

# 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 potentially novel climate conditions, with more extreme events, could disrupt key ecological processes, and potentially drive ecosystems toward critical transitions [2]. Across biomes, recent work has suggested major shifts in pests and pathogens, while the local extirpation of rare species and increase in invaders across taxa has driven biotic homogenization [3, 4, 5]. Forests in particular appear to be shifting dramatically, with increases in adult tree mortality [and insert some other stuff about adult trees or ecosystem-scale carbon stuff] [6, 7, 8]. These shifts make understanding how forests regenerate more important [9, 10].

Regeneration in many temperate and tropical forests depends on the widely observed phenomenon of masting. Masting—defined by ‘boom and bust’ cycles of reproduction that are synchronous across most individuals of a population [11]—occurs across many tree species and is hypothesized to drive fitness benefits during reproduction and the early stages of establishment [12, 13]. 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 [14, 12]. Fitness benefits of masting may also operate earlier in reproduction, by increasing pollen exchange and genetic outcrossing across individuals [15, 16]. While varying in their exact mechanism and lifestage, hypotheses for the fitness benefits of masting are all based on an economy of scale where most individual trees must be synchronous.

Despite the importance of synchrony to yielding fitness benefits, how synchronous masting is and how it occurs remain poorly understood. Most hypotheses for how synchrony emerges focus on shared environmental cues at the species-level CITES. An abundance of work suggests that ideal conditions during bud formation may lead to masting CITES. In temperate systems, this means sufficiently warm temperatures during the growing season when buds develop alongside no cold snaps (e.g., late spring frosts) that cause tissue loss after they form CITES. The alteration of these cues by climate change could disrupt masting dynamics with implications for forest resilience [17, 9], but forecasting this requires better understanding how these cues affect reproductive biology, from buds to fruits.

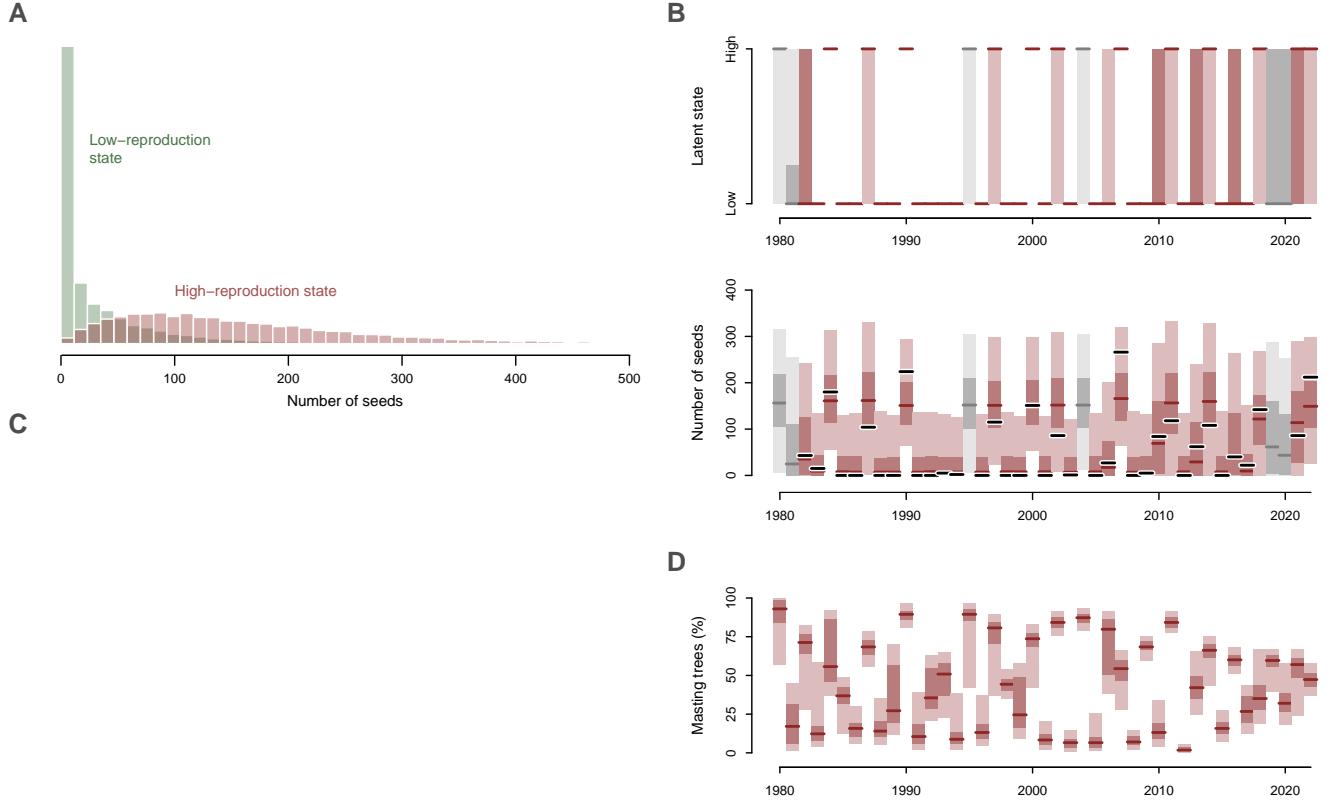
Most temperate woody species develop reproductive buds through a multi-year process. In the common two-year reproductive cycle, bud formation begins the year before flowering and seedset—potentially explaining why summer temperatures from the previous year appear to trigger masting CITES. The following year some of these buds may be lost to spring frost—potentially reducing the number of seeds in what otherwise have been a masting year. This two year cycle, however, also introduces a constraint in most species. Because floral buds for the following year develop simultaneously with current year fruit [18], a large fruit crop year can depress bud initiation [through hormonal inhibition and within-plant resource competition 19, 20]. The result is physiological constraints on flower and fruit development that likely explains why many woody species show alternate bearing—with a large crop year ('on-year') often followed by one or several 'off-years.'

