

1 **Title:** Climate shapes flowering periods across plant communities

2

3 **Short running title:** Plant community flowering periods and climate

4

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17

18 **Acknowledgements:**

19 R.E.S. was supported by funding through the Australian Government's Research Training

20 Program. MJ acknowledges the Australian Research Council DECRA fellowship

21 (DE210101654). We thank all contributors to the AusTraits plant trait database, particularly

22 taxonomists and their supporting institutions for their long-term work describing the flora of

23 Australia. We also acknowledge all contributors to TERN AusPlots for their work in creating an

24 excellent source of reliable plant abundance data for macroecological work in Australia.

25

26 **Abstract:**

27

28 **Aim:** Climate shapes the composition and function of plant communities globally, but it remains  
29 unclear how this influence extends to floral traits. Flowering phenology, or the time period in  
30 which a species flowers, has well-studied relationships with climatic signals at the species level  
31 but has rarely been explored at a cross-community and continental scale. Here, we characterise  
32 the distribution of flowering periods (months of flowering) across continental plant communities  
33 encompassing six biomes, and determine the influence of climate on community flowering  
34 period lengths.

35 **Location:** Australia

36 **Taxon:** Flowering plants

37 **Methods:** We combined plant composition and abundance data from 629 standardised floristic  
38 surveys (AusPlots) with data on flowering period from the AusTraits database and additional  
39 primary literature for 2,983 species. We assessed abundance-weighted community mean  
40 flowering periods across biomes and tested their relationship with climatic annual means and the  
41 predictability of climate conditions using regression models.

42 **Results:** Combined, temperature and precipitation (annual mean and predictability) explain 29%  
43 of variation in continental community flowering period. Plant communities with higher mean  
44 temperatures and lower mean precipitation have longer mean flowering periods. Moreover, plant  
45 communities in climates with predictable temperatures and, to a lesser extent, predictable  
46 precipitation have shorter mean flowering periods. Flowering period varies by biome, being  
47 longest in deserts and shortest in alpine and montane communities. For instance, desert  
48 communities experience low and unpredictable precipitation and high, unpredictable

49 temperatures and have longer mean flowering periods, with desert species typically flowering at  
50 any time of year in response to rain.

51 **Main conclusions:** Our findings demonstrate the role of current climate conditions in shaping  
52 flowering periods across biomes, with implications under climate change. Shifts in flowering  
53 periods across climatic gradients reflect changes in plant strategies, affecting patterns of plant  
54 growth and reproduction as well as the availability of floral resources across the landscape.

55

56 **Keywords:** community assembly, climate, floral traits, flowering phenology, functional  
57 biogeography, macroecology, predictability

58

59 **Main text:**

60

## 61 **1 INTRODUCTION**

62 Climate shapes patterns of community assembly globally, driving the distribution of resources  
63 and the dynamics of interactions that in turn affect the co-occurrence of organisms (Kraft et al.,  
64 2015; Ockendon et al., 2014). As community composition varies along environmental gradients,  
65 so do the functional traits of constituent species (Bruehlheide et al., 2018; Cornwell & Ackerly,  
66 2009; Wieczynski et al., 2019). For example, plant communities are generally taller in the  
67 tropics, and in areas with higher precipitation (Moles et al., 2009), with leaves on average larger  
68 in environments which are warm and wet (Wright et al., 2017). Yet less is known about how the  
69 traits of flowers vary with climate across biomes, continents or globally.

70

71 Previous studies of plant functional biogeography have primarily focussed on a few key traits  
72 thought to be central to plant strategies, particularly leaf size and specific leaf area, plant height  
73 and seed mass (Andrew et al., 2021; Lamanna et al., 2014; Swenson et al., 2012). While such  
74 studies have been extremely productive in describing plant ecological strategies across a wide  
75 range of environmental conditions, recent attention has been drawn to the overlooked role that  
76 flowers and floral traits play in modulating species interactions and shaping patterns of  
77 community assembly (E-Vojtkó, de Bello, Durka, Kühn, & Götzenberger, 2020; Roddy et al.,  
78 2020). Despite some evidence suggesting that floral traits may have weaker links to  
79 macroclimate and landscape patterns than vegetative traits in general (e.g. Kuppler et al., 2020),  
80 flowers and floral traits do respond to biotic and abiotic conditions and thus bear investigation as  
81 “response” traits (Caruso, Eisen, Martin, & Sletvold, 2019; E-Vojtkó et al., 2020; S. Lavorel &

82 Garnier, 2002). At the same time floral traits play important roles in ecological communities,  
83 mediating sexual reproduction by cross-pollination in flowering plant species and the provision  
84 of food and shelter resources for fauna (Fornoff et al., 2017; Lázaro, Gómez-Martínez, Alomar,  
85 González-Estévez, & Traveset, 2020). Thus floral traits also bear investigation as “effect” traits  
86 for their influence on other trophic levels and ecosystem functions (E-Vojtkó et al., 2020; Sandra  
87 Lavorel et al., 2013).

88  
89 Flower phenology has strong connections to climatic signals, at the individual, population,  
90 species and community level (Craine, Wolkovich, & Towne, 2012; Diez et al., 2012; Primack,  
91 1985), and is thus a prime candidate trait for studies of floral functional biogeography. Flowering  
92 phenology is a highly labile trait, with a large amount of intraspecific variation between  
93 populations experiencing different climatic and biotic conditions (Franks, Sim, & Weis, 2007;  
94 Yan, Wang, Chan, & Mitchell-Olds, 2021). Indeed, flowering phenology shifts have been  
95 observed in numerous species worldwide in response to climate warming (e.g. CaraDonna *et al.*,  
96 2014; Prevéy *et al.*, 2019). Flowering phenology also shifts with community composition, and  
97 composition-derived variation in flowering time can explain a significant proportion of  
98 community flowering periods (though less than intraspecific variation; Park, 2014).

99  
100 Recent work suggests that interspecific variation in flowering phenology can be detected at a  
101 landscape scale. For example, flowering and fruiting periods of Chinese angiosperms with  
102 overlapping geographic ranges vary with latitude, elevation and several climatic variables (Du et  
103 al., 2020). However, assessments of variation at grid-cell rather than local patch scale can over-  
104 estimate the influence of macro-environment on trait signals among co-existing species

105 (Bruehlheide et al., 2018). Species with overlapping broad geographic ranges do not necessarily  
106 co-occur in communities at a scale where they are likely to interact, and patterns of trait variation  
107 may differ significantly when species abundances within ecosystems are taken into account  
108 (Wieczynski et al., 2019). It thus remains unclear whether relationships between community  
109 flowering phenology and climatic signals apply to community sorting at the local scale.

110

111 Here, we characterise the continental distribution of flowering periods in plant communities, and  
112 determine the influence of climate on community flowering period lengths. We define flowering  
113 period length as the number of months in which each species has been recorded flowering, which  
114 is not necessarily equivalent to the flowering durations of populations or individuals. We  
115 combine fine-scale plant community richness and abundance data from a network of vegetation  
116 plots across Australia (TERN AusPlots (TERN, 2018)) with flowering period data from the  
117 AusTraits database (Falster et al., 2021), species descriptions and herbarium records. The  
118 Australian continent, though generally low in soil fertility, encompasses a wide array of climatic  
119 regimes from cool temperate to tropical. Vast low relief deserts of the arid interior juxtapose  
120 areas of higher elevation such as the Great Dividing Range of eastern Australia and higher  
121 rainfall habitats with more predictable climates along coastal fringes (Figure 1). Australia has a  
122 latitudinal range of  $>30^\circ$  accompanied by a strong gradient in mean annual temperatures.

123

124 Climatic conditions may influence the length of community flowering periods in several ways.  
125 Higher mean annual temperatures allow pollinators to be active and plants to meet the  
126 physiological costs of producing flowers across a longer period of the year (Primack & Inouye,  
127 1993; Roddy, 2019; Roddy et al., 2020), thus lengthening flowering periods. Low mean annual

128 precipitation, on the other hand, reduces water availability and plant productivity which may  
129 select for ephemeral flowering strategies (Friedel, Nelson, Sparrow, Kinloch, & Maconochie,  
130 1993; Roddy, 2019), thus also lengthening potential flowering periods overall.

