

1 **Temporal trends in the Enhanced Vegetation Index and spring weather predict**  
2 **seed production in Mediterranean oaks**

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19 **Keywords**

20 Seed production; acorns; masting; *Quercus ilex*; EVI; drought

21

22 **Abstract**

23 The extremely year-to-year variable production of seeds (*masting*) is an extended plant reproductive  
24 behaviour important for forest dynamics and food webs. The dependence of these episodes of massive seed  
25 production on recently or long-term photosynthesised carbohydrates, however, remains controversial. In this  
26 paper, we explore whether vegetation (tree canopy) changes, detected using EVI as a proxy of leaf area and  
27 photosynthetic capacity, can provide a reliable estimation of seed production. To complete this analysis, we also  
28 explored the effect of weather both in the trends of EVI and in acorn crop size. To this end, we compared the  
29 trends of the EVI and acorn production over 10 years (2000-2009) in five stands of *Quercus ilex* L. in Barcelona  
30 (Catalonia, NE Spain). We found that acorn production was mainly driven by a combination of: i) a minimum  
31 initial threshold in the EVI values, ii) an increase in EVI in the  $9 \pm 4$  months prior to reproduction, and iii)  
32 appropriate weather conditions (low water stress) during spring. These results indicated, apparently for the first  
33 time, that reproduction in masting species could be detected and partly predicted by remotely sensed vegetative  
34 indices. Our results suggested that this particular reproductive behaviour in Mediterranean oaks was driven by a  
35 combination of two factors, i.e. good and improving vegetation conditions, as shown by a minimum initial  
36 threshold and the increase in EVI needed for large seed crops, and the need of wet weather conditions during  
37 spring. Moreover, our results fully supported recent studies that have associated short-term photosynthate  
38 production with seed production.

39 **Keywords**

40 Seed production; acorns; masting; *Quercus ilex*; EVI; drought

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## 51 **1. Introduction**

52 The synchronous but erratic year-to-year production of seeds, i.e. *masting*, is a widely geographically and  
53 taxonomically extended reproductive behaviour (Kelly and Sork 2002). Masting events have cascading effects  
54 on several forest functions and processes (Ostfeld and Keesing 2000) such as seedling establishment (Negi et al.  
55 1996, Espelta et al. 2009), the regulation of the populations of seed consumers (McShea 2000, Espelta et al.  
56 2008), and the propagation of diseases (e.g. lyme disease (Ostfeld, 1997)). Notwithstanding this, what drives  
57 this phenomenon is one of the most puzzling questions about the dynamics of forest ecosystems (Koenig and  
58 Knops 2005).

59 Whether seed production in masting species is controlled by recently acquired or accumulated resources  
60 (e.g. carbohydrates and nutrients) remains controversial (Koenig and Knops 2000; Kelly and Sork 2002; Sala et  
61 al. 2012). On the one hand, the *resource matching* hypothesis (Sork et al. 1993; Kelly and Sork 2002) states that  
62 plants produce large or poor seed crops in direct response to the immediate availability of resources, i.e. more  
63 favourable weather conditions for photosynthesis would lead to larger harvests (e.g. Espelta et al. 2008; Espelta  
64 et al. 2009). On the other hand, the *resource budget model*, or the *resource accumulation* hypothesis (Sork et al.  
65 1993; Isagi et al. 1997), suggests that plants produce extraordinary seed crops when a resource threshold is  
66 reached after several years of progressive accumulation. This latter hypothesis predicts that plant resources are  
67 depleted to sustain the masting episode, so that flowering and seed production are expected to be very low or  
68 absent in the next growing season, causing a negative autocorrelation between consecutive seed crops (Koenig  
69 and Knops 2000). The consequences of resource depletion after a masting episode may include signs such as a  
70 reduction in the leaf area due to self-thinning (Camarero et al. 2010) or a decrease of nitrogen and phosphorous  
71 concentrations in branches (Sala et al. 2012).

72 Recent studies based on carbon isotopes suggest that seed production in several tree species in temperate  
73 forests depends only on the carbohydrates photosynthesised during the months prior to seeding (Ichie et al.  
74 2013; Hoch et al. 2013). Unfortunately, the measurement of resource availability at a plant level is time-  
75 consuming and expensive and so is difficult to perform at broad spatial and temporal scales. Conversely,  
76 remotely sensed vegetation indices may be useful proxies for monitoring the fluctuations of trees resources at  
77 large temporal and spatial scales. Indeed, spectral indices such as the Normalized Difference Vegetation Index  
78 (NDVI) and the Enhanced Vegetation Index (EVI) provide good descriptions of the state of green vegetation  
79 (e.g. crown cover, leaf area index, and greenness) and its temporal dynamics. These indices have thus been

80 widely used to monitor the functional traits involved in the carbon cycle (Garbulsky et al. 2008) and also as  
81 annual integrators of carbon uptake in forests (Garbulsky et al. 2013). Few studies, however, have yet applied  
82 remotely sensed vegetation indices to predict seed crop production in forest ecosystems, particularly in masting  
83 species (but see Camarero et al., 2010). In this sense, a successful methodology to predict seed crops would  
84 allow managers to better plan management actions in the near future (e.g., wildlife conservation strategies).

85 The aim of this study was to explore whether the pattern of seed production in Mediterranean oak (*Quercus*  
86 spp.) forests could be governed by the temporal dynamics of tree canopies, assessed by means of remote  
87 sensing indices. We hypothesise that vegetation changes, detected using EVI, represent a reliable proxy of the  
88 tree resources available for seed production. Therefore, if an accumulation of resources (e.g. carbohydrates and  
89 nutrients) for several years is a prerequisite for a masting event, EVI should progressively increase during that  
90 period of accumulation. Similarly, if a severe depletion of resources occurs after a masting episode, EVI should  
91 decrease due to the self-thinning of the canopy. In addition, given the nature of the Mediterranean climate, we  
92 hypothesise that weather conditions (e.g. drought) must be an important driver of the temporal dynamics of both  
93 EVI and acorn crop size. To address these questions, we used a data set comprising 12 years (1998-2009) of  
94 acorn production in five oak stands in Collserola Natural Park (Catalonia, NE Spain) and 11 years (2000-2010)  
95 of EVI data derived from MODIS (MODerate Resolution Imaging Spectroradiometer) images of each forest  
96 stand.

