1    **Temporal trends in the Enhanced Vegetation Index and spring weather predict**

2    **seed production in Mediterranean oaks**

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**Abstract**

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

## 1. Introduction

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

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

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

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

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

## 2. Materials and methods

### 2.1. Study area and species

This study was conducted in the Collserola massif (41º26′N, 02º06′E), whose vegetation is dominated by *Q. ilex*. The study area has a Mediterranean climate and a mean annual temperature of $15.7 \pm 1.4$ ºC. January is the coldest month ($8.5 \pm 0.6$ ºC) and August the warmest ($24.3 \pm 0.7$ ºC). Mean annual precipitation reaches $613.8 \pm 34.0$ mm (coefficient of variation (CV) = 0.25; values from the Fabra Observatory at 415 m.a.s.l. for the current climatological standard normal period, 1991-2010). We selected forest stands of *Q. ilex* because it is the most abundant tree species in Collserola, has a strong masting behaviour (Espelta et al. 2008; Fernández-Martínez et al. 2012), and has evergreen leaves that allow continuous monitoring using remotely sensed vegetative indices. Regarding *Q. ilex* fruiting phenology, the pollination period normally starts during the first 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 ± 219 *Q. ilex* stems per hectare), mostly

113 resulting from resprouting and relatively young (ca. 40-60 years), presenting 10.5 ± 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$^2$ (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 (41º25′N, 02º07′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 ($CV_p$) and the individual ($CV_i$) 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 $\Delta EVI$ with $EVI_i$ and

197    $EVI_f$ 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 ($CV_i$)

218    and the population ($CV_p$) levels, and negative temporal autocorrelation (Table 1). No significant differences

219    were found for $r_p$, $r_i$, $CV_p$, $CV_i$, 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 (~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, $SPEI6_{Jn}$). 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 $EVI_i$ 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 ± 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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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 ΔEVI. 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.
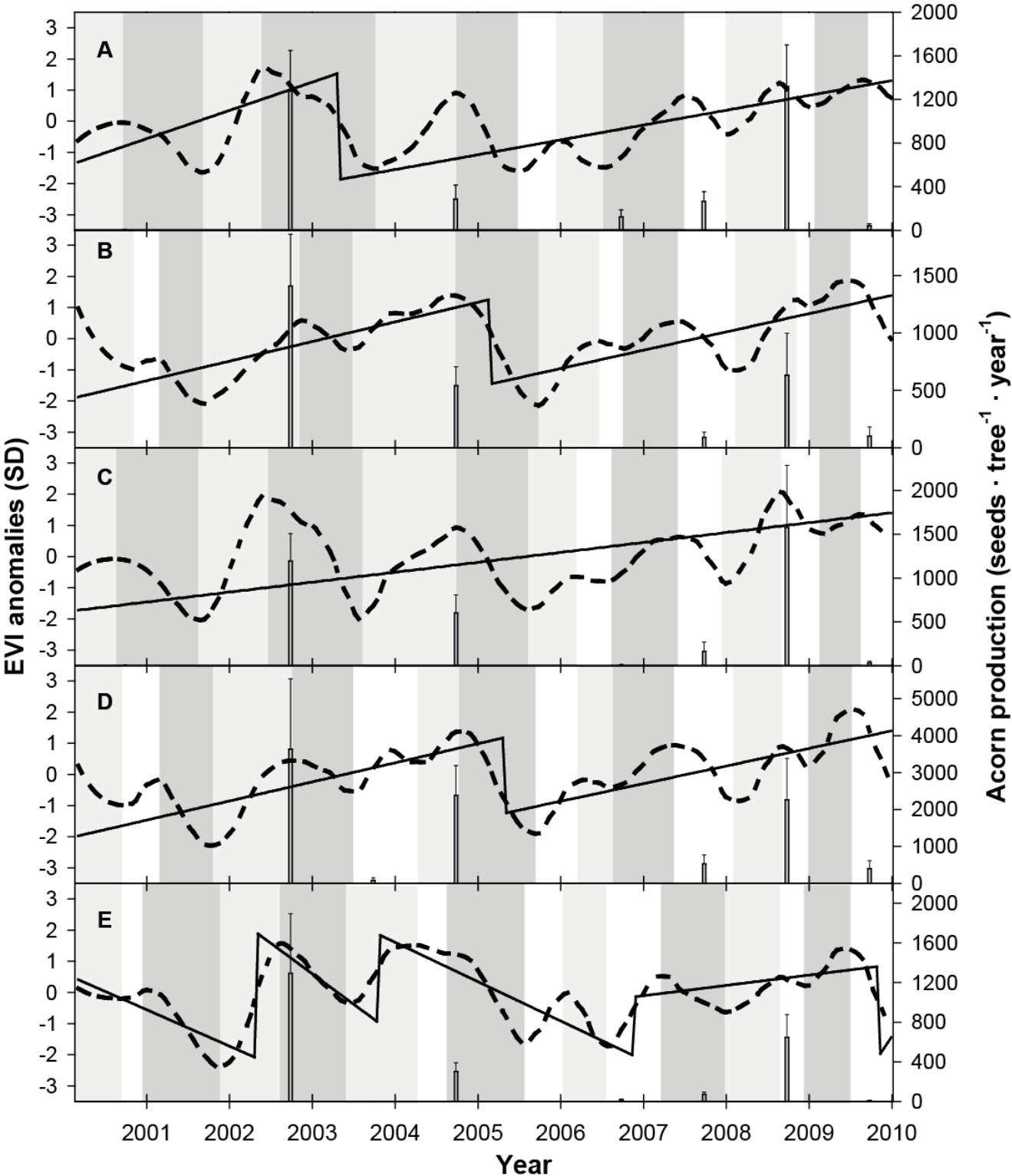
505