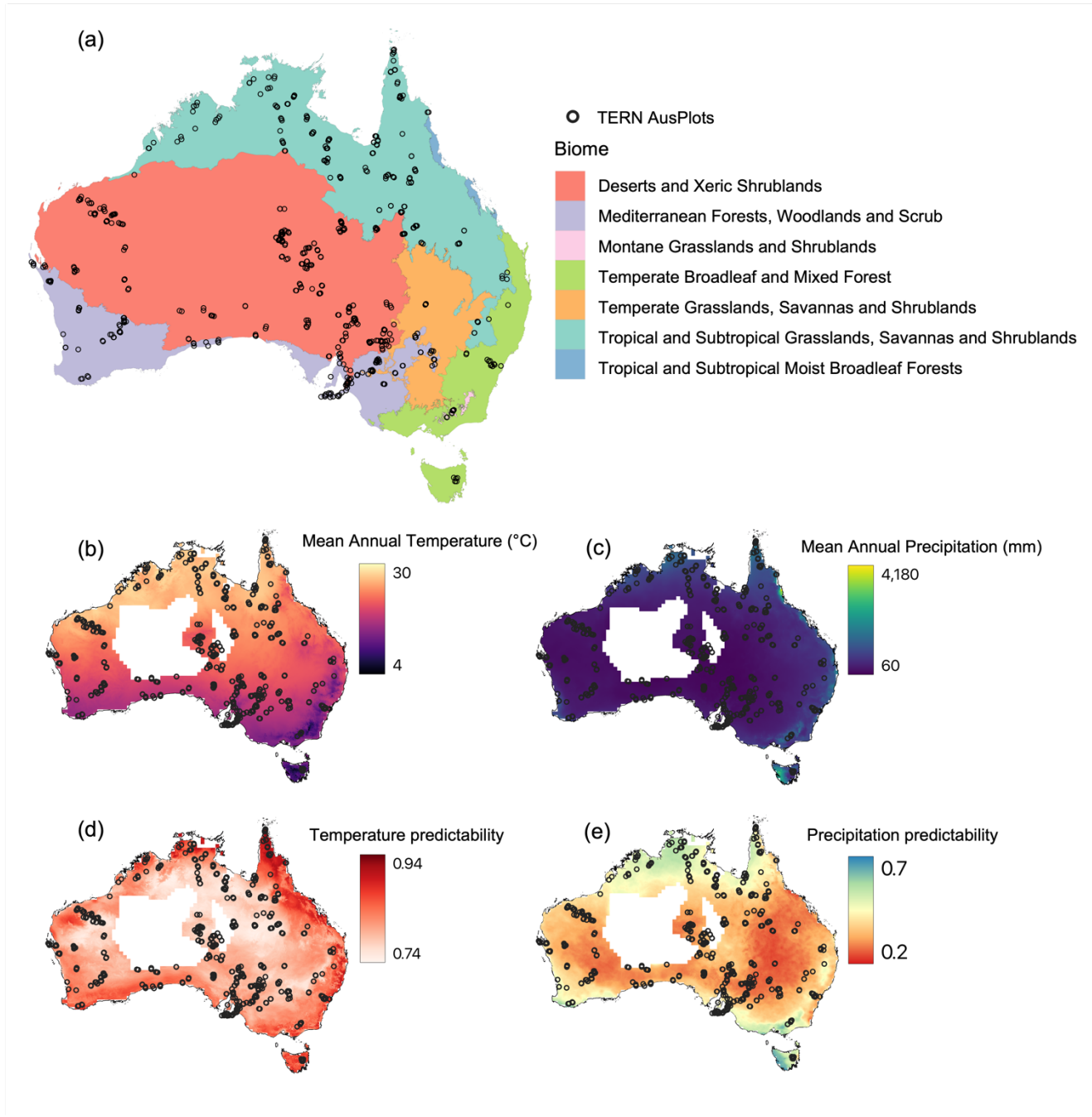
131  
132 In addition to average climate conditions, we hypothesise that the predictability of climatic  
133 phenomena has a strong influence on flowering phenology. We test this idea using the Colwell  
134 index of predictability (Colwell, 1974), which combines both the long-term reliability of  
135 seasonality, known as contingency, and the constancy of aseasonal periodic phenomena into a  
136 single measure of environmental predictability. Predictable environments offer reliable  
137 environmental information to organisms, allowing the timing of events such as flowering to  
138 depend on endogenous factors such as age or condition rather than responding directly to  
139 environmental cues (Wingfield, Hahn, & Doak, 1993). Predictability is therefore a more  
140 complete measure of environmental stochasticity than the more commonly used temperature or  
141 precipitation seasonality, especially in relatively aseasonal continents such as Australia (Jiang,  
142 Felzer, Nielsen, & Medlyn, 2017). Globally temperature predictability follows a latitudinal  
143 gradient, and is uniquely high in Australia, with greater predictability closer to the equator and  
144 coastal areas (Jiang et al., 2017). Precipitation predictability is more geographically variable, and  
145 in Australia is low overall but markedly lowest in the arid inland (Jiang et al., 2017). We expect  
146 that high climatic predictability offers reliable environmental cues and therefore selects for  
147 synchronous biotic responses, with more concentrated and thus shorter community flowering  
148 periods in areas of high predictability. Given that temporal information is preserved by both  
149 flowering periods and climatic predictability, we also anticipate that climatic predictability will  
150 have a stronger relationship with community flowering period lengths than climatic means.

151

152 In summary we predict:

- 153 1. That community flowering periods will be longer with increasing mean annual temperature.
- 154 2. That community flowering periods will be longer with decreasing mean annual precipitation.
- 155 3. That community flowering periods will be shorter with increasing predictability of either  
156 temperature or precipitation.
- 157 4. That community flowering period length will have a stronger relationship with the  
158 predictability of climatic variables than mean climatic measures.





159

160 *Figure 1* The distribution of the 629 AusPlots used in the analysis, across: (a) biomes based on Dinerstein et al. 2017's global  
161 terrestrial ecoregions, aligned to the Australian Interim Biogeographic Regionalisation for Australia (Australian Department of  
162 the Environment and Energy, 2016); (b) mean annual temperature (°C); (c) mean annual precipitation (mm); (d) temperature  
163 predictability; and (e) precipitation predictability. Climate data generated from Australian Water Availability Project (AWAP)  
164 data for 1930-2019. The white area in central Australia in represents a mask where AWAP data were excluded as meteorological  
165 stations are sparse in this area (King et al., 2014).

## 166 **2 METHODS**

167

### 168 **2.1 Community floristic data**

169

170 We accessed data on floristic composition in 810 surveys of 100 m × 100 m vegetation plots  
171 from the Terrestrial Ecosystem Research Network (TERN) AusPlots network using the  
172 `ausplotsR` package (Guerin, Munroe, Saleeba, & Ire, 2020; Munroe et al., 2021; TERN, 2021).  
173 AusPlots are distributed across a representative range of Australian ecosystems and  
174 environments and were surveyed using precise and consistent methods for recording vegetation  
175 species and cover-abundance data between 2011-2020 (Guerin, Williams, Leitch, Lowe, &  
176 Sparrow, 2021; Guerin, Williams, Sparrow, & Lowe, 2020; Sparrow et al., 2020). Plots were  
177 included in analyses if they were located  $\geq 500$  metres from another plot and flowering period  
178 data was available for  $\geq 80\%$  of angiosperm species cover (Borgy et al., 2017; Figure S1). Where  
179 plots had repeat surveys available, the survey with the highest recorded species richness was  
180 retained to maximise representation of species occurring in the system. In total, 629 plots with  
181 2,983 species were retained for analysis (Figure 1). These plots cover a broad and representative  
182 range of Australia's climatic variation (Figure 1) and occur across six globally recognised  
183 biomes (Dinerstein et al., 2017, Figure 1). The number of plots sampled in each biome strongly  
184 correlates with biome size in Australia (Figure S2, ordinary least squares linear regression  $p <$   
185  $0.001$ ,  $R^2 = 0.92$ ).

186

187 All observations were aggregated to the species level, removing any subspecies or variants, after  
188 taxonomic alignment to the Australian Plant Census (Council of Heads of Australasian Herbaria,  
189 2021) following methods in (Falster et al., 2021)).

190

## 191 **2.2 Flowering period**

192

193 Data on flowering periods were accessed from the AusTraits database version 2.1.0 (Falster et  
194 al., 2021) drawn from diverse original sources. The data from AusTraits were supplemented for  
195 627 species from species descriptions in the Flora of Australia (Australian Biological Resources  
196 Study, Canberra, 2021), online state and regional floras ('EUCLID', 2020; Northern Territory  
197 Government, 2021; Royal Botanic Gardens and Domain Trust, Sydney, 2021; Royal Botanic  
198 Gardens Victoria, 2021; State Herbarium of South Australia, 2021; Western Australian  
199 Herbarium, 2021; Zich, Hyland, Whiffin, & Kerrigan, 2020), original species descriptions and,  
200 where flowering period was not available from any of the above sources, herbarium records.

201 Most original sources define flowering periods using a range of months, e.g. "Jun-Oct", "spring-  
202 summer" or "all year round". For analysis, each record was converted into binary vector of  
203 length 12, indicating whether flowering occurred in each month, e.g. "110000000011" for Nov-  
204 Feb.

205

206 Flowering period length was defined as the number of months (i.e. 1-12) in which the species has  
207 been recorded flowering. It therefore refers to the proportion of the year during which a species  
208 potentially flowers, rather than to the length of flowering events. We use the length of flowering  
209 periods as our response variable so as to include the numerous Australian arid-zone species

210 which flower sporadically in response to rain (Friedel et al., 1993; Friedel, Nelson, Sparrow,  
211 Kinloch, & Maconochie, 1994). Mean flowering month cannot be calculated for these species as  
212 midpoint circular means cannot sensibly be calculated for bimodal or equally spaced periods  
213 (Morellato, Alberti, & Hudson, 2010). Where multiple records of flowering period existed for a  
214 single species, data were pooled (e.g. a species reported as flowering in both March-April and  
215 April-May was scored as flowering March-May). This ensured we captured the full scope of  
216 months a species has been reported to flower across its Australian range.

217

### 218 **2.3 Climatic variables**

219

220 Climatic variables were calculated for plot locations using CSIRO Australian Water Availability  
221 Project (AWAP) data from 1930-2019 (Jones, Wang, & Fawcett, 2009; Raupach et al., 2009,  
222 2012). AWAP temperature and precipitation data use records from the Australian Bureau of  
223 Meteorology's network of meteorological stations across Australia, and are modelled at a  
224 resolution of 0.05 degree (~5 km). AWAP data accuracy is reduced for assessments of temporal  
225 variability where the meteorological station network is sparse or has missing data, in years  
226 before 1930 and in areas in central western Australia and locations along the Australian coast  
227 (King et al., 2014). A mask was applied to exclude AWAP data from locations where the  
228 network is sparse (as per King et al., 2014; white areas in Figure 1). Fifty-two AusPlots occurred  
229 in masked areas and so were excluded from analyses with climatic variables.

230

231 Mean annual temperature (°C) (MAT), mean annual precipitation (mm) (MAP) and the Colwell  
232 index of predictability (Colwell, 1974) for temperature and precipitation were calculated from

233 AWAP data for each plot location. The Colwell index of predictability is a simple but elegant  
234 mathematical approach that condenses temporal patterns of variability into single scores that  
235 vary between 0 (completely unpredictable) to 1 (completely predictable). The index has been  
236 widely adopted to characterise climatic, hydrologic and other environmental cues in ecology  
237 (Firman, Rubenstein, Moran, Rowe, & Buzatto, 2020; Wingfield et al., 1993). We calculated  
238 predictability as per Jiang et al. (2017), creating frequency tables for temperature and  
239 precipitation events using monthly time steps and set bins for climatic variables. Decisions  
240 around the binning of continuous climatic variables are fundamental to this method of  
241 calculating predictability (Jiang et al., 2017). Given temperature predictability tends to vary  
242 fairly consistently along a latitudinal gradient globally (Jiang et al., 2017), we chose to bin  
243 temperature by fixed bins of 5°C with two bins of 10°C at each end of the scale to capture rare  
244 extreme values, resulting in a total of ten bins for temperature (i.e. breakpoints at -10, 0, 5, 10,  
245 15, 20, 25, 30, 35, 40, 50). We binned precipitation with a base 3 exponential binning scheme,  
246 considering the large range of precipitation data and creating seven bins in total (0, 3<sup>1</sup>,  
247 3<sup>2</sup>...3<sup>7</sup>).

