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Climate variation, reproductive frequency and acorn yield in English Oaks

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Running Head: Climate and Oak masting behaviour

1 **Abstract**

2 **Aims** – Annually variable, but synchronous production of large seed crops ('masting') is a
3 widespread phenomenon in temperate trees. Mounting concerns about the impacts of
4 anthropogenic climate change (ACC) on plant reproduction, gives urgency to our need to
5 understand better the role of climate on tree reproduction, and in particular, mast events.
6 Unlike our understanding of reproductive phenology however, there is little consensus
7 regarding how climate affects plant reproductive effort, or indeed the actual environmental
8 triggers that underpin masting behaviour.

9 **Methods** - We used a 27-year record of acorn yield from a population of 12 *Quercus robur*
10 trees located in southern England to compare masting frequency and post-dispersal acorn
11 yield each year for each tree, with long-term weather data over the same period. We
12 focussed on discrete or sequential climate cues (temperature, precipitation, and frost days)
13 as likely predictors of oak reproduction.

14 **Important Findings** – Annual post-dispersal acorn crop varied greatly; i.e. no acorns in 14
15 of the 27 years, but there was no sequential pattern of crop versus non-crop years indicating
16 that weather, rather than resource limitation alone, dictated the timing of reproduction.
17 Crop years were instead most closely associated with relatively cool late summer
18 conditions in the preceding year, followed by anomalous summer warmth within crop year.
19 Acorn yield increased following dry April and above average May and June temperatures
20 within crop year. Although our results support a general association between warm late
21 spring and summer conditions, and crop frequency and yield respectively, the influence of

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4 22 cooler later summer conditions in the year prior to masting highlights how a combination of
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7 23 weather cues may dictate the occurrence of mast years. Consequently, our results
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9 24 corroborate not only the hypothesis that temperature differentials between consecutive
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11 25 years, not absolute temperatures, may be the better predictor of mast seeding events, but
12
13 26 lend support also to the suggestion that reproductive failure and resource accumulation
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15
16 27 resulting from a climate-linked environmental veto, drives future reproductive
17
18 28 synchronization in temperate tree species.

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20
21 29 **Keywords** – Anthropogenic climate change; Environmental veto; Moran effect; *Quercus*
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23 30 *robur*; Reproductive effort
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32 INTRODUCTION

33 The synchronous production of seed crops by trees ('masting'), whereby plants display
34 variable between-, but similar within-year high seed yield, is described widely (Salisbury
35 1942; Kelly 1994; Kelly and Sork 2002; Pearse *et al.* 2016). Its occurrence in nature has
36 been ascribed to the adaptive benefit of economies of scale; i.e. plants investing heavily in
37 reproduction in years when con-specifics do the same incur lower costs per surviving
38 offspring (Norton and Kelly 1988, Kelly 1994). **These** so-called 'Ultimate-level' causes
39 (Pearse *et al.* 2016) include predator satiation, whereby infrequent and unpredictable seed
40 production limits putative predator populations (Janzen 1971); increased pollination
41 efficiency, a consequence of synchronised flowering (Smith *et al.* 1990); and
42 environmental prediction, common where large-scale disturbances (fire, hurricanes etc.)
43 generate spatio-temporally limited recruitment opportunity (Kelly 1994). Of these, predator
44 satiation is perhaps the most widely supported (Pearse *et al.* 2016), but whatever adaptive
45 benefit underpins its evolution, successful seedling recruitment and community persistence
46 is, for many long-lived tree species, limited to 'mast' years (Salisbury 1942; Tapper 1992;
47 Crawley and Long 1995). Fluctuations in seed yield also have important cascading effects
48 on ecosystem interactions (Ostfield and Keesing 2000; Pesendorfer and Koenig 2016;
49 Lichti *et al.* 2017). Consequently, an understanding of the causes and consequences of
50 reproductive behaviour is important from the perspectives of tree population biology, forest
51 management, and conservation.

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4 52 While the actual environmental triggers and plant physiological processes underpinning
5
6 53 masting remain unresolved, there is much evidence that climate is the key proximate cue
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9 54 (Koenig and Knops 2005; Pearse *et al.* 2016). Variations in temperature or precipitation do
10
11 55 not necessarily signal better conditions for plant growth or development, but by virtue of a
12
13 56 regional influence, synchronise individual reproductive activity within the wider population
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16 57 (Pearse *et al.* 2016). Consequently, and although reproductive allocation is often moderated
17
18 58 by internal resource budgets (Pearse *et al.* 2016; Bogdziewicz *et al.* 2018), various climate
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20 59 triggers catalyse different developmental processes such as flower formation, pollen
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22 60 release, and/or fruit development that then confer adaptive benefits upon the individual and
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25 61 its progeny (Pearse *et al.* 2016).

