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## Experimental test of the combined effects of water availability and flowering time on pollinator visitation and seed set

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10 set, species interactions, water availability

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15 **Abstract**

16 Climate change is likely to alter both flowering phenology and water availability for plants. Either of  
17 these changes alone can affect pollinator visitation and plant reproductive success. The relative  
18 impacts of phenology and water, and whether they interact in their impacts on plant reproductive  
19 success remain, however, largely unexplored. We manipulated flowering phenology and soil  
20 moisture in a factorial experiment with the subalpine perennial *Mertensia ciliata* (Boraginaceae). We  
21 examined responses of floral traits, floral abundance, pollinator visitation, and composition of visits  
22 by bumblebees versus other pollinators. To determine the net effects on plant reproductive success,  
23 we also measured seed production and seed mass. Reduced water led to shorter, narrower flowers  
24 that produced less nectar. Late flowering plants produced fewer and shorter flowers. Both flowering  
25 phenology and water availability influenced pollination and reproductive success. Differences in  
26 flowering phenology had greater effects on pollinator visitation than did changes in water  
27 availability, but the reverse was true for seed production and mass, which were enhanced by greater  
28 water availability. The probability of receiving a flower visit declined over the season, coinciding  
29 with a decline in floral abundance in the arrays. Among plants receiving visits, both the visitation rate  
30 and percent of non-bumblebee visitors declined after the first week and remained low until the final  
31 week. We detected interactions of phenology and water on pollinator visitor composition, in which  
32 plants subject to drought were the only group to experience a late-season resurgence in visits by  
33 solitary bees and flies. Despite that interaction, net reproductive success measured as seed production  
34 responded additively to the two manipulations of water and phenology. Commonly observed declines  
35 in flower size and reward due to drought or shifts in phenology may not necessarily result in reduced  
36 plant reproductive success, which in *M. ciliata* responded more directly to water availability. The  
37 results highlight the need to go beyond studying single responses to climate changes, such as either  
38 phenology of a single species or how it experiences an abiotic factor, in order to understand how  
39 climate change may affect plant reproductive success.

40 **1 Introduction**

41 Anthropogenic climate change includes both rising global temperatures and changes in precipitation  
42 patterns (IPCC 2014). These abiotic factors have direct physiological effects on plants and animals  
43 that can impact their fitness, but they also influence the timing of key life history events (i.e.,  
44 phenology) of many species (Fitter and Fitter 2002; Walther 2003; Parmesan 2006; Marshall et al.  
45 2008; Hegland et al. 2009; Bartomeus et al. 2011). Species-specific responses to climate change can  
46 also disrupt many ecologically and economically important relationships among species (Memmot et  
47 al. 2007; Forrest and Miller-Rushing 2010; Cardinale et al. 2012; Jamieson et al. 2012; Winfree  
48 2013). The mutualism between plants and their pollinators is among the most vital of these  
49 interactions to maintaining the functional integrity of terrestrial ecosystems (Abrol 2012; Aizen et al.  
50 2009). Understanding how plant-pollinator relationships are being affected by climate change is  
51 therefore of critical importance. Here we focus on the combined influence of changes in water  
52 availability and phenology for plant reproductive success and the extent to which they are mediated  
53 through changes in animal pollination by studying impacts on seed set as well as pollinator visitation.  
54 Each of these factors (water and phenology) have been investigated separately, but how they act in  
55 concert is little known.

56  
57 Phenological shifts among plants and their pollinators can affect plant reproductive success through  
58 the mechanism of seasonal changes in the pollinator visitation rate and the community of potential  
59 pollinators that visit plants (Parsche et al. 2011; Rafferty and Ives 2012). While reduced pollinator  
60 visitation rates are predicted to result in insufficient pollen deposition, changes in the community of  
61 pollinators may increase or decrease pollination success via changes in pollinator effectiveness  
62 (Bruckman and Campbell 2014). Because plants in the same community may not respond in the same  
63 way to environmental changes (CaraDonna et al. 2014), species-level phenological shifts can also  
64 impact the relative abundances of hetero- and conspecific co-flowering plants, altering pollinator  
65 visitation rates (Lázaro et al. 2009; Lázaro and Totland 2010) and the types of pollinators that visit a  
66 plant (Moeller 2005; Mitchell et al. 2009). Changes in pollinator visitation due to experimental  
67 manipulation of flowering phenology are known from several systems (Campbell 1985; Parsche et al.  
68 2011; Rafferty and Ives 2012; Gezon et al. 2016; Eisen et al. 2019).

69  
70 Altered precipitation patterns and changes in temperature are expected to have direct physiological  
71 effects on plants and insect pollinators, which can affect reproductive success through changes in  
72 resource availability for developing offspring. Importantly, changes in water availability can also  
73 affect pollination by altering the capacity of plants to produce a floral display that is attractive to  
74 pollinators, e.g., by changing flower number, size, or reward (Herrera 1995; Galen 2000; Carroll *et*  
75 *al.* 2001; Mal and Lovett-Doust 2005; Caruso 2006; Strauss and Whittall 2006; Burkle and Irwin  
76 2009; Gorden and Adler 2013; Gallagher and Campbell 2017; Suni et al. 2020). Changes in water  
77 availability during the growing season alters the capacity of plants to maintain turgor while  
78 transpiring water during photosynthesis, and also impacts their ability to uptake nutrients by affecting  
79 plant-microbial interactions and mass flow of nutrients in the soil (Galen et al. 1999; Caruso et al.  
80 2005; Burkle and Irwin 2009; Berdanier and Klein 2011; Barber and Soper Gorden 2014). As a  
81 consequence, changes in water availability can affect the ability of plants to attract pollinators  
82 through changes in the emission and composition of floral volatiles (Burkle and Runyon 2016), the  
83 volume and composition of nectar and pollen rewards (Zimmerman and Pyke 1988; Carroll et al.  
84 2001; Nicolson et al. 2007; Burkle and Irwin 2009; Halpern et al. 2010; Waser and Price 2016), and  
85 the overall size of the floral display. These floral responses to experimental changes in water  
86 availability have been shown to impact pollinator visitation in several plant species (Burkle and  
87 Runyon 2016; Glennly et al. 2018; Walter 2020), sometimes in non-linear ways (Gallagher and

88 Campbell 2017).

89

90 Whereas previous studies have experimentally manipulated either flowering phenology or water  
 91 availability and measured impacts on pollinator visitation, these two types of manipulations have  
 92 generally been carried out in separate systems. As a result, we know little about their comparative  
 93 effects on plant reproductive success. And, although each factor can independently affect pollination,  
 94 the extent to which phenological shifts and water availability interact in their effects on pollination  
 95 and reproductive success remains unexplored. Whether the effects of water availability vary with  
 96 timing of flowering will likely depend on a variety of factors. These include seasonal changes in  
 97 pollinator abundance and whether that imposes seasonal variation in pollen limitation, the extent to  
 98 which early and late-season pollinators respond differently to water-mediated changes in floral traits,  
 99 and the extent to which plant reproductive success depends on differences in pollen limitation or  
 100 water resource availability. For example, if flower size and nectar amount have a greater influence on  
 101 pollinators that dominate late in the season than they have on those that are more common early in  
 102 the season, then water availability may have a stronger effect on visitation rate late in the season than  
 103 early in the season. In turn, that response would mean that the effect of water availability on  
 104 pollinator visitation would depend on flowering time. If, however, drought-mediated changes in  
 105 floral traits alter pollinator visitation equally through time, then pollination and seed set may decline  
 106 throughout the season to the same extent when water is limited and when water is abundant, such that  
 107 effects are additive. Changes in water availability and flowering phenology are frequently co-  
 108 occurring responses to climate change. For example, in the southern Rocky Mountains, the trend  
 109 towards reduced snowpack and early snowmelt in the spring (IPCC 2014) advances flowering time  
 110 (CaraDonna et al. 2014) and also reduces soil water in early summer (Blankinship et al. 2014), which  
 111 in turn increases water stress on plants (Sloat et al. 2015). Climate models predict a general decline in  
 112 precipitation compared to evapotranspiration in the region (Seager et al. 2012), which could  
 113 exacerbate that water stress further. It is therefore important to test the relative impacts of phenology  
 114 and water and the extent to which their effects on pollination and plant reproductive success depend  
 115 on each other. Such interactions have not yet been investigated through experimental manipulation.  
 116

