Dryness, wetness and temporary flooding reduce floral resources of plant communities with adverse consequences for pollinator attraction

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Abstract
1. Climate change alters precipitation regimes world-wide and is regarded as a major threat for pollinators and pollination services. Yet, not much is known on how wetter as well as drier conditions affect food resources for pollinators and pollinator attraction in a multi-species community context. It is unclear how community shifts under changed hydrological conditions might affect pollinators.
2. This mesocosm study addresses existing research gaps by investigating effects of drought, wetness and temporary flooding on floral resources and pollinator attraction within a plant community, initially including nine insect-pollinated and six wind-pollinated species. Floral resources were assessed over three growing seasons. I monitored community descriptors (percentage of herbs and herbaceous species richness, presence of flowering insect-pollinated individuals), floral traits (flower height, size and weight, floral sugar content of one key species) and proxies for plant fitness (pollinator attraction, seed and flower weight of one key species).
3. Wetness and especially dryness decreased the species richness and biomass proportion of insect-pollinated herbaceous species and flowering herbaceous plant individuals occurred less frequently. Permanent wetness decreased the floral sugar content of the key species *Trifolium pratense*. Wet, temporary flooded and especially dry communities were visited by pollinators less often. Active pollinators spent less time within wet and flooded communities, while not at all visiting dry communities. Seed and flower weight of the obligate xenogamous *T. pratense* in flooded and dry communities decreased, indicating negative consequences for plant fitness caused by a lack of pollination.
4. Synthesis. While dryness had negative effects for floral resources both in terms of community descriptors and floral traits, negative effects of wetness and temporary flooding were mostly caused by a decrease of insect-pollinated herbaceous species. The study thus indicates that shifts in plant community composition are decisive for a predictive understanding of plant-pollinator interactions under environmental change, but these have been neglected in past research. Changing precipitation patterns will adversely affect floral resources and pollinator attraction in agriculturally
used temperate grassland, which might have widespread negative consequences for pollination services and food security in the coming decades.

**KEYWORDS**
climate change, community level, drought, global change ecology, pollination, pulsed stress, *Trifolium pratense*, waterlogging

## 1 | INTRODUCTION

Pollination is a key ecosystem service, ensuring agricultural food production of the majority of the global main food crop species (Klein et al., 2007), as well as diversity and functioning of natural ecosystems (Bascompte, Jordano, & Olesen, 2006). Grassland covers around 40% of the Earth’s landmass and is amongst the most diverse ecosystems world-wide (Silva, 2008). Agriculturally used grasslands cover 30%–40% of Europe's agricultural area and provide important food sources for pollinators (Carvell et al., 2006; Orford, Murray, Vaughan, & Memmott, 2016), especially in later summer, when the flowering season of main nectar yielding species is over.

The last decades have witnessed a severe decline in insect pollinators (Biesmeijer, 2006; Kovács-Hostyánszki et al., 2017). Climate change is seen as a major threat for pollinators and pollination services in the 21st century, with adverse consequences for agricultural food production, sexual reproduction of the majority of wild plants and plant diversity (Abrol, 2010; Bascompte et al., 2006). Climate change alters precipitation regimes, with already dry regions often receiving less annual precipitation and with high-latitude regions often receiving more. Along with these changes, increases in the frequency of heavy precipitation events as well as of dry spells are observed and predicted to increase further (IPCC, 2012, 2018; Orth, Zscheischler, & Seneviratne, 2016).

Changes in precipitation patterns are likely to impact plants and thereby pollinators, because water availability is key for plant performance and flower production requires large amounts of nutrients, carbon and water (Gallagher & Campbell, 2017; Phillips et al., 2018). Furthermore, water availability determines plant species’ occurrence and abundance, because most species show strong hydrological niche differentiation (Araya et al., 2011). Water availability can therefore impact plant–pollinator interactions not only via changes to an individual plant’s floral traits, but also via changes in the plant community composition. Until now, however, studies on plant–pollinator interactions under precipitation change investigate mainly floral traits of plant individuals. Furthermore, studies focus almost exclusively on dryness effects, despite the higher confidence of climate projections that heavy precipitation will occur more often and more severely in many areas (IPCC, 2018). While one study so far addressed changes in plant–pollinator interactions under permanently wetter conditions (Gallagher & Campbell, 2017), to my knowledge effects of temporary flooding have never been investigated.

