

1 **Variable reproduction goes beyond masting**

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27 **Main text**

28 Kelly's commentary regarding our paper¹, claiming that nutrient scarcity cannot select
29 for masting behaviour in plants, initiated a fruitful discussion on traditionally settled
30 hypotheses about the evolution of reproductive behaviour in plants. In his commentary,
31 Prof. Kelly raises support for a contrasting hypothesis explaining our observation that
32 temporally variable seed production is more pronounced under nutrient scarcity,
33 namely that nutrient scarcity does not directly cause seed production variability, but
34 instead increases variability induced by economies of scale. The commentary hinges
35 mainly on the argument that an economy of scale (EOS) is necessary to select for
36 highly variable seed production. It also points out that there are no mechanisms by
37 which nutrient scarcity would select for that particular trait over generations. In reply to
38 the stimulating comment, we 1) propose a mechanism by which nutrient scarcity may
39 select for highly variable seed production, with weather patterns inducing masting
40 synchrony across populations; 2) further discuss why wind-pollination and predator
41 satiation, the EOS suggested by Kelly, cannot be the only selective pressures that
42 select for highly variable reproduction.

43 (1) There is robust empirical evidence^{2,3} showing that nutrient scarcity, and climate, are
44 long existing evolutionary forces that have selected for multiple plant traits and have
45 constrained the physiology of plants since their early development. Limiting resources,
46 such as water and nutrients, thus trigger the evolution of conservative traits for those
47 limiting factors³. Logically, nutrient availability is a direct determinant of the mean fruit
48 production in agriculture and in the wild⁴. In our paper¹, we hypothesised that low
49 nutrient availability is also an important factor selecting for highly variable and
50 synchronized seed production, the latter in combination with adaptation to variability in
51 long-term climate patterns. Our hypothesis as to why nutrient scarcity may have
52 selected for highly variable seed production in nutrient-poor plants, probably not
53 entirely explained in our original paper, was based on a mechanism linking highly

54 variable seed production in nutrient-poor plant species to increased inter- and
55 intraspecific competitiveness.

56 Because fruits are nutrient-enriched tissues⁵, their production under low fertility implies
57 a reduced allocation of nutrients to growth and defence⁶, and therefore lower
58 competitiveness and survival for the parent plants. Reductions in plant nutrient
59 concentrations after reproduction have been described for several species⁷, in addition
60 to growth and defence-reproductive trade-offs⁶. Therefore, when nutrients are scarce,
61 losing large amounts of nutrients year after year might jeopardize plant growth through
62 reduced photosynthesis, a highly nutrient-dependent process⁸. A constant yearly
63 reproduction would also imply a constant lowering of the availability of nutrients for
64 other processes. In contrast, nutrient accumulation in years with suitable weather
65 conditions for soil organic matter decomposition and mineralization may provide
66 sufficient nutrients to allow a high fruit crop in the following year, which would not come
67 at the expense of reduced competitiveness or increased mortality risk (**Figure 1**).
68 Under these conditions, high temporal variability would thus be beneficial and likely to
69 be selected for. In contrast, under nutrient-rich conditions, plants can potentially
70 reproduce regularly without jeopardising their competitiveness; this is actually one of
71 the reasons for fertilizer addition as a long-existing agricultural practice. This
72 mechanism, which could have originated during the early evolution of plants, may
73 explain why, under low nutrient availability, nutrient-conservative plants with highly
74 variable reproduction may have been preferentially selected in comparison to nutrient-
75 spending plants (with more constant reproduction). Further research including long-
76 term data sets of reproduction, growth and defence allocation, however, is still needed
77 to validate our hypotheses.

78 For a population to exhibit highly variable reproduction over time, a strong synchrony
79 among individuals is required⁹. Synchronous seed production is another important
80 feature of masting behaviour that has been traditionally associated with the benefits of

81 EOS, as it has been suggested to be an adaptive response to improve pollination
82 efficiency or escape seed predation⁷. Synchrony among individuals in a plant
83 population is the rule rather than the exception, as for example in leaf flushing, flower
84 blooming, die-back episodes or simply growth as shown by dendrochronology studies.
85 The most likely mechanism driving the synchrony in phenology, growth or reproduction
86 is the similar response of a population to changing weather patterns, by affecting
87 metabolism and plant resources.

88 Over time, the scientific community has discounted environmental effects based in part
89 on two assumptions that may not hold true, and this has fed the line of thought that
90 EOS benefits are necessary for high variable seed production to evolve. First, a direct
91 role of weather in synchronizing seed production has been discounted in part because
92 interannual variation in weather is much less than variation in seed production. We
93 argue that this line of argument does not hold because the link between weather and
94 seed production in a given year may be highly non-linear¹⁰. In Mediterranean regions,
95 for example, wet spring weather may simultaneously increase both carbon availability
96 through photosynthesis and nutrient availability through mineralization¹¹, boosting plant
97 resources and seed production. Second, proportional allocation has been assumed to
98 describe the passive allocation of resources to reproduction⁷. However, work in the
99 fields of ecological stoichiometry and carbon dynamics suggest that plants allocate
100 resources based on a hierarchy of needs, in which a set portion of resources goes
101 toward tissue maintenance at the expense of all other functions⁴. We, therefore,
102 suggest that interannual variability in reproduction is more likely to have been
103 evolutionary selected than synchrony.