117 In this study, we asked the following major questions: (1) Do changes in water availability or  
 118 differences in flowering phenology have larger effects on pollination and plant reproductive success  
 119 in the same species? and (2) Do the impacts of changes in flowering phenology on pollination and  
 120 reproductive success vary with changes in water availability? To answer these questions, we  
 121 manipulated both flowering onset and water availability to the tall-fringed bluebell, *Mertensia ciliata*  
 122 (Boraginaceae), in a factorial experiment and measured effects on pollinator visitation and female  
 123 reproductive success (i.e., seed set and seed mass). To aid in interpreting mechanisms behind changes  
 124 in visitation, we also measured floral display size and floral morphology.

## 125 2 Materials and Methods

### 126 2.1 Study System

127 Fieldwork was conducted on *Mertensia ciliata* (James ex Torr.) G. Don (Boraginaceae) in a  
 128 subalpine meadow along Rustler Gulch in Gunnison National Forest (38°59'32.68" N, 107°00'23.16"  
 129 W; 3,009 m.a.s.l.) located 4.3 km from the Rocky Mountain Biological Laboratory (RMBL) in  
 130 Gothic, Gunnison County, Colorado, USA. Between 1973-2006, mean spring (April-June)  
 131 temperatures at RMBL have increased by 2.0 °C, and the average date of spring snowmelt has  
 132 advanced by nearly two weeks (Miller-Rushing and Inouye 2009). In many subalpine systems, both  
 133 flowering phenology and summer water availability are largely driven by spring temperatures,

134 snowpack depth, and snowmelt timing (Wielgolaski and Inouye 2013). In the southern Rocky  
135 Mountains, over the next century, temperatures are expected to continue to increase, while both  
136 winter snow fall and total precipitation are expected to decrease (Overpeck and Udall 2010; Pederson  
137 et al. 2011), resulting in earlier snowmelt timing (Saunders et al. 2008) and earlier, longer dry  
138 seasons prior to mid-summer thundershowers.

139  
140 *Mertensia ciliata*, the tall-fringed bluebell, is an herbaceous, rhizomatous perennial of the subalpine  
141 and lower alpine zones of the Rocky and Sierra Nevada Mountains. Plants form compact clones of a  
142 few to several hundred flowering ramets and are commonly found along streams and in wet meadows  
143 (Pelton 1961). The flowers are pendant and tubular, expanding to a wider, lobed mouth, and are  
144 borne in dense clusters of cymes along leafy stems. Flowers are typically open for six days, with  
145 receptive stigmas throughout flowering and can produce a maximum of four one-seeded nutlets  
146 (hereafter seeds). The seeds have elaisomes and so are likely ant-dispersed.

147  
148 Pollen is usually removed within 24-48 hours of anther dehiscence by medium and long-tongued  
149 bumblebees, including *Bombus balteatus* (Dahlbom), *B. bifarius* (Cresson), *B. flavifrons* (Cresson),  
150 and *B. frigidus* (Smith) (Geber 1985; Suzuki 1994; Gallagher and Campbell 2017). *Mertensia ciliata*  
151 flowers are also visited by flies (Bombyliidae, Muscoidea, and Syrphidae) and solitary bees  
152 (Colletidae: *Colletes p. paniscus* Vier. and Megachilidae: *Osmia spp.*) (Pelton 1961; Gallagher and  
153 Campbell 2017). Although *M. ciliata* is self-compatible, seed set is dependent on insect pollination,  
154 with flowers prevented from receiving an insect visit rarely producing seeds and averaging only 8%  
155 as many seeds as those open to insect pollination (Geber 1985).

156  
157 *Mertensia ciliata* flowers from late June through early August in the subalpine meadows around  
158 RMBL. An individual plant flowers for 3 to 5 weeks (Geber 1985). As with many species in this  
159 region, *M. ciliata*'s flowering phenology is strongly correlated with the timing of snowmelt (Miller-  
160 Rushing and Inouye 2009; Wielgolaski and Inouye 2013). In fact, between 1973 and 2006, the  
161 average date of first bloom (DFB) has advanced by 3.3 days per decade (Miller-Rushing and Inouye  
162 2009). Over the same 34-year period, *M. ciliata* has become less common at lower elevations ( $\leq$   
163 2,900 m a.s.l.), and observed declines in peak floral abundance (15 fewer flowers per decade)  
164 correlate with earlier snowmelt timing (1.6 fewer flowers per day earlier snowmelt) (Miller-Rushing  
165 and Inouye 2009). In the plant communities surrounding RMBL, phenological responses to warmer  
166 spring temperatures and early snowmelt are producing a longer mid-season dip in floral abundance  
167 (Aldridge et al. 2011), which may impact pollinator abundance and pollination success of summer-  
168 blooming plants like *M. ciliata*. Over a somewhat longer record of 39 years, its date of peak bloom  
169 advanced by an amount (1.6 days per decade) fairly similar to the average advance in peak bloom  
170 near RMBL (2.5 days per decade; CaraDonna et al. 2014). With some species advancing quickly and  
171 others less so, *M. ciliata* will overlap more with some species and less with others in the future.  
172 Overall, these patterns suggest that changes in spring temperatures and snowmelt timing may alter *M.*  
173 *ciliata* pollination and reproductive success through changes in water availability and flowering  
174 phenology.