Studies addressing effects of dryness on floral traits found mostly negative effects on flower size and flower number (Al-Ghzawi, Zaitoun, Gosheh, & Alqudah, 2009 [one of the two studied species]; Burkle & Runyon, 2016; Carroll, Pallardy, & Galen, 2001; El Balla, Hamid, & Abdelmageed, 2013; Gallagher & Campbell, 2017; Glenny, Runyon, & Burke, 2018; Halpern, Adler, & Wink, 2010), on the amount of viable pollen (Boyer & Westgate, 2004; Turner, 1993) and on nectar volume (Halpern et al., 2010; Turner, 1993; Waser & Price, 2016), Phillips et al. (2018) found less flowers in one of the three studied species, and a lower proportion of nectar-bearing flowers in the other two. Gallagher and Campbell (2017), however, did not find any effects of water availability on flower abundance of one focal species in natural plant communities, but a linear increase of nectar volume with increasing water supply. Nectar sugar concentration or the emission of volatile organic compounds was often found to increase under drought stress conditions. This might increase floral reward and attractiveness for pollinators, although more viscous nectar might increase foraging effort (Burkle & Runyon, 2016; Carroll et al., 2001; Glenny et al., 2018).

Most studies cited above focused on singly growing plants, with the exception of Gallagher and Campbell (2017) and Phillips et al. (2018), investigating some focal species within plant communities and Glenny et al. (2018), studying differences between forb herbaceous species growing alone or growing with three other forb species. It has recently been argued that studies addressing plant–pollinator interactions need to focus more on multi-species plant assemblages and on the community scale (Glenny et al., 2018; Phillips et al., 2018). Because effects of the abiotic and biotic environment on floral resources are often species-specific, studies investigating all flowering species and pollinator attraction within plant communities are urgently needed, yet, do not exist. Effects of hydrology on floral resources and pollinator visitation might differ from the response of plant individuals growing alone, because of changes in the strength of intraspecific plant–plant interactions: Under drought conditions, competition between species often increases in grassland (reviewed in Walter, 2018), and drought effects might as such be even larger when investigated within communities. Complementary resource use, however, might also lead to less stress for plants when growing in communities, for example, when excess water might be exploited more completely, thereby avoiding anoxia. Glenny et al. (2018) showed that climate change effects on pollinator visitation were stronger when plants were growing in multi-species assemblages, compared to single-species assemblages. Changing hydrological conditions are further likely to change the species composition of plant communities, because
most species show strong eco-hydrological niche differentiation (Araya et al., 2011). Shifts in species’ abundances might affect the offer of floral resources for pollinators. It has been shown, for instance, that flooding leads to a dominance of wind-pollinated grasses over often insect-pollinated herbaceous species (Striker, Mollard, Grimoldi, Leon, & Insauti, 2011). Drought, on the other hand, could increase the abundance of specialized herb species with deep roots, but may also lead to local extinctions of species with high food quality. To my knowledge, only one study so far addressed this issue which investigated the floral resources of three key species under drought within a community context in drought-adapted, calcareous grassland (Phillips et al., 2018). This latter study showed decreases in floral species richness in two of the four community types (differing in functional group composition), but did not study consequences for pollinator attraction. These authors also call for studies in more drought-vulnerable habitats, for example, mesophilic grassland.

Studies investigating effects of hydrological change on pollinator attraction, and therefore indirectly on plant fitness, are rare (Gallagher & Campbell, 2017; Walter, 2018). Glenny et al. (2018), Burkle and Runyon (2016) and Al-Ghzawi et al. (2009) found less pollinator visits per plant under dry conditions for some species, although visits per flower also increased for one of the four species in the study by Burkle and Runyon (2016). Contrasting linear increases in floral traits with water supply, Gallagher and Campbell (2017) found peak floral visitation rates at intermediate water availability levels and seed set was partly positively related to visitation rates.

This study addresses existing research gaps: I study changes in floral resources based on floral traits and community shifts and their consequences for pollinator attraction in multi-species mesophilic grassland over three growing seasons. I do not only focus on drought effects, but also on effects of increased precipitation and flooding, as these are relevant scenarios for many temperate grasslands under ongoing climate change.

I hypothesize that (a) hydrological stress under dryness, wetness and temporary flooding (seen by reduced biomass production) will lead to changes in floral traits that reduce floral resources (less, smaller and lower flowers). I further hypothesize that (b) hydrological stress will decrease floral resources of plant communities by reducing the abundance and richness of herbaceous species and by reducing the presence of flowering insect-pollinated plants. (c) Consequently, pollinator attraction will mostly be negatively affected by hydrological stress under dryness, wetness and temporary flooding. (d) This will lead to reductions in flower- and seed weight in pollinator-dependent species.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The mesocosm experiment was conducted at the University of Hohenheim, Stuttgart, Southern Germany (48.71°N, 9.19°E; 389 m a.s.l.) from April 2016 to November 2018. Mean annual precipitation from 1981 to 2010 was 718 mm and mean annual temperature was 9.4°C (Wetter-BW.de, 2019).