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28 62 Although there may be some phylogenetic conservation across species (Koenig *et al.* 2016),
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30 63 even with a single genus (e.g. *Quercus*), crop synchronicity has been associated with a
31
32 64 variety of climate-triggers. For temperate oak species these include; cool summer
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34
35 65 temperatures (*Q. macrocarpa*), or warm spring temperatures 2 years prior to acorn maturity
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37 66 (*Q. rubra*) (Koenig and Knops 2014); cool, wet conditions in the early autumn (*Q. robur*)
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39 67 preceding the event (Crawley and Long 1995); and warm spring temperatures (*Q. robur*)
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41
42 68 within the crop year (Askeyev *et al.* 2005). For the Mediterranean species, *Quercus ilex*
43
44 69 however, acorn crop was more closely associated with rainfall (Perez-Ramos *et al.* 2010)
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46 70 highlighting likely variation between climate triggers in temperate versus Mediterranean-
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49 71 climate regions. Indeed, rather than a single proximate cause, there is consensus that for
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51 72 most plant species, seed crop yield most likely corresponds with a combination or sequence
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54 73 of climate cues (see Allen *et al.* 2014; Buechling *et al.* 2016). Kelly *et al.* (2013) for

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4 74 instance report that for a wide variety of native New Zealand plants (i.e. 15 species from
5
6 75 five families), reproductive effort **was driven by a difference in temperatures between**
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8 **successive years rather than the absolute temperature within a particular year.** Although
9 76
10
11 77 there is mixed support for this so-called ‘ Δt ’ hypothesis (e.g. Koenig and Knops 2014;
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13 78 Pearse *et al.* 2014; Koenig *et al.* 2015; Moreira *et al.* 2015), climate nonetheless likely
14
15 79 provides the main proximate cue for synchrony in reproductive timing and effort (Monks *et*
16
17 80 *al.* 2016; Pearse *et al.* 2016).

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21 81 Notwithstanding the view that climate variation does not explain the ultimate biological
22
23 82 (adaptive) reasons for its evolution (Kelly 1994; Pearse *et al.* 2016), the strong link between
24
25 83 climate and reproductive effort has important implications at a time of Anthropogenic
26
27 84 Climate Change (ACC). A combination of a gradual increase in global temperatures and
28
29 85 shifts in precipitation patterns, coupled with an increased incidence of extreme weather
30
31 86 events (IPCC 2014), have been implicated widely as causes of observed individual tree
32
33 87 mortality and forest dieback (Allen *et al.* 2010; Matusick *et al.* 2013). Although temporal
34
35 88 (ontogenetic) ACC-linked mortality patterns are difficult to resolve (Allen *et al.* 2010), the
36
37 89 fact that for most plant species the regeneration stage represents the most vulnerable life
38
39 90 history phase (Fenner and Thompson 2005) suggests that any climate-linked impacts on
40
41 91 reproduction are critical in understanding tree response to ACC. Despite a wealth of recent
42
43 92 studies documenting the impact of ACC on plant ecophysiology, distributions, phenology,
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45 93 and plant community responses however, there remains a paucity of information on the
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47 94 influence of ACC on plant regeneration, and in particular, reproductive effort (Parmesan
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49 95 and Hanley 2015).

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4 96 Given the importance of masting events for tree population persistence and the likelihood
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6 97 that climate extremes will intensify and increase in frequency over coming decades (IPCC,
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8 98 2014), an understanding of the link between climate and key demographic processes like
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10 99 crop yield would seem to be particularly pressing (Clarke *et al.* 2011; Allen *et al.* 2014).
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12
13 100 Fenner (1991) was one of the first to draw attention to the importance of keeping long-term
14
15 101 records of reproduction in trees to provide a simple bioassay of the effects of climate
16
17 102 change. Remarkably, relatively few studies (see Allen *et al.* 2014; Richardson *et al.* 2015;
18
19 103 Buechling *et al.* 2016; Gaignard *et al.* 2017) have however, looked at how tree crop yields
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21 104 respond to contemporary climate shifts as a basis to predict how future ACC scenarios will
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23 105 likely affect these events into coming decades. We use a 27-year long record of post-
24
25 106 dispersal annual acorn yield (1989-2015) in an even-aged population of 12 *Quercus robur*
26
27 107 L. trees located in southern England to explore how climate variability affects oak
28
29 108 reproductive behaviour. Specifically, we examine whether **mast years** (defined here as
30
31 109 *years where acorn yield exceeded pre- and post-dispersal seed predation*) is associated
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33 110 with any specific individual, combination, or sequence of proximate climate cues.
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43 112 METHODS

44 45 46 113 ***Study Population and annual assessment of acorn yield***

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49 114 In October 1989, twelve mature oaks growing on Southampton Common, Hampshire
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51 115 (50.9262°N, 1.4092°W) were chosen to record variation in annual acorn production. All
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53 116 were isolated specimens with an even branching structure, selected for their uniform size
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4 117 (mean *dbh* = 341 cm (\pm 10.9 cm 1SE)) and ease with which the acorns could be observed
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6 118 and collected from the ground. While the age of the trees was not determined, they most
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9 119 likely date from the early 19th century when grazing ceased on the Common.
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11
12 120 Recording occurred each year in the last week of October (21st to 26th), by which time the
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14 121 trees had shed the bulk of their acorns. Crop samples from each tree were taken from four
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16 122 50cm-wide transects following compass bearings north, south, east and west of the base of
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18 123 the trunk, extending as the canopy edge (mean length 8.28 m (\pm 0.22)). On each sampling
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20 124 occasion, the acorns and other debris were raked together and collected in bags before
21
22 125 samples were cleaned to leave only the acorns (including a small minority infested by gall-
23
24 126 wasps). The fresh weight of these samples was recorded and corresponding dry weight
25
26 127 calculated by oven-drying sub-samples overnight at 105°C. We then used transect length to
27
28 128 calculate acorn yield (Kg) per unit area (m²). By the end of the 27 years of the study, three
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30 129 trees were unusable, either through bramble incursion at the base, or because of branch loss
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35 130 (supplementary Table S1).

