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1 Is forest fecundity resistant to drought? Results from an 18-year rainfall-reduction experiment

2

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12

## 13 **Summary**

- 14 • Recruitment is a primary determinant of the long-term dynamics of plant populations  
15 in changing environments. However, little is known about the effects of anthropogenic  
16 environmental changes on reproductive ecology of trees.
- 17 • We evaluated the impact of experimentally induced 18 years of drought on  
18 reproduction of three contrasting forest trees: *Quercus ilex*, *Phillyrea latifolia*, and  
19 *Arbutus unedo*.
- 20 • Rainfall reduction did not decrease tree fecundity. Drought, however, affected the  
21 allocation of resources in *Q. ilex* and *A. unedo* but not the more drought-tolerant *P.*  
22 *latifolia*. Larger crop production by both *Q. ilex* and *A. unedo* was associated with a  
23 stronger decrease in growth in the rainfall-reduction plots compared to the control  
24 plots, suggesting that these species were able to maintain their fecundity by shifting  
25 their allocation of resources away from growth.
- 26 • Our results indicated resistance to change in tree fecundity in Mediterranean-type  
27 forest subjected to an average 15% decrease in the amount of soil moisture, suggesting  
28 that these ecosystems may adapt to a progressive increase in arid conditions.  
29 However, the species-specific reductions in growth may indirectly affect future  
30 fecundity and ultimately shift community composition, even without immediate direct  
31 effects of drought on tree fecundity.

32

33 **Keywords:** drought, fruit production, global change, mast seeding, rainfall-reduction,  
34 reproduction, tree fecundity,

35

## 36 **Introduction**

37 Anthropogenic environmental changes are exerting increasing pressure on forests worldwide  
38 (Gauthier et al. 2015, Seidl et al. 2017), and accumulating evidence indicates that climate  
39 change is causing dramatic forest diebacks (Allen et al. 2010, Seidl et al. 2017, Lloret and  
40 Kitzberger 2018). The critical question now concerns what ecosystems will follow from these  
41 profound transformations. Few studies, however, have compared the impacts of  
42 environmental change on the reproductive ecology of trees to other effects such as growth,  
43 carbon sequestration, mortality, or phenology (Barbeta et al. 2013, Hacket-Pain et al. 2016,  
44 Zohner et al. 2018, Luo et al. 2019). Ecosystem services, such as mitigating the risk of  
45 avalanches, carbon storage, habitat availability, and value for the economy and recreation, can

46 suffer if reduced reproduction slows forest expansion or limits the recruitment of  
47 merchantable tree species and seed producers that support wildlife (McShea 2000, Ostfeld  
48 and Keesing 2000, Clark et al. 2007, 2019, Bogdziewicz et al. 2016). The volatility of seed  
49 production and our poor understanding of the mechanisms that govern it are challenges for  
50 anticipating change in forest reproduction (Bogdziewicz et al. 2020a). Reliable predictive  
51 models are consequently not available, and the unpredictable recruitment of trees has become  
52 a key obstacle to understanding forest change (Ibáñez et al. 2009, Zhu et al. 2012).

53 Tree reproduction is sensitive to climate change (Mckone et al. 1998, Pearse et al.  
54 2014, Monks et al. 2016, Vacchiano et al. 2017). Observational studies of long-term trends in  
55 fecundity report both increases and decreases in mean reproductive effort in many important  
56 forest-forming species (Richardson et al. 2005, Mutke et al. 2005, Redmond et al. 2012, Allen  
57 et al. 2014, Buechling et al. 2016, Bogdziewicz et al. 2020b). A wide array of statistical tools  
58 used in these studies usually attributes these trends to global warming, but substantial  
59 uncertainty remains, as causality remains unestablished. Experiments that simulate  
60 environmental conditions projected by models of global change are thus useful for predicting  
61 the impacts of environmental global change on the reproductive patterns of forest trees. Such  
62 experiments usually report substantial effects. For example, *Pinus taeda* growing in an  
63 atmosphere enriched in CO<sub>2</sub> produced three-fold as many cones as trees growing under  
64 natural conditions (LaDeau and Clark 2001). Excluding rain reduced the production of seed  
65 biomass in *Quercus ilex* by thirty percent (Pérez-Ramos et al. 2010). Such experimental  
66 studies are nonetheless almost inevitably limited in time. A meta-analysis of global-change  
67 experiments have reported a dampening effect size of treatments (warming, nitrogen  
68 fertilization, or drought) over time (Leuzinger et al. 2011). Monitoring experimental systems  
69 as long as possible is thus desirable for assessing the long-term impacts of global change on  
70 forest fecundity.