248

## 249 **2.4 Data analysis**

250

251 All analyses were performed in R version 4.0.4 (R Core Team, 2021). All data and analysis code  
252 are available at <https://doi.org/10.5281/zenodo.5553530>.

253

254 Trait-environment relationships were analysed according to the Community Weighted Means  
255 (CWM) approach detailed by ter Braak et al. (2018). AusPlots species cover-abundance scores

256 were used to generate CWMs of flowering period lengths for each plot, which were then  
257 regressed using ordinary least squares (OLS) regression against temperature and precipitation  
258 means and predictability for those plots. MAP was log transformed (base 10) prior to analysis.  
259 To ensure that trait-environment relationships were robust, species cover-abundance scores were  
260 also used to calculate weighted Species Niche Centroids (SNC) for each species and each  
261 environmental variable, and these were regressed against species' flowering period lengths. The  
262 highest p-value for each trait-environment relationship (CWM~enviro, SNC~trait) was retained  
263 (pmax) to screen for potential false positive relationships (ter Braak et al., 2018). To assess their  
264 combined predictive power we regressed significant climatic predictors against flowering period  
265 length CWMs using OLS multiple regression.

266

267 To further explore flowering period patterns, we compared flowering period lengths among  
268 biomes. Given the unequal numbers of AusPlots in different biomes, differences in CWM  
269 flowering period lengths between biomes were assessed using a Welch's ANOVA for unequal  
270 variances with Games-Howell posthoc tests. We also compared the difference in flowering  
271 period lengths between woody and herbaceous species using Welch's T-tests, with one t-test for  
272 all species pooled ( $n = 2790$ ) and multiple t-tests with Bonferroni correction ( $\alpha = 0.05/6 =$   
273  $0.008$ ) for species by biome ( $n = 87-1160$ ). Data on woodiness were sourced from AusTraits  
274 (Falster et al., 2021). We also confirmed that species range size was positively correlated with  
275 flowering period length using OLS regressions for all available species ( $n = 2819$ ) as an  
276 indication of the potential intraspecific variation in flowering phenology captured by species-  
277 level data. Range size data (as extent of occurrence, or EOO) was sourced from Gallagher et al.  
278 (2021).

279

## 280 **3 RESULTS**

281

### 282 **3.1 Trait-environment relationships**

283

284 Community weighted mean ( hereafter ‘community’) flowering period lengths increased with

285 MAT and decreased with MAP, precipitation predictability and temperature predictability,

286 though no single relationship explained greater than 20% of community variation (Table 1,

287 Figure 2). The relationship between community flowering period length and environmental

288 variables was strongest for temperature predictability ( $R^2 = 0.17$ ,  $p_{max} < 0.001$ ). MAT and MAP

289 both explained just over 10% of variation in community flowering period lengths ( $R^2 = 0.11$ ,

290  $p_{max} < 0.001$ ). The relationship between precipitation predictability and community flowering

291 period lengths was weaker ( $R^2 = 0.09$   $p_{max} < 0.001$ ). All climatic predictors combined explained

292 29% of variation in community flowering period length (multiple linear regression  $F_{4,572} = 59.53$ ,

293  $p < 0.001$ ,  $R^2 = 0.29$ ). All climatic predictors contributed significantly to the multiple regression

294 ( $p < 0.04$  in each case), with no multicollinearity among predictors ( $VIF < 2.2$  in each case,

295 correlations  $-0.11 - 0.71$ ; Figure S3).

296

297 *Table 1 Results from ordinary least squares regressions of community weighted mean flowering period length versus climatic*

298 *variables. Pmax reports the highest p-value from CWM and SNC regressions for the same climate variable.*

<b>Climate variable</b>	<b>Slope</b>	<b>R<sup>2</sup></b>	<b>F</b>	<b>P<sub>max</sub></b>	<b>Number</b>
			<b>statistic</b>		<b>of plots</b>
<b>Mean Annual Temperature</b>	0.15	0.11	68.92	<b>&lt;0.001</b>	577

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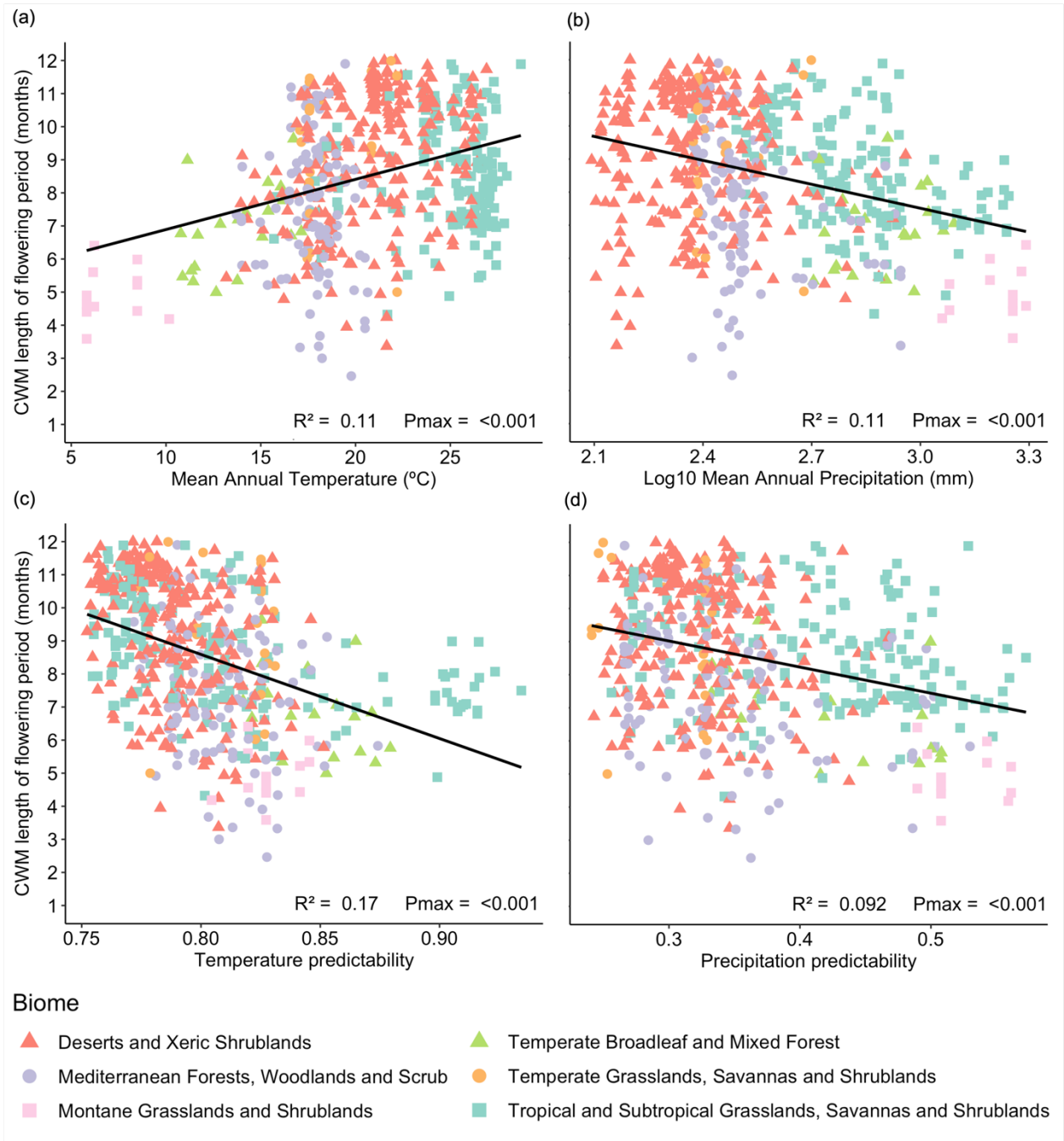
<b>Log10 Mean Annual</b>	-2.41	0.11	68.99	<b>&lt;0.001</b>	577
<b>Precipitation</b>					
<b>Temperature predictability</b>	-25.42	0.17	119.54	<b>&lt;0.001</b>	577
<b>Precipitation predictability</b>	-7.89	0.09	58.42	<b>&lt;0.001</b>	577