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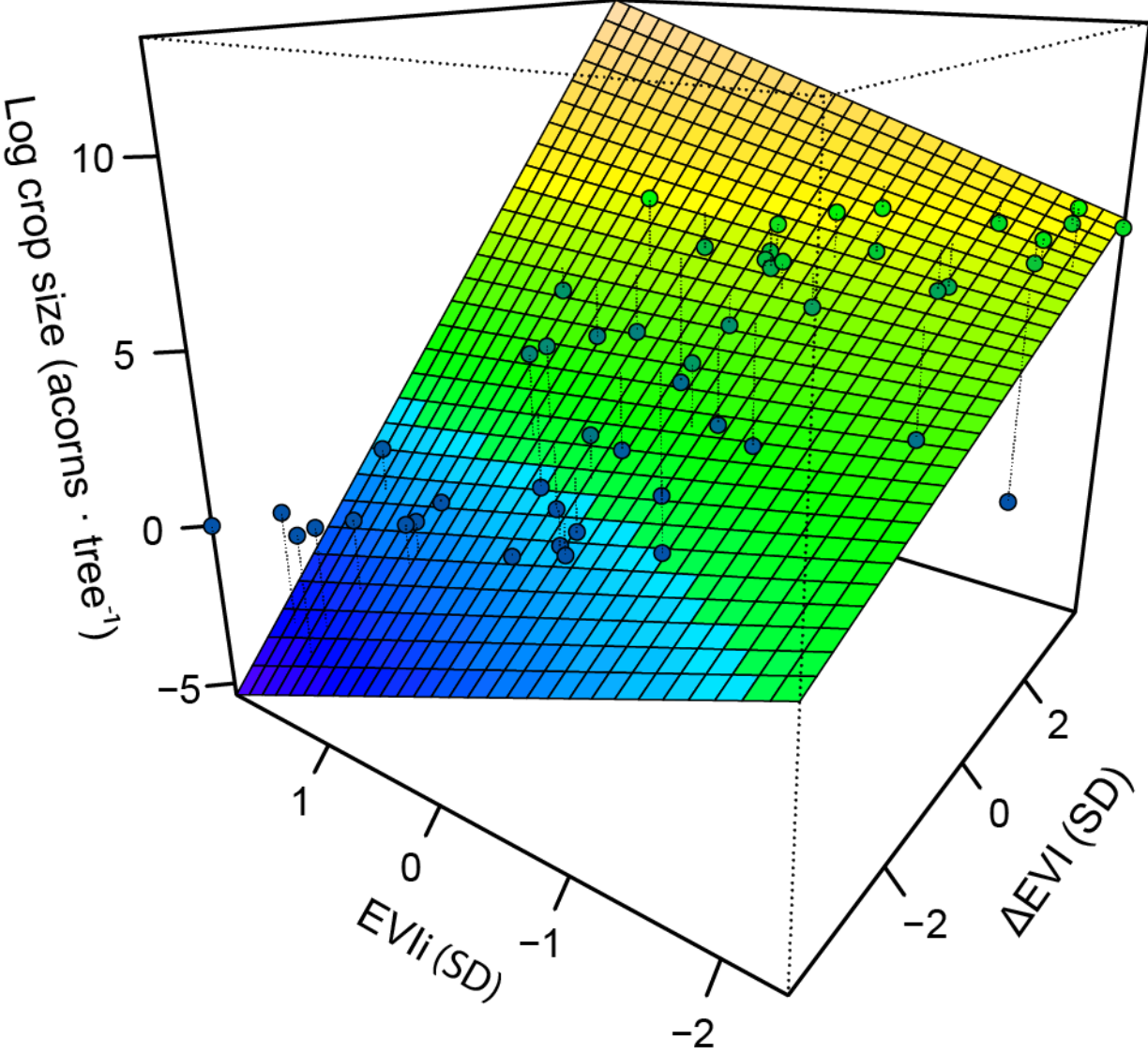507 standard deviation.