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38 131 We did not attempt to exclude post-dispersal seed predators from our samples for two
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40 132 reasons; first, our study site precluded pan traps commonly used in isolated forests (Allen *et*
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42 133 *al.* 2014; Richardson *et al.* 2015; Buechling *et al.* 2016). Second we assumed that as the
43
44 134 most likely ‘ultimate cause’ (Pearse *et al.* 2016), true mast years are by definition, those
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46 135 where acorn crop exceeded predator consumption. **Although this meant we could not**
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48 136 **quantify acorn crops in the non-mast years, by definition these must have been low-acorn**
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50 137 **years, as even if acorns were produced, seed predators were able to remove the whole crop**
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52 138 **before collection.** Moreover, even where previous studies have visually estimated pre-
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4 139 dispersal cone (Moreira *et al.* 2015; Zamorano *et al.* 2017) or seed numbers (Koenig and
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6 140 Knops 2014; Koenig *et al.* 2015), they are unable to draw strong conclusions regarding tree
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9 141 crop yield and post-dispersal predator satiation.

12 142 *Acorn-Climate Analyses*

15 143 To investigate climate influences on the occurrence and productivity of acorn mast years,
16
17 144 we used monthly spring to autumn (i.e. nine months from February to October
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19
20 145 corresponding with the growth/reproductive season) observations of maximum and
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22 146 minimum temperatures, frost days, and rainfall. Climate data were obtained from a
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24 147 meteorological station located at 50.8997°N, 1.39556°W
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26 148 (www.southamptonweather.co.uk/sotonhist.php), 3 km from our oak population. For
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28
29 149 reproductive occurrence, we compared climate data between prior and current crop ($n=13$)
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31 150 and non-crop ($n=14$) years using a two-tailed Student's *t*-test. Since we define 'mast years'
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33 151 as those where acorn crop satiated post-dispersal predation (i.e. acorns were left on the
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35
36 152 ground); all other events were considered to be zero crop years.

39 153 For reproductive effort, we compared monthly climate data against acorn yield ('mast'
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41 154 years only) using Spearman's rank correlations. We recognize that the comparison of oak
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44 155 reproductive behavior with multiple climate variables, increases the likelihood of
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46 156 committing type I error. Nonetheless, we chose not to make the *a priori* assumption that
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48 157 weather for periods known to be strongly associated with reproductive effort in other
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51 158 species and studies, would be the sole drivers of acorn production in our oaks. Rather, we
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53 159 sought to eliminate all possibilities outside of the recognized pollination and seed

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4 160 maturation times and then corroborate *post-priori* any significant ($P < 0.05$) relationships
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6 161 from the literature. Having done this, we then developed a linear regression model to
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9 162 predict acorn crop as a function of seasonal average climate.
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11 12 163 RESULTS

13 14 15 16 164 *Climate and Oak Reproductive Trends*

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18 165 Mast years (thirteen of the total 27 years of observation) occurred synchronously across all
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20 166 trees, except during 2001 when two failed to produce acorns (supplementary Table S1).
21
22 167 The number of trees we were able to observe reduced over time: 12 trees from 1989-1998
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24 168 (4 events), 11 trees from 1999-2005 (4 events), 10 trees from 2006-2014 (5 events), and
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26 169 nine in 2015 (a crop year). Mean acorn production (Figure 1) ranged between a minimum
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28 170 of 0.018 kg m⁻² in 2001 to a maximum of 0.446 kg m⁻² in 1995. Only in 2001-2003 and
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30 171 2010 and 2011 did we record consecutive acorn years. Years 2001 and 2002 (0.053 kg m⁻²)
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32 172 were the two lowest yields recorded, and 2010 (0.124 kg m⁻²) was the sixth lowest, all
33
34 173 below the mean yield calculated across all trees and mast years (0.196 kg m⁻²).
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36 174 Within cropping years, there was a large spread in productivity across trees. For individual
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38 175 events, the largest range occurred in 1995 (0.807 kg m⁻² difference between least and most
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40 176 productive trees) and the smallest in 2001 (0.063 kg m⁻² difference between least and most
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42 177 productive trees). Since seed size is generally aplastic (Fenner and Thompson 2005), and
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44 178 for *Q. robur* in particular unlikely to vary by more than a factor of three (Brookes and
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46 179 Wigston 1979; Nikolić and Orlović 2002), we conclude that observed variation in crop
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48 180 yield was most closely associated with change in acorn number rather than individual size.
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181 *Climate Influence on Mast Year Occurrence*

182 The likelihood of masting occurrence in any given year depends on both favourable
183 environmental conditions (e.g., climate) and internal resource dynamics (Pearse *et al.* 2016;
184 Bogdziewicz *et al.* 2018). If the latter were the sole mechanism, crop and non-crop years
185 would be expected to alternate, as a high reproductive effort in one year would exhaust
186 resources such that a high acorn crop would be unlikely in the following year even if
187 environmental conditions were favourable. To test whether masting/non-masting years
188 alternate more than would be predicted from random, we conducted a Wald–Wolfowitz
189 runs test by converting the masting data to a sequence of ones (masting, $n=13$) and zeros
190 (non-masting, $n=14$). A ‘runs test’ evaluates the probability that a given sequence of events
191 occurs randomly against the alternative hypotheses that events either tend to cluster
192 together or alternate from one trial (year of observation) to the next. Results indicated that
193 the null hypothesis that the sequencing of masting/non-masting events is random cannot be
194 rejected ($z = 1.5796$, $P = 0.11$), suggesting that internal resource limitation was not the sole
195 driver of mast events.