These constraints may limit how climate can affect seed production. Ideal climatic conditions may trigger higher investment in floral buds only for individual trees not already in a high reproductive state ('on-year'). Warm summers would therefore not affect all trees equally, but only those in a low reproductive state ('off-year'), by promoting a transition from 'off-year' to 'on-year' and thus determining the reproductive state for the next year. Spring frosts occur later in the cycle, once a reproductive state has been established. Spring frost damage are conditional on prior reproductive transition the summer before, and should primarily reduce potential seed production in an 'on-year'. These individual-level reproductive dynamics can then scale up to generate population-level synchrony, with mastинг emerging through a combination of climatic variability and reproductive constraints. A mechanistically grounded framework accounting for these differential effects of climate would allow to forecast how climate change may alter mastинг as an emergent phenomenon of individual reproductive cycles.

Here we develop a predictive model that builds from climatic effects on individual trees constrained by their reproductive cycle (through two latent states). Our approach easily scales up these individual dynamics to population-level behavior, to investigate how climate interacts with individual constraints to shape mastинг. Using seed data collected in beech forests of England since 1980, we first tested whether individual trees show evidence for alternative reproductive states that could lead to mastинг at the population level. Then, we examined how synchrony might arise from the combination of reproductive constraints, at the individual-level, and climatic cues that operate over larger scales. Finally, we forecasted how future warming may affect both tree-level seed production and population-level synchrony.

## Results and discussion

Following the paradigm that mastинг 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



**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.

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.