508

509    **Figure 1**

512 **Figure 2**
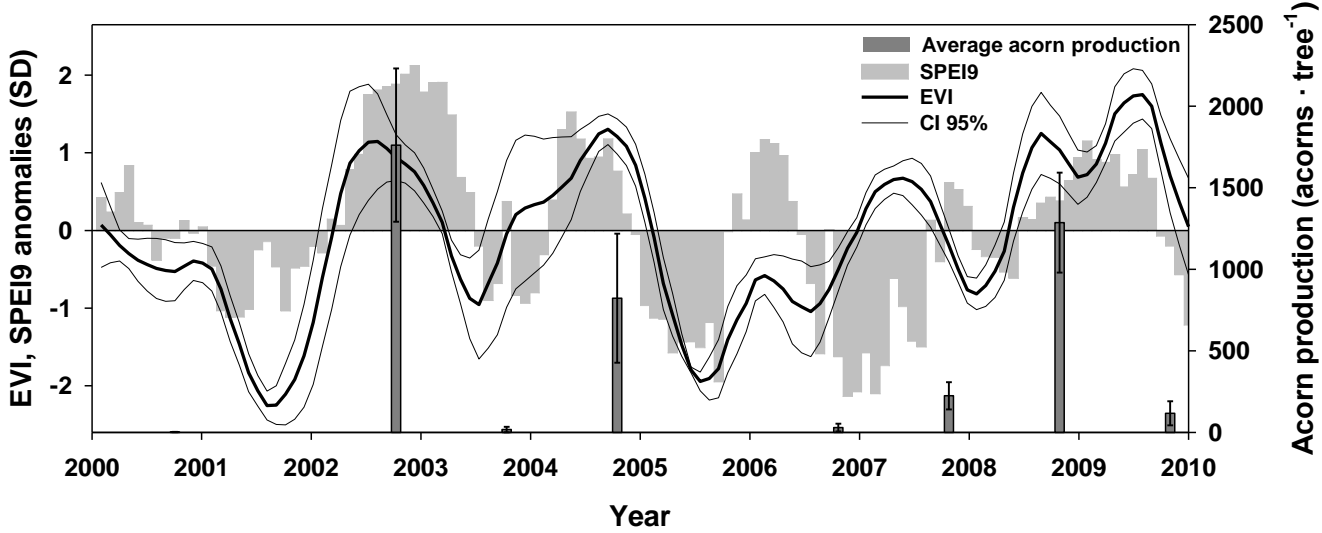
515    **Figure 3**

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 ± 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) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Acorns | A | **0.89 ± 0.26** | **0.64 ± 0.08** | **1.74 ± 0.42** | **2.26 ± 0.14** | **-0.16 ± 0.03** | -0.05 ± 0.03 | **-0.17 ± 0.02** | **-0.09 ± 0.02** | **-0.09 ± 0.03** | **-0.19 ± 0.02** | **-0.20 ± 0.03** |
| | B | **0.85 ± 0.29** | **0.69 ± 0.10** | **1.86 ± 0.49** | **2.17 ± 0.12** | **-0.24 ± 0.02** | 0.03 ± 0.04 | **-0.15 ± 0.03** | **-0.17 ± 0.03** | -0.03 ± 0.04 | **-0.16 ± 0.04** | **-0.29 ± 0.03** |
| | C | **0.91 ± 0.21** | **0.62 ± 0.06** | **1.77 ± 0.48** | **2.27 ± 0.13** | **-0.20 ± 0.02** | 0.02 ± 0.04 | **-0.17 ± 0.02** | **-0.11 ± 0.04** | -0.03 ± 0.04 | **-0.18 ± 0.01** | **-0.22 ± 0.05** |
| | D | **0.84 ± 0.28** | **0.66 ± 0.06** | **1.61 ± 0.47** | **2.06 ± 0.17** | **-0.20 ± 0.02** | 0.02 ± 0.04 | **-0.17 ± 0.02** | **-0.11 ± 0.04** | -0.03 ± 0.04 | **-0.18 ± 0.01** | **-0.22 ± 0.05** |
| | E | **0.89 ± 0.25** | **0.73 ± 0.10** | **2.03 ± 0.52** | **2.12 ± 0.14** | **-0.16 ± 0.04** | 0.00 ± 0.04 | **-0.18 ± 0.02** | -0.06 ± 0.03 | -0.05 ± 0.03 | **-0.18 ± 0.03** | **-0.17 ± 0.04** |
| | mean | **0.87 ± 0.01** | **0.65 ± 0.02** | **1.80 ± 0.07** | **2.18 ± 0.04** | **-0.19 ± 0.01** | 0.00 ± 0.01 | **-0.17 ± 0.01** | **-0.11 ± 0.02** | **-0.05 ± 0.01** | **-0.18 ± 0.01** | **-0.22 ± 0.02** |
| | | | | | | | | | | | | |
| EVI | A | 0.70 ± 0.41 | | **0.05 ± 0.01** | | 0.32 ± 0.30 | -0.04 ± 0.33 | -0.20 ± 0.33 | -0.32 ± 0.34 | -0.16 ± 0.30 | -0.15 ± 0.30 | -0.24 ± 0.30 |
| | B | 0.73 ± 0.49 | | **0.05 ± 0.01** | | 0.22 ± 0.30 | -0.25 ± 0.32 | -0.18 ± 0.33 | -0.05 ± 0.34 | -0.31 ± 0.30 | -0.05 ± 0.30 | -0.08 ± 0.30 |
