi.org/10.1073/pnas.0711567105>
- Gross, N., Sudings, K. N., Lavorel, S., & Roumet, C. (2007). Complementarity as a mechanism of coexistence between functional groups of grasses. *Journal of Ecology*, 95, 1296–1305. <https://doi.org/10.1111/j.1365-2745.2007.01303.x>
- Gubsch, M., Buchmann, N., Schmid, B., Shulze, E.-D., Lipowsky, A., & Roscher, C. (2011). Differential effects of plant diversity on functional trait variation of grass species. *Annals of Botany*, 107, 157–169. <https://doi.org/10.1093/aob/mcq220>
- Halpern, S. L., Adler, L. S., & Wink, M. (2010). Leaf herbivory and drought stress affect floral attractive and defensive traits in *Nicotiana quadrivalvis*. *Oecologia*, 163, 961–971. <https://doi.org/10.1007/s00442-010-1651-z>
- Hanley, M. E., Franco, M., Pichon, S., Darvill, B., & Goulson, D. (2008). Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Functional Ecology*, 22, 592–598. <https://doi.org/10.1111/j.1365-2435.2008.01415.x>
- Hayot Carbonero, C., Mueller-Harvey, I., Brown, T. A., & Smith, L. (2011). Sainfoin (*Onobrychis vicifolia*): A beneficial forage legume. *Plant Genetic Resources*, 9, 70–85. <https://doi.org/10.1017/S1479262110000328>
- Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters*, 12, 184–195. <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- Horn, J., Becher, M. A., Kennedy, P. J., Osborne, J. L., & Grimm, V. (2015). Multiple stressors: Using the honeybee model BEEHAVE to explore how spatial and temporal forage stress affects colony resilience. *Oikos*, 125, 1001–1016.
- IPCC (2014). *Climate change 2014: Impacts, adaptation, and vulnerability*. contribution of working groups I, II and III to the Fifth assessment report of the intergovernmental panel on climate change (eds Core Writing Team, Pachauri RK, Meyer LA). IPCC, Geneva, Switzerland.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., ... Ebeling, A. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577. <https://doi.org/10.1038/nature15374>
- Kaluza, B. F., Wallace, H., Keller, A., Heard, T. A., Jeffers, B., Drescher, N., ... Leonhardt, S. D. (2017). Generalist social bees maximize diversity intake in plant species-rich and resource-abundant environments. *Ecosphere*, 8, e01758. <https://doi.org/10.1002/ecs2.1758>
- Kay, K. M., & Picklum, D. A. (2013). Drought alters the expression of mating system traits in two species of *Clarkia*. *Evolutionary Ecology*, 27, 899–910. <https://doi.org/10.1007/s10682-013-9630-6>
- Klein, A. M., Vaissière, B. E., Cane, J., Steffan-Dewenter, I., Cunningham, S., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B*, 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., ... Klotz, S. R. G. M. (2008). The LEDA Traitsbase: A database of life-history traits of Northwest European flora. *Journal of Ecology*, 96, 1266–1274. <https://doi.org/10.1111/j.1365-2745.2008.01430.x>
- Lee, S. G., & Felker, P. (1992). Influence of water/heat stress on flowering and fruiting of mesquite (*Prosopis glandulosa* var. *glandulosa*). *Journal of Arid Environments*, 23, 309–319.
- Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69, 1–33.
- Levin, D. A. (2010). Environment-enhanced self-fertilization: Implications for niche shifts in adjacent populations. *Journal of Ecology*, 98, 1276–1283. <https://doi.org/10.1111/j.1365-2745.2010.01715.x>
- Ling, T. C., Wang, L.-L., Zhang, Z.-Q., Dafni, A., Duan, Y.-W., & Yang, Y.-P. (2017). High autonomous selfing capacity and flower visitation rates in a subalpine population of *Prunella vulgaris* (Lamiaceae). *Plant Ecology and Evolution*, 150, 59–66. <https://doi.org/10.5091/plecevo>
- Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant/pollinator interactions. *Ecology Letters*, 10, 710–717. <https://doi.org/10.1111/j.1461-0248.2007.01061.x>
- Miller-Struttman, N. E., Geib, J. C., Franklin, J. D., Kevan, P. G., Holdo, R. M., & Ebert-May, D. (2015). Functional mismatch in a bumble bee pollination mutualism under climate change. *Science*, 78, 75–78.