71 The drought experiment in the Prades Mountains in southern Catalonia runs since  
72 1999, and is one of the longest running forest global-change experiments in the world (Wu et  
73 al. 2011, Barbeta et al. 2013, Peñuelas et al. 2018). The experiment is being conducted in a  
74 typical holm oak (*Q. ilex*) forest, where the oak is accompanied by other Mediterranean  
75 woody species with more (*Phillyrea latifolia*) and less (*Arbutus unedo*) drought tolerance  
76 (Peñuelas et al. 2018). Important demographic effects have already been observed, such as a  
77 higher mortality of stems and reduced growth, especially in *Q. ilex* and *A. unedo* (Lloret et al.  
78 2004, Ogaya and Peñuelas 2007b). The differences in the rates of growth and mortality  
79 between drought and control plots recorded at the beginning of the experiment eventually

80 decreased after some years (Barbeta et al. 2013, Liu et al. 2015). Decreased competition with  
81 high mortality after extreme droughts, and possible morphological and physiological  
82 acclimation to drought during the study period, may buffer forests against drier conditions  
83 (Barbeta et al. 2013, Liu et al. 2015, Peñuelas et al. 2018).

84 We evaluated the impact of experimentally induced drought on the fecundity of the  
85 dominant forest trees at our experimental site: *Q. ilex*, *P. latifolia*, and *A. unedo*. All three  
86 species mast at our sites, i.e. reproduced by the synchronous and temporally variable  
87 production of seeds (Kelly 1994). The sensitivity of reproduction of mast-seeding species to  
88 global change is predicted to be especially high, due to hypersensitivity of masting plants seed  
89 production to variation in the weather (Mckone et al. 1998, Monks et al. 2016, Vacchiano et  
90 al. 2017). In addition to the important trends in mean fecundity, changes in the strength of  
91 masting (i.e. the interannual variability and synchrony of reproduction) are crucial for tree  
92 fitness and forest regeneration, because masting is a life-history trade-off among missed  
93 reproductive opportunities in low-seed years, increased pollination efficiency, and decreased  
94 seed predation in mast years (Kelly 1994, Pearse et al. 2016, Bogdziewicz et al. 2020b). We  
95 thus also tested the effects on coupling between plants and variation among years, in addition  
96 to evaluating the effects of drought on mean fruit production. We predicted that drought  
97 would reduce mean reproductive output in *Q. ilex* and *A. unedo* but not *P. latifolia*  
98 (prediction 1) based on studies reporting that *P. latifolia* was much more drought-tolerant  
99 than the other two species (Ogaya and Peñuelas 2007b, Barbeta et al. 2013, Peñuelas et al.  
100 2018). We also predicted that the effect would dampen with time (prediction 2), paralleling  
101 the diminishing effects of drought on growth and mortality (Barbeta et al. 2013). The theory  
102 of mast seeding predicts that more frequent adverse weather would increase the interannual  
103 variability of seed production and strengthen the synchrony of reproductive variation among  
104 trees (Rees et al. 2002, Espelta et al. 2008, Bogdziewicz et al. 2018). We thus predicted an  
105 increase in annual variability and synchrony in all three species on experimental plots relative  
106 to the control, but likely less so in drought-resistant *P. latifolia* than in the other two species  
107 (prediction 3). Finally, we expected that the drought experiment would induce variation in  
108 the strength of the trade-off between growth and reproduction (prediction 4): the trade-off  
109 would be stronger under stressful conditions (drought) (Martín et al. 2015, Berdanier and  
110 Clark 2016, Hacket-Pain et al. 2017).

111

## 112 **Materials and Methods**

### 113 **Rainfall-reduction experiment**

114 We established the experimental site in 1999 on a 25% south-facing slope in the Prades Holm  
115 oak forest in southern Catalonia (northeastern Spain) (41°21'N, 1°2'E; 930 m a.s.l.). As a  
116 result of former coppicing the forest has a very dense multi-stem canopy layer (15433 stems  
117 ha<sup>-1</sup>) dominated by *Q. ilex* (5258 stems ha<sup>-1</sup>), *P. latifolia* (7675 stems ha<sup>-1</sup>), and *A. unedo*  
118 (1100 stems ha<sup>-1</sup>), accompanied by other Mediterranean woody species that usually do not  
119 reach the upper canopy (e.g. *Erica arborea* and *Juniperus oxycedrus*) and occasional isolated  
120 deciduous trees (e.g. *Sorbus torminalis* and *Acer monspessulanum*). Holm oak forests in the  
121 Prades Mountains grow throughout the altitudinal range (400–1200 m), presenting closed  
122 canopies 3–10 m in height depending on site quality. This forest has been managed as a  
123 coppice for centuries but has not been substantially disturbed for the last 70 years.

