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 endogeneous 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 endogeneous 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 endogeneous 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 extremes—years in the high reproduction latent state sometimes have extremely high seed counts, which would almost never be possible in the low reproduction state, while years in the low reproduction state are characterized by extremely low counts that are rarely seed in the high reproductive state. These individual tree-level states scale up to produce population-level seed production that we found was relatively synchronous—further supporting the general definition of masting (CITES): years of high population-level seed production—mast years—were almost always separated by periods of low seed production (Fig. 1D).

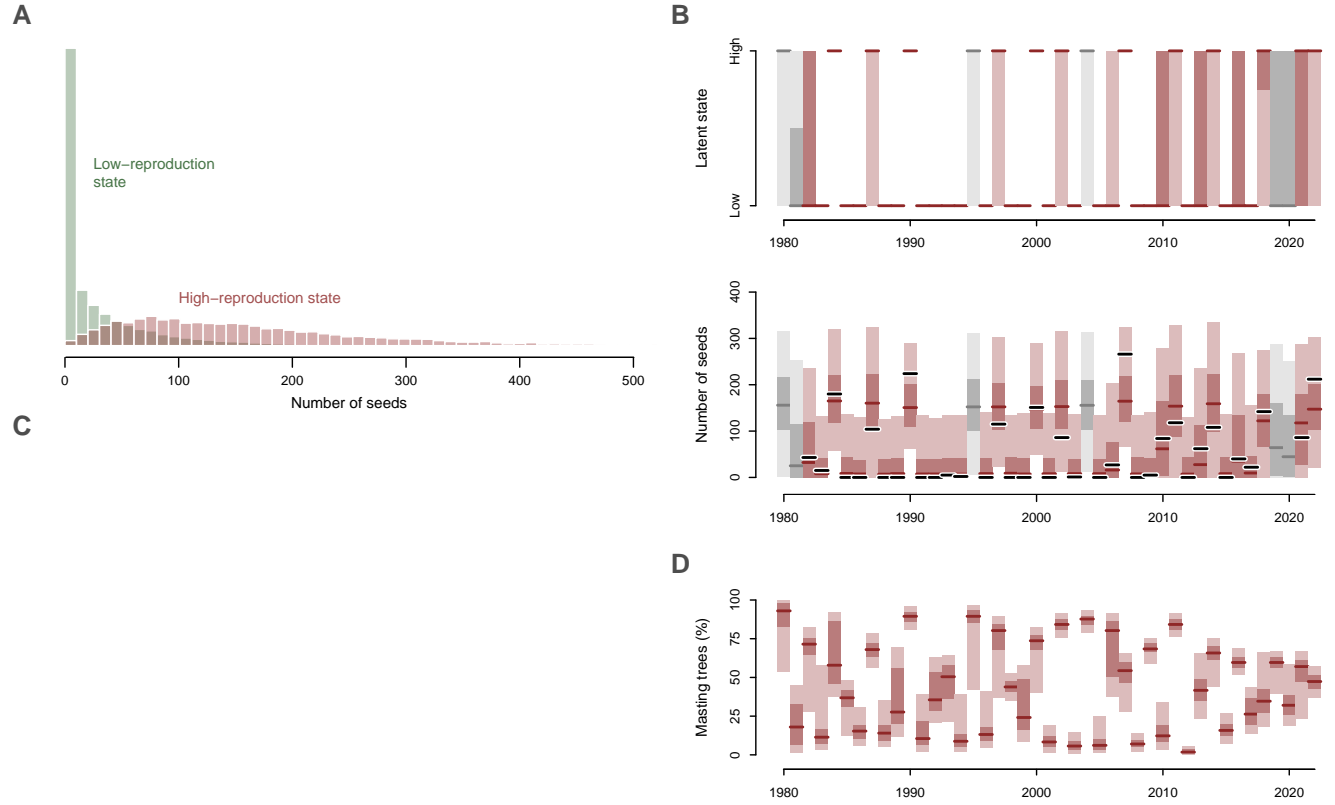Transitioning between reproductive states depended on the state (high or low). In a year with

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 reporesent 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.

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 is 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 state (Fig. 1C). Following a high reproduction year, trees almost systematically go back to a low reproduction state (83%, 90%CI 73 – 91) rather than persisting in a high reproduction state two consecutive years (17%, 90%CI 9 – 27).

Climate strongly affected these transition dynamics. Similar to previous studies (CITE), we found that summer temperature increases the probability that trees in a low-reproduction year transition 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). Following constraints of reproductive biology (because of the competitive overlap of flower bud formation and fruit development), we assumed the transition from a high to a low reproductive state is not affected by climate, which we found strong support for when we relaxed this assumption (Supp. Fig.). Once a tree is in a high-reproduction year, we found that late spring frosts may reduce its seed production. A three-fold increase of growing-degree days until last frost—a metric for late spring frost risk (CITE)—decreased seed production by -15.1% (90%CI -23 – -6.4%, Fig. 2B). In contrast, warmer spring conditions alone had not effect on seed production (Supp. Fig.).