Plant communities were established in March 2016 in the greenhouse in large pots (20 L, 0.28 m height, 0.35 m diameter) filled with sandy loam (14% clay, 70% sand, 16% silt; pH 7.88). They initially comprised 15 grassland species typical for agriculturally managed, mesophilic hay meadows (Arrhenatherion elatioris) that were sown to achieve a density of 90 individuals per pot (i.e. 1,000 individuals per m²), as implemented e.g. by Roscher et al. (2004; six individuals per species, see Table 1).

The number of seeds needed to achieve this density was calculated based on previously measured germination rates of each species. Pots were transported to the field in May 2016. It was made sure that all species were present in each pot with at least one individual in June 2016 (each mesocosm thus containing 15 species) and the estimated percentage of insect-pollinated herbaceous species (in contrast to graminoid species) at the beginning of the water table manipulations was 48.8% ± 0.13 SD across all pots and did not differ between the future hydrological conditions (% of total cover, estimated on 22 June; F3,88 = 0.56; p = .65). Communities were therefore established well and diverse before the start of the hydrological manipulations. With the exception of T. dubium, the herbaceous plants were perennial species and I did not re-sow any species. Non-target species were removed from communities three times per year.

Different hydrological conditions were applied by placing pots in separate 275-L pools and adjusting the water table around them to different water table heights by creating over-flows at the respective height. Pools implementing different hydrological conditions were randomly arranged. Pots had holes at the bottom so that the water table was also achieved inside the pots. To avoid pseudo-replication, only one mesocosm was placed per pool. In the wet treatment (n = 24), the water table was kept at ~5 cm below the soil surface and in the mesic treatment at ~25 cm (n = 24). In the dry treatment, pools contained no water so that pots only received natural rainfall (n = 24). In addition to these permanent manipulations, I tested the effects of a short, extreme flooding pulse by flooding plants up to 2 cm above the ground for 2 weeks in July 2016 and for 3 weeks in July 2017 and 2018, as this might be a realistic scenario given the projected increases in flooding risk and extreme precipitation events. These temporary flooded pots were otherwise kept under mesic conditions for the rest of the growing season (n = 10). On 20 June 2016, hydrological manipulations were initiated and were thereafter applied during each growing season from March to November. Soil moisture was assessed three to four times per year in seven communities per hydrological condition, using a TDR-probe with 0.2-m long rods that were inserted completely into the soil. Mesocosms were placed outside the pools over winter to avoid freezing.

2.2 | Community descriptors

To assess whether hydrological conditions exerted stress on plant communities, total above-ground biomass production was assessed...
self-incompatibility means that selfing and seed set is always hindered via genetic mechanisms (Klotz, Kühn, & Durka, 2002). ±Self-incompatible means that selfing is usually, but not always hindered, self-incompatibility means that selfing and seed set is always hindered via genetic mechanisms.

| Species name               | Wind | Insect | Reward | Self-compatibility | Mating system       |
|----------------------------|------|--------|--------|--------------------|---------------------|
| Achillea millefolium (L.)  | N    | Y      | Nectar | Self-incompatible  | Xenogamous          |
| Bellis perennis (L.)       | N    | Y      | Nectar | Self-compatible    | Autogamous          |
| Centaurea jacea (L.)       | N    | Y      | Nectar | Self-incompatible  | Xenogamous          |
| Crepis biennis (L.)        | N    | Y      | Nectar | ±Self-incompatible | Usually xenogamous  |
| Galium mollugo album (Mill.)| N    | Y      | Nectar | Self-compatible    | Auto- and xenogamous|
| Plantago lanceolata (L.)   | Usually | Seldomly  | Pollen | ±Self-incompatible | Xenogamous          |
| Trifolium dubium sibth (L.)| N    | Y      | Nectar | Self-compatible    | Auto- and xenogamous|
| Trifolium pratense (L.)    | N    | Y      | Nectar | Self-incompatible  | Xenogamous          |
| Vicia cracca (L.)          | N    | Y      | Nectar | Self-compatible    | Usually xenogamous  |
| Alopecurus pratensis (L.)  | Y    | N      | Nectar | Self-incompatible  | Xenogamous          |
| Arrenatherum elatius (L.)  | Y    | N      | Nectar | ±Self-incompatible | Xenogamous          |
| Bromus hordeaceus (L.)     | Y    | N      | Nectar | Self-compatible    | Autogamous          |
| Dactylis glomerata (L.)    | Y    | N      | Nectar | ±Self-incompatible | Xenogamous          |
| Festuca rubra agg. (Nigrescens) | Y    | N      | Nectar | ±Self-incompatible | Xenogamous          |
| Poa pratensis (L.)         | Y    | N      | Nectar | Self-compatible    | Auto- and xenogamous|