124 The site has a Mediterranean climate with a mean annual temperature of 12.4 °C and a  
125 mean annual precipitation of 610 mm during the study period (see Results). Annual and  
126 seasonal precipitation are irregularly distributed, with annual precipitation ranging from 355  
127 to 1021 mm in the 19 years of this study. Spring and autumn are the wettest seasons, and  
128 summer drought usually lasts three months, during which precipitation is ~10% of the annual  
129 total and coincides with the highest temperatures.

130 The experimental system consisted of eight 150-m<sup>2</sup> plots delimited at the same  
131 altitude along the slope. We randomly selected half of the plots to receive the drought  
132 treatment, and the other half had natural conditions. We partially excluded precipitation in the  
133 drought treatment using PVC strips suspended 0.5–0.8 m above the soil and covering  
134 approximately 30% of the plot surfaces, similarly as other drought experiments in  
135 Mediterranean systems (Limousin et al. 2008). We dug a ditch 0.8 m in depth along the top  
136 edge of the plots to intercept water runoff.

137 We installed an automatic meteorological station (Campbell Scientific Inc., Logan,  
138 USA) between the plots to monitor temperature, photosynthetic active radiation, air humidity,  
139 and precipitation, from which we obtained the Standardized Precipitation Evapotranspiration  
140 Index (SPEI) as a measure of atmospheric hydric conditions. SPEI is calculated as the  
141 difference between monthly precipitation and potential evapotranspiration (Beguería et al.  
142 2014). High and low SPEI values therefore indicate wet and drought conditions, respectively.  
143 We selected timescales of 3 (SPEI-3) and 6 (SPEI- 6) months, because they fit our annual  
144 data on plant growth and population dynamics analyzed in earlier studies (Barbeta et al. 2013,  
145 Liu et al. 2015). The SPEI values are provided for month and timescale of calculation (e.g.  
146 SPEI\_May3 refers to the water balance for March, April, and May of a given year). We also  
147 measured soil moisture each month throughout the experiment by time-domain reflectometry

148 (Tektronix 1502C, Tektronix, Beaverton, USA), connecting the time-domain reflectometer to  
149 the ends of three stainless-steel cylindrical rods, 25 cm long and fully driven into the soil, at  
150 four randomly selected locations per plot.

151 We randomly distributed 20 circular baskets (27 cm in diameter with a 1.5-mm mesh)  
152 on the ground in each of the eight plots and collected the fallen litter every two months from  
153 1999 to 2017. Fruits were weighed after drying in an oven at 70 °C to constant weight. We  
154 measured all living stems of all species with diameters >2 cm at a height of 50 cm each winter  
155 since 1999. We then calculated stem basal area increments (BAIs) and began in winter 2009  
156 to also measure the individuals with diameters <2 cm at the beginning of the study but which  
157 then attained or exceeded this size. In total, we measured 735 stems in *Q. ilex*, 842 in *P.*  
158 *latifolia*, 145 in *A. unedo*. Average (SD) number of stems per plot equaled 105 (47) in *Q. ilex*,  
159 128 (90) in *P. latifolia*, and 20 (14) in *A. unedo*.

160

### 161 **Model species**

162 Holm oak (*Quercus ilex* L.) is a drought- tolerant tree widely distributed in the Mediterranean  
163 basin. *Phillyrea latifolia* L. is a small tree associated with *Q. ilex* forests and more resistant to  
164 drought and high temperatures than *Q. ilex* (Ogaya and Peñuelas, 2003; Peñuelas et al. 2018).  
165 *Arbutus unedo* L. is another small tree typical of holm oak forests, less resistant to drought  
166 than *P. latifolia* (Ogaya and Peñuelas, 2003; Peñuelas et al. 2018). The reproductive  
167 phenologies of *Q. ilex* and *P. latifolia* are typical for Mediterranean species. Flowering takes  
168 place in spring, fruit development in summer and fruit maturation and seed dispersal in  
169 autumn (Ogaya and Peñuelas, 2004). In *A. unedo*, flower bud formation occurs in spring, but  
170 flowering takes place in the following autumn, and fruit development continues over a  
171 prolonged period until fruit matures in the autumn of the following year (Ogaya and Peñuelas,  
172 2004).

173

### 174 **Statistical analysis**

175 We evaluated the impact of excluding rain on soil-water content by building a linear  
176 mixed model (LMM), with soil moisture as the response and treatment (control vs drought) as  
177 a fixed effect. Month and year were included as random intercepts.