97

## 98 **2. Materials and methods**

### 99 *2.1. Study area and species*

100 This study was conducted in the Collserola massif (41°26'N, 02°06'E), whose vegetation is dominated by  
101 *Q. ilex*. The study area has a Mediterranean climate and a mean annual temperature of  $15.7 \pm 1.4$  °C. January is  
102 the coldest month ( $8.5 \pm 0.6$  °C) and August the warmest ( $24.3 \pm 0.7$  °C). Mean annual precipitation reaches  
103  $613.8 \pm 34.0$  mm (coefficient of variation (CV) = 0.25; values from the Fabra Observatory at 415 m.a.s.l. for the  
104 current climatological standard normal period, 1991-2010). We selected forest stands of *Q. ilex* because it is the  
105 most abundant tree species in Collserola, has a strong masting behaviour (Espelta et al. 2008; Fernández-  
106 Martínez et al. 2012), and has evergreen leaves that allow continuous monitoring using remotely sensed  
107 vegetative indices. Regarding *Q. ilex* fruiting phenology, the pollination period normally starts during the first  
108 week of April and pollen release reaches its maximum during May (Fernández-Martínez et al. 2012). Pollinated

109 flowers are then ripened until mid-September, when the harvest begins. We selected five 10 m radius stands  
110 (plots A to E), distributed along the Collserola massif, of nearly pure *Q. ilex* stands to maximise the accuracy of  
111 estimates of leaf area (more than 72% of the trees were *Q. ilex* in all plots) being representative of the nearby  
112 area. The selected forests were very dense (coppiced stands of  $1357 \pm 219$  *Q. ilex* stems per hectare), mostly  
113 resulting from resprouting and relatively young (ca. 40-60 years), presenting  $10.5 \pm 0.4$  cm as mean diameter at  
114 breast height and around 3 to 4 m of height.

115

## 116 2.2. *Experimental design and sampling*

### 117 2.2.1. *Acorn crop data*

118 Acorn production was monitored from 1998 to 2009. Fifteen trees per plot were tagged, and the number of  
119 branches per tree was estimated using a regression model between crown projection and the number of branches  
120 previously determined for a subsample of trees (see Espelta et al. 2008). Acorn production on four branches per  
121 tree was recorded each September, i.e. at the peak of seed production in holm oaks before acorns were ripe  
122 enough to fall or to be harvested in appreciable number by birds (see Abrahamson and Layne 2002). The total  
123 number of acorns produced per tree was estimated by multiplying the mean acorn production per branch by the  
124 number of branches per tree (see Espelta et al. 2008 for further details). Since aborted and infested seeds usually  
125 fall much before maturation happens, insect-infested or aborted acorns do only consume a small amount of the  
126 tree resources, mostly insignificant in comparison with those needed in a mast year. Therefore, we did not take  
127 these acorns into account.

128

### 129 2.2.2. *Estimates of canopy cover: satellite data*

130 The NDVI and the EVI can be used to monitor temporal and spatial changes in leaf area and in the fraction  
131 of photosynthetically active radiation (fPAR) intercepted by the canopy (Myneni et al. 2002; Fensholt et al.  
132 2004; Sprintsin et al. 2007). Both indices provide similar information, but we decided to use the EVI because: i)  
133 the NDVI saturates earlier at high levels of greenness (Huete et al. 2002) and our forests were very dense and ii)  
134 because it has been recently demonstrated to successfully monitor biomass in Mediterranean holm oak (Ogaya  
135 et al. 2015). We thus used the EVI values as surrogates of photosynthesising leaf area and the available  
136 resources of the trees. Data were extracted from the Terra MOD13Q1 product of MODIS for the period  
137 between 18 February 2000 and 19 December 2010, with a 16-day periodicity and a spatial resolution of 250 x

138 250 m<sup>2</sup> (pixel size = 6.25 ha), for the pixels that covered each forest stand. The pixels selected were almost  
139 entirely homogeneous with regard to vegetation type and crown cover, thus coinciding with the features of the  
140 sampled trees.

141

### 142 2.2.3. Meteorological data

143 Acorn crop size in Collserola is highly controlled by weather conditions (Fernández-Martínez et al. 2012).  
144 We thus gathered meteorological data from the Fabra Observatory (41°25'N, 02°07'E) to calculate the  
145 Standardized Precipitation-Evapotranspiration Index (SPEI, Vicente-Serrano et al. 2010) on a monthly basis and  
146 for the whole time series for time scales of 1, 3, 6, 9, and 12 months using the SPEI package (Begueria and  
147 Vicente-Serrano 2012) of R (R Core Team 2013). Positive values of the SPEI indicate above-average wet  
148 periods, and negative values indicate drought. Since vegetation may present a lagged responses to prolonged  
149 drought periods (Vicente-Serrano et al. 2013) SPEI was calculated for different time scales to determine the  
150 influence of weather conditions on acorn production and the EVI signal for different periods of time.

151

### 152 2.3. Data analysis

153 We first calculated mean acorn production per tree for each plot and year. Then we described the masting  
154 behaviour of our holm oak populations using the most common metrics (Kelly and Sork 2002): i) the CVs of  
155 seed production as measures of interannual variability at the population (CV<sub>p</sub>) and the individual (CV<sub>i</sub>) levels,  
156 ii) Spearman's  $r$  coefficients as measures of synchrony in seed production among plots ( $r_p$ ) and among  
157 individual trees within a plot ( $r_i$ ), and iii) the mean temporal autocorrelation of seed production of the trees  
158 within a plot using simple and partial autocorrelation functions (ACF and PACF, respectively) to the fourth  
159 time lag. We also calculated these metrics for the mean annual EVI values to check for similarities in the time  
160 series of both acorn production and the EVI. Standard errors of these variables were calculated using the  
161 bootstrap method (Efron 1987).