Twice per year in June and October, mimicking agricultural routines, and starting in October 2016. Therefore, standing biomass was cut at 3 cm above the ground, dried at 60°C for 4 days and weighed. The weight of herbaceous and graminoid species was determined separately at each harvest. To monitor community restructuring, above-ground biomass was sorted per species once per year (October 2016 and 2017; June 2018). Therefore, fresh plant material was directly divided into species after cutting, then dried and weighed specifically. I further assessed the presence of flowering insect-pollinated plant individuals each year by recording presence of open floral units for each species at each harvest and over the growing season, when assessing floral traits of plant individuals (see below). A plant individual was considered as flowering when at least one flower was open (or more than 50% of single florets of one flower head). This was done as flowering of insect-pollinated species (and not only abundance or presence) is the pre-requisite for offering food resources to pollinators.

2.3 | Floral traits

At the beginning of each growing season, one ramet of each herbaceous species in each community was randomly marked and floral traits were assessed approximately monthly for this ramet throughout the growing season. I counted the number of floral units (except for senesced ones) sensu Baldock et al. (2015) and measured the height of the highest open flower or flower head as soon as the species started flowering in one of the treatments. Flower heads were counted as open, as soon as more than 50% of single florets were open. Size of flowers was measured with a ruler (diameter or, for P. lanceolata, length). Because most species did not flower often enough under each condition to obtain enough data for floral traits, these could only be analysed for T. pratense, P. lanceolata and A. millefolium.

To have a proxy for nectar sugar content, I bagged single floral units of T. pratense, the dominant herbaceous species under most hydrological conditions (see Figure 2c and Figure S1), for 24 hr in October 2018 to prevent flower visitation. Flowers were subsequently cut, frozen and pulverized in liquid nitrogen, stored at −20°C and d-glucose, d-fructose and sucrose content of whole floral units were assessed enzymatically. Sugars were determined spectrophotometrically using the UV-method test kit after extraction in water (R Biopharm; no. 10 716 260 035, 340 nm wavelength, glass cuvettes with 1 cm light path) (Perkin Elmer, Lambda 35 UVVIS). I additionally estimated the percentage of vegetation cover in a pot, percentage of wilted plant material and percentage of herbs.

To get an idea on how the community context alters the response of floral resources towards hydrological change, I also assessed floral traits for all nine herbaceous plant species growing alone (only one plant individual per pot) in 2018 (n = 3 per hydrological condition). These single plants were also sown in March 2016, grew in the same-sized pots and were subjected to the same conditions as plant communities since then. Results of this side-experiment are presented in the appendix (Figures S4 and S5).

2.4 | Parameters related to plant fitness

To infer on effects of hydrological conditions for plant fitness, I collected ripe T. pratense floral units (i.e. whole flower heads) in the end
of 2016 and determined the weight of flower heads and seed weight of 20 seeds. To quantify the effects of hydrological conditions on pollinator attraction, the number of pollinators visiting communities and the time they spent in communities was recorded for a total of 17.43 hr on several times during each growing season (23 and 31 August in 2016; 13 June, 25 July and 21 September in 2017; 22 May, 20 June, 16 August and 12 September in 2018). Pollinator visits were assessed between 10.30 and 14.30 on warm, sunny, unwindy days. Following the approach by Hegland and Totland (2005), visitors were counted as pollinators when they stayed on flowers for at least 1 s, because flowers were usually too small to identify if reproductive organs were touched. Data were recorded for 2 min after waiting in silence in front of each community for 1 min. Whenever a pollinator visited a pot at the end of the 2-min period, its total duration of visitation and the flowers it touched were recorded until it left. Although the total visitation time is only 17.43 hr, the more than 4 hr that were spent monitoring each hydrological condition was enough to draw meaningful conclusions. The relatively short monitoring duration is because I only conducted monitoring during the main flowering period (May–September, and later in 2016), because I have restricted the monitoring time per pot to 2 min to include many replicates and because I could usually only monitor once per month, due to weather and time restrictions. I have further tried to monitor pollinators as close as possible to the monthly floral trait measurements, to be able to relate floral resource data to pollinator attraction data. Main visitor groups were identified as *Bombus* spp. (78 visits), non-*bombus* *Apidae* (44 visits) and *Diptera* spp. (58 visits). While the former two groups visited only *T. pratense* and *V. cracca*, the latter also visited *A. millefolium*, *P. lanceolata* and *G. mollugo* flowers.