178 We next evaluated the impact of excluding rain on fruit production (fruit dry mass per  
179 plot) in the model species using LMMs that included log-transformed fruit mass as a  
180 response, with the interaction between treatment and year as fixed effects (prediction 1 & 2).  
181 The interaction was included to test for possible dampening effects of the drought treatment

182 on fruit dry mass production. We built a separate model for each species. Each model also  
183 included plot as a random intercept and SPEI as a covariate. The specific month for each  
184 SPEI was pre-identified for each species by fitting a partial least squares regression (PLS) of  
185 fruit production vs all possible SPEI values. PLS is designed to analyze a large array of  
186 related predictor variables, with insufficient sample sizes relative to the number of  
187 independent variables (Carrascal et al. 2009). The number of plot-years for the analysis was  
188 144 for *Q. ilex* and *P. latifolia* and 126 for *A. unedo*, which was absent in one of the plots.

189 We next evaluated the influence of the experimental drought on the interannual  
190 variability and synchrony of fruit dry mass production (prediction 2). We estimated the  
191 synchrony of fruit production for each treatment by calculating the mean pairwise cross-  
192 correlation of fruit production over all plots of a treatment. The cross-correlations were  
193 calculated using the mSynch function in the ncf package (Bjornstad and Falck 2001). We also  
194 calculated measures of interannual variability for the treatments using the coefficient of  
195 variation (CV) and a proportional variability index (PV) (Heath 2006). We used both indexes  
196 because CV can be skewed by its mean-dependency, while PV is not (Fernández-Martínez et  
197 al. 2018). Yet, CV is widely used to measure inter-annual variation in seed production,  
198 allowing among-studies comparisons. The corresponding 95% confidence intervals (CIs) for  
199 the focal values were calculated by bootstrap resampling with 1000 replications.

200 We built LMMs that included annual stem diameter increment (BAI) as a response to  
201 test whether excluding rain changes the trade-off between growth and fruit dry mass  
202 production in our model species, with the interaction between log-transformed fruit mass and  
203 treatment as a fixed effect (prediction 4). We built a separate model for each species. Each  
204 model included plot and tree as random intercepts. We also included SPEI values as  
205 covariates, which were similarly pre-selected for each species as in the models testing for the  
206 effects of treatment on fruiting. The BAIs were standardized within trees before inclusion in  
207 the models (i.e. we extracted the mean of each value and then divided it by the standard  
208 error). In each model, we also included a matrix for a natural cubic spline (df = 5) of tree size  
209 to account for growth-related trends in BAI, using the ns function from splines package. The  
210 sample sizes for these models, i.e. per stem per year observations, were 11 288 for *Q. ilex* (735  
211 stems measured), 15 301 for *P. latifolia* (842 stems), and 2242 for *A. unedo* (145 stems).

212 We fitted all models using the glmmTMB package (Brooks et al. 2017) in R. Models  
213 were validated, including tests for homoscedasticity and normality of residuals and potential  
214 outliers, using the DHARMA package (Hartig 2019). We also explored all models with



215 temporal autocorrelation structures (ar1) and retained or rejected them based on standard  
216 Akaike information criteria.

217

## 218 **Results**

219 The drought treatment decreased the soil moisture by ~10–30% during the study period ( $z =$   
220  $8.32, p < 0.001$ ), with larger differences during periods of rain (Fig. 1). The drought treatment  
221 decreased the amount of soil moisture by ~20% or more during these periods but by <10%  
222 during dry periods. Median reduction equaled 13%, while mean 15%.

223 The drought treatment did not decrease fruit dry mass production in any of the species  
224 (Fig. 2), contrary to our expectations (prediction 1). The interaction between treatment and  
225 year was not significant for any of the species ( $p > 0.10$ ) (prediction 2). The drought treatment  
226 without the interaction term did not significantly affect fruit production by *Q. ilex* ( $z = -0.64,$   
227  $p = 0.52$ ), *P. latifolia* ( $z = 0.10, p = 0.92$ ), or *A. unedo* ( $z = -1.60, p = 0.11$ ). SPEI was  
228 positively correlated with crop production for all three species (*Q. ilex*: SPEI\_March3,  $z =$   
229  $4.49, p > 0.001$ , *P. latifolia*: SPEI\_March3,  $z = 5.29, p > 0.001$ , *A. unedo*: SPEI\_December3,  
230  $z = 2.59, p = 0.01$ ).

