



Reply to: Nutrient scarcity cannot cause mast seeding

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REPLYING TO D. Kelly *Nature Plants* <https://doi.org/10.1038/s41477-020-0702-7> (2020)

In his recent communication on our original paper^{1,2}, D. Kelly, claiming that nutrient scarcity cannot select for masting behaviour in plants, initiated a fruitful discussion on traditionally settled hypotheses about the evolution of reproductive behaviour in plants. In his commentary, Kelly raises support for a contrasting hypothesis explaining our observation that temporally variable seed production is more pronounced under nutrient scarcity, namely that nutrient scarcity does not directly cause seed production variability but instead increases variability induced by economies of scale (EOS). The commentary hinges mainly on the argument that an EOS is necessary to select for highly variable seed production. It also points out that there are no mechanisms by which nutrient scarcity would select for that particular trait over generations. In reply to the stimulating comment, we (1) propose a mechanism by which nutrient scarcity may select for highly variable seed production, with weather patterns inducing masting synchrony across populations; and (2) further discuss why wind pollination and predator satiation, the EOS suggested by Kelly, cannot be the only selective pressures that select for highly variable reproduction.

There is robust empirical evidence^{3,4} showing that nutrient scarcity and climate, are long-existing evolutionary forces that have selected for multiple plant traits and have constrained the physiology of plants since their early development. Limiting resources, such as water and nutrients, thus trigger the evolution of conservative traits for those limiting factors⁴. Logically, nutrient availability is a direct determinant of the mean fruit production in agriculture and in the wild⁵. In our paper¹, we hypothesized that low nutrient availability is also an important factor selecting for highly variable and synchronized seed production, the latter in combination with adaptation to variability in long-term climate patterns. Our hypothesis as to why nutrient scarcity may have selected for highly variable seed production in nutrient-poor plants, probably not entirely explained in our original paper, was based on a mechanism linking highly variable seed production in nutrient-poor plant species to increased interspecific and intraspecific competitiveness.

Because fruits are nutrient-enriched tissues⁶, their production under low fertility implies a reduced allocation of nutrients to growth and defence⁷, and therefore lower competitiveness and

survival for the parent plants. Reductions in plant nutrient concentrations after reproduction have been described for several species⁸, in addition to growth and defence–reproductive trade-offs⁷. Therefore, when nutrients are scarce, losing large amounts of nutrients year after year might jeopardize plant growth through reduced photosynthesis, a highly nutrient-dependent process⁹. Constant yearly reproduction would also imply a constant lowering of the availability of nutrients for other processes. In contrast, nutrient accumulation in years with suitable weather conditions for soil organic matter decomposition and mineralization may provide sufficient nutrients to allow a high fruit crop in the following year, which would not come at the expense of reduced competitiveness or increased mortality risk (Fig. 1). Under these conditions, high temporal variability would thus be beneficial and likely to be selected for. In contrast, under nutrient-rich conditions, plants can potentially reproduce regularly without jeopardizing their competitiveness; this is actually one of the reasons for fertilizer addition as a long-existing agricultural practice. This mechanism, which could have originated during the early evolution of plants, may explain why, under low nutrient availability, nutrient-conservative plants with highly variable reproduction may have been preferentially selected in comparison to nutrient-spending plants (with more constant reproduction). Further research, including long-term datasets of reproduction, growth and defence allocation, however, is needed to validate our hypotheses.

For a population to exhibit highly variable reproduction over time, a strong synchrony among individuals is required¹⁰. Synchronous seed production is another important feature of masting behaviour that has been traditionally associated with the benefits of EOS, as it has been suggested to be an adaptive response to improve pollination efficiency or escape seed predation⁸. Synchrony among individuals in a plant population is the rule rather than the exception, as for example in leaf flushing, flower blooming, die-back episodes or simply growth as shown by dendrochronology studies. The most likely mechanism driving the synchrony in phenology, growth or reproduction is the similar response of a population to changing weather patterns, by affecting metabolism and plant resources.

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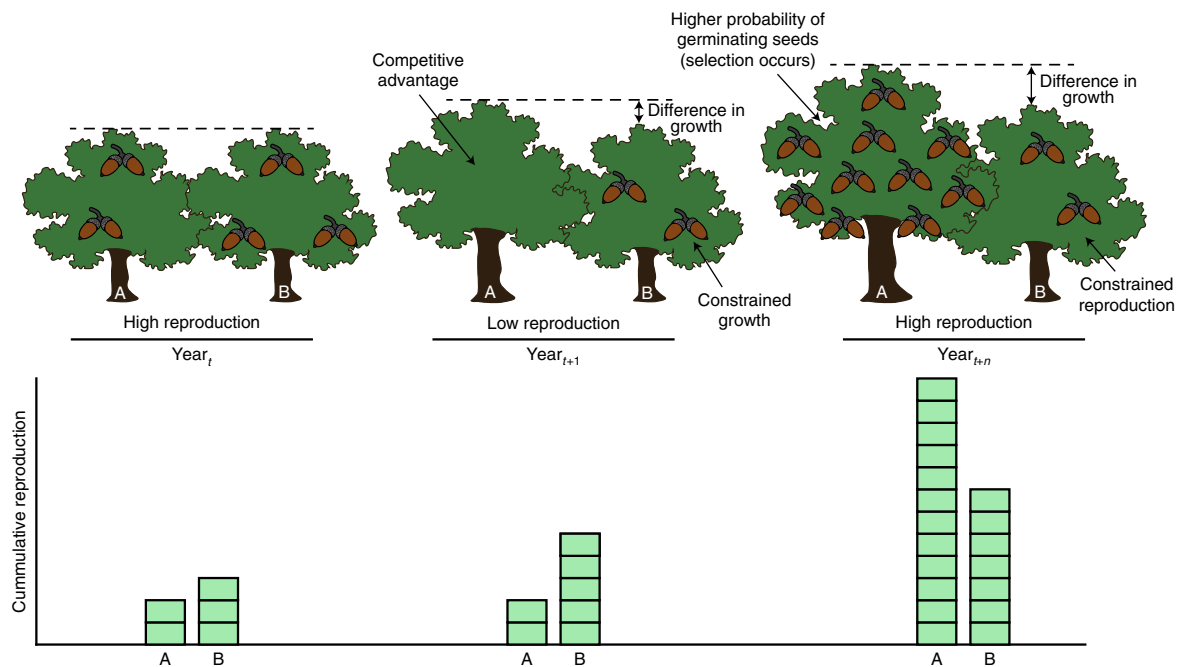