162

#### 163 2.3.1. Testing the effect of weather on EVI time series

164 We tested the effect of weather on the EVI by two methods. i) We first calculated the standardised and  
165 deseasonalised monthly EVI time series using an additive seasonal decomposition. These time series indicated  
166 whether a particular month (e.g. January 2000) was above or below the mean for that month (January) in units

167 of standard deviations (SDs). We then smoothed the EVI time series using local regressions (LOESS, Cleveland  
168 1979) to remove noise and identify trends or low-frequency periodicities in the time series. This methodology  
169 would also help to deal with potential noise addition in the estimation of EVI as a consequence of the flowering  
170 intensity (Shen et al. 2014). Finally, we correlated the smoothed EVI time series with the SPEI time series (1, 3,  
171 6, 9, and 12) using Pearson correlations. ii) We calculated the seasonally averaged EVI and SPEI values (e.g.  
172 winter EVI: mean EVI from January to March) for each year to correlate with each other (EVI vs. SPEI) to  
173 identify the season in which the SPEI was better correlated with the EVI. Spearman correlations were used for  
174 this procedure. To avoid increasing false discovery rate,  $P$  values were adjusted using the Bonferroni correction.

175

### 176 *2.3.2. Testing the effect of weather and the EVI on seed production*

177 We performed a two-step analysis to determine the relationships among weather, the EVI, and acorn  
178 production. First, we explored the relationships of seasonally averaged SPEI and EVI time series with acorn  
179 production to identify the season when SPEI has the largest effect on EVI. Then, we tested the correlation  
180 between acorn production and the seasonally averaged time series of SPEI and EVI. We used Spearman  
181 correlations for this procedure because the acorn-production data were not normally distributed. Second, we  
182 used the smoothed EVI time series to test whether tree resources increased before large seed crops (i.e. masting  
183 events) by looking for evidence of an increasing EVI prior to masting. We identified all changes in the trends  
184 (e.g. from increasing to decreasing EVI) of the smoothed time series and considered an EVI trend to be the  
185 period between two of these points of change (peaks or valleys). We chose not to calculate trends for fixed  
186 periods of time because weather drives the phenology of these trees from year to year (Fernández-Martínez et  
187 al. 2012), and the periods of resource accumulation might thus occur during slightly different periods depending  
188 on the particular meteorological characteristics of the year. Then we assigned each trend to the most plausibly  
189 influenced harvest, starting at least five months (spring) before the harvest season (October). We also calculated  
190 the initial and final EVI values ( $EVI_i$  and  $EVI_f$ , respectively, units in SD) and the increment in the EVI (i.e.  
191  $\Delta EVI = EVI_f - EVI_i$ ) of each trend.

192 To test the influence of weather, the EVI, and previous acorn harvests on acorn production, we constructed  
193 a generalised linear mixed model (GLMM) fitted using the negative binomial distribution, using the natural  
194 logarithm as the link function, to correct for overdispersion. The model included the plot as a five-level random  
195 factor. The fixed effects were an SPEI variable (best correlated with acorn production),  $\Delta EVI$ ,  $EVI_i$ ,  $EVI_f$ , and

196 the acorn production of the previous year as covariates. We also included the interaction of  $\Delta\text{EVI}$  with  $\text{EVI}_i$  and  
197  $\text{EVI}_f$  to test for possible synergic effects of an increasing EVI and the initial or final level reached in the EVI.  
198 The inclusion of the acorn production of the previous year allows the testing for a negative autocorrelation in  
199 seed production that would suggest a depletion of resources after mast years (Sork et al. 1993). The minimum  
200 adequate model was achieved by deleting all non-significant predictors and minimising the Akaike information  
201 criterion. The models were fitted using the R package *lme4* (Bates et al. 2013).

202

#### 203 *2.3.4. Testing for the reduction of leaf area after large seed crops*

204 To test whether the crowns of trees were self-thinned after mast seeding, we analysed the entire 16-day  
205 EVI time series with the Breaks For Additive Seasonal and Trend (BFAST) methodology using the R package  
206 *bfast* (Verbesselt et al. 2010a; Verbesselt et al. 2010b). We used this technique due to its ability to integrate the  
207 decomposition of time series into trend, seasonal, and residual components with methods for detecting changes  
208 in trends and seasonal behaviour. We configured BFAST to detect one break per year because we expected to  
209 find breaking points in the deseasonalised EVI time series after episodes of mast seeding.

210

### 211 **3. Results**

#### 212 *3.1. Synchrony, interannual variability, and temporal autocorrelation in acorn production and the EVI*

213 Two clear mast seeding episodes occurred in our experimental plots, in 2002 and 2008 (Figures 1 and 2).  
214 Another masting event of extremely high acorn production occurred in plot D in 2004, but the other stands  
215 produced moderate amounts of acorns, so that we could not clearly define 2004 as a mast year for our holm oak  
216 plots (Figure 2). The time series of acorn production in all forest stands, however, presented a typical masting  
217 profile: high synchrony ( $r_i$  among trees and  $r_p$  among plots), high interannual variability at the individual ( $\text{CV}_i$ )  
218 and the population ( $\text{CV}_p$ ) levels, and negative temporal autocorrelation (Table 1). No significant differences  
219 were found for  $r_p$ ,  $r_i$ ,  $\text{CV}_p$ ,  $\text{CV}_i$ , and temporal autocorrelation among plots (using bootstrapped standard errors of  
220 the means). The average synchrony ( $r_p$ ) in the mean annual EVI was  $0.68 \pm 0.03$  (Table 1). The CVs of the EVI  
221 values were very low ( $\sim 0.05$ ) and did not differ from zero (were not significant) due to error propagation,  
222 although the  $r$  values were quite high.

223

#### 224 *3.2. Effects of weather and an increasing EVI on acorn production*



225 Droughts and wet periods (i.e. negative and positive SPEI9 values – SPEI for a 9-month window) were  
226 correlated with low and above-average EVI values, respectively (Figure 1). The correlation analysis confirmed  
227 that the EVI could be driven by the cumulative effect of weather conditions during the previous nine months ( $r$   
228  $= 0.50$ ,  $P < 0.001$ ; Table 3). Additionally, acorn crops were larger after wetter seasons and when they were  
229 preceded by larger increases in the EVI during the previous months (Figures 1 and 2). Acorn crop sizes,  
230 however, were still very low when these periods of increasing EVI began from very low EVI values and did not  
231 reach above-average values (Figures 1 and 2).

