Climatic drivers and intrisic biological processes shape masting dynamics...

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1 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. These two characterisics—variability and synchrony—define masting. Masting is hypothesized to have strong fitness benefits, mostly because high seed production could overwhelm seed predators—i.e. a higher proportion of seeds and seedlings could escape predation and establish [7]. 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 [8, 9].

Abrupt disruption of masting timing by climate change could trigger cascading effects on forest resilience [10, 11]. Masting is a population-level characteristic that require individual trees to respond similarly to environmental cues in order to reproduce together within a certain distance—which should match with predator foraging range. Tree species that mast have likely evolved under colder climates, and global warming could modify the cues that allowed for both reproductive variability and synchrony across a population.

Understanding the reproductive behavior that arises at the population level requires to study individual trees' responses to their environment. Reproductive success requires that a tree experienced favorable environmental conditions—and in particular no late spring frosts and sufficiently warm temperatures during the growing season. Yet, the alternation between favorable and unfavorable years is not invariant and cannot explain the regular intervals at which masting can occur [12].

At the individual level, the alternating reproductive cycle may mainly arise from endogeneous factors. In many tree species, floral buds are initiated the year before flowering, simultaneously as fruits of the current year start developing [13]. During a large crop year, the presence of many fruits could depress floral initiation because of hormonal inhibition and resource 'competition' for photosynthetic assimilates [14, 15]. 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 inherent alternation leads to masting behavior at the population scale [16, 14]. Floral bud initiation requires warm summer temperatures [17]. Unfavorable or favorable summer conditions could 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. [Add some hypotheses/predictions here?]. Reliable forecasts of its potential consequences for long-term population-level synchrony requires 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 interacted with endogenous constraints to impact masting.

The model separates out two distinct modalities of seed production in beech forests in England, supporting the existence of two reproductive states at the tree level. Alternance between these states at the tree level generates high variability in seed production at the population scale. 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 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.

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). 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%. 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 [18, 11]. Trees are expected to be more frequently in a high-reproduction state, and years with low seed production to become rarer—potentially at the cost of individual tree growth [19]. 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.

Endogenous constraints inherently prevent individuals from producing a high number of seeds every year. Climate impacts on reproduction are not independent of the reproductive state of trees. Warm summer temperatures can improve floral bud initiation, but they do not suppress the trade-off imposed by a large fruit load. [Say a bit more?] Because masting behavior arise from tree-level reproductive cycles, individual constraints cannot be ignored when forecasting population-scale dynamics.

Despite these constraints, synchrony across populations still appears to go down in the last two decades. The year 2006 was previously identified as a year of abrupt change, marked by a desynchronization across England [18]. 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. Disentangling these two scales is critical for understanding masting. 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 [20]. 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.

To write... Not very fun.

To write, more fun!

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