

# Climatic drivers and endogeneous biological constraints shape masting dynamics

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## Introduction

The acceleration of climate change is predicted to have abrupt ecological effects worldwide [1]. Rapid shifts to novel climate conditions, with more extreme events, could disrupt key ecological processes — and potentially drive ecosystems toward critical transitions [2]. In particular, many forest ecosystems are showing signs of increased sensitivity to biotic and abiotic disturbances [3, 4]. Forests could adapt only if they can rely on their regeneration capacity, which promotes post-disturbance recolonization with individuals that may be better adapted to new conditions [5, 6].

Regeneration in many temperate and tropical forests depends the widely observed phenomenon of masting. Masting—which is defined by ‘boom and bust’ cycles of reproduction that are synchronous across most individuals of a population [7]—is hypothesized to drive fitness benefits [8, 9]. The most commonly invoked fitness benefit, ‘predator satiation,’ hypothesizes that years of high seed production overwhelm seed predators and thus allow a higher proportion of seeds and seedlings to escape predation and establish [10, 8]. Masting, however, has many other potential avenues to increase fitness, including through increasing greater pollen exchange and genetic outcrossing across individuals, potentially favoring adaptive evolution via the production of new phenotypes more suitable in novel climates [11, 12].

Masting is a population-level phenomenon that requires individual trees to respond similarly to environmental cues, in order to reproduce together within a certain area. Tree species that mast have likely evolved under colder climates, with specific cues that allowed for synchrony in reproduction. The alteration of these cues by climate change could disrupt masting dynamics and trigger cascading effects on forest resilience [13, 14].

Forecasting how masting will respond to climate change requires to understand how population-level reproductive dynamics emerge from individual tree behaviors. While masting is well established as a phenomenon driven by synchronous trees, modeling this reality has proven challenging. Each tree may respond differently to the same climatic conditions depending on its own reproductive cycle, yet many models treat all trees identically — which could mask the true impact of climate. Capturing individual-level responses is therefore essential for predicting masting at the population scale.

At the individual level, the alternating reproductive cycle is constrained by endogenous factors. In many tree species, floral buds are initiated the year before flowering, simultaneously as fruits of the current year start developing [15]. During a large crop year, the presence of many fruits could depress floral initiation because of hormonal inhibition and resource "competition" for photosynthetic assimilates [16, 17]. These physiological constraints on flower and fruit development could explain while trees often show alternate bearing—with a large crop year ('on-year') often followed by one or several 'off-years'.

The combination of endogenous constraints and local climatic conditions could explain how individual-level intrinsic alternation leads to masting behavior at the population scale [18, 16].

Anthropogenic climate change could alter the climatic cues that synchronize individual reproductive cycles. Without any constraints, novel climatic conditions could disrupt masting and its evolutionary benefits [13, 14]. Reliable forecasts of long-term population-level synchrony thus require to model how individual endogenous constraints and climate act together.

We developed a model in which individual trees may alternate between two latent reproductive states. These states explicitly encode endogenous constraints, i.e. the alternate bearing because of the temporal overlap between floral bud initiation and fruit development. For each observed tree and each year, the model estimates the reproductive state—given the previous state—and the subsequent seed production. Climate is included as an explicit driver of both state transitions (probability matrix), and seed production (number of seeds). From these individual reproductive dynamics, the model allows to scale up to population-level behavior and investigate how climate interacts with endogenous constraints to impact masting. We apply this model to seed data collected in beech forests of England, since 1980.

## Results and discussion

Following the paradigm that masting is defined by of 'boom and bust' reproduction, our model identified high and low reproductive years as alternative latent states (Fig. 1A-B). In high ('boom') reproductive years, individual trees produced XX seeds on average (give some RANGE), while in low ('bust') reproductive years they most often produced 0 (?? seeds, give mode and then maybe man and range in parentheses). Seed number per tree in low and high reproductive years, however, overlapped significantly (both distributions spanned seed numbers of XX-YY), even for the same individual tree. The difference between these two states thus occurs mostly in the opposite extremes—years in the high reproduction latent state included extremely high seed counts, which would almost never be possible in the low reproduction state, while years in the low reproduction state were characterized by extremely low counts rarely seen in the high reproductive state.