232 The selected periods of increasing or decreasing EVI values (Figure 2, shaded periods) lasted, on average,  $9$   
233  $\pm 4$  months (range: 4-16 months). Most of these periods began during the summer or autumn of the previous  
234 year or during the winter of the year in which acorns were produced, and they ended mostly in summer (Figure  
235 2). Acorn crop size was positively correlated with  $SPEI6_{jn}$ ,  $EVI_i$ , and  $\Delta EVI$  (Table 2). The best model  
236 predicting acorn production included  $SPEI6_{jn}$  (i.e. SPEI comprising six months from January to June),  $EVI_i$ ,  
237  $\Delta EVI$ , and a positive interaction between  $EVI_i$  and  $\Delta EVI$ . In this model, the effect of acorn production in the  
238 previous years was negligible. These results confirmed the visual inspection of Figures 1 and 2: large acorn  
239 crops were correlated with both wet spring periods and a previous trend of increasing EVI but depended on the  
240 values at which this trend started. Interestingly, the positive interaction between  $EVI_i$  and  $\Delta EVI$  on acorn  
241 production (Table 2; Figure 3) highlighted the importance of reaching an initial EVI threshold before the  
242 beginning of the increasing EVI period.

243

### 244 *3.3. Effects of masting events on crown condition*

245 The BFAST methodology failed to identify a clear pattern of abrupt decreases in the trend of the EVI after  
246 the two observed masting events (Figure 2). Two stands (B and D) presented a break during 2005, and one plot  
247 (A) presented a break after 2003, possibly associated with the severe droughts that occurred in those years.  
248 Another plot (C) did not present any breaks during any time series, and only two of the five plots (A and E)  
249 presented one break that could be associated with the masting episode of 2002.

250

## 251 **4. Discussion**

252 To our knowledge, we report for the first time that mast seeding events can be detected and, to some extent,  
253 predicted using remotely sensed vegetative indices such as the EVI. The masting events observed in this study

254 followed an average period of increase in the EVI (a surrogate of potential photosynthetic capacity) of  $9 \pm 4$   
255 months but also required favourable weather conditions in spring (low levels of water stress, SPEI<sub>6,m</sub>). In  
256 addition to these two factors, the initial EVI value at the start of an EVI increase period was also important, i.e.  
257 a large increase in the EVI did not lead to a masting event unless it departed from a minimum EVI<sub>i</sub> threshold  
258 (Table 2; Figures 1, 2, and 3). This initial EVI threshold may suggest the need of a minimum amount of  
259 previously stored resources to produce buds before a mast seeding event, while the importance of the seasonal  
260 increase in the EVI and the favourable weather conditions in spring supports the relevance of the immediate  
261 availability of resources for triggering the masting episode. Our results thus fully agree with those recently  
262 found for deciduous trees in studies that applied isotopic analyses to show that the main photosynthates spent in  
263 the production of seed crops were those accumulated during the last growing seasons (within 17 months) (Ichie  
264 et al. 2013; Hoch et al. 2013).

265

#### 266 *Short-time resource accumulation and masting*

267 The need of a minimum threshold of the EVI to produce large seed crops at the beginning of the increasing  
268 or decreasing EVI periods, despite the increase in the EVI during the last months before reproduction, supports  
269 the hypothesis that trees require a minimum level of stored resources to produce buds that will eventually ripen  
270 and produce seeds (Sork et al. 1993; Isagi et al. 1997; Kelly and Sork 2002). This minimum EVI value is in line  
271 with many studies reporting a relevant role of the conditions of the previous years (e.g. canopy growth, bud  
272 development, and temperatures) to account for a future masting episode (Alla et al., 2011, Sánchez-Humanes et  
273 al. 2011, Kelly et al., 2013). Moreover, the negative autocorrelation coefficients among consecutive acorn crops  
274 (Table 1, lags 1, 3, and 4) also support the premise that large crop sizes are driven by endogenous cycles of  
275 resource accumulation-depletion. When taking into account the EVI temporal dynamics and SPEI, however, the  
276 negative autocorrelation at lag 1 was not significant (Table 2), which indicates the relatively small importance  
277 of these endogenous cycles in comparison with the paramount role of the current year's weather conditions. The  
278 BFAST analyses, in contrast to Camarero et al. (2010), did not indicate that leaf area decreased due to crown  
279 self-thinning after a masting episode. The lack of such an effect in our oak stands could be due to several  
280 reasons: i) the low number of acorns produced in these moderately young forests (coppiced stands of ca. 40-60  
281 years; see Espelta et al. 2008; Espelta et al. 2009) relative to the number produced in older forests, ii) oaks in  
282 the mild Mediterranean climate of our study area can even photosynthesise in autumn and early winter after the

283 seeding season (Sánchez-Humanes 2009; Ogaya et al. 2014), thus replenishing a certain amount of the  
284 resources spent in reproduction and allowing to preserve more leaf area, and iii) the frequent droughts in our  
285 study area (see the values for SPEI9 in Figure 1) may be a much more relevant factor accounting for the  
286 changes in leaf area than the amount of resources invested in acorn production.

287       Once a minimum threshold of EVI was reached, the increase in EVI during the months ( $9 \pm 4$ ) previous to  
288 reproduction also influenced acorn production. The relationship between the leaf area index and gross primary  
289 production is well established (Gower et al. 2001; Law et al. 2002; Fernández-Martínez et al. 2014), and the  
290 EVI is proficient at estimating forest growth in Mediterranean evergreen forests (Garbulsky et al. 2013), but we  
291 cannot determine the part of the increase in the EVI that corresponds to an increase in leaf area or  
292 photosynthesis. The increase in leaf area during spring leads to higher rates of carbon fixation, thus generating  
293 the pool of carbohydrates needed to sustain a mast seeding event (Figures 1 and 2). These recently synthesised  
294 carbohydrates could be those identified in isotopic studies (Ichie et al. 2013; Hoch et al. 2013). However, since  
295 only deciduous species were used in these studies, caution should be taken when extrapolating these  
296 conclusions for the evergreen *Q. ilex*. The relatively short time periods of increasing EVI values (i.e. acquisition  
297 of resources) mediated by favourable weather conditions (e.g. low water stress) could be a consequence of  
298 drought episodes (see Figure 1, negative SPEI9 values for years 2005 and 2007) that may often interrupt a more  
299 constant accumulation of resources through the years. These results are consistent with the nature of the  
300 Mediterranean climate in which the growth of vegetation is mostly limited by severe shortages of water  
301 (Kramer et al. 2000). The effect of weather on Mediterranean forests, however, may not only be of relevance for  
302 water availability. Precipitation may also increase mineralisation rates in soils (Jarvis et al. 2007) and nutrient  
303 availability to plants (Sardans and Peñuelas 2007; Smaill et al. 2011) in Mediterranean areas. The combined  
304 pulse of water and nutrient availability may thus produce a synergic effect boosting large seed crops in these  
305 forests. Accordingly, the reproductive behaviour of *Q. ilex* would be mostly aligned with that of a *putative*  
306 masting species that mimics the behaviour of the weather (*sensu* Koenig and Knops, 2000).