Fig. 1 | Scheme showing the hypothesized mechanism by which nutrient scarcity may act as a selective pressure of variable reproduction. When nutrients are scarce, delaying reproductive efforts may provide a competitive advantage given by the lower rate of nutrient loss through reproductive structures. Losing nutrients through reproduction may reduce growth in the short term by decreasing photosynthetic rates. Under low nutrient availability, nutrient-conservative plants (A, with more variable reproduction) outcompete, by vegetative growth, nutrient-spending plants (B, less variable reproduction). This competition may thus increase the probability of seed germination in nutrient-conservative plants and therefore potentially select for nutrient-conservative traits such as high interannually variable reproduction. Synchronous reproduction would then be the logical response to reproducing only when weather is optimal and also selected for during evolution. $Year_t$ indicates a given year, $Year_{t+1}$ indicates the following year and $Year_{t+n}$ indicates n years after a given year.

Over time, the scientific community has discounted environmental effects based in part on two assumptions that may not hold true and this has fed the line of thought that EOS benefits are necessary for high variable seed production to evolve. First, a direct role of weather in synchronizing seed production has been discounted in part because interannual variation in weather is much less than variation in seed production. We argue that this line of argument does not hold because the link between weather and seed production in a given year may be highly nonlinear¹¹. In Mediterranean regions, for example, wet spring weather may simultaneously increase both carbon availability through photosynthesis and nutrient availability through mineralization¹², boosting plant resources and seed production. Second, proportional allocation has been assumed to describe the passive allocation of resources to reproduction⁸. However, work in the fields of ecological stoichiometry and carbon dynamics suggest that plants allocate resources based on a hierarchy of needs, in which a set portion of resources goes toward tissue maintenance at the expense of all other functions⁵. We, therefore, suggest that interannual variability in reproduction is more likely to have been evolutionary selected than synchrony.

From evolutionary and theoretical bases, that highly variable reproduction can only be selected because of wind pollination and predator satiation does not hold either. For that to be true, we would have to accept that the common ancestors of plants, before the trait of wind pollination and their seed predators evolved, did not show variable seed production. In fact, it implies that the reproductive efforts of organisms other than vascular plants, which do not produce pollen or may not have important predators of their offspring, cannot be temporally variable unless, for other reasons, it evolved later in these clades. However, there is evidence suggesting that other organisms that reproduce sexually are also temporally synchronized and variable (Fig. 2). Some bryophytes tend to produce sporophytes more frequently than others¹³ and their production



Fig. 2 | Four examples of interannually variable sexual reproduction.

a, Sporophytes of *Plagiomnium undulatum* (a species that produces sporophytes only rarely). **b**, Acorn production by a *Quercus ilex* tree (often considered a masting species). **c**, Mushroom production by *Hypholoma fasciculare* (fungal reproduction is highly interannually synchronized within and across species). **d**, A mother wild boar with four piglets (sow fertility rates depend on the availability of food, such as acorns, during *Quercus* mast years). The photographs in **a** and **b** were taken by Catherine Preece, the photograph in **c** was taken by Jordi Corbera and the photograph in **d** was taken by M.F.-M.

is mainly controlled by weather variability, as in vascular plants¹⁴, being synchronized in time and space. The same happens with mushroom communities, being highly synchronized, interannually

variable and highly dependent on weather conditions¹⁵. Even the rates of animal fertility vary amongst years depending on the amount of resources available, such as fertility rates of wild boars¹⁶. Given that temporally variable sexual reproduction in nature seems to be common, we should conclude that factors others than wind pollination and predator satiation may have played a role in shaping this reproductive trait. We suggest that one of these potential factors triggering highly variable seed production, before wind pollination and predators evolved, may have been nutrient scarcity because of its role in determining the physiology of a broad range of organisms⁴. Later on, wind pollination and predator satiation may have evolved, reinforcing highly variable seed production of vascular plants. To better understand the evolutionary history of highly variable reproduction in vascular plants, the field of masting will benefit from broadening its scope and looking for inspiration in different disciplines and exploring examples from other groups of organisms.

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Author contributions

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

Competing interests

The authors declare no competing interests.

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