104 (2) From evolutionary and theoretical bases, that highly variable reproduction can only
105 be selected because of wind pollination and predator satiation does not hold either. For
106 that to be true, we would have to accept that the common ancestors of plants, before
107 the trait of wind pollination and their seed predators evolved, did not show variable

108 seed production. In fact, it implies that the reproductive efforts of organisms other than
109 vascular plants, which do not produce pollen or may not have important predators of
110 their offspring, cannot be temporally variable unless, for other reasons, it evolved later
111 in these clades. However, there is evidence suggesting that other organisms that
112 reproduce sexually are also temporally synchronised and variable (**Figure 2**). Some
113 bryophytes tend to produce sporophytes more frequently than others¹², and their
114 production is mainly controlled by weather variability, like in vascular plants¹³, being
115 synchronised in time and space. The same happens with mushroom communities,
116 being highly synchronised, interannually variable, and highly dependent on weather
117 conditions¹⁴. Even the rates of animal fertility vary amongst years depending on the
118 amount of resources available, such as fertility rates of wild boars¹⁵. Given the fact that
119 temporally variable sexual reproduction in nature seems to be common, we should
120 conclude that factors others than wind pollination and predator satiation may have
121 played a role in shaping this reproductive trait. We suggest that one of these potential
122 factors triggering a highly variable seed production, before wind pollination and
123 predators evolved, may have been nutrient scarcity because of its role in determining
124 the physiology of a broad range of organisms³. Later on, wind pollination and predator
125 satiation may have evolved, reinforcing a highly variable seed production of vascular
126 plants. In order to better understand the evolutionary history of highly variable
127 reproduction in vascular plants, the field of masting will benefit from broadening its
128 scope and looking for inspiration in different disciplines and exploring examples from
129 other groups of organisms.

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173 **Conflict of interest**

174 The authors declare no conflict of interest.

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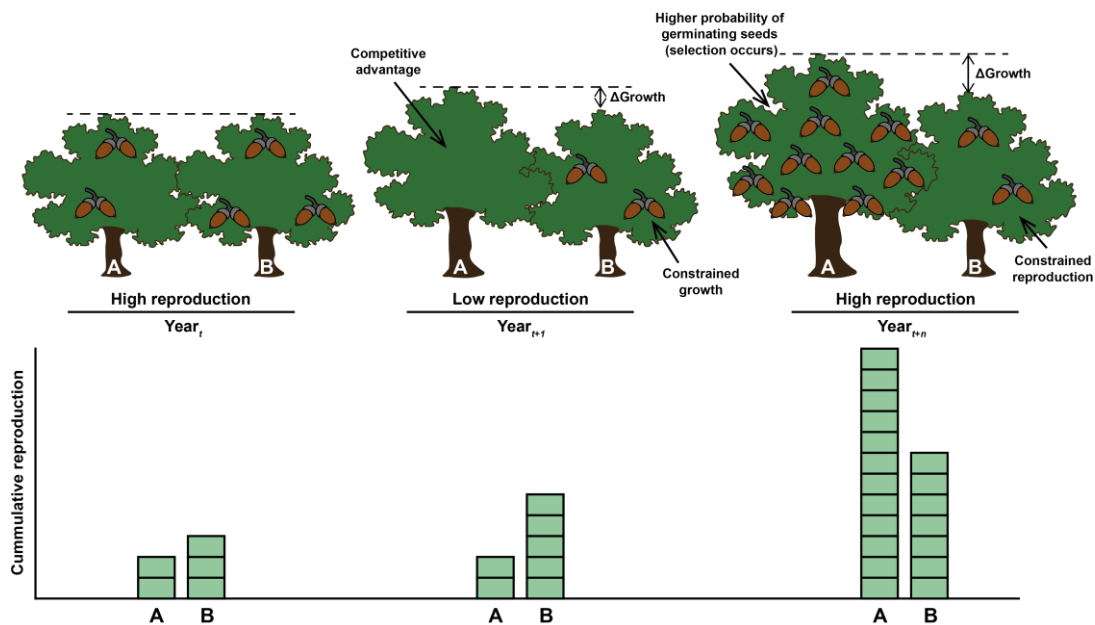
176 **Author contribution**

177 M.F-M., J.S., J.P., J.M.E., J.P. and I.A.J., conceived the paper. All authors contributed
178 equally to the writing of the manuscript.

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180 **Figure captions**

181 **Figure 1: Scheme showing the hypothesised mechanism by which nutrient**
182 **scarcity may act as a selective pressure of variable reproduction.** When nutrients
183 are scarce, delaying reproductive efforts may provide a competitive advantage given by
184 the lower rate of nutrient loss through reproductive structures. Losing nutrients through
185 reproduction may reduce growth in the short term by decreasing photosynthetic rates.
186 Under low nutrient availability, nutrient-conservative plants (A, with more variable
187 reproduction) outcompete, by vegetative growth, nutrient-spending plants (B, less
188 variable reproduction). This competition may thus increase the probability of seed
189 germination in nutrient-conservative plants and therefore potentially select for nutrient-
190 conservative traits such as high interannually variable reproduction. Synchronous
191 reproduction would then be the logical response to reproducing only when weather is
192 optimal and also selected for during evolution.



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195 **Figure 2: Four examples of interannually variable sexual reproduction.** (a)
196 Sporophytes of *Plagiomnium undulatum* (a species that produces sporophytes only
197 rarely); (b) acorn production by a *Quercus ilex* tree (often considered a *masting*
198 species); (c) mushroom production by *Hypholoma fasciculare* (fungal reproduction is
199 highly interannually synchronised within and across species); (d) a mother wild boar
200 with four piglets (sow fertility rates depend on the availability of food, such as acorns,
201 during *Quercus* mast years). The photographs in (a) and (b) were taken by Catherine
202 Preece, the photograph in (c) was taken by Jordi Corbera, and the photograph in (d)
203 was taken by M.F-M.

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