196 To investigate possible climate triggers for masting, we compared climate between crop-
197 and non-crop years. Although temperature in the year prior to masting had no discernible
198 influence, July conditions were on average, warmer during the actual mast year (Figure 2:
199 left and centre columns). When recalculated as the difference between the current and
200 previous year, however, the strongest potential triggers were maximum and mean
201 temperatures during July ($T_{\max} P = 0.028$; $T_{\text{mean}} P = 0.0364$) and August ($T_{\max} P =$
202 0.038 ; $T_{\text{mean}} P = 0.007$) (Figure 2: right column). This suggests mast years tend to occur

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4 203 when cold summer conditions during previous year, were followed by anomalous warmth
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6 204 in the same months in the mast year. We found less association between mast seeding
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8 205 occurrence and either the number of frost days or rainfall (Figure 3), the only significant
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10 206 anomalous occurrence being April rainfall ($P = 0.001$) where mast years were more
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13 207 common in drier conditions.
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16 208 *Climate Influence on Acorn Yields*

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19 209 To estimate climate effects on acorn production while accounting for changes in the
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21 210 number of trees observed, we estimated an average per tree acorn yield in each mast year.
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23 211 Of all climate variables, concurrent year monthly mean temperatures were most strongly
24
25 212 related to total acorn production. The strongest correlations were with May (Spearman's r
26
27 213 = 0.66; $P = 0.01$) and June ($r = 0.75$; $P = 0.003$) temperatures, indicating that warm
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29 214 conditions during these months were associated with larger acorn crops. Averaging mean
30
31 215 temperatures together for May and June, we developed a simple linear regression model for
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33 216 acorn yield per tree (Figure 4). The regression was highly significant with large explanatory
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35 217 power ($P = 0.002$, $r^2 = 0.61$) and corresponds with the peak pollination period for oak in
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37 218 southern England (Grime *et al.* 2007). From the slope of the regression, we estimate that
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39 219 acorn yield per tree increases by about 0.11 kg m⁻² per °C of warming.
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48 221 DISCUSSION

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51 222 Despite observing the relatively large between-tree variation in acorn crops reported
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53 223 elsewhere (Herrera *et al.* 1998; Crawley and Long 1995; Koenig and Knops 2000;
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4 224 Zamorano *et al.* 2017), our oaks exhibited uniform variation in seed crop yield across the
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6 225 population. For example, eight of the 13 mast years, including 2015, were followed by non-
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8 226 mast years (i.e. no acorns survived post-dispersal predation) for all individuals.

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11 227 Nonetheless, we found no evidence that high reproductive allocation in one year was
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13 228 followed sequentially by a low acorn crop the next. Although at face value this may seem
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15 229 to contradict the view that internal resource dynamics prevent individuals from producing
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17 230 sequential mast crops (Herrera *et al.* 1998; Kelly and Sork 2002; Crone and Rapp 2014), a
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19 231 combination of internal resource dynamics and climate may nonetheless, together trigger
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21 232 masting behaviour.