231 The variability of fruit production among years was high for all species, with positive  
232 pairwise cross-correlations in fruiting among plots (mean cross-correlation >0.60 for all  
233 species, Fig. 3). Both interannual variability, as measured by either PV or CV, and synchrony,  
234 were unaffected by excluding rain for all three species ( $p > 0.05$ ), contrary to our expectations  
235 (prediction 3).

236 Excluding rain affected reproductive allocation for *Q. ilex* and *A. unedo* but not *P.*  
237 *latifolia* (Fig. 4) (prediction 4). *Q. ilex* fruit production was positively correlated with growth  
238 in the control plots ( $\beta$  [SE] = 0.06 [0.005];  $z = 10.85, p < 0.001$ ), but the slope of the  
239 relationship ( $\beta$  [SE] = 0.04 [0.005];  $z = 7.50, p < 0.001$ ) was lower in the drought plots  
240 (interaction term:  $z = -5.57, p < 0.001$ ). Fruit production by *A. unedo* was similarly positively  
241 correlated with growth in the control plots ( $\beta$  [SE] = 0.05 [0.009];  $z = 5.86, p < 0.001$ ), but the  
242 slope of the relationship ( $\beta$  [SE] = 0.02 [0.01];  $z = 2.06, p = 0.04$ ) was lower in the drought  
243 plots (interaction term:  $z = -2.15, p = 0.03$ ). *P. latifolia* growth was positively correlated with  
244 reproduction ( $\beta$  [SE] = 0.05 [0.003];  $z = 14.78, p < 0.001$ ), and the induced drought did not  
245 affect this pattern (interaction term:  $z = -0.97, p = 0.33$ ). Cubic splines of size were not  
246 significant predictions of BAI in all three species ( $p < 0.10$ ).

247

## 248 **Discussion**

249 The 18-year experimental rainfall reduction did not decrease tree fecundity, contrary to  
250 predictions. The year-to-year variability and synchrony of reproduction was also unaffected  
251 the levels of drought induced by our experiment. Drought, however, affected the allocation of  
252 resources in *Q. ilex* and *A. unedo* but not the more drought-tolerant *P. latifolia*. Production of  
253 larger crop size by both *Q. ilex* and *A. unedo* was associated with a stronger decrease in  
254 growth in the rainfall-reduction plots compared to the control plots, suggesting that these  
255 species were able to maintain their fecundity by shifting their allocation of resources away  
256 from growth.

257 Theory predicts that tree reproduction will be sensitive to climate change, due to  
258 strong correlations between seed production and annual variation in the weather (Pearse et al.  
259 2016). Fruit production by the three species studied here was previously correlated with  
260 drought severity (Ogaya and Peñuelas 2007a, Espelta et al. 2008, Bogdziewicz et al. 2017b),  
261 but fecundity was resistant to the level of drought induced by this experiment. One possibility  
262 is that water stress induced by natural drought also includes decrease in atmospheric water  
263 availability. While our rainfall reduction treatment cannot affect that, both soil moisture and  
264 atmospheric demand for water independently limit and affect vegetation productivity and  
265 water use during periods of hydrologic stress (Novick et al. 2016). What is more, the  
266 synchrony and interannual variability of reproduction were consequently also unaffected.  
267 More frequent adverse weather, such as drought, should increase variability and synchrony  
268 among years by decreasing reproduction in some years, thus strengthening the reinforcing  
269 effects of stored resources on the synchrony of reproductive variation among trees (Rees et al.  
270 2002, Espelta et al. 2008, Bogdziewicz et al. 2018, 2019). Such effect is, however, only  
271 expected in the case of very intense drought episodes when reproductive failures happen more  
272 frequently (Espelta et al. 2008), which was not the case in our forest.

273 Our results imply that the maintenance of fecundity under drought stress was possible  
274 by decreasing growth in *Q. ilex* and *A. unedo*, indicated by changes in the trade-off between  
275 growth and reproduction with and without stress. The slope of the positive relationship  
276 between fruit production with growth was reduced by over 30% in *Q. ilex*, and 60% in *A.*  
277 *unedo* in drought treatment compared to control. *P. latifolia* was in turn able to sustain both  
278 growth and reproduction under induced drought. Stem growth in the drought treatment was  
279 >60% lower for *A. unedo*, >17% lower for *Q. ilex*, and was unaffected for *P. latifolia*  
280 compared to the control plots (Barbeta et al. 2013). Drought reduces transpiration by stomatal  
281 closure in *Q. ilex* and *A. unedo*, which decreases the assimilation of carbon (Limousin et al.  
282 2009, Ripullone et al. 2009). Drought also increases litterfall, likely due to xylem cavitation