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300





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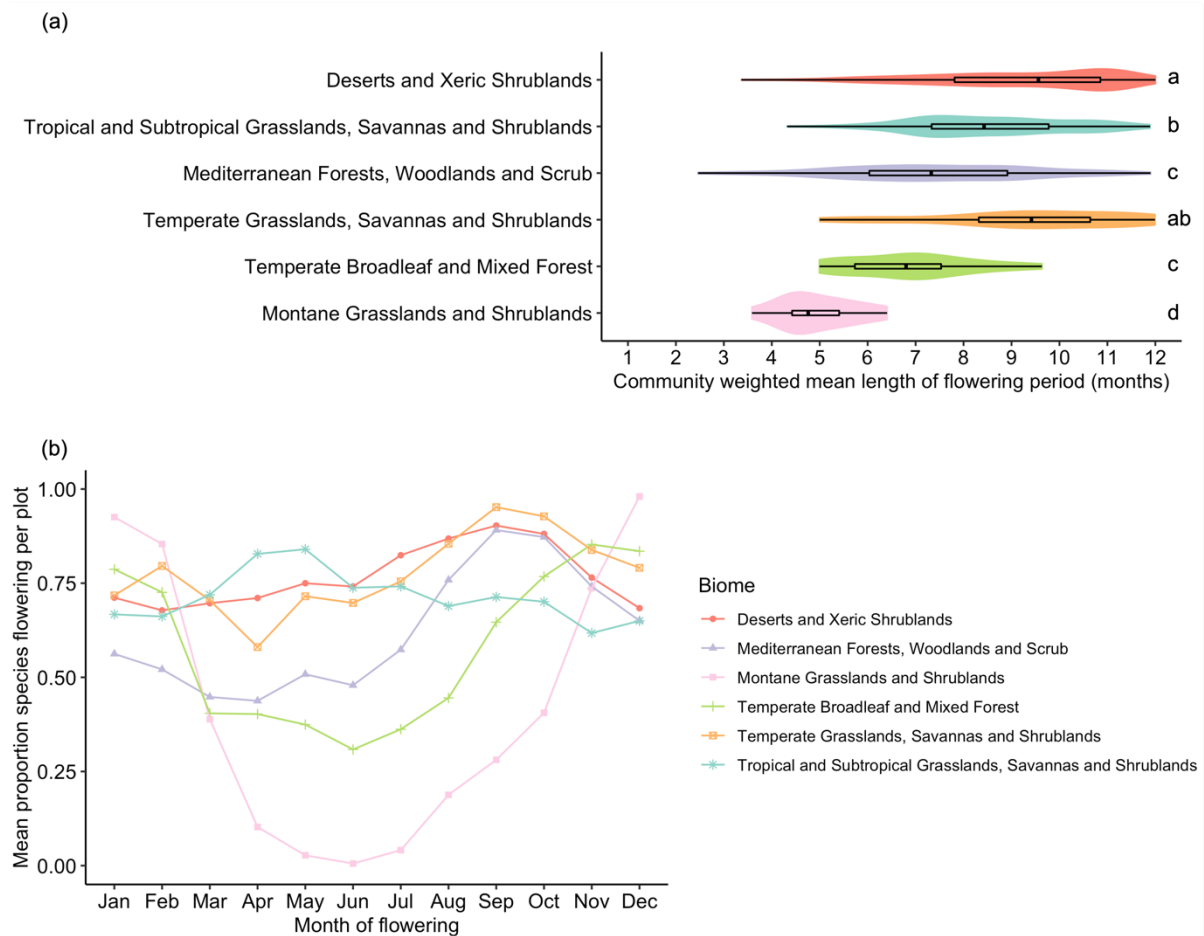
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306

*Figure 2 Relationships between mean annual temperature ( $^{\circ}C$ ) (a) mean annual precipitation (mm) (b), temperature predictability (c), precipitation predictability (d), and community weighted means (CWM) of the length of flowering periods (months).  $P_{max}$  values report the highest  $P$  value for both SNC and CWM regressions.*

### 3.2 Flowering periods by biome

307 Community flowering period lengths differed significantly by biome (Welch's ANOVA for  
 308 unequal variances  $F_{5,64.82} = 63.25$ ,  $P < 0.001$ ; Figure 3). Community flowering periods were  
 309 longest on average in Deserts and Xeric Shrublands, closely followed by Temperate Grasslands,  
 310 Savannas and Shrublands and Tropical and Subtropical Grasslands, Savannas and Shrublands  
 311 (Figure 3; Table S2). Community flowering periods were shortest in Montane Grasslands and  
 312 Shrublands (Figure 3; Table S2).  
 313

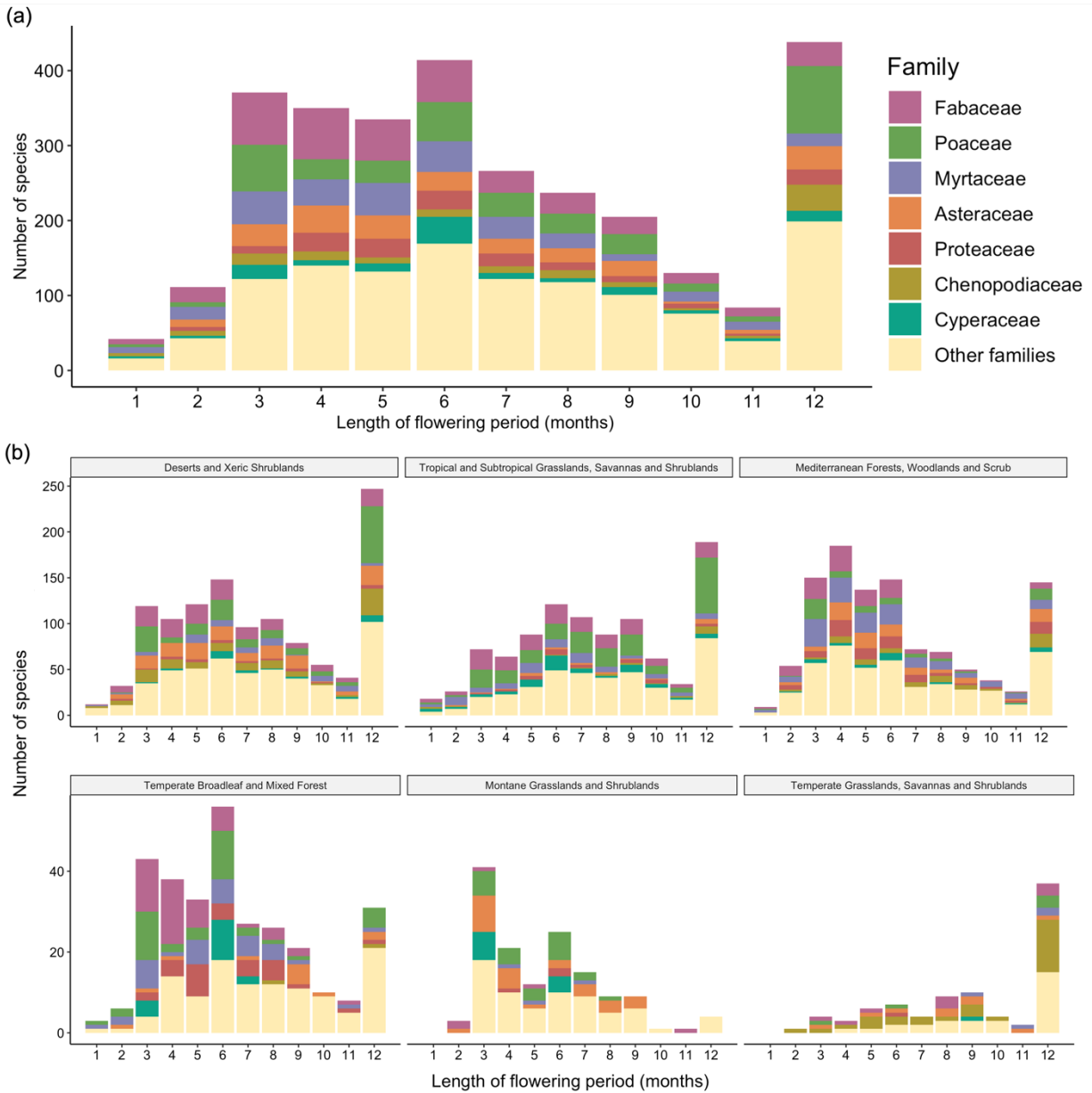


314  
 315 *Figure 3 Flowering periods by biome: a) community weighted mean flowering period lengths. Letters indicate significantly*  
 316 *different groups according to Games-Howell posthoc tests; b) monthly pattern of flowering as mean proportion of species cover*  
 317 *flowering per site per month.*

318 Montane Grassland and Shrubland sites show a strongly seasonal pattern of flowering, followed  
319 by Temperate Broadleaf and Mixed Forest (Figure 3). In contrast, Tropical and Subtropical  
320 Grasslands, Savannas and Shrublands; Temperate Grasslands, Savannas and Shrublands; and  
321 Desert and Xeric Shrubland biomes all show aseasonal patterns of flowering (Figure 3). When  
322 considering the geographic distribution of community flowering period lengths, central and  
323 northern Australia show generally longer community flowering periods, with shorter community  
324 flowering periods in southwest Western Australia and south-eastern Australia (Figure S5).

325  
326 Flowering period lengths across all species and among biomes are shown in Figure 4. The plant  
327 families contributing most species, occurrences and proportionate cover in study plots were  
328 Fabaceae (414 species, 1626 occurrences, 88 cumulative proportional cover), Poaceae (374  
329 species, 2743 occurrences, 196 cover) and Myrtaceae (287 species, 1033 occurrences, 125 cover;  
330 Table S1, Figure 4). Some families had relatively low species richness but high cover, including  
331 Casuarinaceae (13 species with 15 cover) and Scrophulariaceae (54 species with 11 cover). The  
332 distribution of flowering period lengths has peaks at three months, six months and twelve  
333 months, with most values falling between three and six months (Figure 4). Flowering periods of  
334 twelve months were particularly common for Poaceae and Chenopodiaceae species, whilst  
335 flowering periods of three to six months were more common for species in the Fabaceae and  
336 Myrtaceae (Figure 4). Different species flowering period lengths among AusPlots biomes  
337 therefore reflect the uneven distribution of plant families among biomes (Figure 4).