### 307 308 *Rethinking the influence of weather on masting behaviour*

309       Previous studies have suggested that weather could rarely be the most important factor driving masting due  
310 to the bimodality usually presented by seed production (Norton and Kelly 1988; Herrera et al. 1998), given the  
311 absence of bimodality in weather variables, and due to the higher variability of seed production compared to the

312 variability of weather variables such as rainfall (Kelly and Sork 2002; Koenig and Knops 2005). These  
313 assumptions are unquestionably true for linear relationships between weather and seed production but not for  
314 non-linear relationships, as a consequence of *Jensen's inequality* (Jensen 1905; Ruel and Ayres 1999). The key  
315 role of weather found in this study, presenting a logarithmic relationship with acorn production, suggests that  
316 non-linear relationships between weather and seed production might be the cause of these differences in the  
317 distribution of seed production and weather data. For example, if seed production can be modelled as an  
318 exponential function of rainfall, the variability in seed production will easily be much higher than the variability  
319 in rainfall. Similarly, a sigmoid relationship between weather and seed production would lead that bimodality to  
320 appear in the data for seed production (e.g. flowering intensity of *Chionochloa* sp. in McKone et al. (1998)).  
321 The *Moran Effect* or synchronisation using weather cues (Ranta et al. 1997; Kelly et al. 2013) could also  
322 account for this non-linear effect of weather variability and seed production. These exosomatic signals may act  
323 as triggers for mobilising stored reserves in plants to produce seeds. We do not suggest (or report) that weather  
324 is the only driver of seed production and its extreme variability, but we call for a renewed view of the effect of  
325 weather and a reinforcement of its influence in conditioning masting behaviour either as a cue (Kelly et al.  
326 2013) or as providing good conditions for photosynthesis (Fernández-Martínez et al. 2012).

327

328 *Are remotely sensed vegetative indices suitable for monitoring masting?*

329 Our results clearly indicate that mast seeding events in *Q. ilex* can be detected by the analysis of trends in  
330 remotely sensed vegetative indices such as the EVI. According to our results, large seed crops in *Q. ilex* might  
331 be anticipated when detecting large increasing trends in the deseasonalised EVI, mostly since the winter prior to  
332 seed harvest, especially if the trend begins at high EVI values and weather conditions during spring are mostly  
333 wet. Other authors have suggested that remotely sensed vegetative indices could predict yields in annual  
334 agricultural crops (Zhao et al. 2007), but to our knowledge, this study is the first to demonstrate that seed  
335 production in forest ecosystems can also be detected using satellite imagery and weather data. Nevertheless, the  
336 study of species with different cycles of flowering, pollination, and maturation of seeds (e.g. red oaks that  
337 require more than one year from the onset of flowering to seed maturation), may require a different approach.  
338 Likewise, the study of deciduous forests may also require different methodologies, because these species may  
339 respond differently. For example, a drastic reduction in crown cover was detected in two birch species (*Betula*  
340 *alleghaniensis* and *B. papyrifera*) during a mast year (Gross 1972), and *Fagus* sp. has also shown drastic

341 reductions in crown conditions due to large seed harvests (Innes 1992; Ferretti et al. 1998; Han et al. 2008;  
342 Vicca et al. 2014). In these kind of forests, masting could be detected after substantial decreases in the EVI not  
343 explained by weather conditions (Vicca et al. 2014). Various approaches may thus be needed to monitor and  
344 predict seed production in different plant species according to their contrasting functional and life-history traits.  
345 Establishing a reliable methodology for predicting masting events in forest ecosystems for extensive and remote  
346 areas will help to improve pest controls, wildlife management and hunting policies.

347

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354

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- 491
- 492

493 **Figure captions**

494 **Figure 1.** Smoothed and deseasonalised anomalies of EVI time series averaged for all five plots overlaid to  
495 SPEI9. Humid periods (positive SPEI9) lead to positive anomalies in the EVI ( $r = 0.50$ ,  $P < 0.001$ ). Grey bars  
496 indicate the average annual acorn production of the five plots. Error bars indicate standard errors. SD, standard  
497 deviation; CI, confidence interval.