283 that accelerates foliar senescence (Choat et al. 2012, Liu et al. 2015). Defoliation in turn  
284 decreases the carbon content of plant tissues (Rosas et al. 2013), suggesting that drought  
285 stress decreased resource availability in *Q. ilex* and *A. unedo* and forced the trees to partition  
286 the limited resources to reproduction at the expense of growth, providing experimental  
287 evidence for intraspecific variability and phenotypic plasticity in the cost of reproduction due  
288 to habitat differences. Alternatively, the positive association between growth and fruit  
289 production could follow from both growth and reproduction responding similarly to water  
290 availability. If in the drought treatment decreases variability in water availability, it could  
291 weaken the correlation between growth and fruiting. However, our data suggest that the  
292 variance in soil moisture was similar in both treatments (Levene's Test,  $F = 0.44$ ,  $p = 0.51$ ;  
293 Fig. 1d). Another important implication of these findings is that *Q. ilex* has avoided reduced  
294 growth associated with reproduction throughout most of its range (Pérez-Ramos et al. 2010,  
295 Fernández-Martínez et al. 2015), but our results imply that it may not continue do so in the  
296 near future due to the progressive increase in drought frequency predicted by models of global  
297 change.

298         Generally positive relationship between growth and reproduction in all three species,  
299 indicate that favorable meteorological conditions could increase the accumulation of  
300 resources and their subsequent allocation to both growth and reproduction in certain years  
301 (Norton and Kelly 1988, Vergotti et al. 2019). Nonetheless, the maintenance of reproduction  
302 at the expense of growth, together with the previously established link between drought,  
303 reduced growth, and elevated mortality at our site (Ogaya and Peñuelas 2007b, Barbeta et al.  
304 2013, Liu et al. 2015), well supports the theory of the cost of reproduction in plants, where  
305 current reproductive allocation at the expense of growth is predicted to influence the  
306 probability of future survival (Obeso 2002). The lack of direct effects of drought on fecundity  
307 thus does not preclude indirect costs of fecundity from sustained lower growth rates, which  
308 may influence future reproduction.

309         The results of this study indicated substantial resistance of tree fecundity in a *Q. ilex*  
310 dominated forest subjected to an average 15% (median 13%) decrease in the amount of soil  
311 moisture. The length of the study provides consistency to these results. Growing evidence  
312 indicates that *Q. ilex* dominated forests are resistant to an increase in drought to some extent,  
313 suggesting that these ecosystems may adapt to a progressive increase in arid conditions  
314 (Peñuelas et al. 2018). Our study, however, comes with an important warning. The species-  
315 specific reductions in growth and increased mortality (Ogaya and Peñuelas 2007b, Barbeta et

316 al. 2013) may indirectly affect future fecundity and ultimately shift community composition,  
317 even without immediate direct effects of drought on tree fecundity.

318

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325

### 326 **Author Contribution**

327 All authors conceived the study, RO and JP collected data, MB and MFM ran the analysis, all  
328 authors participated in the evaluation of the results, MB drafted the manuscript, and all  
329 authors participated in the editing and approved the final version.