175  
176 Previous field experiments with *M. ciliata* revealed that both changes in water availability and  
177 changes in flowering phenology can independently affect pollination success in this species. Floral  
178 responses to experimental changes in water availability altered pollinator visitation rates, but the  
179 effects were non-linear, with visitation peaking at intermediate water levels (Gallagher and Campbell  
180 2017). In a separate experiment, shifts in timing of flowering onset affected the pollination of plants,  
181 such that early-flowering plants received a higher frequency and diversity of pollinator visitors than  
182 did late-flowering plants. Those pollinators that visited late-flowering plants were more effective

183 pollinators than their early-season counterparts, resulting in no net difference in seed set between  
 184 early- and late-flowering plants (Gallagher and Campbell 2020). In this system we expected that  
 185 water availability would have less effect on pollinator visitation early in the season, when pollinators  
 186 are abundant and diverse, allowing visitation to all size flowers and perhaps less choosy visitors due  
 187 to competition for nectar. But later in the season, when visits are dominated by worker bumblebees,  
 188 including *B. flavifrons* which shows preferences based on flower size (Campbell et al. 2014), we  
 189 predicted that differences in water-mediated floral traits (e.g., size, nectar) would more likely impact  
 190 pollinator visitation rates.  
 191

## 192 2.2 Experimental design

193 To test the extent to which effects of phenology on pollination and reproductive success vary with  
 194 co-occurring changes in water availability, we manipulated both flowering onset and water  
 195 availability in a factorial experiment using potted *M. ciliata* plants. Between 2012 and 2015, 120  
 196 plants were collected from a large *M. ciliata* population in Rustler Gulch and potted using native soil  
 197 in 2-gallon plastic pots (actual volume: 1.593 Gallons, Nursery Supplies, Inc.). A portion of the  
 198 plants were used for other studies in 2013 and 2015, but otherwise remained in trenches and  
 199 overwintered in the ground under snow at RMBL until their use for this experiment. In 2016, potted  
 200 plants were randomly assigned to one of three water treatments, dry, average, and wet. To inhibit  
 201 flowering, potted plants were moved to Schofield Pass (39°00'54.98" N, 107° 2'49.40" W; 3,263  
 202 m.a.s.l.) in early June, where they were placed in a shaded snowbank under a mesh shade-shelter.  
 203 Each week, 30 randomly selected plants, 10 per water treatment, were moved back to RMBL, where  
 204 the higher light and warmer temperatures at low elevation induced them to flower at the  
 205 experimentally chosen time (typically within 5-7 days after being moved to RMBL).  
 206

207 Each week, thirty plants in their first week of flowering (10 per water treatment) were moved from  
 208 RMBL to a meadow near the original source population in Rustler Gulch. Plants were arranged 30  
 209 cm apart into five randomized arrays of six plants, set 30 cm apart in a single line, with 2 m between  
 210 arrays. Each array included two plants of each water treatment. In week four, 12 plants stopped  
 211 flowering mid-week and therefore we re-randomized the plants that had flowers remaining into three  
 212 new arrays with six plants each. Where appropriate, we calculated the mean values per array of week  
 213 four plants before and after the plants were rearranged, and then averaged those two values for each  
 214 plant. To create distinct experimental populations, arrays were located 50 meters away from  
 215 unmanipulated *M. ciliata* populations. Plants remained in the arrays for one week before being  
 216 replaced by the next group. This period was the only time when their flowers were available for  
 217 pollination. A total of 114 plants flowered and were included in the experiment, for a total of four  
 218 phenology treatment groups spanning four weeks (June 20 — July 17).  
 219

220 The water manipulations were maintained through the growing season (June 10 – August 1) and  
 221 discontinued once seeds were collected. We watered pots manually with watering cans slowly and  
 222 evenly to avoid pooling, in the mid to late afternoon to coincide with the timing of July  
 223 thundershowers. Throughout the experiment, we measured soil moisture as volumetric water content  
 224 (VWC) every third day using a 12 cm Campbell Scientific “HydroSense” probe inserted into the  
 225 center of each pot (if done on the day of watering, always before applying water). We used these  
 226 VWC measurements to maintain soil moistures within the pots at levels that correspond with VWC  
 227 levels in a previous water manipulation experiment with *M. ciliata* (Gallagher and Campbell 2017)  
 228 performed at a nearby site with similar soil. In that study, plants within naturally occurring  
 229 populations received either 50% reduction in precipitation (hereafter “dry”), additional rainfall equal

230 to the historic average rainfall during July from 1990 to 2009 (hereafter “wet”; based on long-term  
 231 data reported in Campbell and Wendlandt 2013), or ambient conditions (“control”). In that previous  
 232 field study, VWC had averaged 9.4%, 11.7%, and 15.4%, respectively. In the end, we watered wet  
 233 pots daily, control pots every other day, and dry pots every third day, achieving  $10.4 \pm 0.4\%$ ,  $12.7 \pm$   
 234  $0.4\%$ , and  $17.5 \pm 0.6\%$  average VWC in the soil for dry, control, and wet pots respectively (Mean  $\pm$   
 235 SEM). Whereas these values for VWC resembled those for in situ plants in our earlier study, the  
 236 measured values may slightly underestimate actual average soil moisture depending on the  
 237 relationship between soil moisture and time between watering and measurement, as well as the  
 238 impact of variable rain events. Average VWC values for plots were analyzed with a linear mixed  
 239 model with the main and interactive effects of water treatment and phenology week as fixed effects,  
 240 and array nested in phenology week as a random effect. The resultant gradient in soil moisture did  
 241 not vary significantly among phenology weeks (Water:  $\chi^2_2 = 106.3$ ,  $P < 0.0001$ , Phenology:  $\chi^2_3 = 5.2$ ,  
 242  $P = 0.2$ , Water  $\times$  Phenology:  $\chi^2_6 = 1.44$ ,  $P = 0.96$ , Figure 1A).

243  
 244 Note that we manipulated both factors within a realistic range of natural variation. The four  
 245 phenology weeks corresponded closely with the range of flowering time onset in nearby natural  
 246 populations (Gallagher and Campbell 2020). The water treatments of adding 100% or subtracting  
 247 50% of average rainfall fell within the range of summer precipitation over the past few decades  
 248 (Campbell and Wendlandt 2013).

249

### 250 **2.3 Measurements of reproductive traits, pollinator visitation, and reproduction**

251 For each phenology week, we measured reproductive traits, including total abundance of flowers  
 252 open during the phenology week, corolla size, and nectar volume and sugar concentration. We  
 253 measured corolla width at the opening of the tube and corolla length from the base of the calyx to a  
 254 randomly chosen corolla lobe for an average of  $4.4 \pm 0.4$  flowers per plant. Corollas were measured  
 255 on the second or third day of each phenology week. All flowers within an array were measured at the  
 256 same time, and the order in which arrays were measured was randomized each week. At the end of  
 257 each week, after pollination observations were complete, individual flowers in each phenology group  
 258 were labeled and all flowering stems were bagged with fine mesh jewelry bags (Uline, Pleasant  
 259 Prairie, WI, USA) to prevent further pollination and loss of seeds, and to provide a count of the total  
 260 number of flowers open during that phenology week. For plants with flowers remaining at the end of  
 261 each week, we measured nectar volume and percent sugar concentration 48 hours after plants were  
 262 bagged (N = 71 plants). For an average of  $2.6 \pm 0.2$  flowers per plant, we measured nectar volume  
 263 using 5  $\mu$ l microcapillary tubes (Kearns and Inouye 1993) and percent sugar concentration using a  
 264 handheld nectar refractometer (Bellingham + Stanley Ltd., Basingstoke, Hants, UK). No flowers  
 265 remained for nectar measurements in week four; therefore, we only include nectar data from  
 266 phenology weeks 1-3 in our analyses. To select which flowers to measure, we marked the calyx of  
 267 buds to track when flowers opened and then chose at random among available flowers of the same  
 268 age. For each floral trait, we calculated the mean trait value of each potted plant, to be used as the  
 269 response variable in our analyses.

270

271 Plants in each phenology group were open to pollination for one week. During that time, we  
 272 conducted pollinator observations and tracked pollinator identity and the number of flowers visited  
 273 during multiple 30-minute observation periods between the hours of 9:00 and 16:00. At the  
 274 beginning of each observation period, we counted the number of open flowers per potted plant. We  
 275 calculated mean pollinator visitation rate per plant as (total number of flowers visited) / (number of  
 276 flowers available per hour of observations) averaged across the phenology week. Visitors were



277 counted as pollinators if they crawled inside the flower corolla. For each 150-minute round of  
 278 observations to the five arrays we randomized the order of observations among arrays.  
 279 In total, we completed 25 hours of pollinator observations per phenology group.

