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 sign 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 on tree species that have a high reproductive variability across years, and where most individuals of a population reproduce synchrounously [7]. These two characterisics—variability and synchrony—define masting, where reproduction occurs in so-called 'boom and bust' cycles hypothesized to drive fitness benefits [8, 9]. The most commonly involved fitness benefit is the 'predator satiation' hypothesis, where high seed production could overwhelm seed predators—i.e. a higher proportion of seeds and seedlings could escape predation and establish [10, 8]. Masting could also increase 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]. Floral bud initiation requires warm summer temperatures [19]. Unfavorable or favorable summer conditions could act as a hinge point to synchronize individual reproductive cycles within a population, and this synchrony may then persist over several years.

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]. However, endogenous constraints linked to reproductive biology could buffer the effects of climate change. Reliable forecasts of long-term population-level synchrony thus require to model how individual endogeneous constraints and climate act together.

Results and discussion

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.

The model separates out two distinct modalities of seed production in beech forests in England (Fig. 1A), supporting the existence of two reproductive states at the tree level (Fig. 1B). Alternance between these states at the tree level generates high variability in seed production at the population scale (Fig. 1D). Individual reproductive behaviors are relatively synchronous: years of high population-level seed production—mast years—are separated by periods of low seed production. Under average climatic conditions, a tree has a probability of X of transitioning from a low-reproduction to a high-reproduction state, and a low probability of Y of remaining in that state in the following year (Fig. 1C).

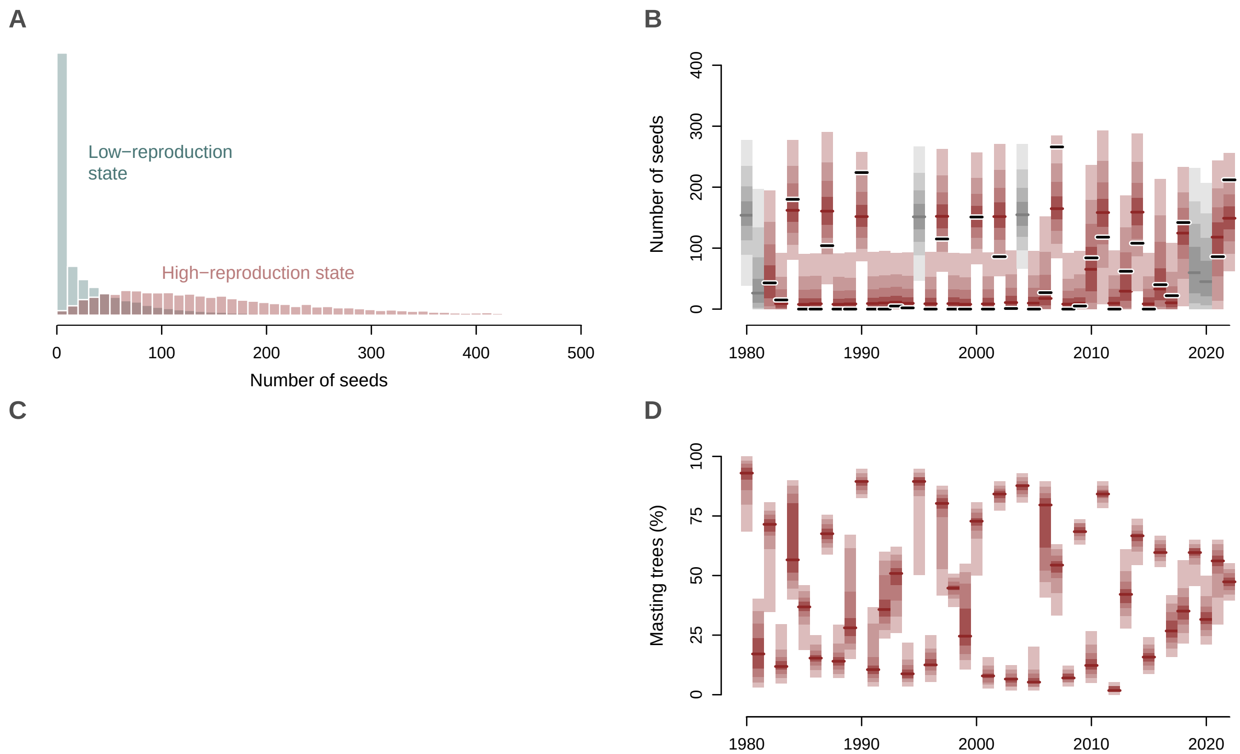

Figure 1: Distinct tree reproductive states generates variability at the population level.