338



339  
 340 *Figure 4 The distribution of species flowering period lengths, coloured by family: a) total and b) separated by biome. Note in (b)*  
 341 *the different scales between the larger (top row) and smaller (bottom row) biomes.*

342

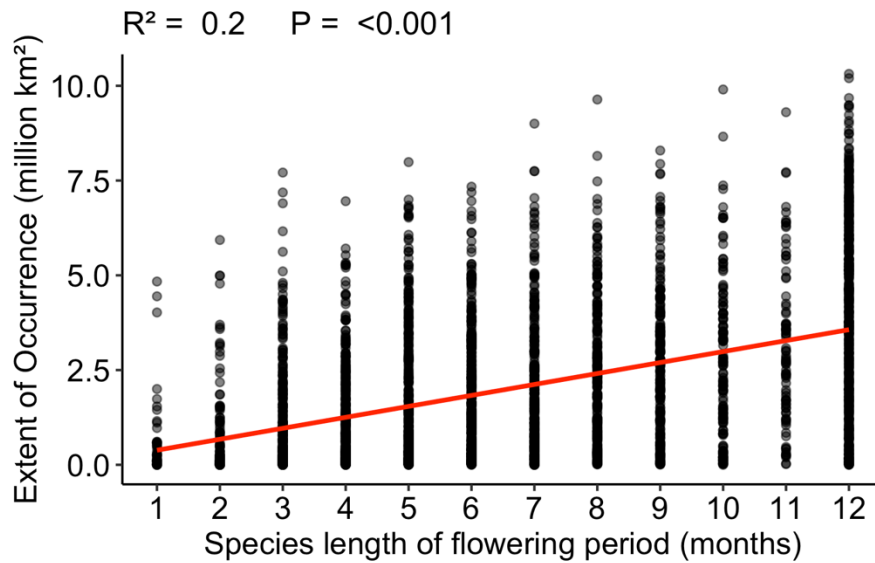
343 Flowering periods were longer in species with larger extents of occurrence ( $R^2 = 0.2$ ,  $p < 0.001$ ;

344 Figure 5). Mean flowering periods were longer for herbaceous species (mean = 6.8) than woody

345 species (mean = 6.5;  $t_{2786} = -2.73$ ,  $p = 0.01$ ; Figure S4). Mean flowering periods did not differ

346 significantly between woody and herbaceous species within different biomes (alpha with  
347 Bonferroni correction = 0.008,  $p = 0.03-0.49$ ).

348



349

350 *Figure 5 Species length of flowering period (months) against species extent of occurrence (million km²).*

351

#### 352 4 DISCUSSION

353

354 We show that climate plays a significant role in determining flowering period of plant  
355 communities, not just their constituent species, across six biomes, 23°C of MAT and 1,800 mm  
356 of MAP variation. Biome level differences in community flowering periods are driven in part by  
357 temperature and precipitation, both means and predictability. Four climate variables explained  
358 29% of variation in community flowering period lengths (i.e. MAT, MAP, and the predictability  
359 of temperature and precipitation). As hypothesised, plant communities with higher MAT and  
360 lower MAP typically exhibit longer mean flowering periods, whereas plant communities with  
361 predictable temperatures and precipitation exhibit shorter mean flowering periods. While the

362 relationship with temperature predictability was the strongest observed, the relationship with  
363 precipitation predictability was weaker than those with climatic means, perhaps due to the  
364 extreme variability and low predictability observed in precipitation across the Australian  
365 continent (Table 1). Our results show that shifts in flowering period with climate previously  
366 documented at the species level also operate in plant communities with implications for  
367 community assembly processes under both current and future climates.

368

369 Community flowering responses to climate are a product of the flowering phenologies of  
370 constituent species, which in turn depend on the flowering phenologies of constituent  
371 populations and individuals (Craine et al., 2012; Primack, 1985). Localised climatic conditions  
372 directly shape the flowering periods of the plant populations in an area, contributing to  
373 intraspecific variation, which then affects the flowering period recorded at the species level  
374 (Craine et al., 2012; Park, 2014). Though we could not test it directly, the effect of intraspecific  
375 variation on flowering period length is suggested in our results, as species with larger ranges  
376 have longer flowering periods (Figure 5). This illustrates how the use of species-level flowering  
377 periods as opposed to site-specific data may shape our results: as species range size increases, the  
378 specificity of flowering time observations decreases. Larger species' ranges encompass a broader  
379 array of climatic conditions, which should lead to longer periods of time in which different  
380 populations may experience suitable conditions for flowering. Thus, intraspecific responses to  
381 climate likely affect our results indirectly, shaping the species flowering periods that in turn  
382 contribute to community level flowering periods.

383

384 At the community scale, climate conditions can influence the co-occurrence of species with  
385 particular flowering periods via environmental filtering (Du et al., 2020; Park, 2014). Though the  
386 influence of climate is typically weaker when examining interspecific relative to intraspecific  
387 flowering times, composition-derived shifts in flowering time can explain up to 49.3% of  
388 community phenological variation (Park, 2014). Phenology can be a major determinant of  
389 species distributions, setting geographic limits on the environmental conditions a species requires  
390 to complete its life cycle (Chaine, 2010). In our study different plant families predominate in  
391 different biomes, and these compositional shifts correspond with shifts in flowering periods  
392 among biomes (Figure 3, Figure 4). In addition, community mean flowering periods vary with  
393 climate, suggesting that flowering phenology may be one of several traits determining species  
394 co-occurrence in plant communities, along with more commonly investigated traits such as plant  
395 height and specific leaf area (Guerin et al., In review). This is supported by Du et al. (2020)'s  
396 finding that flowering and fruiting phenology varies with environment across China, and shows  
397 that climate-community phenology relationships can be detected even in local, co-occurring  
398 plant communities, despite the influence of stochastic events on local community assembly  
399 (Bruehlheide et al., 2018). As such, our results clearly demonstrate the signal of environmental  
400 filtering in community flowering phenology, as different flowering strategies predominate across  
401 the breadth of plant communities and biomes explored.

402

#### 403 **4.2 Flowering period as a “response” trait**

404

405 Flowering periods are longest in Desert and Xeric Shrubland communities, and in communities  
406 with low and unpredictable MAP. This reflects longstanding observations about the flowering

407 phenology of desert communities, which is typically opportunistic in response to sporadic  
408 rainfall (Noy-Meir, 1973). The long flowering periods of desert biomes do not imply long  
409 flowering durations. Instead, longer flowering periods reflect the fact that desert species flower  
410 at any time of year in response to rainfall, which shows high inter-annual variability across  
411 Australia's arid regions (Friedel et al., 1993; King et al., 2014). For plants to be able to meet the  
412 physiological costs of flower production and maintenance (both water and carbon, see Roddy *et*  
413 *al.* (2020)), and resulting seed production, they must respond to water when it is available. Plants  
414 respond to this unpredictable rainfall differently: desert annuals and herbaceous perennials often  
415 germinate, flower and fruit following rainfall, with annuals completing their full life cycle while  
416 soil moisture is available (Nano & Pavey, 2013; Noy-Meir, 1973). Woody species typically have  
417 deeper root systems with access to more stable soil moisture, and can thus access resources to  
418 flower in more predictable windows, but still respond to stochastic rainfall events for flowering  
419 and reproduction (Friedel et al., 1993, 1994; Nano & Pavey, 2013; Noy-Meir, 1973). These  
420 differences in woody and herbaceous species' flowering may explain the slightly longer  
421 flowering periods found for herbaceous species, which showed a larger proportion of species  
422 with 12 month flowering periods than woody species (Figure S4), though this relationship did  
423 not hold within Deserts and Xeric Shrublands or any other biome.

424

425 In contrast to desert communities, mean flowering periods are shorter in Montane Grasslands and  
426 Shrublands, and in communities with low MAT, high MAP and predictable temperature and  
427 precipitation. Alpine plant communities experience strong climatic boundaries, with low  
428 temperatures and snow cover in the winter months preventing plant growth or reproduction.  
429 These strong climatic boundaries limit the window for flowering, pollination and seed



430 production in alpine plant communities, which must be completed before autumn snowfall  
431 (Inouye & Pyke, 1988). Reflecting this, alpine plant communities experience the most seasonal  
432 flowering of any Australian biome, with peak flowering in December-January and no flowering  
433 in June, the month of the Southern Hemisphere's winter solstice (Figure 3). The strength and  
434 specificity of this flowering pattern also reflects the smaller ranges of Australian alpine species  
435 (R. V. Gallagher, 2016). Australia's montane biome covers a small proportion of the country's  
436 terrestrial surface area (~0.16%, Figure 1) and is a centre of floral endemism in Australia (Crisp,  
437 Laffan, Linder, & Monro, 2001). Our findings confirm the combination of highly seasonal  
438 flowering, tight climate relationships and high rates of endemism which have made montane  
439 biomes the subject of intense research into the impacts of climate change on flowering  
440 phenology in recent decades (CaraDonna et al., 2014; R. Gallagher, Hughes, & Leishman, 2009).  
441 Some impacts of climate change on flowering phenology in Australian montane habitats have  
442 been detected, and these may lengthen community flowering periods in this biome in the future  
443 (R. Gallagher et al., 2009; Green, 2010).

444

445 Community mean flowering periods decreased with increasing predictability of both temperature  
446 and precipitation, as hypothesised. Precipitation predictability had less explanatory power than  
447 climatic means, while temperature predictability explained the most variance in community  
448 flowering periods (Table 1). Flowering is highly responsive to temperature cues, with flowering  
449 in many species initiated by increases in ambient temperatures (Capovilla, Schmid, & Posé,  
450 2015). It is thus unsurprising that more predictable temperature cues equal more regular, and thus  
451 shorter, community flowering periods, although Australian temperatures are highly predictable  
452 compared to other regions of the world (Jiang et al., 2017). In contrast, precipitation in Australia

453 is highly variable both geographically and year-to-year, driven by climatic modes such as the El  
454 Niño-Southern Oscillation, and this contributes to low levels of precipitation predictability (King  
455 et al., 2014). Temperate Broadleaf and Mixed Forest biomes in Australia, for example, are  
456 globally unique for their low precipitation predictability, and in particular their low precipitation  
457 contingency (Jiang et al., 2017). Australian vegetation is correspondingly opportunistic, with  
458 growth and flowering events often closely tracking water availability (Duursma et al., 2016;  
459 Nano & Pavey, 2013). Though community flowering periods decrease with precipitation  
460 predictability as predicted, this relationship was weaker than that with other climatic predictors,  
461 perhaps due to the extreme heterogeneity of precipitation across the Australian continent. Overall  
462 the relationship between climatic predictability and community plant phenology across Australia  
463 suggests climatic factors shaping plant community assembly beyond the climatic means typically  
464 considered.