Synchronization depends not only on climate but also on previous reproductive states. This mechanism provides a simple physiological explanation for previous findings that temperature difference between the two previous summers mattered for masting (ΔT model; 19). Rather than complex molecular pathways such as 'epigenetic summer memory' [20], a cold summer followed by a warm summer generates synchrony simply because cold temperatures leave most trees in a low-reproduction state, allowing them to respond consistently to following warm temperatures that promote floral induction (Fig. 4B).

Increasing summer temperatures with climate change have been predicted to disrupt masting by reducing variability and synchrony—a phenomenon previously called breakdown [22, 14]. Trees are expected to be more frequently in a high-reproduction state, and years with low seed production to become rarer [14], potentially at the cost of individual tree growth [23, 24]. However, even with a significant and continuous 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).

Since our initial model allowed summer temperatures to affect only transitions from low- to high-reproduction state, we additionally tested whether warm summer influences the probability of persistence in a high-reproduction state and found a weak effect (Supp. Fig.). Even with this additional effect, trees cannot get stuck indefinitely in a highly reproductive state. On the contrary, 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).

Climate impacts on reproduction are not independent of the reproductive state of trees. Endoge-
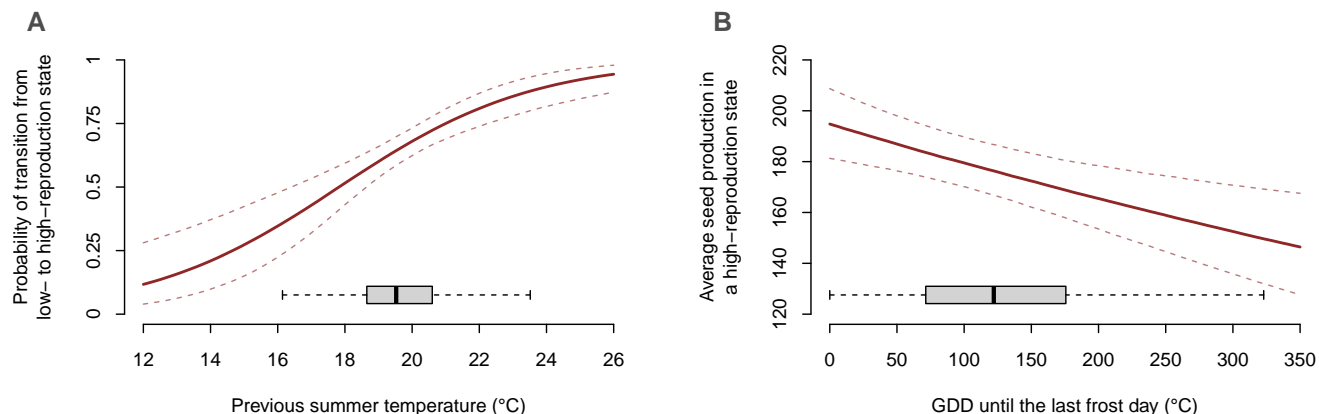
Figure 2: **Climate conditions impact both transition probabilities between states and seed production in a high reproduction state. (A)** Average maximum temperature in July and August of the previous year increases the probability of transition from a low-reproduction to a high-reproduction state. **(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 [21]. 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).

nous constraints intrinsically prevent individuals from producing a high number of seeds every year. Warm summer temperatures can improve floral bud initiation, but do not suppress the trade-off imposed by a large fruit load. Because masting behavior arise from tree-level reproductive cycles, these constraints cannot be ignored when forecasting population-scale dynamics. The biological constraints underlying tree reproduction could slow down the increase of reproduction sensitivity to climate change, potentially preventing unlimited amplification of climate effects and an abrupt collapse of masting.

Despite these constraints, synchrony across populations still appears to go down in the last two decades (Fig. 1D). The year 2006 was previously identified as a year of abrupt change, marked by a desynchronization across England [22]. A lower synchrony may mask different processes operating at different scales: it could be caused either by a desynchronization among trees within populations or by a desynchronization between populations. The evolutionary benefits of masting depend on the spatial scale at which trees reproduce synchronously, and this scale in turn depends on the evolutionary hypothesis that we consider [26]. To overwhelm seed predators, synchrony scale should be on the order of predators foraging ranges (typically X km), making synchrony within a forest more relevant than synchrony across distant populations.