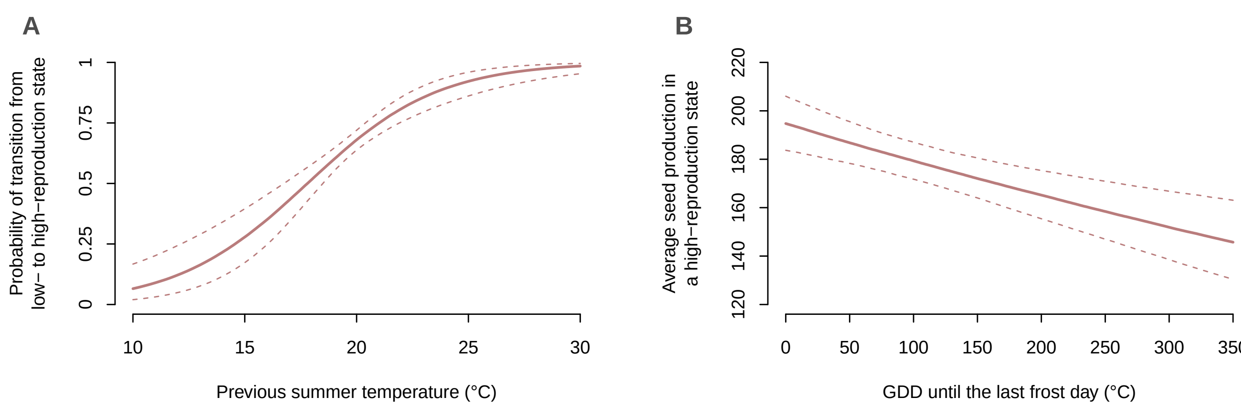

Figure 2: Effects of climate.

Reproductive dynamics are impacted by climate. In a warm summer (XdegC), trees in a low-reproduction state are X times more likely to transition to a high-reproduction state than during cold summers (XdegC, Fig. 2A). Once in a high-reproduction state, a two-fold increase of spring frost risk—measured as growing-degree days until last frost—can decrease seed production by X% (Fig. 2B). However, warmer spring conditions have no effects on seed production.

Increasing summer temperatures with climate change have been predicted to disrupt masting by reducing variability and synchrony—a phenomenon previously called breakdown [20, 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 [21, 22]. However, by modeling explicit latent states and transitions, we found that trees cannot get stuck indefinitely in a highly reproductive state. Even in a much warmer world (+XdegC, Figure), a high-reproduction year would be often followed by a low-reproduction year.

Since our initial model allowed summer temperatures to affect only transitions from low- to high-reproduction year, we additionally tested whether warm summer influences the probability of persistence in a high-reproduction state, and found a weak effect (). 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 (Figure).

Climate impacts on reproduction are not independent of the reproductive state of trees. Endogenous 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 processes 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 [20]. 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 [23]. 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. 3A). Some years—such as 2018—appear desynchronized because of high uncertainty on tree-level reproductive states within populations, whereas

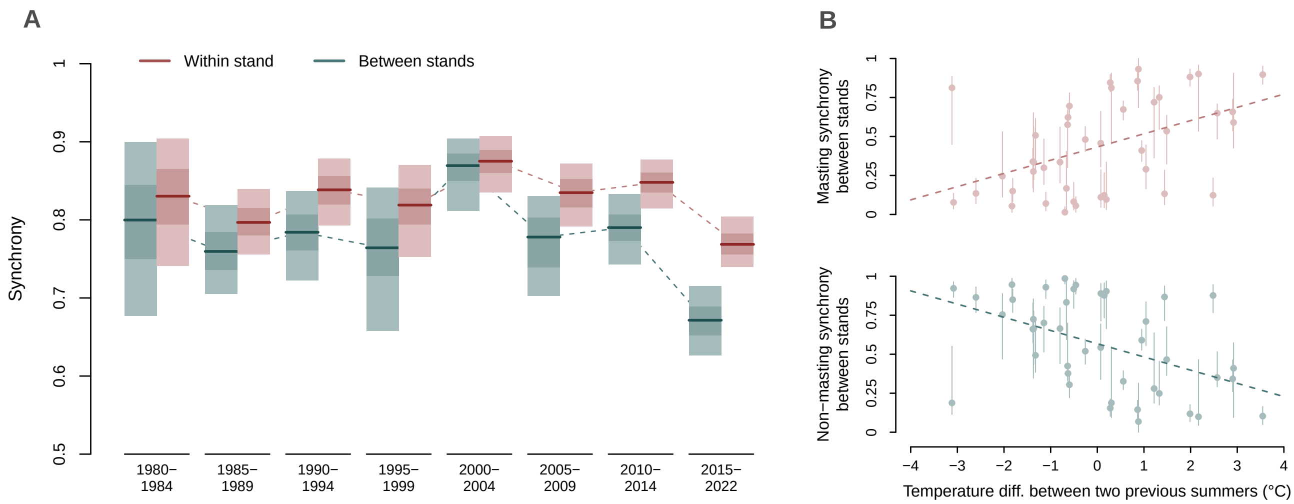

Figure 3: How synchrony arises from two scales!

in other years—such as 2019—populations are desynchronized but trees within the same population remain synchronized.

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; 24). Rather than complex molecular pathways such as 'epigenetic summer memory' [25], 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. 3B).

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.

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