465

#### 466 **4.3 Flowering period as an “effect” trait**

467

468 What do our results about flowering period imply for pollinators and pollination? Pollination is  
469 spatially heterogeneous: for example, wind pollination is thought to be more common in areas  
470 with lower MAT and MAP (Rech et al., 2016). For animal-pollinated species, different pollinator  
471 assemblages are active in different areas and different climatic conditions (Ollerton, 2017). Areas  
472 with higher MAT likely have more months of the year in which pollinator species are active  
473 (Primack & Inouye, 1993), and thus increased flowering periods in these communities is likely  
474 matched by increased windows of pollinator activity.

475

476 Relationships between pollinator activity and precipitation are more complicated. Though areas  
477 with higher precipitation have increased water availability which can increase floral traits  
478 associated with pollinator attraction and reward, rainfall itself typically impedes pollinator  
479 activity, diluting flower nectar, degrading pollen and preventing insect pollinators from flying  
480 (Lawson & Rands, 2019). Pollinator activity likely varies with climatic predictability much as  
481 flowering periods do, though pollinator phenology is less frequently or consistently studied  
482 (Neave, Brown, Batley, Rao, & Cunningham, 2020). In desert biomes, for example, bird  
483 abundance and species richness tracks unpredictable rainfall (Jordan, James, Moore, & Franklin,  
484 2017), and pollinators in cold or montane environments experience similar periods of reduced  
485 activity, either migrating away or else overwintering as larvae during the cold months (Inouye &  
486 Pyke, 1988; Stemkovski et al., 2020). Thus, climate shapes community flowering periods but  
487 also the activity of pollinators that visit flowers, not to mention the activity of the many  
488 florivorous animals that do not effect pollination (e.g. see McCall & Irwin, 2006).

489

#### 490 **4.4 Implications and future directions**

491

492 Community flowering strategies may shift with climate change, either as species adapt to new  
493 conditions or as community composition changes via localised extinctions and range shifts. In  
494 Australia climate change is causing higher temperatures overall, with an increase in heavy  
495 precipitation in northern Australia and an increase in drought in southern Australia (IPCC, 2021).  
496 Communities with shorter flowering periods will be more susceptible to the impacts of current  
497 and future climate change, as mismatches in the timing of flowering, pollinator emergence and  
498 climatic conditions over time may select for communities with longer, more responsive

499 flowering periods (e.g. Stenkovski *et al.*, 2020). Indeed, there are already reports that lower and  
500 less predictable rainfall is affecting plant community composition through dieback in southwest  
501 Australia (Hoffmann *et al.*, 2019), and that higher temperatures are shifting flowering dates in  
502 alpine southeast Australia (R. Gallagher *et al.*, 2009; Hoffmann *et al.*, 2019).

503

504 Flowering is just one part of a plant's reproductive phenology, and flowering phenology is just  
505 one aspect of a plant's floral strategy. Seed size may influence the timing of fruiting and  
506 flowering, as flowers must be pollinated in time to allow suitable conditions for fruit  
507 development, which takes longer in larger-seeded species, and seed dispersal (Chuine, 2010; Du  
508 *et al.*, 2020). Evidence for this hypothesis is equivocal, however, and recent field investigations  
509 in montane habitats found no association between phenological events and seed size, though they  
510 did find a strong association with plant height (Liu *et al.*, 2021). A landscape scale comparison  
511 between plant traits, fruiting time and flowering period would require either more specific  
512 measures of population flowering duration, or else measurement only in strongly seasonal  
513 environments where flowering periods experience definite constraints. A more fruitful approach  
514 in aseasonal landscapes might be to investigate community-level variation in other floral traits, in  
515 particular traits related to trade-off spectra such as floral longevity, floral mass or floral mass per  
516 area (Roddy *et al.*, 2020).

517

## 518 **5 Conclusion**

519

520 Climate has long been known to affect plant strategies across biomes. Here we have shown that  
521 climate similarly contributes to strategies around the timing of plant flowering. Plant

522 communities in climatically predictable areas, with higher mean precipitation and lower mean  
523 temperatures, favour shorter, more concentrated flowering periods. Species in these communities  
524 likely time their flowering to match pollinator activity and optimal conditions for pollination and  
525 seed development. In contrast, plant communities in areas with unpredictable climates, with  
526 lower mean precipitation and higher mean temperatures, have longer, more dispersed flowering  
527 periods, as species in these harsher conditions must respond whenever water is available to  
528 enable flowering. Filtering for these divergent flowering strategies may limit which species can  
529 co-exist in communities, resulting in signals of flowering in the processes of community  
530 assembly. Future studies may further reveal how different flowering strategies affect pollination,  
531 plant reproduction and community turnover, as well as the availability of floral resources across  
532 the landscape.

533

534 **Data availability statement:**

535 All data used in this study and primary analysis R code are available via an archived GitHub  
536 repository at <https://doi.org/10.5281/zenodo.5553530>.

537 **References**

- 538 Andrew, S. C., Mokany, K., Falster, D. S., Wenk, E., Wright, I. J., Merow, C., ... Gallagher, R. V.  
539 (2021). Functional diversity of the Australian flora: Strong links to species richness and  
540 climate. *Journal of Vegetation Science*, 32(2), e13018. <https://doi.org/10.1111/jvs.13018>
- 541 Australian Biological Resources Study, Canberra. (2021). Flora of Australia. Retrieved 1 March  
542 2021, from <http://www.ausflora.org.au>
- 543 Australian Department of the Environment and Energy. (2016). *Interim Biogeographic*  
544 *Regionalisation for Australia (IBRA), Version 7*. Retrieved from  
545 [https://data.gov.au/data/dataset/interim-biogeographic-regionalisation-for-australia-](https://data.gov.au/data/dataset/interim-biogeographic-regionalisation-for-australia-ibra-version-7-regions)  
546 [ibra-version-7-regions](https://data.gov.au/data/dataset/interim-biogeographic-regionalisation-for-australia-ibra-version-7-regions)
- 547 Borgy, B., Violle, C., Choler, P., Garnier, E., Kattge, J., Loranger, J., ... Viovy, N. (2017). Sensitivity  
548 of community-level trait–environment relationships to data representativeness: A test  
549 for functional biogeography. *Global Ecology and Biogeography*, 26(6), 729–739.  
550 <https://doi.org/10.1111/geb.12573>
- 551 Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., ...  
552 Jandt, U. (2018). Global trait–environment relationships of plant communities. *Nature*  
553 *Ecology & Evolution*, 2(12), 1906–1917. <https://doi.org/10.1038/s41559-018-0699-8>
- 554 Capovilla, G., Schmid, M., & Posé, D. (2015). Control of flowering by ambient temperature.  
555 *Journal of Experimental Botany*, 66(1), 59–69. <https://doi.org/10.1093/jxb/eru416>
- 556 CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape a  
557 subalpine plant community. *Proceedings of the National Academy of Sciences*, 111(13),  
558 4916–4921. <https://doi.org/10.1073/pnas.1323073111>

- 559 Caruso, C. M., Eisen, K. E., Martin, R. A., & Sletvold, N. (2019). A meta-analysis of the agents of  
560 selection on floral traits. *Evolution*, 73(1), 4–14. <https://doi.org/10.1111/evo.13639>
- 561 Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of*  
562 *the Royal Society B: Biological Sciences*, 365(1555), 3149–3160.  
563 <https://doi.org/10.1098/rstb.2010.0142>
- 564 Colwell, R. K. (1974). Predictability, Constancy, and Contingency of Periodic Phenomena.  
565 *Ecology*, 55(5), 1148–1153. <https://doi.org/10.2307/1940366>
- 566 Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait  
567 distributions across an environmental gradient in coastal California. *Ecological*  
568 *Monographs*, 79(1), 109–126. <https://doi.org/10.1890/07-1134.1>
- 569 Council of Heads of Australasian Herbaria. (2021). The Australian Plant Census (APC). Retrieved  
570 1 March 2021, from <https://biodiversity.org.au/nsl/services/search/taxonomy>
- 571 Craine, J. M., Wolkovich, E. M., & Towne, E. G. (2012). The roles of shifting and filtering in  
572 generating community-level flowering phenology. *Ecography*, 35(11), 1033–1038.  
573 <https://doi.org/10.1111/j.1600-0587.2012.07625.x>
- 574 Crisp, M. D., Laffan, S., Linder, H. P., & Monro, A. (2001). Endemism in the Australian flora.  
575 *Journal of Biogeography*, 28(2), 183–198. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2699.2001.00524.x)  
576 [2699.2001.00524.x](https://doi.org/10.1046/j.1365-2699.2001.00524.x)
- 577 Diez, J. M., Ibáñez, I., Miller-Rushing, A. J., Mazer, S. J., Crimmins, T. M., Crimmins, M. A., ...  
578 Inouye, D. W. (2012). Forecasting phenology: From species variability to community  
579 patterns. *Ecology Letters*, 15(6), 545–553. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2012.01765.x)  
580 [0248.2012.01765.x](https://doi.org/10.1111/j.1461-0248.2012.01765.x)

- 581 Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., ... Saleem, M.  
582 (2017). An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm.  
583 *BioScience*, 67(6), 534–545. <https://doi.org/10.1093/biosci/bix014>
- 584 Du, Y., Mao, L., Queenborough, S. A., Primack, R., Comita, L. S., Hampe, A., & Ma, K. (2020).  
585 Macro-scale variation and environmental predictors of flowering and fruiting phenology  
586 in the Chinese angiosperm flora. *Journal of Biogeography*, 47(11), 2303–2314.  
587 <https://doi.org/10.1111/jbi.13938>
- 588 Duursma, R. A., Gimeno, T. E., Boer, M. M., Crous, K. Y., Tjoelker, M. G., & Ellsworth, D. S.  
589 (2016). Canopy leaf area of a mature evergreen Eucalyptus woodland does not respond  
590 to elevated atmospheric [CO<sub>2</sub>] but tracks water availability. *Global Change Biology*,  
591 22(4), 1666–1676. <https://doi.org/10.1111/gcb.13151>
- 592 EUCLID: Eucalypts of Australia [Electronic resource]. (2020). Retrieved 1 March 2021, from  
593 <https://apps.lucidcentral.org/euclid/text/intro/index.html>
- 594 E-Vojtkó, A., de Bello, F., Durka, W., Kühn, I., & Götzenberger, L. (2020). The neglected  
595 importance of floral traits in trait-based plant community assembly. *Journal of*  
596 *Vegetation Science*, jvs.12877. <https://doi.org/10.1111/jvs.12877>
- 597 Falster, D., Gallagher, R., Wenk, E. H., Wright, I. J., Indiarso, D., Andrew, S. C., ... Ziemińska, K.  
598 (2021). AusTraits, a curated plant trait database for the Australian flora. *Scientific Data*,  
599 8(1), 254. <https://doi.org/10.1038/s41597-021-01006-6>
- 600 Firman, R. C., Rubenstein, D. R., Moran, J. M., Rowe, K. C., & Buzatto, B. A. (2020). Extreme and  
601 Variable Climatic Conditions Drive the Evolution of Sociality in Australian Rodents.  
602 *Current Biology*, 30(4), 691–697.e3. <https://doi.org/10.1016/j.cub.2019.12.012>