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26 233 Aside from dry April conditions, precipitation and the number of frost days had no
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28 234 detectable influence on acorn production; both phenomena can be relatively localised and
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30 235 consequently thought not to impose the uniform regional climate cue needed to ensure
31
32 236 regional synchronisation (Norton and Kelly 1988; Kelly *et al.* 2013). Temperature signals
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34 237 in either the previous, or current, years alone were only weakly related to masting
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36 238 occurrence. Masting was, however, strongly associated with a combination of temperature
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38 239 cues across these years; specifically relatively cool conditions in the summer of the year
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40 240 before masting when followed by relatively warmer temperatures during the period of the
41
42 241 actual mast year, together promoted mast occurrence. In addition, warm, dry May and June
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44 242 weather within the mast year were associated with relatively high acorn crops, results
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46 243 corroborating studies that associate warm late spring/early summer conditions to high tree
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48 244 seed yield. Askeyev *et al.* (2005), Bogdziewicz *et al.* (2017) and Caignard *et al.* (2017) for
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50 245 example, reported that ‘within-year’ warm spring and summer conditions promoted
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4 246 increased acorn production in Russian, Polish, and French *Q. robur* populations
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6 247 respectively. Similar relationships were described for the Californian *Q. lobata* (Koenig *et*
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8 248 *al.* 2015), and Scandinavian *Picea abies* and *Betula* species (Zamorano *et al.* 2017).
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10 249 Consequently, it seems likely that our analyses identified *bona fide* biological relationships
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12 250 between reproductive effort and monthly weather data, rather than generating ‘significant’
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14 251 correlations due simply to type I error (see Cabin & Mitchell 2000).
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19 252 The long-accepted explanation for the link between warm, dry spring conditions and high
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21 253 reproductive output in temperate oak species is that this weather promotes pollen transfer in
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23 254 anemophilous trees (Norton and Kelly 1988; Smith, *et al.* 1990). This explanation
24
25 255 underpins the *Moran effect* hypothesis; i.e. pollination success and thus reproductive
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27 256 output, is decoupled from mechanisms affecting flower production but is instead,
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29 257 associated with environmental conditions during flowering (Koenig 2012; Pearse *et al.*
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31 258 2016; Bogdziewicz *et al.* 2017). In addition to warm dry conditions favouring pollination,
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33 259 warm early summer growing conditions in July and August may also promote increased
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35 260 photosynthesis and so increase the resources available for reproductive allocation (Norton
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37 261 and Kelly 1988; Kelly and Sork 2002).
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43 262 The apparent influence of the summer temperature difference anomaly on acorn crops, also
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45 263 highlights however, the potential importance of *pollen coupling*; i.e. pollination success and
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47 264 seed yield are functions of environmental and/or resource constraints that dictate the parent
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49 265 tree’s ability to produce flowers (Satake and Iwasa 2000; Kelly *et al.* 2001; Monks *et al.*
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51 266 2016). Bogdziewicz *et al.* (2018) developed this idea further by suggesting that the
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53 267 environment has a ‘veto’ effect on reproductive allocation. Put simply, reproductive failure
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4 268 brought about by poor environmental conditions in one year, facilitates the accumulation of
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6 269 resources that plants can then allocate to subsequent (increased) reproductive output.
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9 270 Consequently, masting may not simply arise from the occurrence of favourable
10
11 271 environmental conditions. Instead Bogdziewicz *et al.* (2018) argue that masting it is a
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13 272 combination of unfavourable environmental conditions (that limit reproduction),
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15 273 subsequent resource accumulation (more to spend on reproduction), and the environmental
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17 274 triggering of resource release to reproduction when weather conditions are favourable. The
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19 275 cool late summer conditions the year prior to mast (likely reducing seed development and
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21 276 maturation) may have facilitated resource accumulation and high reproductive output when
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23 277 coincidental with above-average summer conditions in mast year. Since a good summer
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25 278 does not predictably follow a bad one, resource accumulation alone cannot dictate acorn
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27 279 yield, and so explain why we failed to detect any sequential pattern of crop/non-crop years.
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29 280 Certainly, our results corroborate a growing consensus that the initiation of masting results
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31 281 from a combination or sequence of climate cues (Allen *et al.* 2014; Buechling *et al.* 2016).
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33
34 282 Given the close association between oak masting (occurrence and amount), and spring and
35
36 283 summer weather we elucidate here, the likely increased temperatures and shifts in
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38 284 precipitation associated with ACC would be expected to affect greatly reproductive timing
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40 285 and output. Our data and analysis suggest a 0.11 kg m⁻² per tree increase in acorn yield per
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42 286 °C of warming; we recognise however, that a scenario of continual increased masting is
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44 287 highly unlikely to unfold. As Buechling *et al.* (2016) point out; positive climate/masting
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46 288 relationships must eventually be constrained by inherent physiological limitations. Indeed,
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48 289 there is an emerging consensus that in order to best understand masting behaviour,
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4 290 predictive models based on environmental cues for flowering, pollination success and acorn
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6 291 production, must incorporate also a term for internal parental resource budgets (Koenig et
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8 292 al 2015; Pesnedorfer *et al.* 2016; Bogdziewicz *et al.* 2017, 2018). In addition, changes in
9
10 293 the abundance and activity of seed and seedling predators, and extrinsic factors affecting
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12 294 germination and seedling dormancy (Newbold and Goldsmith 1981), are additional
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14 295 complexities that serve to highlight the fact that we still understand remarkably little
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16 296 regarding the impacts of ACC on plant regeneration biology (Parmesan and Hanley 2015).
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28 299 SUPPLEMENTARY MATERIAL

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31 300 Supplementary material (Table S1) is available at *Journal of Plant Ecology* online.
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36 37 302 REFERENCES