280  
 281 During 100 hours of pollinator observations to six plants at a time, we observed 340 floral visitors to  
 282 experimental plants. The most common pollinators, bumblebees (*Bombus spp.*) and solitary bees  
 283 (*Osmia spp.*), accounted for 92.6% of floral visitors, with flies (Muscoidea and Syrphidae 7.1%) and  
 284 a moth (0.3%) making up the rest. We excluded the moth from our analyses. For a metric of  
 285 pollinator type, for each potted plant we calculated mean percent of visitors that were bumblebees as  
 286  $(100\% \times \text{number of visitors that were bumblebees}) / (\text{total number of flower visitors per hour of}$   
 287  $\text{observation})$  averaged across the phenology week.

288  
 289 All plants remained in the field until seeds were collected to standardize conditions after pollination  
 290 exposure. We counted the total number of seeds produced per marked flower (as described by Forrest  
 291 and Thomson 2010). We calculated the average seeds per flower for each potted plant as (number of  
 292 mature seeds / number of flowers). Mature seeds from tagged flowers were collected in coin  
 293 envelopes and transported to the University of California, Irvine to be weighed. We calculated mean  
 294 seed mass for each plant as (mass of collected seeds / number of collected seeds). Seed mass included  
 295 the mass of the elaiosome. All field procedures followed RMBL permitting guidelines.  
 296

## 297 2.4 Statistical analysis

298 We tested whether experimental changes in flowering phenology and water availability had  
 299 interactive effects on floral traits, pollinator visitation and percent of visitors that were bumblebees  
 300 (i.e., pollinator type), and seed set. For each response variable, we tested whether the effects of  
 301 flowering timing varied with changes in water availability using a model with main and interactive  
 302 effects of water treatment and phenology week as fixed effects, and array nested in phenology week  
 303 as a random effect. Both water and phenology treatments were treated as factors.

304  
 305 Residuals of the analyses for flowers per array, corolla width and length, nectar concentration, seed  
 306 set, and seed mass were all approximately normally distributed, and we used linear mixed model  
 307 (LMM) analyses to test whether changes in those traits resulting from differences in water  
 308 availability differed among phenology weeks. We used generalized linear mixed models (GLMM)  
 309 with a Poisson distribution (log link) to test for main and interactive effects of phenology week and  
 310 water treatment on floral abundance per plant (i.e., flowers per plant) and nectar volume, the latter  
 311 after multiplying by 100 and rounding to an integer.

312  
 313 We first attempted to test the fixed effects of phenology week and water treatment and the random  
 314 effect of array on pollinator visitation using zero-inflated mixed models due to excess zeroes.  
 315 Employing the *glmmTMB* package in R (Brooks et al. 2017), models using conditional distributions  
 316 of Poisson or truncated generalized Poisson (on integer data) failed to converge even when the  
 317 random effect of array was removed from the zero-inflated portion to reduce over-parameterization,  
 318 and negative binomial distributions gave poor fits judging by Q-Q plots. We therefore ran separate  
 319 analyses of the probability that a plant would receive a visit and the visitation rate to plants that  
 320 received at least one visit. These analyses were performed using Proc Glimmix in SAS (v 9.3; SAS  
 321 Institute, Inc., Cary, NC, USA). We tested whether the likelihood of receiving a pollinator visit  
 322 differed among treatments in a GLMM with a binomial distribution and logit link. For plants  
 323 receiving at least one visit, we tested the effects of water treatment and phenology week on pollinator

324 visitation rate using a log-normal distribution, which provided a better fit than a Poisson, negative  
 325 binomial, or normal distribution, based on a low value for Aikake's information criterion (AIC), a  
 326 low ratio of Pearson chi-square to df, and lack of pattern to a plot of residuals versus predicted  
 327 values.

328

329 For the analysis of pollinator type, we used the mean percent of visitors that were bumblebees for the  
 330 two plants in each array that belonged to the same water treatment, as the response variable in our  
 331 analyses. This averaging eliminated the need to designate array nested in phenology week as a  
 332 random effect and allowed us to test the effects of phenology week and water treatment on pollinator  
 333 type using a model with normally distributed residuals, which provided a good fit based on a plot of  
 334 residuals versus predicted values.

335

336 The floral abundance among arrays during the first three weeks ranged from 15 to 71, with a mean of  
 337  $44.26 \pm 1.9$  (Mean  $\pm$  SEM) flowers per array (Figure 1B). The floral abundance per array for week  
 338 four plants, however, averaged  $15 \pm 1.3$  flowers and was significantly lower than in the previous  
 339 three weeks ( $\chi^2_3 = 29.47$ ,  $P < 0.0001$ ). We assessed whether these differences in floral abundance  
 340 influenced pollination by repeating the analyses on pollination with floral abundance per array added  
 341 to each of the models.

342

343 Seed set is expected to be positively correlated with both pollinator visitation rate (Engel and Irwin  
 344 2003; Sahli and Conner 2006; Sahli and Conner 2007) and soil moisture (Burkle and Irwin 2009;  
 345 Berdanier and Klein 2011). To test whether seed set increased with pollinator visitation rate, and  
 346 whether the influence of pollinator visitation rate on seed set differed among water treatments, we  
 347 performed a second analysis on seed set, adding mean pollinator visitation rate and the interaction  
 348 between mean pollinator visitation rate and water treatment to the model. Because the interaction  
 349 between mean pollinator visitation rate and water treatment was not significant ( $P > 0.05$ ), we reran  
 350 the model without the interaction to simplify interpretation.

351

352 Analyses were conducted using R (R Core Team 2016), except where noted otherwise. We used the  
 353 *lme4* package in R (Bates et al. 2015) for all GLMM and LMM analyses and tested the models with  
 354 type III Wald likelihood ratio tests using the *car* package in R (Fox and Weisberg 2011). In the event  
 355 of significant main effects, we performed Tukey post hoc comparisons across the levels of each  
 356 effect using the *lsmeans* package (Lenth 2016). For analyses of pollinator visitation, we used Proc  
 357 Genmod and Proc Glimmix (when a random effect was included) in SAS (v 9.3; SAS Institute, Inc.,  
 358 Cary, NC, USA).

### 359 **3 Results**

#### 360 **3.1 Effects on reproductive traits**

361 Water availability influenced corolla and nectar traits the same way regardless of phenology week ( $P$   
 362  $> 0.05$  for phenology  $\times$  water interaction in all cases, Table 1). The dry treatment reduced corolla  
 363 length, corolla width, and nectar volume compared to the other water treatments (Tukey pairwise  
 364 comparison among water treatments,  $P < 0.05$ , Figure 2A, B, C). Late season plants (week 4) also  
 365 produced flowers that were  $1.24 \pm 0.01$  mm shorter than those in week two (Tukey pairwise  
 366 comparison among phenology weeks,  $P < 0.01$ ), but corolla width and nectar volume did not differ  
 367 among phenology weeks.