- 603 Fornoff, F., Klein, A.-M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H. M., & Ebeling, A.  
604 (2017). Functional flower traits and their diversity drive pollinator visitation. *Oikos*,  
605 126(7), 1020–1030. <https://doi.org/10.1111/oik.03869>
- 606 Franks, S. J., Sim, S., & Weis, A. E. (2007). Rapid evolution of flowering time by an annual plant  
607 in response to a climate fluctuation. *Proceedings of the National Academy of Sciences*,  
608 104(4), 1278–1282. <https://doi.org/10.1073/pnas.0608379104>
- 609 Friedel, M. H., Nelson, D. J., Sparrow, A. D., Kinloch, J. E., & Maconochie, J. R. (1993). What  
610 Induces Central Australian Arid Zone Trees and Shrubs to Flower and Fruit? *Australian*  
611 *Journal of Botany*, 41(3), 307–319. <https://doi.org/10.1071/bt9930307>
- 612 Friedel, M. H., Nelson, D. J., Sparrow, A. D., Kinloch, J. E., & Maconochie, J. R. (1994). Flowering  
613 and fruiting of arid zone species of Acacia in central Australia. *Journal of Arid*  
614 *Environments*, 27(3), 221–239. <https://doi.org/10.1006/jare.1994.1060>
- 615 Gallagher, R., Hughes, L., & Leishman, M. (2009). Phenological trends among Australian alpine  
616 species: Using herbarium records to identify climate-change indicators. *Australian*  
617 *Journal of Botany*, 57(1), 1–9. <https://doi.org/10.1071/BT08051>
- 618 Gallagher, R. V. (2016). Correlates of range size variation in the Australian seed-plant flora.  
619 *Journal of Biogeography*, 43(7), 1287–1298. <https://doi.org/10.1111/jbi.12711>
- 620 Gallagher, R. V., Allen, S., Mackenzie, B. D. E., Yates, C. J., Gosper, C. R., Keith, D. A., ... Auld, T.  
621 D. (2021). High fire frequency and the impact of the 2019–2020 megafires on Australian  
622 plant diversity. *Diversity and Distributions*, 27(7), 1166–1179.  
623 <https://doi.org/10.1111/ddi.13265>

- 624 Green, K. (2010). Alpine taxa exhibit differing responses to climate warming in the Snowy  
625 Mountains of Australia. *Journal of Mountain Science*, 7(2), 167–175.  
626 <https://doi.org/10.1007/s11629-010-1115-2>
- 627 Guerin, G. R., Gallagher, R. V., Wright, I. J., Andrew, S. C., Falster, D. S., Wenk, E., ... Lowe, A. J.  
628 (In review). Environmental associations of abundance-weighted functional traits in  
629 Australian plant communities. *Basic and Applied Ecology*.
- 630 Guerin, G. R., Munroe, S., Saleeba, T., & Ire. (2020). *AusplotsR: TERN AusPlots Analysis Package*  
631 *(Archive v1.2)*. Zenodo. <https://doi.org/10.5281/zenodo.4059195>
- 632 Guerin, G. R., Williams, K. J., Leitch, E., Lowe, A. J., & Sparrow, B. (2021). Using generalised  
633 dissimilarity modelling and targeted field surveys to gap-fill an ecosystem surveillance  
634 network. *Journal of Applied Ecology*, 58(4), 766–776. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2664.13814)  
635 [2664.13814](https://doi.org/10.1111/1365-2664.13814)
- 636 Guerin, G. R., Williams, K. J., Sparrow, B., & Lowe, A. J. (2020). Stocktaking the environmental  
637 coverage of a continental ecosystem observation network. *Ecosphere*, 11(12).  
638 <https://doi.org/10.1002/ecs2.3307>
- 639 Hoffmann, A. A., Rymer, P. D., Byrne, M., Ruthrof, K. X., Whinam, J., McGeoch, M., ... Williams,  
640 S. E. (2019). Impacts of recent climate change on terrestrial flora and fauna: Some  
641 emerging Australian examples. *Austral Ecology*, 44(1), 3–27.  
642 <https://doi.org/10.1111/aec.12674>
- 643 Inouye, D. W., & Pyke, G. H. (1988). Pollination biology in the Snowy Mountains of Australia:  
644 Comparisons with montane Colorado, USA. *Australian Journal of Ecology*, 13(2), 191–  
645 205. <https://doi.org/10.1111/j.1442-9993.1988.tb00968.x>

- 646 IPCC. (2021). Summary for Policymakers. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L.  
647 Connors, C. Péan, S. Berger, ... B. Zhou (Eds.), *Climate Change 2021: The Physical Science*  
648 *Basis. Contribution of Working Group I to the Sixth Assessment Report of the*  
649 *Intergovernmental Panel on Climate Change*. Cambridge University Press. Retrieved  
650 from <https://www.ipcc.ch/report/ar6/wg1>
- 651 Jiang, M., Felzer, B. S., Nielsen, U. N., & Medlyn, B. E. (2017). Biome-specific climatic space  
652 defined by temperature and precipitation predictability. *Global Ecology and*  
653 *Biogeography*, 26(11), 1270–1282. <https://doi.org/10.1111/geb.12635>
- 654 Jones, D., Wang, W., & Fawcett, R. (2009). High-quality spatial climate data-sets for Australia.  
655 *Australian Meteorological and Oceanographic Journal*, 58(04), 233–248.  
656 <https://doi.org/10.22499/2.5804.003>
- 657 Jordan, R., James, A. I., Moore, D., & Franklin, D. C. (2017). Boom and bust (or not?) among  
658 birds in an Australian semi-desert. *Journal of Arid Environments*, 139, 58–66.  
659 <https://doi.org/10.1016/j.jaridenv.2016.12.013>
- 660 King, A. D., Klingaman, N. P., Alexander, L. V., Donat, M. G., Jourdain, N. C., & Maher, P. (2014).  
661 Extreme Rainfall Variability in Australia: Patterns, Drivers, and Predictability. *Journal of*  
662 *Climate*, 27(15), 6035–6050. <https://doi.org/10.1175/JCLI-D-13-00715.1>
- 663 Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community  
664 assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*,  
665 29(5), 592–599. <https://doi.org/10.1111/1365-2435.12345>
- 666 Kuppler, J., Albert, C. H., Ames, G. M., Armbruster, W. S., Boenisch, G., Boucher, F. C., ... Junker,  
667 R. R. (2020). Global gradients in intraspecific variation in vegetative and floral traits are

- 668 partially associated with climate and species richness. *Global Ecology and Biogeography*,
- 669 29(6), 992–1007. <https://doi.org/10.1111/geb.13077>
- 670 Lamanna, C., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B., imova, I., ... Enquist, B. J. (2014).
- 671 Functional trait space and the latitudinal diversity gradient. *Proceedings of the National*
- 672 *Academy of Sciences*, 111(38), 13745–13750. <https://doi.org/10.1073/pnas.1317722111>
- 673 Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem
- 674 functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16(5), 545–
- 675 556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- 676 Lavorel, Sandra, Storkey, J., Bardgett, R. D., Bello, F. de, Berg, M. P., Roux, X. L., ... Harrington, R.
- 677 (2013). A novel framework for linking functional diversity of plants with other trophic
- 678 levels for the quantification of ecosystem services. *Journal of Vegetation Science*, 24(5),
- 679 942–948. <https://doi.org/10.1111/jvs.12083>
- 680 Lawson, D. A., & Rands, S. A. (2019). The effects of rainfall on plant–pollinator interactions.
- 681 *Arthropod-Plant Interactions*, 13(4), 561–569. [https://doi.org/10.1007/s11829-019-](https://doi.org/10.1007/s11829-019-09686-z)
- 682 09686-z
- 683 Lázaro, A., Gómez-Martínez, C., Alomar, D., González-Estévez, M. A., & Traveset, A. (2020).
- 684 Linking species-level network metrics to flower traits and plant fitness. *Journal of*
- 685 *Ecology*, 1365-2745.13334. <https://doi.org/10.1111/1365-2745.13334>
- 686 Liu, Y., Li, G., Wu, X., Niklas, K. J., Yang, Z., & Sun, S. (2021). Linkage between species traits and
- 687 plant phenology in an alpine meadow. *Oecologia*, 195(2), 409–419.
- 688 <https://doi.org/10.1007/s00442-020-04846-y>