- Oliver, T. H., Isaac, N. J. B., August, T. A., Woodcock, B. A., Roy, D. B., & Bullock, J. M. (2015). Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications*, 6, 10122. <https://doi.org/10.1038/ncomms10122>
- Oliver, T. H., Marshall, H. H., Morecroft, M. D., Brereton, T., Prudhomme, C., & Huntingford, C. (2015). Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change*, 5, 941–945. <https://doi.org/10.1038/nclimate2746>
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Petanidou, T., & Smets, E. (1996). Does temperature stress induce nectar secretion in Mediterranean plants? *New Phytologist*, 133, 513–518. <https://doi.org/10.1111/j.1469-8137.1996.tb01919.x>
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D., R Core Team (2016). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-128. Retrieved from <http://CRAN.R-project.org/package=nlme>
- Pinheiro, C., & Chaves, M. M. (2011). Photosynthesis and drought: Can we make metabolic connections from available data? *Journal of Experimental Botany*, 62, 869–882. <https://doi.org/10.1093/jxb/erq340>
- Prather, C. M., Pelini, S. L., Laws, A., Rivest, E., Woltz, M., Bloch, C. P., ... Parsons, S. (2013). Invertebrates, ecosystem services and climate change. *Biological Reviews*, 88, 327–348. <https://doi.org/10.1111/brv.12002>
- Prýs-Jones, O. E., & Corbet, S. A. (1991). *Bumblebees*. Slough, UK: The Richmond Publishing Co., Ltd..
- R Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Rodwell, J. S. (1992). *British plant communities. 3 grasslands and Montane communities*. Cambridge, UK: Cambridge University Press.
- Roulston, T. H., & Goodell, K. (2011). The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, 56, 293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>
- Royal Botanic Gardens Kew (2016). *Seed Information database (SID)*. Version 7.1. Retrieved from: <http://data.kew.org/sid/>

- Schweiger, O., Biesmeijer, J. C., Bommarco, R., Hickler, T., Hulme, P. E., Klotz, S., ... Petanidou, T. (2010). Multiple stressors on biotic interactions: How climate change and alien species interact to affect pollination. *Biological Reviews*, *85*, 777–795.
- Settele, J., Bishop, J., & Potts, S. G. (2016). Climate change impacts on pollination. *Nature Plants*, *2*, 16092. <https://doi.org/10.1038/nplants.2016.92>
- Takkis, K., Tscheulin, T., Tsalkatis, P., & Petanidou, T. (2015). Climate change reduces nectar secretion in two common Mediterranean plants. *AoB PLANTS*, *7*, plv111. <https://doi.org/10.1093/aob/pla/plv111>
- Thomson, D. M. (2016). Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters*, *19*, 1247–1255. <https://doi.org/10.1111/ele.12659>
- Vaudo, A. D., Tooker, J. F., Grozinger, C. M., & Patch, H. M. (2015). Bee nutrition and floral resource restoration. *Current Opinion in Insect Science*, *10*, 133–141. <https://doi.org/10.1016/j.cois.2015.05.008>
- Villarreal, A. G., & Freeman, E. (1990). Effects of temperature and water stress on some floral nectar characteristics in *Ipomopsis longiflora* (polemoniaceae) under controlled conditions. *Botanical Gazette*, *151*, 5–9. <https://doi.org/10.1086/337797>
- Vogel, A., Fester, T., Eisenhauer, N., Scherer-Lorenzen, M., Schmid, B., Weisser, W. W., & Weigelt, A. (2013). Separating drought effects from roof artifacts on ecosystem processes in a grassland drought experiment. *PLoS ONE*, *8*, e70997. <https://doi.org/10.1371/journal.pone.0070997>
- Waser, N. M., & Price, M. V. (2016). Drought, pollen and nectar availability, and pollination success. *Ecology*, *97*, 1400–1409. <https://doi.org/10.1890/15-1423.1>
- Woodcock, B. A., Edwards, M., Redhead, J., Meek, W. R., Nuttall, P., Falk, S., ... Pywell, R. F. (2013). Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. *Agriculture, Ecosystems and Environment*, *171*, 1–8. <https://doi.org/10.1016/j.agee.2013.03.005>
- Wyatt, R., Broyles, S. T., & Derda, G. S. (1992). Environmental influences on nectar production in milkweeds (*Asclepias syriaca* and *A. exaltata*). *American Journal of Botany*, *79*, 636–642. <https://doi.org/10.1002/j.1537-2197.1992.tb14605.x>
- Yee, T. W. (2010). The VGAM package for categorical data analysis. *Journal of Statistical Software*, *32*, 1–34.
- Zimmerman, M., & Pyke, G. H. (1988). Experimental manipulations of *Polemonium foliosissimum*: Effects on subsequent nectar production, seed production and growth. *Journal of Ecology*, *76*, 777–789. <https://doi.org/10.2307/2260573>
- Zwicke, M., Picon-Cochard, C., Morvan-Bertrard, A., Prud'homme, M. P., & Volaire, F. (2015). What functional strategies drive drought survival and recovery of perennial species from upland grassland? *Annals of Botany*, *116*, 1001–1015. <https://doi.org/10.1093/aob/mcv037>

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Phillips BB, Shaw RF, Holland MJ, et al. Drought reduces floral resources for pollinators. *Glob Change Biol.* 2018;24:3226–3235. <https://doi.org/10.1111/gcb.14130>