368

369 The number of flowers that plants produced (i.e., floral abundance per plant) differed among

370 phenology weeks, and that effect of phenology week differed among water treatments (Figure 3), as  
 371 illustrated by a significant interaction ( $P < 0.001$ , Table 1). Floral abundance peaked in week two,  
 372 with plants producing an average of 52% more flowers than plants in other weeks. Week four plants  
 373 produced fewer flowers than those in the other phenology weeks (Tukey pairwise comparison among  
 374 phenology weeks,  $P < 0.001$ , Figure 3). Control plants made 65% more flowers than plants in the dry  
 375 treatment in week one, but dry plants made 61% more than control plants in week four (Tukey  
 376 pairwise comparison of water x phenology interaction,  $P < 0.001$ , Figure 3).  
 377

### 378 3.2 Effects on pollinator visitation

379 The probability that a plant received a pollinator visit differed among phenology weeks and water  
 380 treatments, but these effects were approximately additive (Table 2, Figure 4A). Between week two  
 381 and week four, the likelihood of receiving a visit decreased by an average of 61% among plants in all  
 382 water treatments (Figure 4A). Across all weeks, plants in the wet treatment were 11% more likely to  
 383 receive a visit than plants in the other water treatments (Figure 4A). In a separate model that also  
 384 included floral abundance per array, the probability that a plant received a pollinator visit increased  
 385 with the number of flowers in the array ( $F_{1,86} = 5.8$ ,  $P = 0.02$ ), but in this model, the effects of  
 386 phenology week and water treatment were no longer significant ( $P > 0.7$ ). The decline in the  
 387 probability of receiving a visit after week two (Figure 4A) coincided with the decline in floral  
 388 abundance in the arrays (Figure 1B). These data suggest that pollinators were attracted to arrays  
 389 based on the overall floral abundance, which differed among phenology weeks ( $\chi^2_3 = 29.47$ ,  $P <$   
 390  $0.0001$ ).  
 391

392 Once a pollinator visited a plant in the arrays, floral abundance no longer had a significant influence  
 393 on pollinator visitation rates ( $F_{1,52} = 0.96$ ,  $P = 0.3$ ). Among those plants that received visits, timing of  
 394 flowering and water treatment had significant, additive effects on pollinator visitation rates (Table 2,  
 395 Figure 4B). Visitation rates decreased by an average of 77% after the first phenology week for plants  
 396 in all water treatments (Tukey pairwise comparison among phenology weeks,  $P < 0.001$ ), and  
 397 remained consistently low until the final week, when dry treatment plants alone experienced a non-  
 398 significant resurgence in pollinator visits (Table 2). On average across all four weeks, plants in the  
 399 wet treatment were visited at a 40% higher rate than those in the control treatment (Tukey pairwise  
 400 comparison among water treatments,  $P < 0.003$ ). Visitation to dry plants had higher variance, which  
 401 meant that differences in visitation between plants in dry and wet treatments could only be detected  
 402 in week three (Tukey pairwise comparison among water treatments in a given week,  $P < 0.05$ ).  
 403

404 Water availability and flowering time had a significant interactive effect on the types of pollinator  
 405 visitors, as measured by percent bumblebees (Table 1). Over the four phenology weeks, the  
 406 composition of pollinator visitors generally shifted from a diverse array of solitary bees, flies and  
 407 bumblebees to 100% bumblebees among all water treatments, except for dry plants which received a  
 408 resurgence of visits by flies and solitary bees in week four and to a lesser extent in week 2 (Table 1,  
 409 Figure 4C). We separated contributions to the interaction by re-running the model with a single fixed  
 410 factor with 12 levels corresponding to the combinations of weeks and water availability, and using  
 411 the contrast statement in Proc Genmod to specify individual contrasts. Differences between week 1  
 412 and week 2 and 4 were smaller for the dry treatment than for the other treatments ( $P < 0.05$ ; details in  
 413 legend to Figure 4C). The percent of pollinator visitors that were bumblebees was not significantly  
 414 influenced by the number of flowers available in the array ( $\chi^2 = 1.01$ ,  $P = 0.3$ ).  
 415

### 416 3.3 Effects on seed set

417 In a model with fixed factors of flowering phenology and water availability and a random effect of  
418 array, both fixed factors influenced *M. ciliata* reproductive success, however, there was no  
419 significant interaction between the two factors for either seed set or seed mass (Table 1). Flowering  
420 phenology affected both the number of seeds produced per flower as well as seed mass (Table 1).  
421 Over four weeks, seed set decreased by an average of 15% (Figure 5A). While this decline in seed set  
422 coincided with the decline in pollinator visitation rate (Figure 4B), the relationship of seed set to  
423 visitation rate was not significant ( $\chi^2 = 3.14$ ,  $P = 0.08$ ). Seeds from week four plants were  $0.54 \pm$   
424  $0.09$  mg heavier than those produced by plants in the previous two weeks (Tukey pairwise comparison  
425 among phenology weeks,  $P < 0.05$ , Figure 5B). Water availability had a significant, positive effect on  
426 both metrics of *Mertensia ciliata* reproductive success (Table 1). Plants in the wet treatment  
427 produced an average of 40% more seeds per flower, which were an average of  $0.74 \pm 0.02$  mg  
428 heavier than seeds produced by plants in the dry treatment (Tukey pairwise comparison among water  
429 treatments,  $P < 0.001$ , Figure 5).

## 430 4 Discussion

431 Changes in flowering phenology and water availability for plants are two likely co-occurring  
432 responses to anthropogenic global change, but have been rarely, if ever, manipulated together. By  
433 manipulating flowering onset and water availability in factorial combination for the same subalpine  
434 plant species, we generated two major results. First, whereas flowering onset had a stronger impact  
435 on pollinator visitation than did water availability, the reverse was true for seed production and seed  
436 mass in this system. Second, these two factors had additive impacts on major fitness components  
437 such as seed production, even though an interaction was observed for composition of floral visitors.  
438 One caveat is that our manipulation of phenology focused on a specific aspect, the timing of onset of  
439 blooming, and we measured visitation only during the first week of bloom for each plant. It is  
440 possible that other aspects of flowering phenology would have impacts different from those observed  
441 here.

442

### 443 4.1 Comparative impacts of phenology and water availability on pollinator visitation

444 By manipulating both factors together, we found that flowering onset time had a stronger average  
445 effect on pollinator visitation, while water availability more strongly affected seed production. The  
446 impact on both the probability of a plant receiving a visit and the per-flower visitation rate was  
447 greater for the manipulation of flowering onset, even though increased water availability had strong  
448 effects on floral traits. This result suggests that the frequently observed impacts of water availability  
449 on floral traits might not always translate into substantial effects on pollinator visitation. In the few  
450 other systems that have investigated this question, drought reduced pollinator visitation in three of  
451 five species (Burkle and Runyon 2016; Glenny et al. 2018; Rering et al. 2020).

