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. 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 [7, 8].

Disruption of masting timing by climate change could trigger cascading effects on forest resilience [9, 10]. 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 [11].

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 [12]. During a large crop year, the presence of many fruits could depress floral initiation because of hormonal inhibition and resource 'competition' for photosynthetic assimilates [13, 14]. 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 [15, 13]. Floral bud initiation requires warm summer temperatures [16]. 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 separated 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 generated 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.

Climate impacted both transitions between states and seed production. In a warm summer (XdegC), trees in a low-reproduction state were 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—could decrease seed production by X%. However, warmer spring conditions had no effects on seed production.

- Our projections vs current studies
  - current studies: ACC leads to more seeds via more masting
  - but even if you drive warming way upp you still get a plateau
  - this even happens with summer temp effect on M to M (figure proj)
  - To actually ahve a breakdown, we would nee the parameter valeu on M to M to be at least as important as NM to M

- How constraints prevent breakdown!
  - ...
- But synchrony does appear to go down
  - Review previous results and overall figure
  - these years look less synchrone...
  - but here, it could be driven both by within and between asynchrony
  - (what level of between-stand synchrony predict..?)
  - evolutionary benefits of mating depends on scale of synchrony *rightarrow* which scale depends on which evolutionnary model you consider, but for seed predators... should be quite small (foraging distance = X km)
- Asynchrony indeed driven by multiple factors
  - within between
  - discuss results... maybe figure with %?
- What drives synchrony?
  - bad years could act as precise cue, and with biol. constraints it would explain the following synchrony
  - how ACC could change those dynamics, and on which scale?
  - (Unclear how breakdown at tree and then at stand level?)
  - basically, we need to figure out the biology useful for predictions with ACC

References

[1] Christopher H. Trisos, Cory Merow, and Alex L. Pigot. The projected timing of abrupt ecological disruption from climate change. *Nature*, 580(7804):496–501, April 2020. ISSN 1476-4687. doi: 10.1038/s41586-020-2189-9.

[2] Thomas Wernberg, Scott Bennett, Russell C. Babcock, Thibaut de Bettignies, Katherine Cure, Martial Depczynski, Francois Dufois, Jane Fromont, Christopher J. Fulton, Renae K. Hovey, Euan S. Harvey, Thomas H. Holmes, Gary A. Kendrick, Ben Radford, Julia Santana-Garcon, Benjamin J. Saunders, Dan A. Smale, Mads S. Thomsen, Chenae A. Tuckett, Fernando Tuya, Mathew A. Vanderklift, and Shaun Wilson. Climate-driven regime shift of a temperate marine ecosystem. *Science*, 353(6295):169–172, July 2016. ISSN 1095-9203. doi: 10.1126/science.aad8745.

[3] Katharina Albrich, Werner Rammer, and Rupert Seidl. Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology*, 26(7):4013–4027, May 2020. ISSN 1365-2486. doi: 10.1111/gcb.15118.

[4] Giovanni Forzieri, Vasilis Dakos, Nate G. McDowell, Alkama Ramdane, and Alessandro Cescatti. Emerging signals of declining forest resilience under climate change. *Nature*, 608 (7923):534–539, July 2022. ISSN 1476-4687. doi: 10.1038/s41586-022-04959-9.

[5] Camille S. Stevens-Rumann, Kerry B. Kemp, Philip E. Higuera, Brian J. Harvey, Monica T. Rother, Daniel C. Donato, Penelope Morgan, and Thomas T. Veblen. Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters*, 21(2):243–252, December 2017. ISSN 1461-0248. doi: 10.1111/ele.12889.

[6] Monica G. Turner and Rupert Seidl. Novel disturbance regimes and ecological responses. *Annual Review of Ecology, Evolution, and Systematics*, 54(1):63–83, November 2023. ISSN 1545-2069. doi: 10.1146/annurev-ecolsys-110421-101120.

[7] Stephanie M. Carlson, Curry J. Cunningham, and Peter A.H. Westley. Evolutionary rescue in a changing world. *Trends in Ecology & Evolution*, 29(9):521–530, September 2014. ISSN 0169-5347. doi: 10.1016/j.tree.2014.06.005.

[8] Megan Bontrager and Amy L. Angert. Gene flow improves fitness at a range edge under climate change. *Evolution Letters*, 3(1):55–68, February 2019. ISSN 2056-3744. doi: 10.1002/evl3.91.

[9] Michał Bogdziewicz, Dave Kelly, Andrew J. Tanentzap, Peter Thomas, Jessie Foest, Jonathan Lageard, and Andrew Hacket-Pain. Reproductive collapse in european beech results from declining pollination efficiency in large trees. *Global Change Biology*, 29(16):4595–4604, May 2023. ISSN 1365-2486. doi: 10.1111/gcb.16730.

[10] Jessie J. Foest, Michał Bogdziewicz, Mario B. Pesendorfer, Davide Ascoli, Andrea Cutini, Anita Nussbaumer, Arne Verstraeten, Burkhard Beudert, Francesco Chianucci, Francesco Mezzavilla, Georg Gratzer, Georges Kunstler, Henning Meesenburg, Markus Wagner, Martina Mund, Nathalie Cools, Stanislav Vacek, Wolfgang Schmidt, Zdeněk Vacek, and Andrew Hacket-Pain. Widespread breakdown in masting in european beech due to rising summer temperatures. *Global Change Biology*, 30(5), May 2024. ISSN 1365-2486. doi: 10.1111/gcb.17307.

[11] Daniel H Janzen. Seeding patterns of tropical trees. In *Tropical trees as living systems*, pages 83–128. Cambridge University Press Cambridge, 1978.

[12] Monica A. Geber, Maxine A. Watson, and Hans de Kroon. *Organ Preformation, Development, and Resource Allocation in Perennials*, pages 113–141. Elsevier, 1997. ISBN 9780120834907. doi: 10.1016/b978-012083490-7/50006-2.

[13] S.P. Monselise and E.E. Goldschmidt. Alternate bearing in fruit trees, January 1982.

[14] Anton Milyaev, Julian Kofler, Yudelsy Antonia Tandron Moya, Janne Lempe, Dario Stefanelli, Magda-Viola Hanke, Henryk Flachowsky, Nicolaus von Wirén, and Jens-Norbert Wünsche. Profiling of phytohormones in apple fruit and buds regarding their role as potential regulators of flower bud formation. *Tree Physiology*, 42(11):2319–2335, August 2022. ISSN 1758-4469. doi: 10.1093/treephys/tpac083.

[15] J. D. Matthews. The influence of weather on the frequency of beech mast years in england. *Forestry*, 28(2):107–116, 1955. ISSN 1464-3626. doi: 10.1093/forestry/28.2.107.

[16] Giorgio Vacchiano, Andrew Hacket-Pain, Marco Turco, Renzo Motta, Janet Maringer, Marco Conedera, Igor Drobyshev, and Davide Ascoli. Spatial patterns and broad-scale weather cues of beech mast seeding in europe. *New Phytologist*, 215(2):595–608, May 2017. ISSN 1469-8137. doi: 10.1111/nph.14600.