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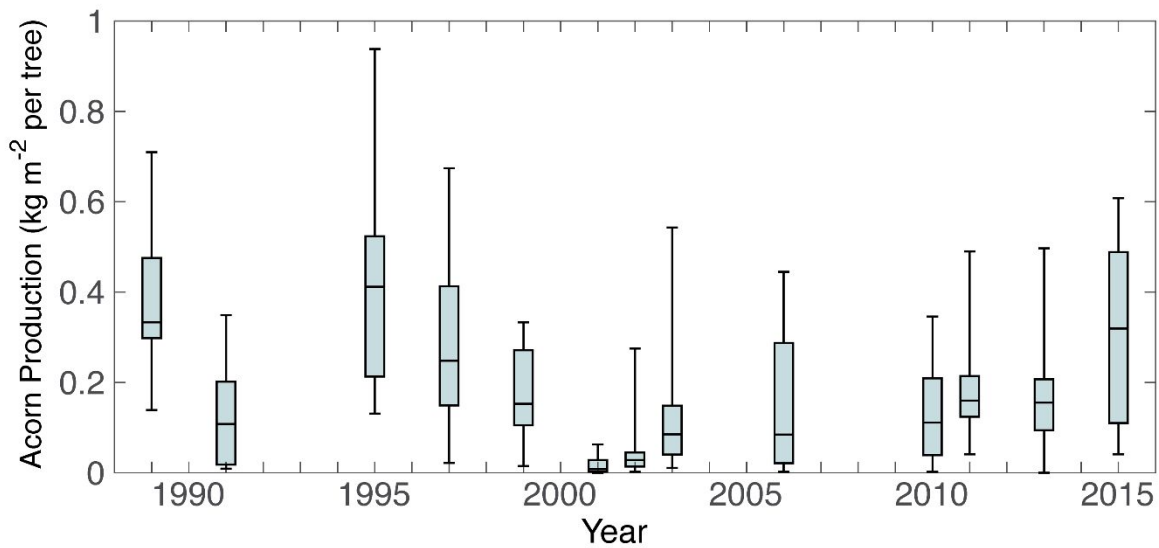
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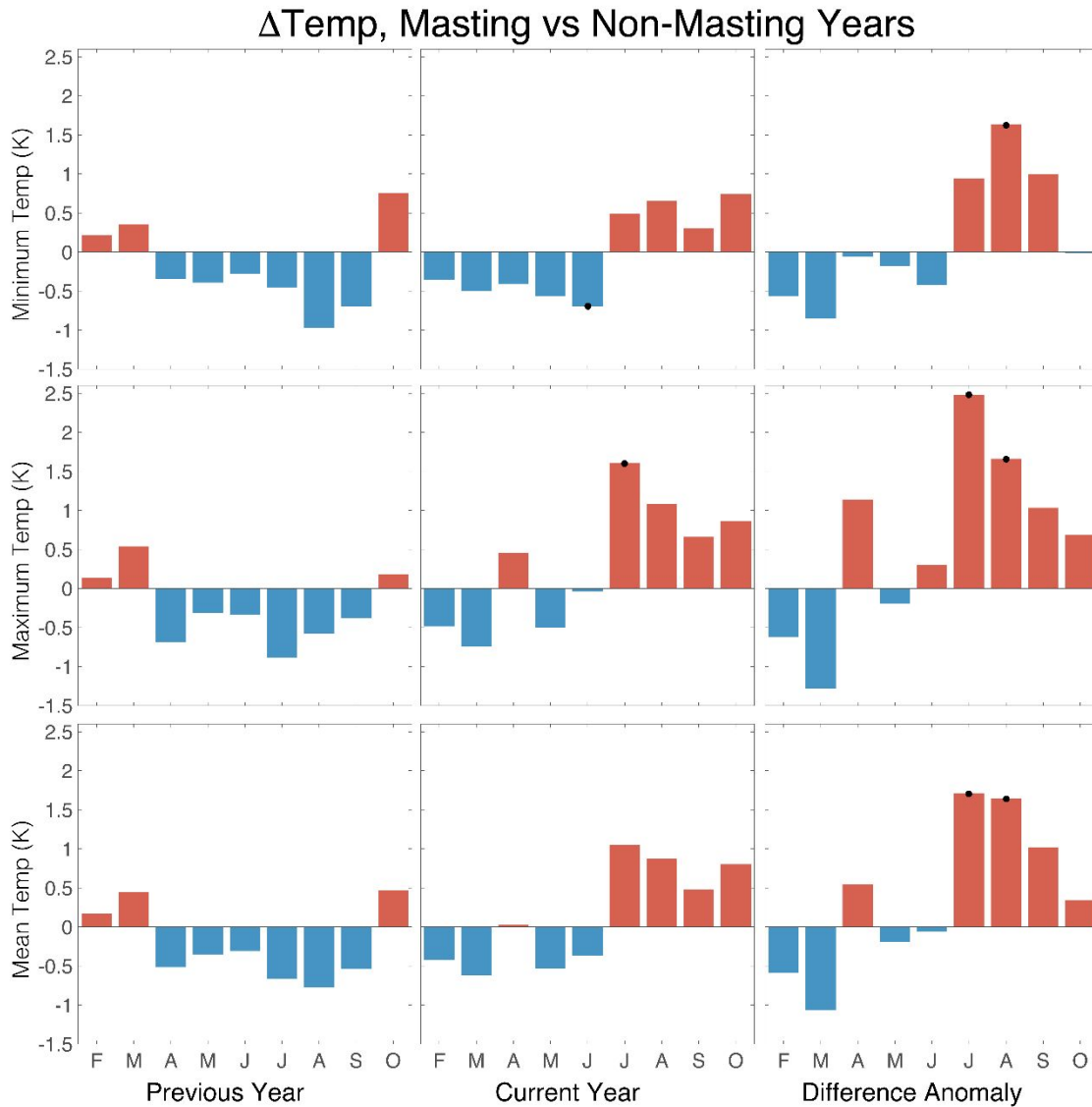
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443 **Figure 1.** Acorn production (kg m⁻²) across individual trees during mast seeding events444 recorded from 1989 to 2015 for a population of *Quercus robur* trees growing in