452

453 In *M. ciliata* the likelihood that a plant would receive a pollinator visit declined over the course of  
454 four weeks and was influenced by the July decline in the number of flowers per plant, as also seen in  
455 our previous work (Gallagher and Campbell 2020). This positive relationship between the density  
456 and diversity of floral resources and flower visitor activity is common (Rathcke 1983; Laverly 1992;  
457 Johnson et al. 2003; Ghazoul 2006; Feldman 2008; Hegland and Boeke 2006). The decline in visits,  
458 however, also coincided with an increase in floral abundance and diversity throughout the  
459 surrounding plant community (Gallagher and Campbell 2020). Although *Mertensia ciliata* is a  
460 summer-blooming subalpine perennial, at our study site, its onset of flowering begins about a week

461 earlier than most other summer-blooming species (Gallagher and Campbell 2020). It is possible that  
 462 *M. ciliata* receives more frequent pollinator visits early in the season, because it is one of the few  
 463 floral resources available at that time. As floral abundance increases in the entire community,  
 464 pollinators may become more selective when visiting different plant species (Schmitt 1983; Lázaro et  
 465 al. 2013), which may account not only for the decline in the number of plants in our arrays that  
 466 received visits, but also the change in visitation rates and assemblages of pollinators once they were  
 467 in the arrays. Among plants that received at least one visit, pollinator visitation rates also declined  
 468 greatly over the course of the flowering season, although this change in per flower visit rate was not  
 469 influenced by the number of flowers in the array. Water-mediated changes in pollinator visitation  
 470 were not only less pronounced than those due to flowering onset, they also coincided with  
 471 simultaneous changes in individual floral traits, including corolla width and nectar production. In an  
 472 earlier study in this system, pollinator visitation peaked at an intermediate value for both corolla  
 473 length and corolla width at the site most similar in elevation to the current one (Gallagher and  
 474 Campbell 2017).  
 475

#### 476 **4.2 Comparative effects of phenology and water on seed set and mass**

477 In contrast to pollinator visitation, both seed set and seed mass were more strongly affected by water  
 478 availability than by flowering time. Seed set declined over the four weeks, with fewer, heavier seeds  
 479 in week four compared to all other weeks. This decline in seed set over the four weeks was not well  
 480 explained by the coincident decrease in pollinator visitation rate, however. In fact, plants in the wet  
 481 treatment made significantly more seeds than dry plants, even in week 4 when dry plants received  
 482 more visits than wet plants. Examinations of pollen receipt from single visits to virgin flowers  
 483 revealed that flowers likely require very few visits to receive enough pollen to develop all four ovules  
 484 in each *M. ciliata* flower (Gallagher and Campbell 2020). In a previous study of this system, seed set  
 485 depended on pollinator visitation only when those rates were low, with seed set leveling off strongly  
 486 at higher visitation levels (Gallagher and Campbell 2017). Plants in the current study experienced  
 487 higher pollinator visitation rates than those in our previous study, which may explain why we did not  
 488 detect an effect of pollinator visitation on seed set. We maintained similar soil moisture levels across  
 489 treatments in both experiments, which resulted in similar effects on floral attractants. The differences  
 490 in pollinator visitation rates among years, therefore, can likely be attributed to natural variation in  
 491 pollinator availability across years and sites.  
 492

493 Another potential explanation for the decrease in seed set over the four weeks is differences in  
 494 pollinator effectiveness, that is the capacity of different pollinators to deposit sufficient, compatible  
 495 pollen on the stigmas of flowers (Ne'eman et al. 2010). Single-visit pollinator effectiveness studies  
 496 revealed differences in the amount of pollen deposited and seed set among the various pollinator taxa  
 497 that visit *M. ciliata*. Bumblebee and solitary bee visitors contribute more per visit to the reproductive  
 498 success of plants, than do flies (Gallagher and Campbell 2020). Differences in effectiveness cannot  
 499 however, explain why seed set of wet plants was higher than for dry plants in week one, as the  
 500 proportion of total visits by bumblebees, solitary bees, and flies for plants in wet and dry treatments  
 501 were nearly equal (Figure 4C). This pattern further supports the hypothesis that water availability,  
 502 and not pollinator visitation or composition, has a larger effect on seed set in *M. ciliata*.  
 503

504 It is possible that changes in water availability may have an outsized effect on seed set in this system  
 505 because plants are not highly pollen-limited. In systems where plants are more pollen-limited, and the  
 506 majority of tested plant species show some pollen-limitation (Knight et al. 2005), changes in  
 507 pollinator visitation and pollinator effectiveness can have substantial effects on seed set. For

508 example, experimental shifts in flowering phenology of the spring-blooming, subalpine herb,  
509 *Claytonia lanceolata*, altered both the assemblage and visitation rates of pollinators with the result  
510 that late-flowering plants experienced higher levels of pollen-limitation and lower seed set (Gezon et  
511 al. 2016). Thus, the potential for changes in flowering phenology to affect seed set may increase in  
512 systems that are more pollen limited.

513  
514 Not only seed set but also seed mass was enhanced by increasing water availability. Seed mass  
515 included the elaiosome in our study, and although ant-dispersal of seeds has not been studied in *M.*  
516 *ciliata*, the ant *Formica* sp. removes seeds from its congener *M. fusiformis* in similar locales  
517 (Turnbull et al. 1983). In some other species with elaiosomes, the chance that ants remove seeds for  
518 dispersal is greater for larger seeds (Mark and Olesen 1996). These observations suggest the  
519 hypothesis that drought associated with climate change may reduce the chance of seed dispersal for  
520 *M. ciliata*. To test that hypothesis and others about combined effects of pollination and water  
521 availability on plant reproductive success, we need more studies of impacts on the whole pathway  
522 from floral traits to pollinator visitation to seed production to seed dispersal and seedling  
523 establishment.

524

### 525 **4.3 Interactions between flowering time and water availability**

526 In this system, effects of phenology and water availability on total pollinator visitation were additive,  
527 but the percent of visitors that were bumblebees did show an interaction. Plants in the dry treatment  
528 experienced a resurgence in relative visitation by small insects late in the season (week 4) while  
529 plants in other water treatments received visits during week 4 only by bumblebees. This resurgence  
530 in visits by small insects was unexpected, as in a previous study of phenology in which water was not  
531 manipulated, such late-blooming plants had only been visited by worker bumblebees (Gallagher and  
532 Campbell 2017). Flowers declined monotonically in corolla length over the season, suggesting that a  
533 generalist plant, like *M. ciliata*, may be able to attract pollinators of different taxa or castes, both  
534 when flowers are small or large.

535

536 Despite the interaction in effects on visitor assemblage, we saw no interaction in the effects of  
537 phenology and water availability on either total pollinator visitation or seed set. We had predicted  
538 that water availability would have less effect on pollinator visitation for plants that bloom early in the  
539 season when a diverse array of pollinators are available, whereas later in the season when visits are  
540 dominated by worker bumblebees, water-mediated changes in floral traits would have a stronger  
541 effect on pollinator visitation rate. Instead, dry plants with short corollas proved unexpectedly  
542 attractive to small insects at the end of the season, so that their visitation was relatively high, just as it  
543 had been early in the season, compared to well-watered plants that were visited only by bumblebees.  
544 Regardless of the interactive effect on visitor assemblage, we detected no interaction in the effect on  
545 total visitation. The weak or non-existent interactions on seed set and seed mass further suggest that  
546 impacts of climate change on plant reproduction may often be predictable through separate studies of  
547 flowering time and water availability. At the same time, both phenology and direct effects of abiotic  
548 factors are potentially critical factors in climate change, and so neither should be assumed more  
549 important to pollination-mediated changes in reproduction. Since we didn't detect an interaction on  
550 seed set, it is worth considering the potential for situations where such an interaction might occur.  
551 One example would be in a generalized pollinator system in which pollinator type changes  
552 systematically across the season, such that one pollinator type is available only early in the season  
553 and a different one, with different responses to water-mediated floral traits, is available only late. In  
554 many cases, different pollinators of the same plant species differ in visitation responses to flower

555 size, as seen for bees versus flies (Galen et al. 1987; Strauss et al. 1996), and bees versus butterflies  
 556 and moths (Thompson 2001), making this mechanism plausible although not yet demonstrated.  
 557 Another potential mechanism is a change in the flowering or pollinator community over the season,  
 558 causing a pollinator to change its preference for large versus small flowers seasonally. Seasonal  
 559 changes in competition with other pollinators can influence a bumblebee's use of plant species  
 560 (Shiribata and Kudo 2020). Whether that extends to changes in trait preferences within a natural plant  
 561 population is unknown, but competition with other pollinators sometimes affects trait preferences of  
 562 hummingbirds (Temeles et al. 2016). Finally, the extent of pollen limitation could vary between  
 563 plants that bloom early versus those that bloom late (Campbell 1985; Gezon et al. 2016), potentially  
 564 altering the response of seed production to water availability.