Transitioning between reproductive states across years depended on a tree's state in the previous year (high or low). In a year with average climatic conditions (GIVE mean temp here? Or some quick definition of what is average climate in parentheses), a tree in a low reproductive state was most likely to transition to a high reproductive state the next year, with a probability of 66% (90%CI 60 – 71), with a 1.9 times lower probability (34%, 90%CI 29 – 40) of staying in a low reproductive

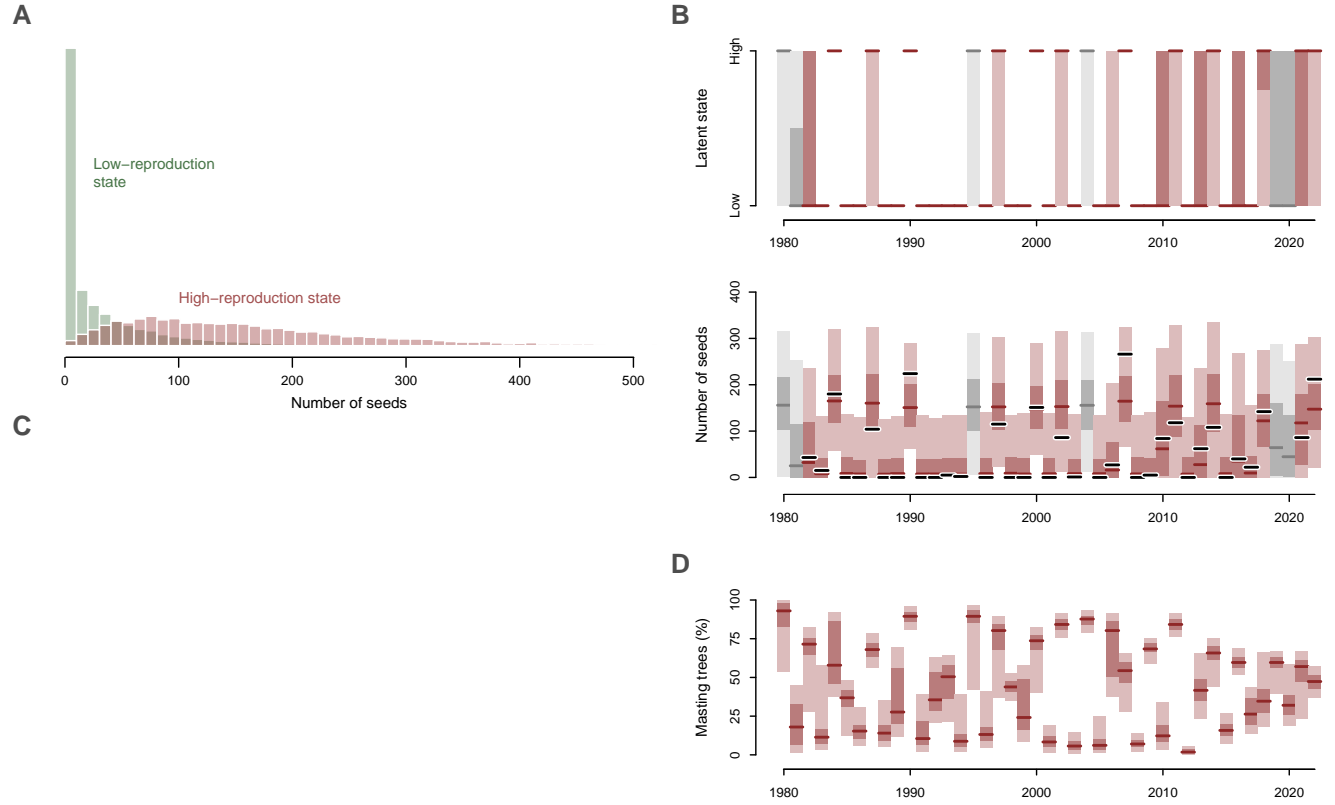


Figure 1: **Distinct tree reproductive states generates variability at the population level.**