445 Southampton, southern England. Years without a box = zero acorns post-predation.

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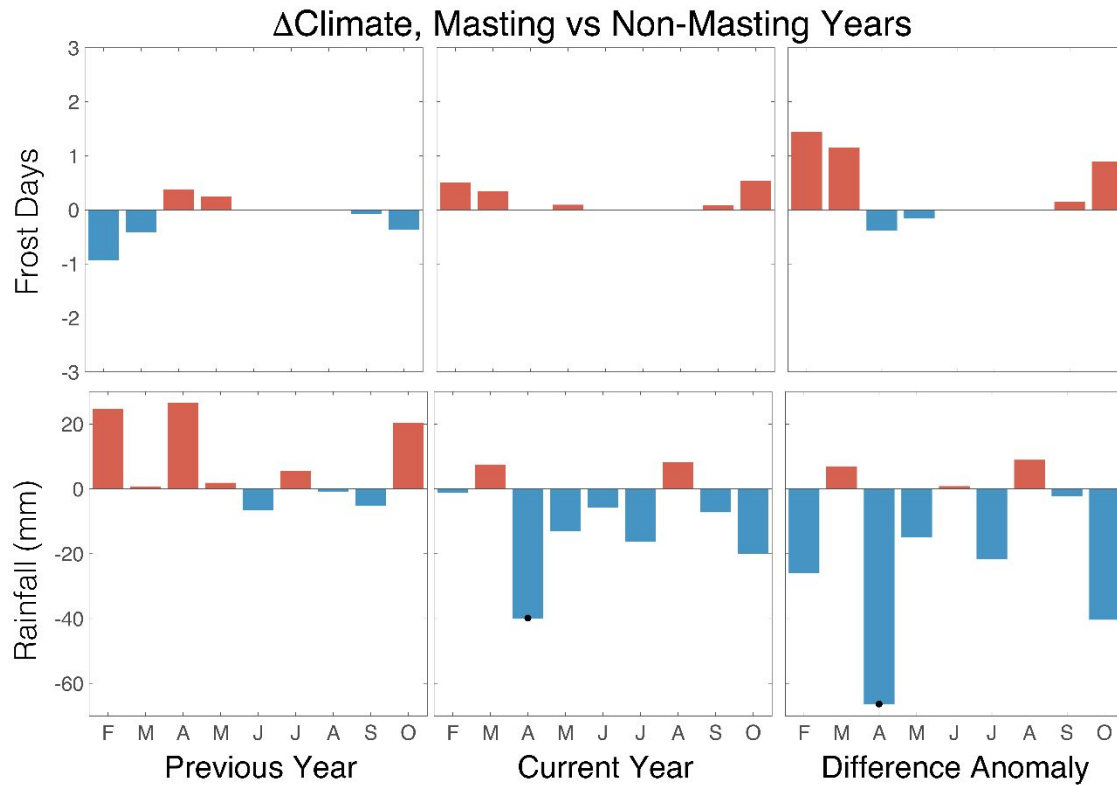
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Figure 2. Monthly minimum, maximum, and mean temperature anomalies (significance assessed with a two-sided Student' t -test and indicated by black ($P < 0.05$) dots) associated with mast and non-years for a population of *Quercus robur* trees growing in Southampton, southern England. Results are shown for years prior to the mast

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6 455 (right column).
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Figure 3. Anomalies (assessed with a two-sided Student' *t*-test and indicated by black ($P < 0.05$) dots) in frost days and rainfall associated with mast and non-mast years for a population of *Quercus robur* trees growing in Southampton, southern England. Results are shown for years prior to the mast year (left column); the mast year (centre column); the difference between the two (right column).

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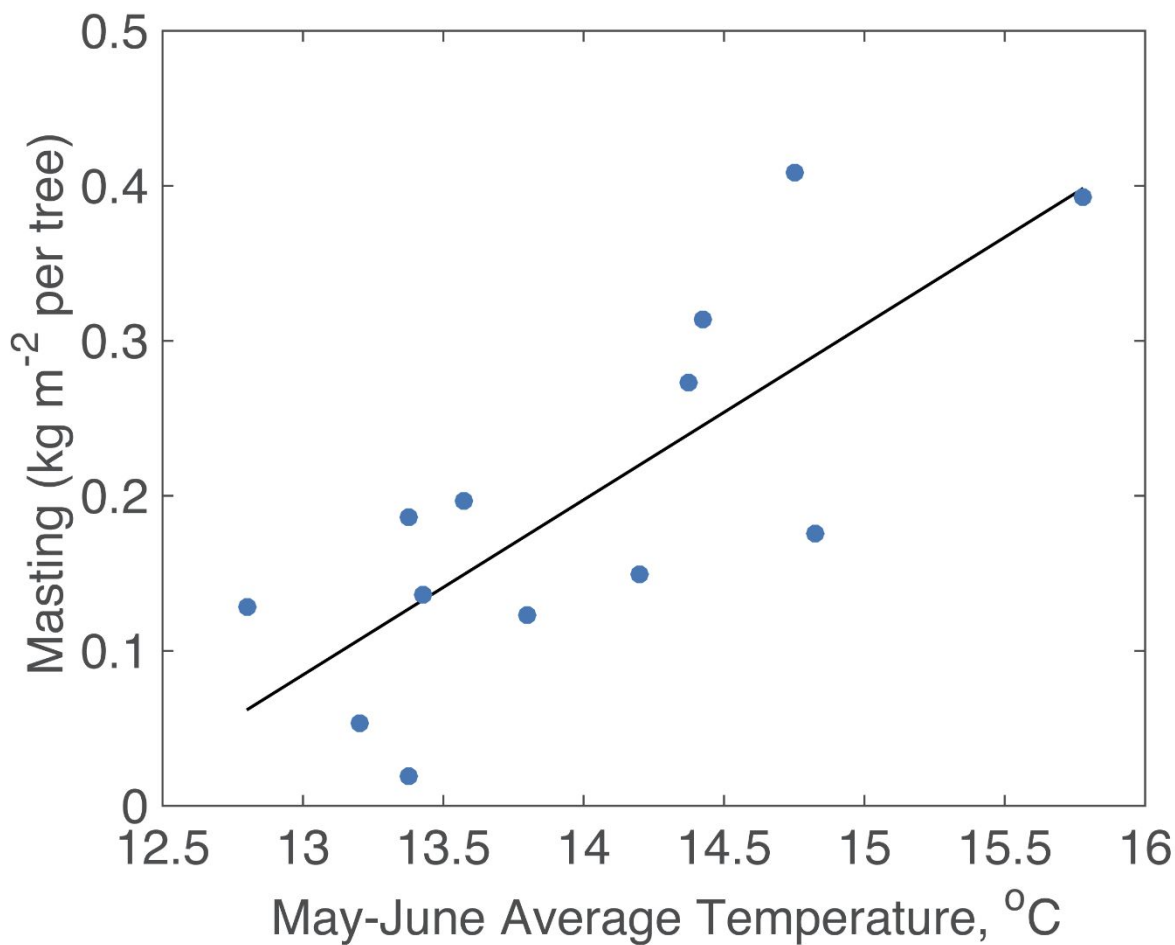