565  
 566 Interactive effects on plant-animal interactions between any two factors likely to change with climate  
 567 change are not often studied. We are unaware of other such studies involving plant phenology and  
 568 water, and results are mixed for combinations of other factors. Herbivory and warming had non-  
 569 additive effects on seed mass of *Oenothera biennis* (Lemoine et al. 2017), as did herbivory and  
 570 drought for yield in *Vicia minor* (Raderschall et al. 2020) while having only additive effects on seed  
 571 production in *Centaurea stoebe* (Ortega et al. 2012). To consider joint effects of multiple species  
 572 interactions, such as pollination and seed dispersal, it will be especially important to consider  
 573 multiple aspects of environmental change because each species interaction could be more responsive  
 574 to a different abiotic factor.  
 575

#### 576 4.4 Implications for climate change

577 Pollinator responses to both phenology and water availability are likely to differ depending on the  
 578 magnitude of changes in those factors. We manipulated both factors within a realistic range of natural  
 579 variation over the past few decades, but future climate change will likely eventually push conditions  
 580 outside of the historical envelope. Furthermore, climate change will likely impact other plant species  
 581 and pollinators in ways that we did not manipulate in this study. Nevertheless, we can make an  
 582 estimate of how flowering onset and water availability to *M. ciliata* in the absence of other impacts  
 583 might affect pollinator visitation under near-term climate change. Note that we are not here  
 584 attempting to predict the integrated effects of climate change, which could also depend on other  
 585 factors such as change in phenologies of other plant species. Furthermore, we are assuming that  
 586 pollinators would respond to changes to conditions for *M. ciliata* over a wide spatial range in the  
 587 same way that they responded to a small set of potted plants near a larger unmanipulated population.  
 588 That assumption may not hold, as the *Bombus* spp. and *Osmia* spp. that were common pollinators  
 589 typically forage over a range of nearly a km (Greenleaf et al. 2007). In that simplified scenario with  
 590 an absence of changes in pollinators, the difference between week 2 control plants and week 1 dry  
 591 plants in our experiment would approximate the expected effect of two decades of climate change,  
 592 for the following reasons. Week 2 corresponds approximately with the current peak flowering time  
 593 (Gallagher and Campbell 2020). Since the onset of first bloom for *M. ciliata* has advanced by 3.3  
 594 days per decade over the past three decades (Miller-Rushing and Inouye 2009), week 1 corresponds  
 595 to expected peak blooming in two decades. At the same time, climate projections for the Colorado  
 596 River headlands, which includes this location, indicate that surface water will decline by 0 to 0.1  
 597 mm/day per decade in the near future (Seager et al. 2012), which is comparable over two decades to  
 598 the difference of 0.175 mm/day between our dry and control treatments. Climate change over two  
 599 decades may then approximate the shift from week 2 control plants to week 1 dry plants, implying a  
 600 short-term increase in the probability of receiving a pollinator visit and rate of pollinator visitation  
 601 and little change in either seed set or seed mass, in the absence of changes in other factors.

602  
603 For a summer-blooming, generalist perennial, like *M. ciliata*, there may be a significant benefit to  
604 flowering early in terms of pollination success, but an increased risk that reproductive success may  
605 be affected by changes in water availability, depending on the severity of the drought. Spring-  
606 blooming plants can face a similar trade-off when flowering early, between increased pollinator  
607 visitation and an increased risk of exposure to late spring storms or frost events (Inouye 2008; Gezon  
608 et al. 2016). With further climate change and earlier snowmelt, not only would *M. ciliata* plants  
609 flower earlier (Miller-Rushing and Inouye 2009), but those early-flowering plants may be more likely  
610 to have shorter, smaller corollas with less nectar due to lower water availability in the soil prior to  
611 mid-summer thundershowers (Blankinship et al. 2014).

612  
613 The impact of climate change will ultimately depend on how it influences other species that interact  
614 with *M. ciliata*. We only manipulated conditions for the focal plant species in our study and not for  
615 other plant species in the community, nor for the pollinators. In our study, pollinators had the option  
616 to visit flowers of other species that were not water limited. But if the entire region were to undergo  
617 early snowmelt or drought, floral traits throughout the community might be affected, which may  
618 drive pollinators to make different choices about which plant species to visit. Of the 10 other plant  
619 species reported to overlap in blooming time and share pollinators with *M. ciliata* at our study site  
620 (Gallagher and Campbell 2020), four species are expected to move towards more overlap in  
621 flowering time with *M. ciliata* over the short-term and six species towards less overlap  
622 (Supplementary Table S1). Because of this mixed response, and because little is known about the  
623 potential for competition for pollination with *M. ciliata*, it is difficult to predict how changes in  
624 community phenology would alter visitation to *M. ciliata*. More studies of community-wide  
625 manipulation of climatic factors would be very informative. In one rare community-wide  
626 manipulation of water in mesocosms, plant species richness was altered, and pollinators visited both  
627 flooded and dry mesocosms less often than intermediate ones (Walter 2020).

628  
629 Climate change can also influence abundance or phenology of the insect pollinator populations  
630 themselves in this locality, in part due to indirect effects of floral resource phenology (Ogilvie et al.  
631 2017), and climate-induced changes in insect populations were not included in our manipulations.  
632 Comparisons of bee phenology across time in this locality suggest that emergence of solitary bees is  
633 advancing by 4.9 days per decade (Stemkovsky et al. 2020), which may be faster than that of *M.*  
634 *ciliata*. Syrphid fly emergence responds to date of snowmelt, making earlier emergence likely in the  
635 future even though it has not yet been demonstrated (Iler et al. 2013). On the other hand, timing of  
636 bumblebees has not shifted appreciably (Pyke et al. 2016). Given that most visits to *M. ciliata* are by  
637 bumblebees, with solitary bees common only early in the season, our manipulation of phenology for  
638 the plant but not its pollinators likely captured the main essence of how the phenological relationship  
639 will be disrupted under climate change.