- 689 McCall, A. C., & Irwin, R. E. (2006). Florivory: The intersection of pollination and herbivory.  
690 *Ecology Letters*, 9(12), 1351–1365. <https://doi.org/10.1111/j.1461-0248.2006.00975.x>
- 691 Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., ... Leishman,  
692 M. R. (2009). Global patterns in plant height. *Journal of Ecology*, 97(5), 923–932.  
693 <https://doi.org/10.1111/j.1365-2745.2009.01526.x>
- 694 Morellato, L. P. C., Alberti, L. F., & Hudson, I. L. (2010). Applications of Circular Statistics in Plant  
695 Phenology: A Case Studies Approach. In I. L. Hudson & M. R. Keatley (Eds.), *Phenological*  
696 *Research: Methods for Environmental and Climate Change Analysis* (pp. 339–359).  
697 Dordrecht: Springer Netherlands. [https://doi.org/10.1007/978-90-481-3335-2\\_16](https://doi.org/10.1007/978-90-481-3335-2_16)
- 698 Munroe, S., Guerin, G., Saleeba, T., Martín-Forés, I., Blanco-Martin, B., Sparrow, B., &  
699 Tokmakoff, A. (2021). ausplotsR: An R package for rapid extraction and analysis of  
700 vegetation and soil data collected by Australia’s Terrestrial Ecosystem Research  
701 Network. *Journal of Vegetation Science*, 32(3), e13046.  
702 <https://doi.org/10.1111/jvs.13046>
- 703 Nano, C. E. M., & Pavey, C. R. (2013). Refining the ‘pulse-reserve’ model for arid central  
704 Australia: Seasonal rainfall, soil moisture and plant productivity in sand ridge and stony  
705 plain habitats of the Simpson Desert. *Austral Ecology*, 38(7), 741–753.  
706 <https://doi.org/10.1111/aec.12036>
- 707 Neave, M. J., Brown, J., Batley, M., Rao, S., & Cunningham, S. A. (2020). Phenology of a bee  
708 (Hymenoptera: Apoidea) community over a 10 year period in south-eastern Australia.  
709 *Austral Entomology*, 59(3), 602–611. <https://doi.org/10.1111/aen.12488>

- 710 Northern Territory Government. (2021). EFlora NT: Northern Territory Flora Online. Retrieved 1  
711 March 2021, from <http://eflora.nt.gov.au/>
- 712 Noy-Meir, I. (1973). Desert Ecosystems: Environment and Producers. *Annual Review of Ecology*  
713 *and Systematics*, 4(1), 25–51. <https://doi.org/10.1146/annurev.es.04.110173.000325>
- 714 Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., ... Pearce-  
715 Higgins, J. W. (2014). Mechanisms underpinning climatic impacts on natural  
716 populations: Altered species interactions are more important than direct effects. *Global*  
717 *Change Biology*, 20(7), 2221–2229. <https://doi.org/10.1111/gcb.12559>
- 718 Ollerton, J. (2017). Pollinator Diversity: Distribution, Ecological Function, and Conservation.  
719 *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 353–376.  
720 <https://doi.org/10.1146/annurev-ecolsys-110316-022919>
- 721 Park, I. W. (2014). Impacts of differing community composition on flowering phenology  
722 throughout warm temperate, cool temperate and xeric environments. *Global Ecology*  
723 *and Biogeography*, 23(7), 789–801. <https://doi.org/10.1111/geb.12163>
- 724 Prev y, J. S., Rixen, C., R ger, N., H ye, T. T., Bjorkman, A. D., Myers-Smith, I. H., ... Wipf, S.  
725 (2019). Warming shortens flowering seasons of tundra plant communities. *Nature*  
726 *Ecology & Evolution*, 3(1), 45–52. <https://doi.org/10.1038/s41559-018-0745-6>
- 727 Primack, R. B. (1985). Patterns of Flowering Phenology in Communities, Populations,  
728 Individuals, and Single Flowers. In J. White (Ed.), *The Population Structure of Vegetation*  
729 (pp. 571–593). Dordrecht: Springer Netherlands. [https://doi.org/10.1007/978-94-009-](https://doi.org/10.1007/978-94-009-5500-4_24)  
730 [5500-4\\_24](https://doi.org/10.1007/978-94-009-5500-4_24)

- 731 Primack, R. B., & Inouye, D. W. (1993). *Factors affecting pollinator visitation rates: A*  
732 *biogeographic comparison*. 7.
- 733 R Core Team. (2021). R: A language and environment for statistical computing (Version 4.0.4).  
734 Vienna, Austria: R Foundation for Statistical Computing. Retrieved from [https://www.R-](https://www.R-project.org/)  
735 [project.org/](https://www.R-project.org/)
- 736 Raupach, M. R., Briggs, P. R., Haverd, V., King, E. A., Paget, M., & Trudinger, C. M. (2009).  
737 Australian Water Availability Project (AWAP): CSIRO Marine and Atmospheric Research  
738 Component: Final Report for Phase 3. *CAWCR Technical Report No. 013*, 67.
- 739 Raupach, M. R., Briggs, P. R., Haverd, V., King, E. A., Paget, M., & Trudinger, C. M. (2012).  
740 Australian Water Availability Project. Retrieved from CSIRO Marine and Atmospheric  
741 Research, Canberra, Australia website: <http://www.csiro.au/awap>
- 742 Rech, A. R., Dalsgaard, B., Sandel, B., Sonne, J., Svenning, J.-C., Holmes, N., & Ollerton, J. (2016).  
743 The macroecology of animal versus wind pollination: Ecological factors are more  
744 important than historical climate stability. *Plant Ecology & Diversity*, 9(3), 253–262.  
745 <https://doi.org/10.1080/17550874.2016.1207722>
- 746 Roddy, A. B. (2019). Energy Balance Implications of Floral Traits Involved in Pollinator Attraction  
747 and Water Balance. *International Journal of Plant Sciences*, 180(9), 944–953.  
748 <https://doi.org/10.1086/705586>
- 749 Roddy, A. B., Martínez-Perez, C., Teixido, A. L., Cornelissen, T. G., Olson, M. E., Oliveira, R. S., &  
750 Silveira, F. A. O. (2020). Towards the flower economics spectrum. *New Phytologist*.  
751 <https://doi.org/10.1111/nph.16823>

- 752 Royal Botanic Gardens and Domain Trust, Sydney. (2021). PlantNET (The NSW Plant Information  
753 Network System). Retrieved 1 March 2021, from <https://plantnet.rbgsyd.nsw.gov.au>
- 754 Royal Botanic Gardens Victoria. (2021). VicFlora: Flora of Victoria. Retrieved 1 March 2021,  
755 from <https://vicflora.rbg.vic.gov.au/>
- 756 Sparrow, B. D., Foulkes, J. N., Wardle, G. M., Leitch, E. J., Caddy-Retalic, S., van Leeuwen, S. J., ...  
757 Lowe, A. J. (2020). A Vegetation and Soil Survey Method for Surveillance Monitoring of  
758 Rangeland Environments. *Frontiers in Ecology and Evolution*, *8*, 157.  
759 <https://doi.org/10.3389/fevo.2020.00157>
- 760 State Herbarium of South Australia. (2021). EFlora SA: Electronic Flora of South Australia.  
761 Retrieved 1 March 2021, from <http://www.flora.sa.gov.au/index.html>
- 762 Stemkovski, M., Pearse, W. D., Griffin, S. R., Pardee, G. L., Gibbs, J., Griswold, T., ... Irwin, R. E.  
763 (2020). Bee phenology is predicted by climatic variation and functional traits. *Ecology*  
764 *Letters*, ele.13583. <https://doi.org/10.1111/ele.13583>
- 765 Swenson, N. G., Enquist, B. J., Pither, J., Kerkhoff, A. J., Boyle, B., Weiser, M. D., ... Nolting, K. M.  
766 (2012). The biogeography and filtering of woody plant functional diversity in North and  
767 South America. *Global Ecology and Biogeography*, *21*(8), 798–808.  
768 <https://doi.org/10.1111/j.1466-8238.2011.00727.x>
- 769 ter Braak, C. J. F., Peres-Neto, P. R., & Dray, S. (2018). Simple parametric tests for trait–  
770 environment association. *Journal of Vegetation Science*, *29*(5), 801–811.  
771 <https://doi.org/10.1111/jvs.12666>
- 772 TERN. (2021). AusPlots ecosystem surveillance monitoring dataset. Retrieved 2 August 2021,  
773 from <http://aekos.org.au/>



- 774 Western Australian Herbarium. (2021). Florabase—The Western Australian Flora. Retrieved 1  
775 March 2021, from <https://florabase.dpaw.wa.gov.au/>
- 776 Wieczynski, D. J., Boyle, B., Buzzard, V., Duran, S. M., Henderson, A. N., Hulshof, C. M., ...  
777 Savage, V. M. (2019). Climate shapes and shifts functional biodiversity in forests  
778 worldwide. *Proceedings of the National Academy of Sciences*, *116*(2), 587–592.  
779 <https://doi.org/10.1073/pnas.1813723116>
- 780 Wingfield, J. C., Hahn, T. P., & Doak, D. (1993). Integration of environmental factors regulating  
781 transitions of physiological state, morphology and behaviour. In P. J. Sharp (Ed.), *Avian*  
782 *endocrinology* (pp. 111–122). Bristol, UK: Society for Endocrinology.
- 783 Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., ... Wilf, P. (2017). Global  
784 climatic drivers of leaf size. *Science*, *357*(6354), 917–921.  
785 <https://doi.org/10.1126/science.aal4760>
- 786 Yan, W., Wang, B., Chan, E., & Mitchell-Olds, T. (2021). Genetic architecture and adaptation of  
787 flowering time among environments. *New Phytologist*, *230*(3), 1214–1227.  
788 <https://doi.org/10.1111/nph.17229>
- 789 Zich, F. A., Hyland, B. P. M., Whiffin, T., & Kerrigan, R. A. (2020). Australian Tropical Rainforest  
790 Plants, Edition 8. Retrieved 1 March 2021, from <https://apps.lucidcentral.org/rainforest/>  
791

792 **Biosketch:**

793 Ruby E. Stephens is a plant ecologist with broad interest in the macroecology of plants and  
794 pollination. This work is part of her PhD on the macroecology and macroevolution of flowers  
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798 respective universities and lab groups.

799

800 **Author contributions:** R.E.S., R.V.G. and H.S. conceived the project; G.R.G. provided example  
801 code and assistance with AusPlots data, D.F. assisted with taxonomic name matching, M.J.  
802 calculated climate data. R.E.S. analysed the data; R.E.S. led the writing with assistance and  
803 review from all other authors.