330

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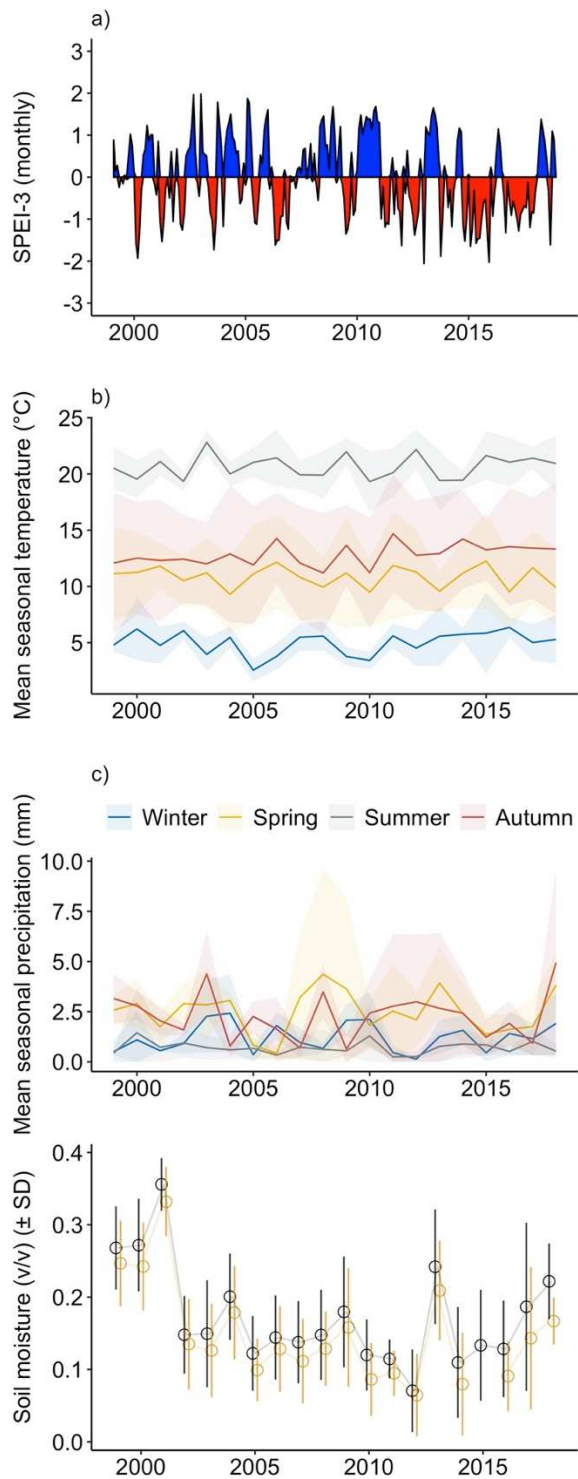
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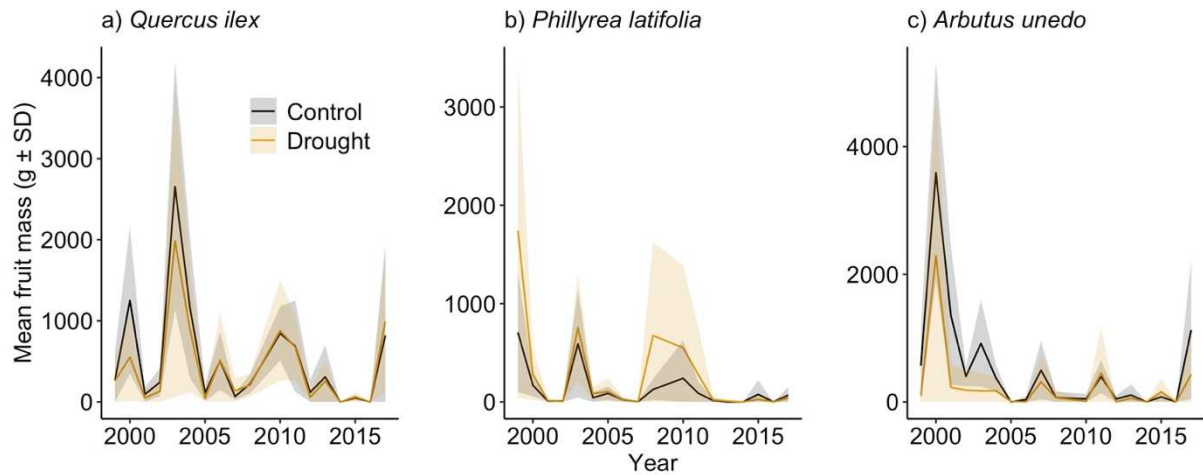
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533 Figure 1. Abiotic conditions at the experimental site in the Prades Mountains in southern  
534 Catalonia. a) SPEI-3, b) temperature, c) precipitation, and d) soil moisture. Data for soil  
535 moisture was not collected in 2015 due to equipment malfunction.