640

## 641 4.5 Conclusions

642 Climate change may affect plant-pollinator interactions through a variety of mechanisms, including  
643 direct effects of precipitation patterns, temperature, and CO<sub>2</sub> levels, as well as indirect effects of  
644 those abiotic factors on phenology (Hoover et al. 2012; Gornish and Tylianakis 2013; Forrest 2015).  
645 Here we considered the simultaneous effects that two of these, potentially co-occurring mechanisms  
646 have on the pollination and seed set of a subalpine wildflower. We found that changes in water  
647 availability interacted with differences in flowering time in their effects on pollinator taxonomic  
648 composition, but their effects on pollinator visitation and seed set were additive. Moreover, in our



649 system, the strength of these two mechanisms differed, with phenological shifts having a greater  
650 effect on the likelihood and frequency of pollinator visits and water availability having a greater  
651 effect on seed set and seed mass. This study illustrates the necessity of examining the relative  
652 strength and potential interactive effects of co-occurring mechanisms, and monitoring multiple  
653 fitness components, to address the potential reproductive consequences of climate change.  
654

655

656 **5 Data Availability Statement**657 Data available from the Dryad Digital Repository: <https://doi.org/10.7280/D16D7Z>.658 **6 Conflict of Interest**659 The authors declare that the research was conducted in the absence of any commercial or financial  
660 relationships that could be construed as a potential conflict of interest.661 **7 Author Contributions**662 MKG and DC designed the study, and revised and edited the manuscript. MKG performed the  
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672673 **10 Supplementary Material**674 The Supplementary Material for this article can be found online at  
675

676 **11 Literature Cited**

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915 **Figure Legends**

916

917 Figure 1 Mean (A) soil moisture of three water treatments and (B) floral abundance per array of  
 918 *Mertensia ciliata* plants across four phenology weeks (N = 114). Soil moisture measured as  
 919 volumetric water content (VWC), assessed every third day, and when applicable, always before  
 920 applying water. The center of the boxplot represents the median value, the edges of the box indicate  
 921 the 25th and 75th percentiles, the whiskers represent the 5th and 95th percentiles of the distributions,  
 922 and the points indicate outlying values.

923

924 Figure 2 Effects of experimental variation in soil moisture and flowering phenology on (A) corolla  
 925 width, (B) corolla length, (C) nectar volume and (D) nectar sugar concentration of *Mertensia ciliata*.  
 926 Corolla traits include all four phenology weeks (N = 106), whereas nectar measurements were only  
 927 collected for three phenology weeks (N = 63). (A), (B), and (C): Wet differed from control and dry  
 928 treatments (Tukey pairwise comparison among water treatments,  $P < 0.05$ ). (B): Week 4 (July 11)  
 929 differed from the earlier three weeks (Tukey pairwise comparison among phenology weeks,  $P <$   
 930  $0.01$ ). Boxplots follow the same conventions as in Figure 1.

931

932 Figure 3 Effects of experimental variation in soil moisture and flowering phenology on *Mertensia*  
 933 *ciliata* floral abundance per plant (N = 114). Week 4 (July 11) differed from the other three weeks  
 934 (Tukey pairwise comparison among phenology weeks,  $P < 0.001$ ). Significant interaction terms ( $P <$   
 935  $0.05$ ) were: week 1 versus week 4 in wet versus control, as well as control versus dry treatments;  
 936 week 1 versus week 2 in dry versus wet as well as dry versus control treatments; week 2 versus week  
 937 3 in wet versus control; all treatment combinations in week 2 versus week 4; all treatment  
 938 combinations in week 3 versus week 4. Boxplots follow the same conventions as in Figure 1.

939

940 Figure 4 Effects of experimental variation in soil moisture and flowering phenology on visitation. (A)  
 941 the likelihood that a plant received a pollinator visit. Wet differed from control (Tukey pairwise  
 942 comparison among water treatments,  $P < 0.0001$ ). Week 1 differed from weeks 3 and 4 (Tukey  
 943 pairwise comparison among phenology weeks,  $P < 0.0001$ ). (B) the mean pollinator visitation rate  
 944 per plant among plants that received at least one visit, calculated as (total number of flowers visited /  
 945 number of flowers available per hour of observation) averaged across the phenology week. Wet  
 946 differed from control ( $P < 0.010$ ). Week 1 differed from all other weeks ( $P < 0.001$ ). (C) the percent  
 947 of total pollinator visits that were comprised of bumblebees, flies, and solitary bees, (N = 114).  
 948 Significant interaction terms ( $P < 0.05$ ) were: week 1 versus week 2 in control versus dry treatment,  
 949 week 1 versus week 2 in wet versus dry treatment, and week 1 versus 4 in control versus dry  
 950 treatment. Boxplots follow the same conventions as in Figure 1.

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952 Figure 5 Effects of experimental variation in soil moisture and flowering phenology on (A) seeds set  
 953 per flower, calculated as (number of mature seeds / number of flowers), and (B) seed mass,  
 954 calculated as (mass of collected seeds / number of collected seeds) (N = 114). (A) and (B): Wet  
 955 differed from control and dry treatments (Tukey pairwise comparison among water treatments,  $P <$   
 956  $0.005$ ). (A): Week 4 (July 11) differed from the first two weeks (June 20 and June 27) (Tukey  
 957 pairwise comparison among phenology weeks,  $P < 0.05$ ). Boxplots follow the same conventions as in  
 958 Figure 1.

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**Tables**

Table 1. Results from analyses testing the effects of experimental variation in phenology and water treatments on floral traits, percent of visitors that were bumblebees (i.e., pollinator type), seed set, and seed mass. Linear mixed models and generalized linear mixed models included main and interactive effects of water treatment and phenology week as fixed effects, and array nested in phenology week as a random effect. Mean percent bumblebee visitors was calculated for the two plants in each array that belonged to the same water treatment, instead of each separate plant, and therefore was analyzed with a linear model including main and interactive effects of water treatment and phenology week as predictors. Models were tested with type III Wald likelihood ratio tests in R, with df given in parentheses following the test statistic ( $\chi^2$ ).

	Phenology Treatment $\chi^2$ (3)	Water Treatment $\chi^2$ (2)	Phenology x Water $\chi^2$ (6)
Corolla width	3.85	78.69 ***	11.84 .
Corolla length	19.01 ***	36.84 ***	4.55
Nectar volume ‡	4.35	41.93 ***	4.48
Nectar concentration	3.74	2.60	1.83
Floral abundance per plant ‡	51.03 ***	2.92	119.48 ***
Pollinator type	21.76 ***	3.02	12.64 *
Seed set	16.11 **	11.31 **	1.87
Seed mass	18.17 ***	18.84 ***	1.37

Significance codes: \*\*\* P < 0.001; \*\* P < 0.01; \* P < 0.05  
‡ GLMM Poisson distribution

973

974 Table 2. Results from analyses testing the effects of experimental variation in phenology and water  
 975 treatments on the likelihood that a plant received a pollinator visit and the pollinator visitation rate to  
 976 plants that received at least one visit, calculated as (total number of flowers visited / number of  
 977 flowers available per hour of observation) averaged across the phenology week. Models included  
 978 main and interactive effects of water treatment and phenology week as fixed effects, and array nested  
 979 in phenology week as a random effect. Models were tested with Wald type III F ratio tests using Proc  
 980 Glimmix in SAS.  
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	Phenology Treatment			Water Treatment			Phenology x Water		
	F	df	<i>P</i>	F	df	<i>P</i>	F	df	<i>P</i>
Likelihood of pollinator visit ‡	63.9	3, 16	<0.001	95.1	2, 87	<0.001	0.5	5, 87	0.8
Pollinator visitation rate *	24.8	3, 15	<0.001	6.1	2, 52	0.004	1.9	6, 52	0.1

‡ Proc Glimmix binomial distribution  
 \* Proc Glimmix log normal distribution

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