### 2.5 Data analyses

Statistical analyses were performed with R 3.5.1. (R Core Team, 2018). For analysing community descriptors and pollinator attraction (biomass proportion and occurrence of flowering insect-pollinated plant species proportion of herbs, number of pollinator visits, time spent by pollinators) mixed effects models were fitted using the lme4 R package (Bates, Maechler, Bolker, & Walker, 2015). Hydrological conditions and year of the study were fixed effects, and occurrence of flowering insect-pollinated plant species as random effects. Using time or year of the study as fixed factors allows for investigating changes over time, by including the interaction between hydrological conditions and time. A significant interaction then shows that effects of hydrological conditions changed over time. Generalized linear mixed effects models with a binomial error structure were used to analyse the presence of flowering insect-pollinated individuals, and generalized linear mixed effect models with Poisson error structure were used to analyse the number of pollinator visits and the time they spent in communities (see Table S1 for all models, necessary transformation and the statistical results). For analysing the occurrence of flowering insect-pollinated plant species, I did not differentiate whether species were not flowering or simply not present any more, because species loss and lack of flowering have basically the same consequences for pollinators (no food resources).

For number and height of floral units, mixed effects models were used with water and species as fixed effects and pot as a random effect. Number of flowers were analysed using a generalized linear mixed effect model with a negative-binomial error distribution, because of over-dispersion of count data.

Weight of floral units, 20-seed weight and sugar content of *T. pratense* flowers were analysed using linear models with hydrological conditions as the fixed factor. Sucrose was usually not detectable in flowers and was not, unlike α-fructose and α-glucose, analysed separately, but was included in total sugar sum, by adding the concentrations of all three sugar types. Because only few flowers from mesic, temporarily flooded and wet communities could be sampled in late summer 2018 for analysing the floral sugar content, temporarily flooded and mesic flowers were pooled in the analyses for flower sugar content, because communities were both kept under mesic conditions at this time (flooding pulse was over since 8 weeks) and did not show any significant differences in sugar content anymore.

To account for zero-inflation (excess zeros) of data for biomass proportion of insect-pollinated species, number of flowers and the number of pollinator visits, generalized linear mixed effect models including a zero-inflation term were fitted for these response variables using template model builder (r package glmmTMB; Brooks et al., 2017).

To test for significance of main effects, likelihood ratio tests were performed for generalized linear mixed effects models between the model with and without the interaction term (interaction between hydrological conditions and time), and, when the interaction was non-significant, between the model including and not including the main factors. In case of one-factorial models likelihood ratio tests were performed between the model including the factor and the null-model. ANOVA were performed for linear (mixed effects) models, using Satterthwaite correction for degrees of freedom for mixed effects models (Kuznetsova, Brockhoff, & Christensen, 2017).

To identify best explaining independent predictors of community performance and floral traits for number of pollinator visits and time spent within communities, data on pollinator visits were combined with data of the nearest date for floral trait assessments (usually 1 week before or after pollinator assessments). Hierarchical partitioning was applied to analyse which of the predictors of floral resources and vegetation (number, height and diameter of the highest open *T. pratense* flower, overall number of open flowers of marked plant individuals of all species, percentage cover, percentage wilting and percentage of herbs) best explained pollinator visits, using R package hier.part (Walsh & Mac Nally, 2013). Hierarchical partitioning allows for identifying predictors that are independently correlated with the dependent variable, rather than being only dependently correlated via co-linearity with other predictors. It considers all possible models of a multiple regression and evaluates their goodness of fit. As such, problems of collinearity between predictors are avoided (Mac Nally, 2000).
Response variables were transformed when necessary to reach homoscedacity and normality of errors (see Table S1). Whenever the main effect of hydrological conditions was significant, post hoc tests were performed with TukeyHSD correction (package lsmeans; Lenth, 2016).

Data for singly growing plants of 2018 were analysed using the models and methods described above, with species as additional random effect.

3 RESULTS

In 2016, the first year of the study, June was exceptionally wet (115 mm rainfall) and was followed by a dry period from July to September (117 mm in the three months). The year 2017 was a rather moist year, with almost 90 mm more rainfall than the long-term 30-year average (1981–2010) during the growing season. Also, 2018 had a record-breaking dry and hot summer (+2.3 K and 90 mm less precipitation than the long-term average from April to November) (Wetter-BW.de, 2019). Soil moisture reacted to the applied hydrological treatments as expected, showing lowest moisture under dry and highest moisture under wet conditions, with peaks in soil moisture in the temporary flooded communities during the flooding pulse (Figure 1a). Soil moisture under dry and mesic conditions resembled the values of other experiments that were conducted in the field (Kreyling, Wenigmann, Beierkuhnlein, & Jentsch, 2008; Walter et al., 2012).