(A) The model identifies two distinct reproductive latent states that correspond to two different level of seed production. (B) At the tree level (illustrated here for one random tree), the alternation between these two latent states across time (upper plot) generates low and high seed production years (lower plot). (C) The differences in transition probabilities between states reflect endogenous constraints that shape tree-level reproductive cycles. (D) these individual cycles generate some amount of variability and synchrony in seed production across years. In (B) and (D), the red line represents the median model prediction, while the shaded areas represent the 25–75% and 5–95% quantile ranges. The black lines represent the observed seed counts, and the grey lines and areas indicate model predictions for years when observations were missing.

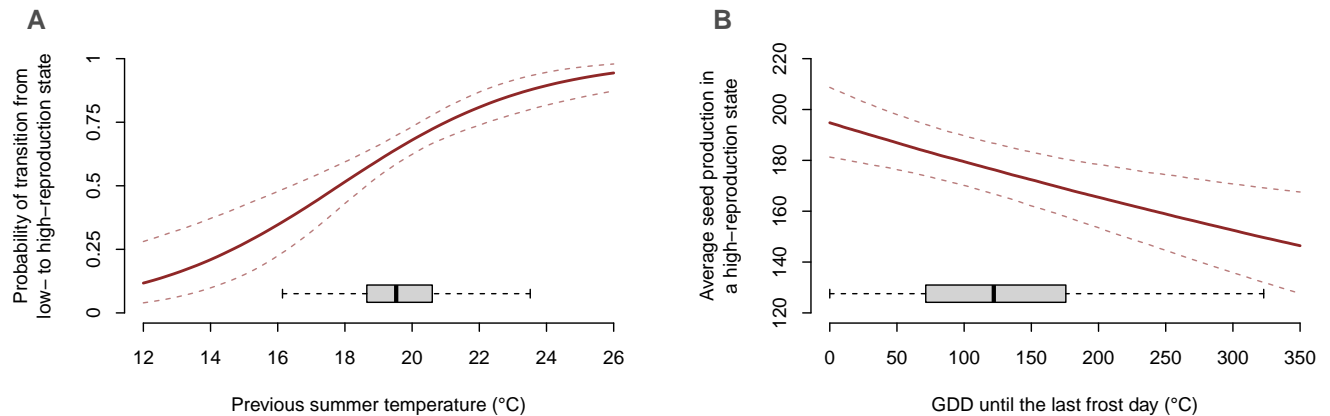
state (Fig. 1C). Under the same average climate, a tree in a high reproductive state was even more likely to transition, with a probability of 83% (90%CI 73 – 91) that it would transition to a low reproductive state, and much less likely to remain in the same state (17%, 90%CI 9 – 27). These results suggest that trees on average shift into a new reproductive state most years, but are more likely to remain in a low reproductive state, supporting the idea of non-mast years being more frequent than mast years (CITES).

Climate strongly affected these transition dynamics. Similar to previous studies (CITE), we found that warm summer temperatures increased the probability that trees in a low-reproduction state transitioned to a high-reproduction state (Fig. 2A). For example, the transition probability during a warm summer at 23°C (86, 90%CI 78 – 91) was 2 times higher than during a 17°C summer (43, 90%CI 32 – 53). Given the reproductive constraints that prevent beeches and many other woody plants from repetitive years of high fruit (from the competitive overlap of flower bud formation and fruit development CITES), we assumed the transition from a high to a low reproductive state was not affected by climate (we found strong support for this when we relaxed this assumption, Supp. Fig.). Trees in a high reproductive state may not necessarily produce abundant seeds, however, if conditions are not favorable for flower and/or fruit development (CITES). We found support for the common hypothesis that spring frosts may limit seed production (CITES), with seed production for trees in a high reproductive state reduced -15.1% (90%CI -23 – -6.4%, Fig. 2B) given a three-fold increase in a metric of frost risk (growing-degree days until last frost, CITES), but no evidence that warm springs affected seed production (Supp. Fig.).