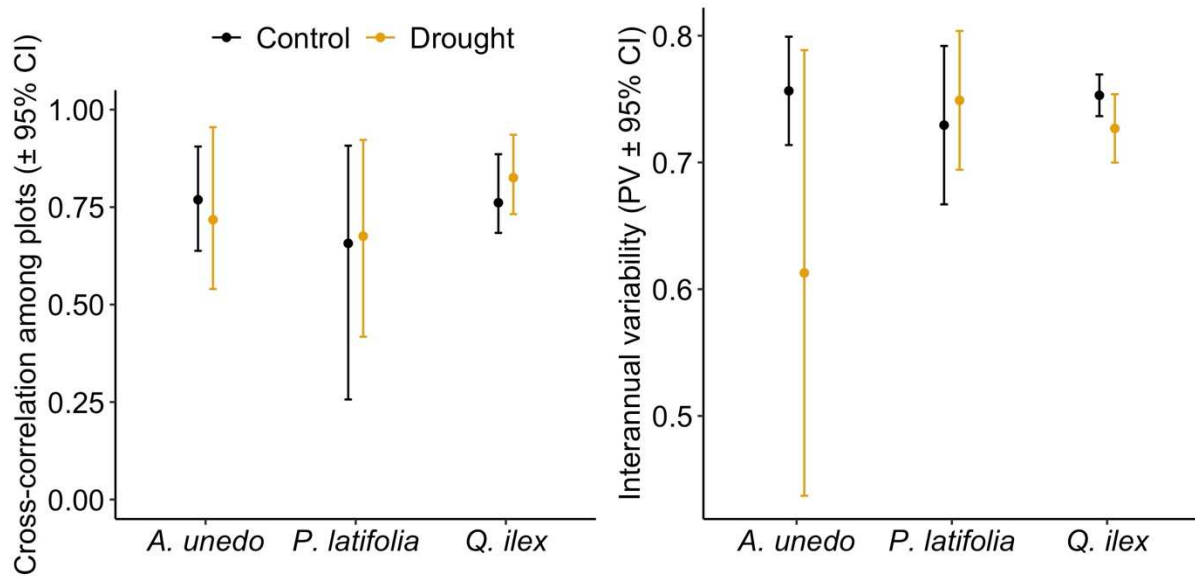
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537 Figure 2. Fruit production by a) *Quercus ilex*, b) *Phillyrea latifolia*, and c) *Arbutus unedo* in  
538 the control and drought plots. The solid lines and shaded areas are annual means and  
539 associated standard deviations, respectively. The number of observations of reproductive  
540 events is 144 (plot-years) for *Q. ilex* and *P. latifolia* and 126 for *A. unedo*, which was absent  
541 in one of the plots. *Q. ilex* and *P. latifolia* were observed at 8 plots, while *A. unedo* at 7.



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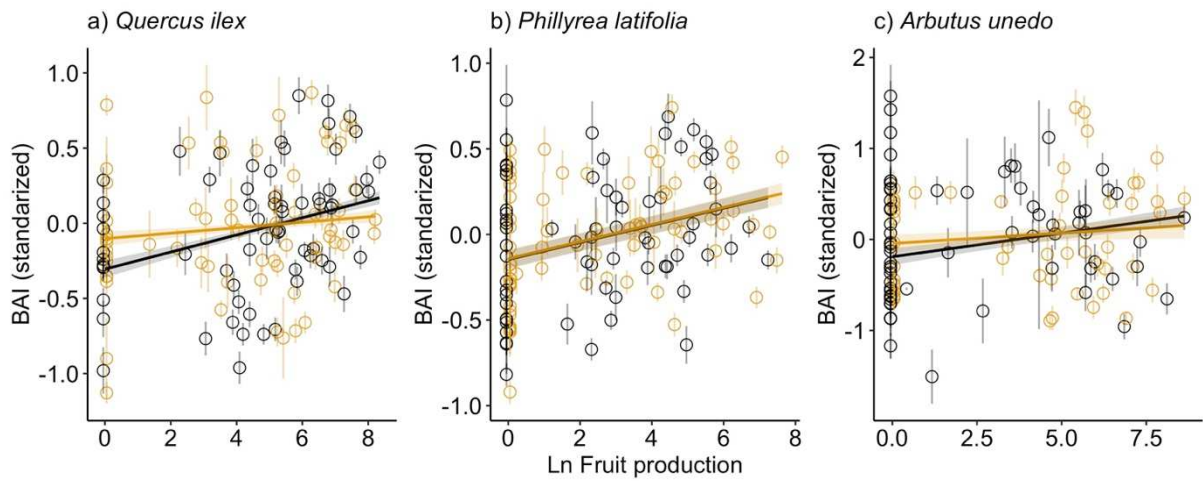
550 Figure 3. Synchrony and interannual variability (PV) of fruit production by *Quercus ilex*,  
551 *Phillyrea latifolia*, and *Arbutus unedo* in the control and drought plots. Synchrony was  
552 measured by mean pairwise Pearson correlation among plots. CV not shown.



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555 Figure 4. Scatterplots of standardized basal area increment (BAI) and fruit production for a)  
556 *Quercus ilex*, b) *Phillyrea latifolia*, and c) *Arbutus unedo* in the control and drought plots.  
557 The lines and shaded areas are the linear mixed model predictions and associated 95%  
558 confidence intervals, respectively. Points and whiskers are plot-year means and associated  
559 standard errors, respectively. Black represents the control, and yellow represents experimental  
560 rainfall exclusion. The sample sizes for these models are 11288 for *Q. ilex* (735 stems  
561 measured), 15301 for *P. latifolia* (842 stems), and 2242 for *A. unedo* (145 stems).  
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