Generally, plant communities were most stressed by dry conditions, and to a lesser extent under permanently wet and temporary flooded conditions, as shown by decreases in biomass production ($F_{3,86} = 161.25; p < .001$; Figure 1b). Effects varied with time (interaction hydrological conditions: year: $F_{12,294} = 5.09; p < .003$): While dryness and permanent wetness had negative effects on biomass production throughout the study period, temporary flooding had only negative effects in October of the first 2 years, but not in June (which was before flooding was applied each year) and also not in the very hot and dry 2018 (see Table S2 for results of post hoc tests and additionally Table S3 for estimates of all models).

All the herbaceous species produced most biomass in the mesic treatment, with the exception of *Bellis perennis*, producing slightly more biomass during the dry treatment (see Figure S1).

3.1 Community descriptors: Floral species richness, presence of flowering insect-pollinated plants, proportion of herbs

Species richness of insect-pollinated species was significantly affected by hydrological conditions (Chisq$_3 = 73.89; p < .001$; Figure 2a): average number of insect-pollinated species was 5 ($\pm 0.27$ SE) in mesic communities, marginally significantly less in wet and temporary flooded communities (4 $\pm 0.25$ SE; post hoc $p = .08$; and 3.7 $\pm 0.47$ SE; post hoc $p = .07$, respectively), and significantly less in dry communities (1.6 $\pm 0.18$ SE; post hoc $p < .001$). The proportion of herbaceous species in relation to graminoids showed a similar pattern, with a lower proportion of herbs under wet, flooded and dry conditions ($F_{3,84} = 52.4; p < .001$) and effects changing over time ($F_{12,286} = 8.08; p < .001$; Figure 2b): While negative effects of dryness on the proportion of herbs were already apparent at the end of the first year, effects of waterlogging showed up from June of the
FIGURE 2 Effects of hydrological conditions on (a) the richness of insect-pollinated species within communities, (b) the proportion of herbs (in relation to graminoid species) over the course of the study and (c) the presence of flowering insect-pollinated plants. The latter indicates for each species the proportion of communities in which flowering of the respective species was observed in a given year of the study (light grey = dry; grey = mesic; dark grey = waterlogged; black = temporary flooded (short flooding pulse and otherwise mesic conditions). Note that for (a), data have been square-root-transformed for visualization, to account for the skewness of the Poisson-distributed data. Means ± 1 SE are shown. Lower case letters signify significant, or in (a) marginally significant, differences between the hydrological conditions (Am = Achillea millefolium; Bp = Bellis perennis; Cb = Crepis biennis; Cj = Centaurea jacea; Gm = Galium mollugo; Pl = Plantago lanceolata; Td = Trifolium dubium; Tp = Trifolium pratense, Vc = Vicia cracca).

The role of hydrological conditions on the height of the highest open flower could only be evaluated for P. lanceolata and T. pratense, as only these showed enough open flowers across all hydrological conditions. Hydrological conditions modified the height of floral units ($F_{3,439} = 1.27; p = .28$) over all years, but differed significantly between species ($F_{3,439} = 8.56; p = .004$) (see Table S3 for estimates and standard errors). Average flowers in case these species were still present in the communities ($\text{Chisq}_3 = 31.09; p < .001$), but effects varied with species (interaction term: $\text{Chisq}_3 = 57.9; p < .001$; Figure 3a). While A. millefolium did not show a clear effect of hydrological conditions on the number of flowers ($\text{Chisq}_3 = 0.52; p = .91$), T. pratense and P. lanceolata showed strong effects of hydrological conditions, yet in opposite directions ($\text{Chisq}_3 = 62; p < .001$; $\text{Chisq}_3 = 17.19; p < .001$). While P. lanceolata had most flowers under dry conditions, T. pratense had most flowers under mesic conditions.

3.2 Floral traits: Number and height of flowers and floral sugar content

Only three species were sufficiently flowering over the 3 years across all hydrological conditions to analyse the number of flowers at the individual plant scale depending on hydrological condition (compare Figure 2c). Hydrological conditions affected the number of
flower size of \( T. \text{ pratense} \) was \( 16.26 \text{ mm} \pm 0.48 \text{ SE} \), and of \( P. \text{ lanceolata} \) was \( 12.4 \text{ mm} \pm 0.71 \text{ SE} \).