| | C | 0.57 ± 0.58 | | **0.04 ± 0.01** | | 0.06 ± 0.30 | 0.08 ± 0.30 | -0.39 ± 0.31 | -0.06 ± 0.35 | 0.08 ± 0.30 | -0.40 ± 0.30 | -0.01 ± 0.30 |
| | D | 0.76 ± 0.42 | | **0.05 ± 0.01** | | 0.32 ± 0.30 | -0.15 ± 0.33 | -0.04 ± 0.34 | 0.00 ± 0.34 | -0.29 ± 0.30 | 0.14 ± 0.30 | -0.10 ± 0.30 |
| | E | 0.64 ± 0.55 | | **0.04 ± 0.01** | | 0.17 ± 0.30 | -0.41 ± 0.31 | -0.48 ± 0.36 | 0.00 ± 0.41 | -0.45 ± 0.30 | -0.39 ± 0.30 | -0.06 ± 0.30 |
| | mean | **0.68 ± 0.03** | | **0.05 ± 0.01** | | **0.22 ± 0.05** | **-0.16 ± 0.08** | **-0.26 ± 0.08** | **-0.09 ± 0.06** | **-0.23 ± 0.09** | -0.17 ± 0.10 | **-0.10 ± 0.04** |

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 |
| --- | --- | --- | --- |
| **Plot** | Intercept | 0.1203 | 0.3469 |
| **Residual** | | 0.7708 | 0.8779 |

**Fixed effects**

| | Estimate | SE | t value | *P* value |
| --- | --- | --- | --- | --- |
| **Intercept** | 4.31 | 0.30 | 14.48 | <0.0001 |
| **$\Delta$EVI** | 1.12 | 0.26 | 4.38 | <0.0001 |
| **$EVI_i$** | -0.47 | 0.41 | -1.15 | 0.2515 |
| **$SPEI6_{Jn}$** | 1.01 | 0.46 | 2.20 | 0.0278 |
| **$\Delta$EVI\* $EVI_i$** | 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$_{Jn}$), and summer EVI (EVI$_{sm}$). Pearson correlations were used for EVI vs. SPEI9 and EVI$_{sm}$ vs.

530    SPEI6$_{Jn}$, 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

| Plot | EVI vs. SPEI9 | AP vs. EVI$_{sm}$ | AP vs. SPEI6$_{Jn}$ | EVI$_{sm}$ vs. SPEI6$_{Jn}$ |
|------|---------------|-------------------|---------------------|------------------------------|
| A | 0.48*** | 0.69* | 0.68* | 0.74** |
| B | 0.42*** | 0.85** | 0.82** | 0.81** |
| C | 0.41*** | 0.94*** | 0.74* | 0.70* |
| D | 0.36*** | 0.81** | 0.82** | 0.72* |
| E | 0.50*** | 0.75* | 0.75* | 0.94*** |

533