Individual tree-level reproductive states (high or low) scaled up to produce population-level seed production that was synchronous, both within and between populations (sites). Within populations, 82% (80 – 85%) of trees shared the same reproductive state on average each year, while synchrony across populations was only slightly lower (the proportion of trees in the same state across all populations was 77%, 73 – 80%). This high level of synchrony across populations could suggest that synchrony occurs across wide spatial scales, as sometimes suggested (CITES), but given that these populations were not widely separated spatially (Supp. Mat.), it only supports the idea of synchrony over smaller spatial scales, as often suggested (CITES).

Climatic cues—especially cold summers—appeared critical to synchronizing the reproductive cycle of individual trees to produce the population-level synchrony that often defines masting (CITES). While XX% of trees in a low reproductive state are likely to stay in that state, cold summer temperatures prevent an additional subset from transitioning to a high reproductive state (because cold summer temperatures reducing reduce the probability of transition to a high reproductive state). Thus natural reproductive constraints combined with cold summers leave most trees in a low reproductive state (Fig. 2A). This synchrony of low reproduction can then drive synchrony of high reproduction when a cold summer is followed by a warm summer; in such years most trees responded consistently to the warm temperatures that promote floral induction, and transition together into a high reproductive state (FIGURE DELTA T), thus generating a mast year at the population scale. The interplay between individual-level constraints and population-level climatic cues provides a physiological mechanism for reproductive synchrony that can persist

over multiple years, and offers a simple explanation for previous findings that masting depends on the temperature difference between successive summers (the  $\Delta T$  model; 19).



**Figure 2: Climate conditions impact both transition probabilities between states and seed production in a high reproduction state. (A)** Average maximum temperature in July and August of the previous year increases the probability of transition from a low-reproduction to a high-reproduction state. **(B)** The accumulated growing-degree days (GDD) until the last frost day decreases the number of seeds produced in a high-reproduction state. Plants that have accumulated more GDD before a frost event are phenologically more advanced and thus face a higher risk of frost injury [20]. In **(A)** and **(B)**, the solid red line and dashed lines respectively represent the median and the 5% and 95% quantiles, while the gray boxplots show observed conditions (1980–2022).

Our results superficially support the hypothesis that increasing summer temperatures with climate change could disrupt masting [21, 14]. This hypothesis—previously called breakdown [21, 14]—predicts that warm summers will drive trees to be in high reproductive state more frequently and thus years of low reproduction will become rarer, potentially leading to lower individual tree growth [22, 23] and reducing variability and synchrony in seed production at the population level. While we do find that warmer summers increase the probability of trees transitioning into a high reproductive state—and thus increasing summer temperatures would increase the frequency of high seed production years—reproductive constraints prevent major shifts in the frequency of high seed production years and should not necessarily drive lower synchrony. Indeed, we found even with extreme summer warming (7°C in one century), only 56% (90%CI 44 to 69.5%) of trees in a population would mast in any given year (Fig. 3). This result remains even when we relax reproductive constraints and allow warm summers to increase the probability of trees staying a high-reproductive state (Supp. Fig.). Even with this additional effect, trees cannot get stuck indefinitely in a highly reproductive state. On the contrary, we found a ‘breakdown’ because of climate change would require summer warming to have a similar impact on both transition and persistence into a high-reproduction year — an hypothesis not supported by the data we used here (Fig. 3).