The apparent desynchronization of beech populations does not always arise from the same spatial scale. In the recent years (2015-2022), synchrony between populations has decreased more than synchrony within populations (Fig. 4A). Some years—such as 2018—appear desynchronized
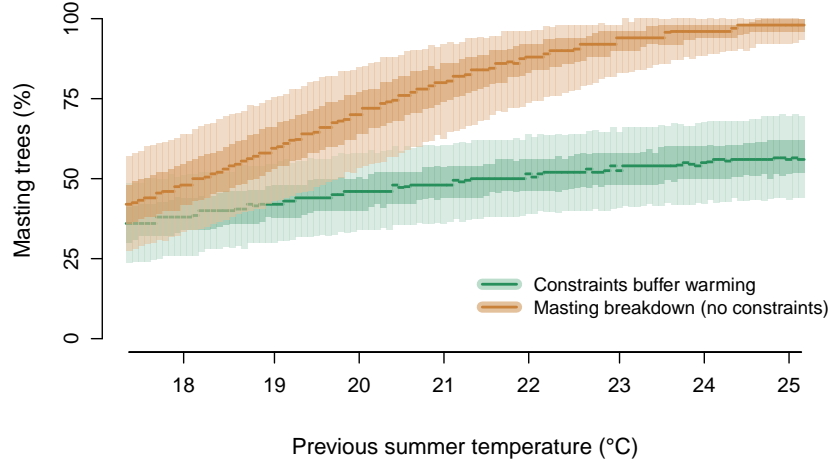
Figure 3: **Endogeneous constraints prevent masting breakdown under a significant summer warming.** We predicted the percentage of masting trees for 50 new trees in an average population in England under a strong summer warming of 7℃ in one century—which corresponds to the warmest regional climate model projections [25]. 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.
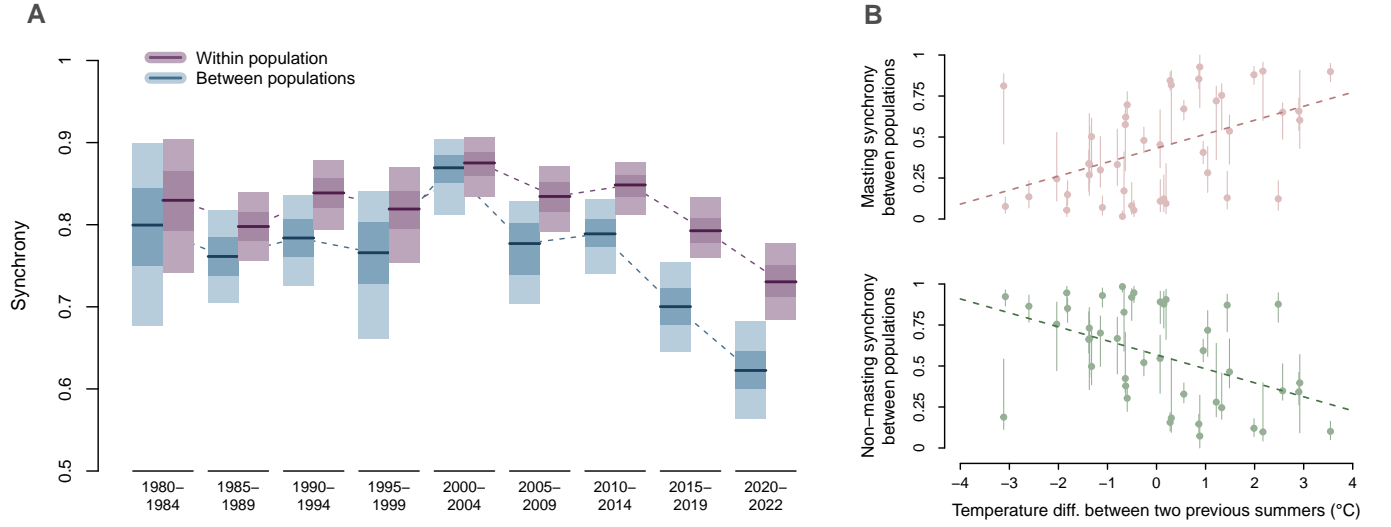
Figure 4: **Reproductive synchrony arises from populations of individual trees. (A)** Blue line and shaded areas (median, 25–75% and 5–95% quantile ranges) represent the synchrony within population, i.e. the average proportion of trees of the same population that are in the same state. Some populations 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.

because of high uncertainty on tree-level reproductive states within populations, whereas in other years—such as 2019—populations are desynchronized but trees within the same population remain synchronized (Supp. Fig.).

Masting is driven by the interaction of endogenous constraints at the individual level and climatic factors acting at a broader spatial scale. Constraints prevent endless amplification of individual reproduction with warming summers, but alone do not allow for synchrony between trees. [How synchrony arises... coordination of individual cycles] Anthropogenic climate change could change those dynamics, and potentially disrupt benefits of masting. Determining which biological processes are relevant for prediction—and at which spatial scale synchrony is important—is critical to anticipate these effects and understand how forests will regenerate under climate change.

1 References

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