Figure 4. Relationship between average acorn yield (kg m^{-2}) and local May-June average temperature for a population of *Quercus robur* trees growing in Southampton, southern England. Each dot represents one mast year.

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Tree Number	Year																										
	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
1	0.304	0	0.109	0	0	0	0.156	0	0.416	0	0.153	0	0.005	0.016	0.169	0	0	0.063	0	0	0	0.029	0.490	0	0.379	0	0.464
2	0.435	0	0.102	0	0	0	0.131	0	0.288	0	0.289	0	0.000	0.275	0.076	0	0	0.106	0	0	0	0.039	0.146	0	0.094	0	
3	0.376	0	0.349	0	0	0	0.193	0	0.029	0	0.144	0	0.062	0.004	0.021	0	0	0.021	0	0	0	0.274	0.371	0	0.149	0	0.608
4	0.310	0	0.013	0	0	0	0.233	0	0.022	0	0.015	0	0.002	0.025	0.037	0	0	0.002	0	0	0	0.002	0.174	0	0.000	0	0.041
5	0.347	0	0.199	0	0	0	0.432	0	0.410	0	0.187	0	0.033	0.042	0.126	0	0	0.287	0	0	0	0.125	0.124	0	0.207	0	0.319
6	0.292	0	0.010	0	0	0	0.502	0	0.087	0	0.083	0	0.007	0.013	0.085	0	0	0.044	0	0	0	0.097	0.041	0	0.162	0	0.403
7	0.710	0	0.023	0	0	0	0.647	0	0.236	0	0.234	0	0.014	0.028	0.085	0	0	0.019	0	0	0	0.166	0.214	0	0.183	0	0.218
8	0.674	0	0.273	0	0	0	0.938	0	0.419	0																	
9	0.516	0	0.204	0	0	0	0.392	0	0.218	0	0.333	0	0.063	0.046	0.543	0	0	0.402	0	0	0	0.346	0.192	0	0.497	0	0.563
10	0.289	0	0.142	0	0	0	0.295	0	0.211	0	0.284	0	0.010	0.002	0.011	0	0										
11	0.139	0	0.009	0	0	0	0.545	0	0.674	0	0.105	0	0.000	0.094	0.156	0	0	0.445	0	0	0	0.209	0.083	0	0.124	0	0.117
12	0.319	0	0.107	0	0	0	0.439	0	0.260	0	0.106	0	0.008	0.038	0.051	0	0	0.106	0	0	0	0.070	0.132	0	0.070	0	0.090
Total (kg)	4.710	0	1.540	0	0	0	4.904	0	3.270	0	1.934	0	0.203	0.584	1.359	0	0	1.496	0	0	0	1.359	1.966	0	1.864	0	2.822
Mean (kg)	0.428	0	0.140	0	0	0	0.446	0	0.297	0	0.176	0	0.018	0.053	0.124	0	0	0.136	0	0	0	0.124	0.179	0	0.169	0	0.257
SE (kg)	0.048	0	0.032	0	0	0	0.067	0	0.054	0	0.029	0	0.007	0.023	0.043	0	0	0.048	0	0	0	0.033	0.039	0	0.043	0	0.061
Median (kg)	0.333	0	0.108	0	0	0	0.412	0	0.248	0	0.153	0	0.008	0.028	0.085	0	0	0.085	0	0	0	0.111	0.160	0	0.155	0	0.319

Table S1 - Annual acorn yield (Kg m⁻²) for a population of 12 *Quercus robur* trees growing on Southampton Common (50.9262°N, 1.4092°W), southern England. Acorn yield was quantified using four transects placed north, south, east and west extending from the base of the trunk to the edge of the canopy for each tree. Trees 8 and 10 became engulfed by brambles; tree 2 suffered major branch damage. Acorn yield from each 'sample' and the estimate for the 'total' for each individual tree (i.e. sample mass × 14.7) are shown. Hanley, Cook & Fenner (July 2017)