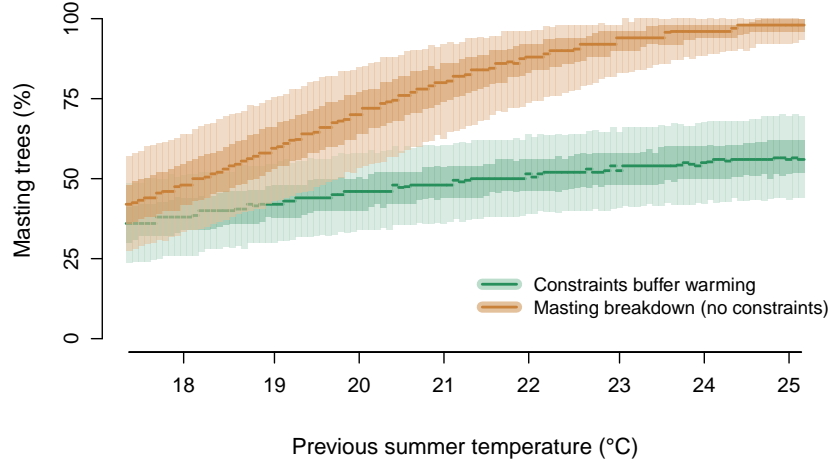


Figure 3: **Endogeneous constraints prevent masting breakdown under a significant summer warming.** We predicted the percentage of masting trees for 50 new trees in an average population in England under a strong summer warming of  $7^{\circ}\text{C}$  in one century—which corresponds to the warmest regional climate model projections [24]. The green line and shaded areas (median, 25–75% and 5–95% quantile ranges) represent the predictions with the model fitted on the data used in this paper. With this model, the fitted transition probabilities indicate that trees cannot remain continuously in a high-reproduction state. The orange line and shaded areas (median, 25–75% and 5–95% quantile ranges) represent the predictions from an hypothetical model where summer warming increases the probability of persisting into a high-reproduction state — and would lead to most trees masting every year (i.e. reproductive breakdown). These predictions are not supported by the data used here.

These results highlight how biological constraints on plant reproduction may limit the runaway effects of climate change sometimes proposed. At the individual level, floral bud initiation is promoted by warm summer temperatures, potentially leading to a higher number of flowers and fruits in the following year (CITE). However, in the next summer, the development of a larger fruit load inherently imposes a trade-off that limits the tree ability to initiate a large number of floral buds again (CITE). These individual-level constraints scale up to the population level by preventing the entire population from producing large seed crops every year—preventing an unlimited amplification of climate effects on masting. Our results highlights that constraints at the individual level are critical for accurate forecasts of population-scale dynamics (CITE?); further this approach can help identify the spatial scale at which changes occur, including possible shifts in synchrony.

In contrast to previous results we found no strong evidence of declines in synchrony within populations. Synchrony across trees within a population varied over time but has not clearly changed in recent periods (recent declines in 2015 onward are within the 90% range of previous periods, Fig. 4A). In contrast, synchrony between populations has declined in recent years, from a previous mean of XX to one of YY since 2015. This suggests understanding potential desynchronization [21] requires disentangling these two scales—within versus between populations—and better evidence of what scale actually matters to forest regeneration. Most hypotheses for the fitness benefits of masting require synchrony at the population-level, but exactly what that spatial scale matters for fitness benefits depends on the exact hypothesis (e.g., predator satiation or pollination efficiency) and the species-level attributes [e.g. predators foraging ranges or wind dispersal distances, which depend on seed shape, size and the local landscape 25]. Thus, if beech masting in England mainly serves to overwhelm seed predators, such as XX species (ask Eleonore?), then masting synchrony at the population level (given that sites are XX km apart) should be sufficient to maintain the regeneration benefits of masting.

While we find no evidence for a positive feedback of summer warming that would trigger an abrupt runaway seed production, our results suggest possible changes in synchrony as we lose the cold summers—the potential hinge points for population synchronization. Several consecutive years without cold summers could progressively decrease synchrony within a population (Fig. X). Determining the extent to which this will happen in the coming decades, and producing robust spatiotemporal forecasts, will require improved metrics of synchrony and better measurements of the scale at which synchrony appears and disappears across years.