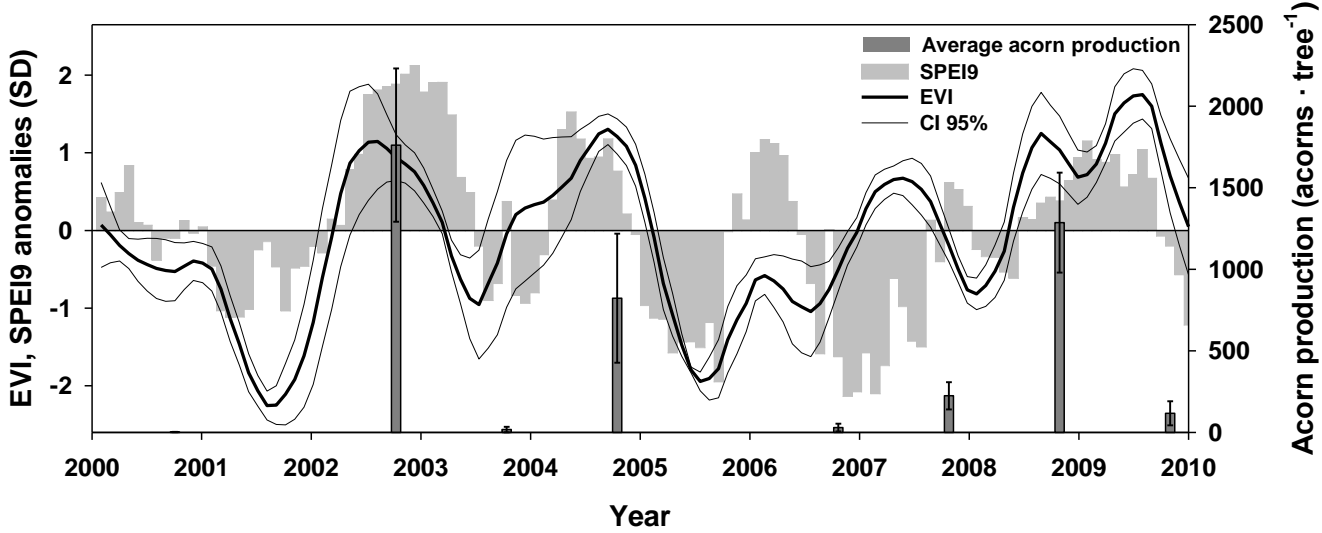
498

499 **Figure 2.** Temporal dynamics of the EVI time-series anomalies, BFAST trends identified in the EVI time  
500 series, and acorn production from 2000 to 2010 for each forest stand (A-E). Dashed lines represent the  
501 deseasonalised, smoothed EVI anomalies, solid lines show the BFAST trends of the series, and bars indicate  
502 annual acorn production. Light and dark shading indicate the periods used to calculate  $\Delta$ EVI. Unshaded periods  
503 were not used to calculate these increments (see section 2.3.2 for information about the selection of periods).  
504 Error bars indicate standard errors.

505

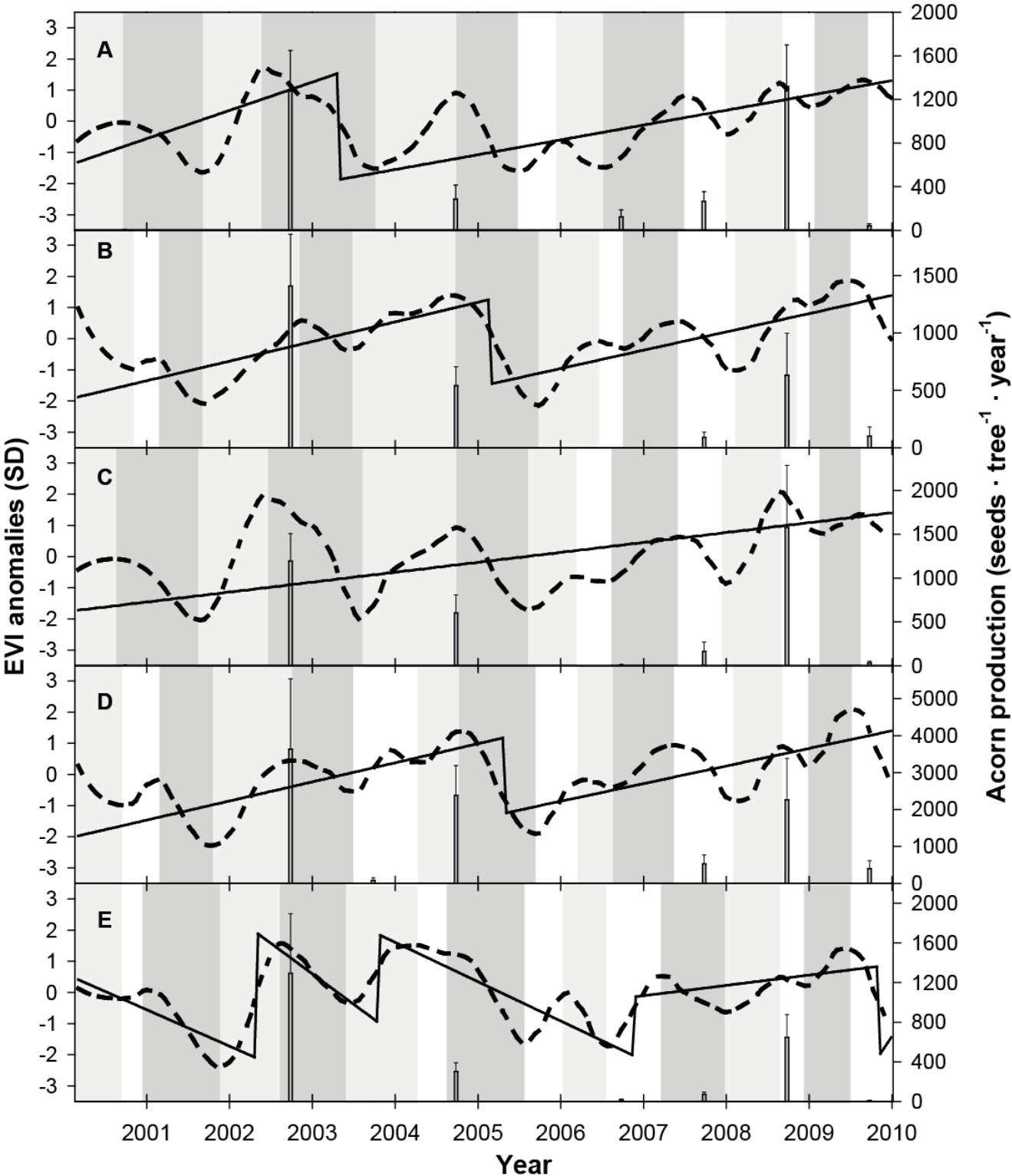
506 **Figure 3:** 3D representation of the response surface of acorn production to changes in  $\Delta$ EVI and  $EVI_i$ . SD,  
507 standard deviation.