The glucose content of \( T. \text{ pratense} \) flowers did not differ between flowers collected under wet conditions and collected under mesic conditions (flowers for analysing flower sugar content were collected 8 weeks after the temporary flooding pulse; \( F_{1,15} = 2.66; \ p = .12 \)).

Fructose content as well as sum of all sugars, however, was higher in flowers collected under mesic conditions than in flowers from wet communities (\( F_{1,15} = 5.97; \ p = .03 \); Table 2). Because no flowers were present in late summer 2018 in dry communities, the role of dry conditions for floral sugar content could not be evaluated for that year.

### 3.3 | Plant fitness proxies

Weight of ripe flower heads of \( T. \text{ pratense} \), collected in late summer 2016, was affected by hydrological conditions (\( F_{3,24} = 18.8; \ p < .001 \)). Flower heads were significantly heavier under wet and mesic compared to dry and temporarily flooded conditions (Table 2).

TABLE 2 | Effects of hydrological conditions on the glucose, fructose and overall sugar content (glucose + fructose + sucrose) of flower heads of \( T. \text{ pratense} \), herbaceous key species of all communities, collected in October 2018 and weight of whole flower heads and of 20 seeds of \( T. \text{ pratense} \), collected in late summer 2016. No flowers were available in 2018 in dry communities. Values in bold show significant or marginally significant deviations from the mesic control values (\( p < .1 \)).

| Hyd. condition | Glucose (g/100 g) | Fructose (g/100 g) | Sugar sum (g/100 g) | Weight (g) | Seed weight (mg) |
|----------------|------------------|-------------------|---------------------|------------|------------------|
| Dry            | NA               | NA                | NA                  | 0.087 ± 0.0155 | 0.019 ± 0.003 |
| Mesic          | 1.24 ± 0.279     | 1.82 ± 0.23       | 3.09 ± 0.465        | 0.211 ± 0.0163 | 0.028 ± 0.0019 |
| Wet            | 0.81 ± 0.216     | 1.11 ± 0.263      | 1.93 ± 0.49         | 0.234 ± 0.0107 | 0.029 ± 0.0019 |
| Flooded        | 1.7 ± 0.298      | 1.9 ± 0.201       | 3.6 ± 0.46          | 0.116 ± 0.0218 | 0.016 ± 0.0033 |

Hydrological conditions significantly influenced the number of pollinators visiting plant communities (\( \text{Chisq}_3 = 43.01; \ p < .001 \); Figure 4a): Mesic communities were visited most often, while wet and flooded communities were visited not even half as often, and a dry community was only visited once by three dipteran species foraging on \( P. \text{ lanceolata} \). Excluding this singularity from the data, insects stayed on average 39 s (±7 SE) within mesic and only 27 s in wet (±10) or pulsed flooded (±11.8 SE) communities, but this difference was non-significant (\( \text{Chisq}_3 = 3.7; \ p = .16 \)). Yet, when restricting the data to active pollinators moving between flowers (excluding visits in which dipteran species rested on one flower for more than 60 s), hydrological conditions modified the time these active pollinators spent in communities (\( \text{Chisq}_3 = 8.89; \ p = .01 \); Figure 4b); staying in mesic communities for 35 s (±5.9 SE), in temporarily flooded for 18 s (±6.3) and in very wet communities for 15 s (±3.3).

Best explaining independent predictor for the number of pollinators visiting communities was the percentage of wilted plant material, with more pollinators visiting pots with less wilted plant material (independently explaining 34% of variation in the number of visiting pollinators). For the time active pollinators spent in communities, the overall number of open flowers was the best explaining independent predictor (independently explaining 30%; see Figure S3).
in a community context under dry conditions, with the exception of growing in communities indicates that stress is exacerbated on plants on floral traits of non-drought-tolerant species when plants were methods M1 in appendix. The stronger negative effects of dryness for number of flowers and biomass proportion of species show that negative competition effects might decrease under harsh conditions. Species-specific results for number of flowers and biomass proportion of species show that negative competition effects might decrease under harsh conditions for stress-adapted species (like P. lanceolata, however, whose biomass proportion in the communities was benefitted by dryness, had also most and highest flowers under dry conditions. Species-specific results for number of flowers and biomass proportion of species show that negative competition effects might decrease under harsh conditions for stress-adapted species (like P. lanceolata), driven by an overall decrease in community biomass (in accordance with the stress-gradient hypothesis, e.g. Walter, 2018). This is also supported by the different findings for floral traits of species growing singly compared with the same species growing in plant communities (see Figures S4–S6 and methods M1 in appendix). The stronger negative effects of dryness on floral traits of non-drought-tolerant species when plants were growing in communities indicates that stress is exacerbated on plants in a community context under dry conditions, with the exception of the dryness-tolerant species P. lanceolata. Contrastingly, the weaker negative effects of wetness in communities in contrast to singly growing species indicate facilitative interactions between plants when growing in communities under wetness, as reviewed in Walter (2018). Facilitation under wetness stress in communities might occur because of higher transpiring biomass or increased root penetration, allowing for better oxygen supply. These results show that interactions between plants shape responses of floral traits towards hydrological conditions (Glenny et al., 2018). Yet, the importance of the percentage of wilted plant material for pollinator attraction, and the very strong decline in abundance and biomass proportion of herbaceous species suggest that community shifts and the disappearance of herbaceous species might be more important to floral resources than changes in floral traits.