Understanding future forest regeneration requires moving across scales and life stages. At the tree level, a better understanding of the climatic drivers of masting will not be possible without a finer decoupling of the constraints acting on different stages of reproduction, including bud formation, flowering, and flower or bud abortion (frost damage of trees about to mast), rather than relying only on seed production data. One possible way to start disentangling these temporal constraints is to compare species with different reproductive cycles (e.g. two-year versus three-year cycles), and investigate whether they respond differently to climate—using a similar modeling approach as the one we proposed here. More broadly, understanding changes in reproductive dynamics will re-

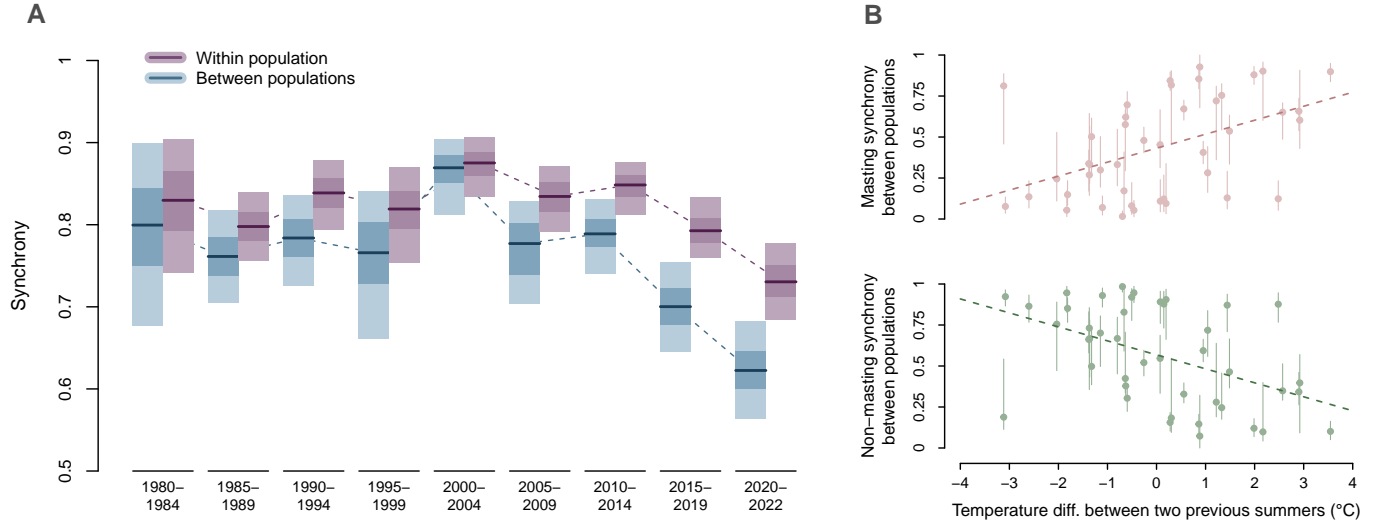


Figure 4: **Reproductive synchrony arises from populations of individual trees.** (A) Blue line and shaded areas (median, 25–75% and 5–95% quantile ranges) represent the synchrony within population, i.e. the average proportion of trees of the same population that are in the same state. Some populations can be in a non-masting year, while some population can mast. Purple line and shaded areas (median, 25–75% and 5–95% quantile ranges) represent the synchrony across populations, i.e. the proportion of trees that are in the same state across all populations. Since our model includes only two states, the minimum synchrony is 0.5 (i.e. at least 50% of the trees are in the same state). (B) The interactions of previous summer conditions and previous latent states explains the apparent two-year lag effect of climate on observed synchrony across populations.



quire replacing masting within a wider life-cycle context. Seed production represents only the first step toward a successful forest regeneration, and climate change may lead into failures in seedling establishment and tree recruitment even in forests where seed production remains synchronous.

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