508



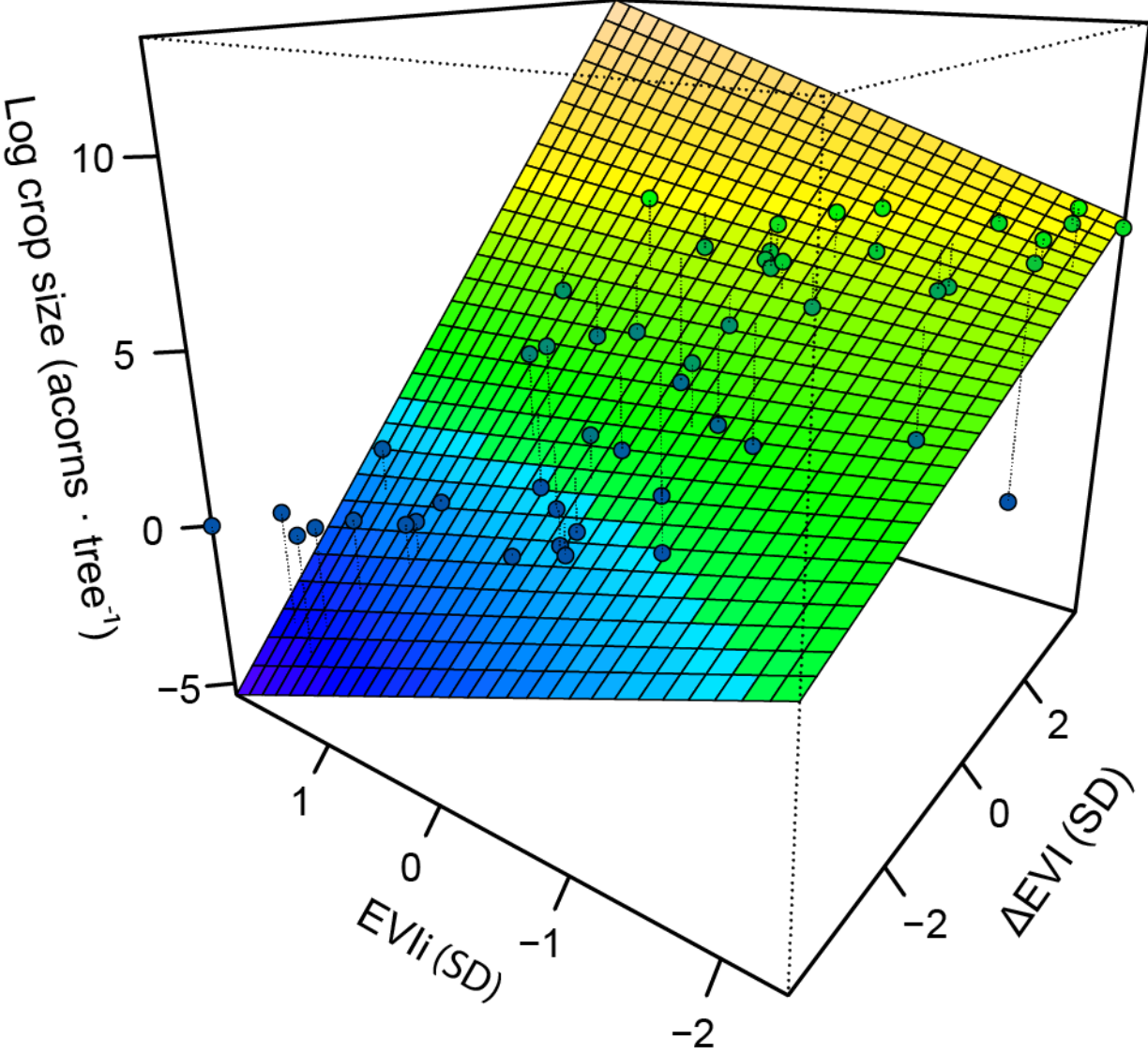
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511



515 **Figure 3**

516



517

518

519 **Table 1.** Synchrony ( $r_p$  among plots and  $r_i$  among trees), variability at the population ( $CV_p$ ) and individual ( $CV_i$ ) levels, and temporal autocorrelation (simple and  
520 partial (P)) of acorn production and EVI time series (mean  $\pm$  SE). No significant differences were found among plots. Values different from zero are in bold type.  
521