Generally, community shifts observed under wetness and dryness were consistent with the expectations and with the few other studies, showing that dryness reduces floral species richness (Phillips et al., 2018) and that flooding increases the dominance of grass-species (Striker et al., 2011). Yet, the fast and strong reaction of communities, especially under dryness, but also under permanent wetness, was unexpected. Communities in mesocosms might react stronger towards hydrological conditions, as their rooting depth and available soil volume is restricted. The reaction of temporary flooded and wet communities, however, depended on stress severity, with smaller effects in the very dry year of 2018, when effects of temporary flooding and permanent wetness on soil moisture and biomass production were less severe.

Patterns of pollinator visitation were consistent with the observed community shifts, with strongest effects on dry communities, but less visitors and less time spent in communities also under
permanent wetness and temporary flooding stress. This is consistent with Gallagher and Campbell (2017) showing highest pollinator visitation rates of one focal species at intermediate levels of water supply. Gallagher and Campbell (2017) showed increased nectar volume with increased water supply, but my results suggest that sugar concentration in nectar might be lower under wetness, which might also explain their findings of increased pollinator visitation rates under intermediate water supply, despite higher nectar volume under wetness. When sugar concentration is lower under wetness, the overall resources might still be highest under intermediate water supply.

In my experiment, unstressed and stressed communities were closely together in one common garden. While under dry conditions, almost no nectar-bearing flowers were available for pollinators, it might be that under natural conditions, pollinators would visit wetness-stressed communities more often (without an adjacent mesic and unstressed alternative), yet still finding less food resources within (less flowers, lower sugar concentration). Temporary flooding, despite its short duration relative to the perennial species lifetime, had profound consequences for pollinator attraction and seed and flower weight. Surprisingly, the percentage of wilted plant material that reflected higher mortality under stress conditions seemed most influential for pollinator attraction, and not floral traits. Parallel decreases in seed and flower weight suggest that plant fitness might be negatively affected by decreases in pollinator visitations associated with hydrological stress, at least in obligate xenogamous species that rely on insect pollen vectors, such as *T. pratense*. It has already been shown that declines in pollinators are paralleled by declines in insect-pollinated plant species (Biesmeijer, 2006).

4.1 | Conclusions: Consequences of hydrological change for pollinators and plants

Most experiments investigating effects of precipitation change for ecosystem functioning focus on dryness, which is projected to increase over many areas (IPCC, 2018). Yet, there is even higher confidence that the frequency and intensity of extreme precipitation events will increase in many regions, contributing to an increase in floods (IPCC, 2018). This study shows that both, wetness and dryness stress will decrease floral food resources for pollinators in temperate, mesophilic grassland, by decreasing herbaceous species, presence of flowering plant individuals, flower number and nectar sugar content under hydrological stress. Consequences of precipitation change for pollinators caused by shifts in plant community composition might be quite severe, especially since these community shifts occur fast, probably leaving no time for specialized and adapted floral plant species to fill the gap left by floral species loss. One dry year might already severely reduce food resources offered by mesophilic grasslands for pollinators, caused by community shifts. Declines in pollinator attraction accompanied hydrological stress and were related to reductions in flower and seed weight under dryness and after temporary flooding. This indicates adverse consequences for the sexual reproduction and fitness of flowering plants.

Therefore, precipitation change might also contribute to pollinator decline in the future. Yet, studies at larger spatial and temporal scales are needed to investigate if and under which circumstances species turnover towards more stress-prone species might counteract negative consequences at the community level. Ultimately, provisioning of many ecosystem services offered by pollinators will be affected when changes in precipitation lead to widespread and negative consequences for floral resources in mesophilic, agriculturally used grassland.

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AUTHORS’ CONTRIBUTIONS

J.W. conceived the ideas and designed methodology, organised data collection, analysed the data and wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.m905qfjxf (Walter, 2020).

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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