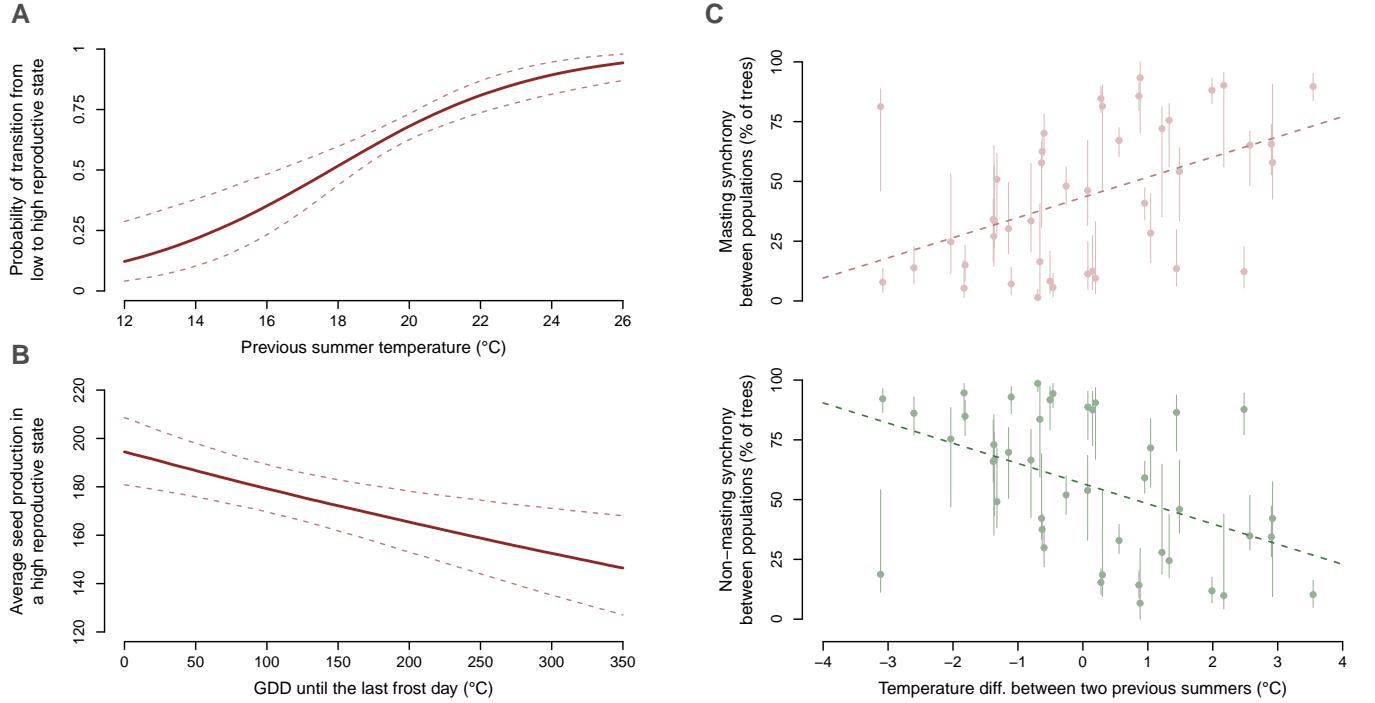
Transitioning between reproductive states across years depended on a tree’s state in the previous year (high or low). In a year with average climatic conditions (GIVE mean temp here? Or some quick definition of what is average climate in parentheses), a tree in a low reproductive state was most likely 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 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-reproductive state transitioned to a high-reproductive 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 33 – 54). 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 -14.9% (90%CI -23 – -6.1%, 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%, 74 – 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 (Fig. 2C), 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; 21).



**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-reproductive state to a high-reproductive state. **(B)** The accumulated growing-degree days (GDD) until the last frost day decreases the number of seeds produced in a high-reproductive state. Plants that have accumulated more GDD before a frost event are phenologically more advanced and thus face a higher risk of frost injury [22]. **(C)** The interactions of previous summer conditions and previous latent states explains the apparent two-year lag effect of climate on observed synchrony across populations. 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 [23, 9]. This hypothesis—previously called breakdown [23, 9]—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 [24, 10] 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—our results suggest that reproductive constraints prevent major shifts in the frequency of high seed production years; warm summers may thus not drive lower synchrony. Indeed, we found even with extreme summer warming ( $7^{\circ}\text{C}$  in one century, well beyond predictions of the current high emissions scenario for this region, 25), 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).

These results highlight how biological constraints on plant reproduction may limit runaway effects of climate change. For masting, floral bud initiation at the individual tree level 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—and thus also 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 in recent decades, during a period of significant warming (CITE). 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 78.9% (75.4 – 82.4%) to one of 67% (62.8 – 71.5%) since 2015. This suggests understanding potential desynchronization [23] 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