	Plot	$r_p$	$r_i$	$CV_p$	$CV_i$	lag 1	lag 2	lag 3	lag 4	lag 2 (P)	lag 3 (P)	lag 4 (P)
<b>Acorns</b>	<b>A</b>	<b>0.89 <math>\pm</math> 0.26</b>	<b>0.64 <math>\pm</math> 0.08</b>	<b>1.74 <math>\pm</math> 0.42</b>	<b>2.26 <math>\pm</math> 0.14</b>	<b>-0.16 <math>\pm</math> 0.03</b>	-0.05 $\pm$ 0.03	<b>-0.17 <math>\pm</math> 0.02</b>	<b>-0.09 <math>\pm</math> 0.02</b>	<b>-0.09 <math>\pm</math> 0.03</b>	<b>-0.19 <math>\pm</math> 0.02</b>	<b>-0.20 <math>\pm</math> 0.03</b>
	<b>B</b>	<b>0.85 <math>\pm</math> 0.29</b>	<b>0.69 <math>\pm</math> 0.10</b>	<b>1.86 <math>\pm</math> 0.49</b>	<b>2.17 <math>\pm</math> 0.12</b>	<b>-0.24 <math>\pm</math> 0.02</b>	0.03 $\pm$ 0.04	<b>-0.15 <math>\pm</math> 0.03</b>	<b>-0.17 <math>\pm</math> 0.03</b>	-0.03 $\pm$ 0.04	<b>-0.16 <math>\pm</math> 0.04</b>	<b>-0.29 <math>\pm</math> 0.03</b>
	<b>C</b>	<b>0.91 <math>\pm</math> 0.21</b>	<b>0.62 <math>\pm</math> 0.06</b>	<b>1.77 <math>\pm</math> 0.48</b>	<b>2.27 <math>\pm</math> 0.13</b>	<b>-0.20 <math>\pm</math> 0.02</b>	0.02 $\pm$ 0.04	<b>-0.17 <math>\pm</math> 0.02</b>	<b>-0.11 <math>\pm</math> 0.04</b>	-0.03 $\pm$ 0.04	<b>-0.18 <math>\pm</math> 0.01</b>	<b>-0.22 <math>\pm</math> 0.05</b>
	<b>D</b>	<b>0.84 <math>\pm</math> 0.28</b>	<b>0.66 <math>\pm</math> 0.06</b>	<b>1.61 <math>\pm</math> 0.47</b>	<b>2.06 <math>\pm</math> 0.17</b>	<b>-0.20 <math>\pm</math> 0.02</b>	0.02 $\pm$ 0.04	<b>-0.17 <math>\pm</math> 0.02</b>	<b>-0.11 <math>\pm</math> 0.04</b>	-0.03 $\pm$ 0.04	<b>-0.18 <math>\pm</math> 0.01</b>	<b>-0.22 <math>\pm</math> 0.05</b>
	<b>E</b>	<b>0.89 <math>\pm</math> 0.25</b>	<b>0.73 <math>\pm</math> 0.10</b>	<b>2.03 <math>\pm</math> 0.52</b>	<b>2.12 <math>\pm</math> 0.14</b>	<b>-0.16 <math>\pm</math> 0.04</b>	0.00 $\pm$ 0.04	<b>-0.18 <math>\pm</math> 0.02</b>	-0.06 $\pm$ 0.03	-0.05 $\pm$ 0.03	<b>-0.18 <math>\pm</math> 0.03</b>	<b>-0.17 <math>\pm</math> 0.04</b>
	<b>mean</b>	<b>0.87 <math>\pm</math> 0.01</b>	<b>0.65 <math>\pm</math> 0.02</b>	<b>1.80 <math>\pm</math> 0.07</b>	<b>2.18 <math>\pm</math> 0.04</b>	<b>-0.19 <math>\pm</math> 0.01</b>	0.00 $\pm$ 0.01	<b>-0.17 <math>\pm</math> 0.01</b>	<b>-0.11 <math>\pm</math> 0.02</b>	<b>-0.05 <math>\pm</math> 0.01</b>	<b>-0.18 <math>\pm</math> 0.01</b>	<b>-0.22 <math>\pm</math> 0.02</b>
<b>EVI</b>	<b>A</b>	0.70 $\pm$ 0.41		<b>0.05 <math>\pm</math> 0.01</b>		0.32 $\pm$ 0.30	-0.04 $\pm$ 0.33	-0.20 $\pm$ 0.33	-0.32 $\pm$ 0.34	-0.16 $\pm$ 0.30	-0.15 $\pm$ 0.30	-0.24 $\pm$ 0.30
	<b>B</b>	0.73 $\pm$ 0.49		<b>0.05 <math>\pm</math> 0.01</b>		0.22 $\pm$ 0.30	-0.25 $\pm$ 0.32	-0.18 $\pm$ 0.33	-0.05 $\pm$ 0.34	-0.31 $\pm$ 0.30	-0.05 $\pm$ 0.30	-0.08 $\pm$ 0.30
	<b>C</b>	0.57 $\pm$ 0.58		<b>0.04 <math>\pm</math> 0.01</b>		0.06 $\pm$ 0.30	0.08 $\pm$ 0.30	-0.39 $\pm$ 0.31	-0.06 $\pm$ 0.35	0.08 $\pm$ 0.30	-0.40 $\pm$ 0.30	-0.01 $\pm$ 0.30
	<b>D</b>	0.76 $\pm$ 0.42		<b>0.05 <math>\pm</math> 0.01</b>		0.32 $\pm$ 0.30	-0.15 $\pm$ 0.33	-0.04 $\pm$ 0.34	0.00 $\pm$ 0.34	-0.29 $\pm$ 0.30	0.14 $\pm$ 0.30	-0.10 $\pm$ 0.30
	<b>E</b>	0.64 $\pm$ 0.55		<b>0.04 <math>\pm</math> 0.01</b>		0.17 $\pm$ 0.30	-0.41 $\pm$ 0.31	-0.48 $\pm$ 0.36	0.00 $\pm$ 0.41	-0.45 $\pm$ 0.30	-0.39 $\pm$ 0.30	-0.06 $\pm$ 0.30
	<b>mean</b>	<b>0.68 <math>\pm</math> 0.03</b>		<b>0.05 <math>\pm</math> 0.01</b>		<b>0.22 <math>\pm</math> 0.05</b>	<b>-0.16 <math>\pm</math> 0.08</b>	<b>-0.26 <math>\pm</math> 0.08</b>	<b>-0.09 <math>\pm</math> 0.06</b>	<b>-0.23 <math>\pm</math> 0.09</b>	-0.17 $\pm$ 0.10	<b>-0.10 <math>\pm</math> 0.04</b>

522 **Table 2:** Output of the generalised linear mixed model using a negative binomial distribution ( $\theta = 0.4013$ )  
 523 relating acorn crop size,  $SPEI6_{Jn}$ ,  $EVI_i$ , and  $\Delta EVI$ , with plot as a random effect. SD, standard deviation; SE,  
 524 standard error.  
 525

**Random effects**

Groups	Name	Variance	SD
<b>Plot</b>	Intercept	0.1203	0.3469
<b>Residual</b>		0.7708	0.8779

**Fixed effects**

	Estimate	SE	t value	P value
<b>Intercept</b>	4.31	0.30	14.48	<0.0001
<b><math>\Delta EVI</math></b>	1.12	0.26	4.38	<0.0001
<b><math>EVI_i</math></b>	-0.47	0.41	-1.15	0.2515
<b><math>SPEI6_{Jn}</math></b>	1.01	0.46	2.20	0.0278
<b><math>\Delta EVI * EVI_i</math></b>	0.45	0.13	3.52	0.0004

526

527

528 **Table 3.** Correlation coefficients for the SPEI9 and EVI time series, annual acorn production (AP), SPEI6 from  
 529 June (SPEI6<sub>Jn</sub>), and summer EVI (EVI<sub>sm</sub>). Pearson correlations were used for EVI vs. SPEI9 and EVI<sub>sm</sub> vs.  
 530 SPEI6<sub>Jn</sub>, and Spearman correlations were used for the AP relationships (due to the non-normal distribution of  
 531 the data). \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

532

<b>Plot</b>	<b>EVI vs. SPEI9</b>	<b>AP vs. EVI<sub>sm</sub></b>	<b>AP vs. SPEI6<sub>Jn</sub></b>	<b>EVI<sub>sm</sub> vs. SPEI6<sub>Jn</sub></b>
A	0.48 <sup>***</sup>	0.69 <sup>*</sup>	0.68 <sup>*</sup>	0.74 <sup>**</sup>
B	0.42 <sup>***</sup>	0.85 <sup>**</sup>	0.82 <sup>**</sup>	0.81 <sup>**</sup>
C	0.41 <sup>***</sup>	0.94 <sup>***</sup>	0.74 <sup>*</sup>	0.70 <sup>*</sup>
D	0.36 <sup>***</sup>	0.81 <sup>**</sup>	0.82 <sup>**</sup>	0.72 <sup>*</sup>
E	0.50 <sup>***</sup>	0.75 <sup>*</sup>	0.75 <sup>*</sup>	0.94 <sup>***</sup>

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