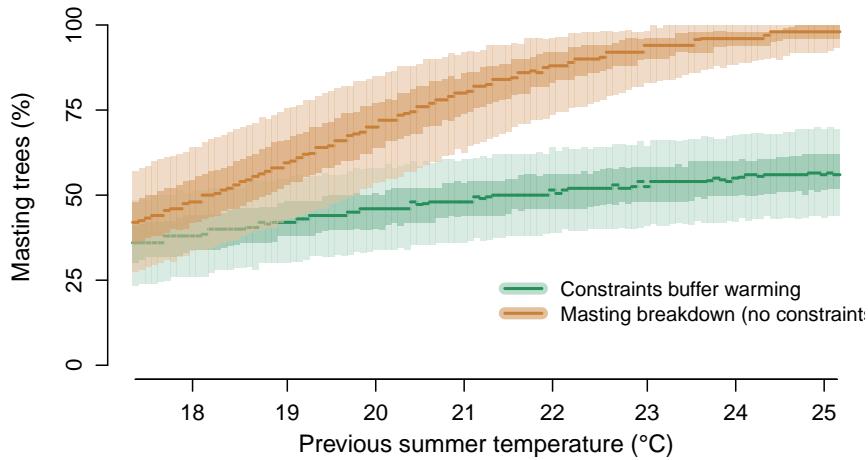
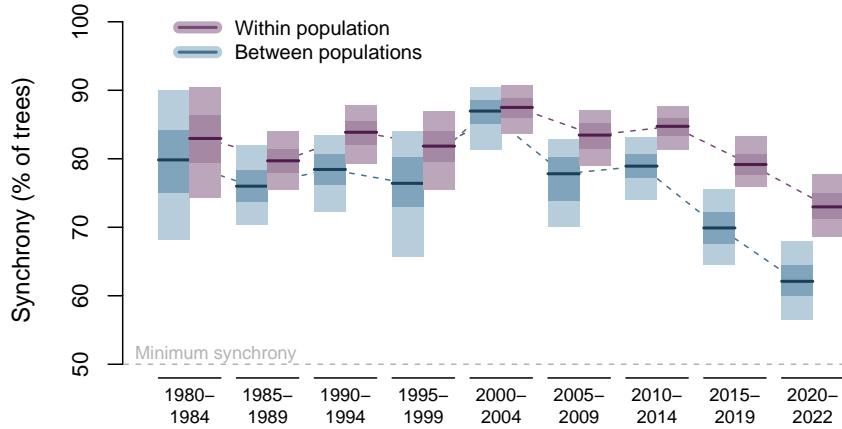


Figure 3: **Endogeneous constraints prevent masting breakdown under a significant summer warming.** We predicted the percentage of masting trees for 50 new trees in an average population in England under a strong summer warming of 7°C in one century—which corresponds to the warmest regional climate model 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.

depend on seed shape, size and the local landscape 26]. 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.



**Figure 4: Reproductive synchrony arises from populations of individual trees.** 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).

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. 5). This result is consistent with our previous finding that only 56% of trees mast in years with very warm summers (Fig. 3), resulting in low synchrony—whereas synchrony would remain high if all trees were stuck in a high reproductive state every year. Determining the extent to which synchrony decrease 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 (CITE?).

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

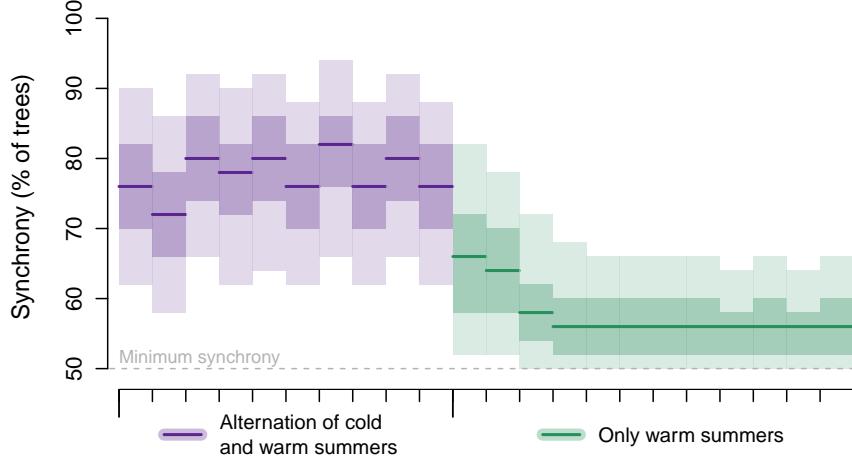


Figure 5: **Cold summers synchronize reproduction at the population level.** We predicted the percentage of masting trees for 50 new trees, that first experience a perfect alternation of cold (around 15°C) and warm summers (around 24°C), in purple, and then only warm summers, in green.

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 require replacing mastining within a wider life-cycle context (CITE). Seed production represents only the first step toward forest regeneration, and climate change may lead into failures in seedling establishment and tree recruitment [27], even in forests where seed production remains synchronous.

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