

Modeling masting

From individual tree behavior to population-level synchrony

1 The motivations behind the project

💡 The ecological motivation

Understanding the reproductive behavior that arises at the population level requires to study individual trees' responses. We believe that integrating reproductive biology (i.e. biological **constraints**) and environmental **cues** at the *individual* level can help us investigating the drivers of the variability and synchronicity of reproduction at the *population* scale. Our final goal is to understand to what extent climate change could really disrupt forest regeneration—and provide better forecasts!

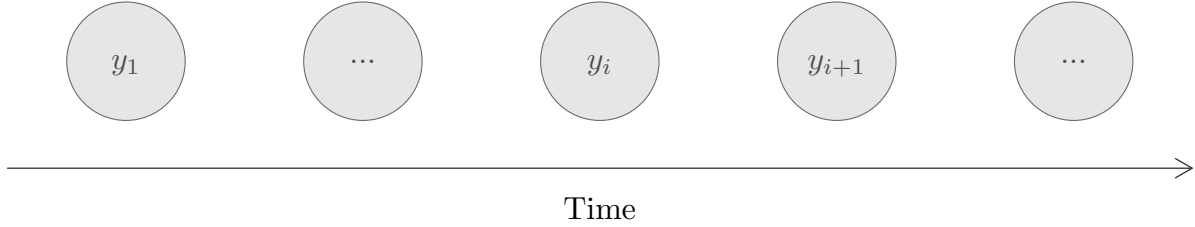
💡 The technical motivation

Bayesian magic! Our approach models the (latent) reproductive states of each *individual* tree, and the consequent amount of seed production. The states explicitly encode the **constraints** that shape tree reproduction – in particular, the fact that most trees need at least two years between flower bud differentiation and fruit maturation. We do not standardize away the complexities of individual-level reproduction (e.g. with normalized stand-level indices between 0 and 1...). On the contrary, modeling tree-level reproduction allows us to obtain *population* estimates — and thus direct inferences on the population-level variability and synchronicity! And the cherry on top: we incorporate climatic **cues** at different key moments of the reproductive cycle.

2 A generative model for masting

2.1 Previous approaches and limitations

The observations we have—whether for an individual tree or a seed trap—are a time series of yearly seed counts y_i .



The following quote illustrates the current approach of statistical model of masting:

“We fitted a zero-inflated, negative binomial mixed model to the annual number of initiated seeds in each tree, with fixed factors that included summer temperatures in 1 and 2 years before seedfall, [...] and seed production in the previous year to account for possible resource depletion. [...] We included [...] a first-order temporal autocorrelation structure.”

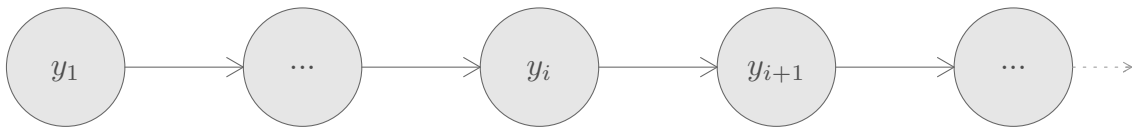
If we ignore the zero-inflated part, we could write this model as something like:

$$y_i \sim \text{NegBin}(\mu_i, \phi)$$

$$\mu_i = \alpha + \beta_{n-1}^{\text{summer}} \cdot X_{i-1}^{\text{summer}} + \beta_{n-2}^{\text{summer}} \cdot X_{i-2}^{\text{summer}} + \beta_{n-1}^{\text{seed}} \cdot y_{i-1} + \rho \cdot \epsilon_{i-1} + \epsilon_i$$

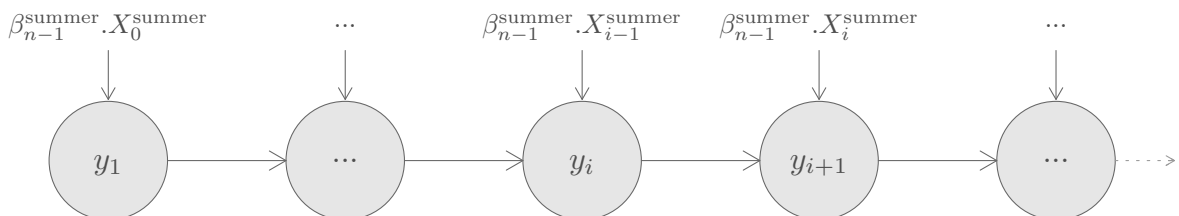
$$\epsilon_i \sim \mathcal{N}(0, 1)$$

The idea is to introduce some dependency between the seed counts:



The inclusion of both a lagged response of $\beta_{n-1}^{\text{seed}} \cdot y_{i-1}$ and a first-order autocorrelation structure on the residuals $\rho \cdot \epsilon_{i-1}$ seems... quite tricky.

But more importantly, the effect of summer temperature does not directly depends on the previous state. In other words, whatever the value of $\beta_{n-1}^{\text{seed}} \cdot y_{i-1}$, a tree that experiences a warm summers would be predicted to have an increasing seed production—regardless of the previous reproductive state.

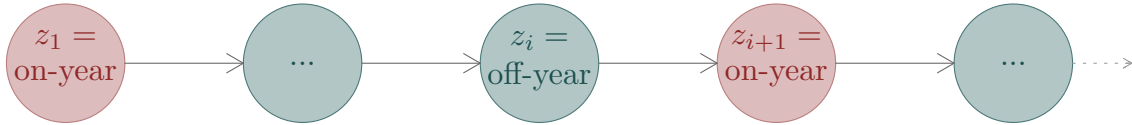


This issue arises because we does not explicitly simulate the reproductive state of an individual tree. The model does not allow to differentiate effects of climate during a non-masting year or a masting year. Moreover, without modeling individual-level states, it is not possible to infer reproductive behavior at the population scale—including the degree of potential synchrony.

2.2 A new approach grounded in biology

Researchers have worked on the reproductive biology of trees for decades—and in particular fruit trees. In parallel, people working on masting have defined characteristics of masting and developed clear hypotheses about the evolutionary mechanisms that could cause masting. There is thus a great opportunity to develop more generative models, that explicitly incorporate biological knowledge of flower and fruit development in order to better understand how masting works.

To understand the reproductive behavior that arises at the population level, we need to model individual trees' reproduction. At the tree level, floral buds are initiated the year before flowering—in the same time as fruits of the current year start developing. During a large crop year (an “on”-year), the presence of many fruits depress flower initiation because of hormonal inhibition and resource trade-off. Thus, the next year will likely be an “off”-year. This behavior is called **alternate bearing**. It is not always a 2-year cycle, as an “on”-year can be followed by several “off”-years. This clearly defines two states for a tree.



Each state z_{i+1} is dependent **only on the preceding state** z_i (which is called the *Markovian* assumption). These states are latent, because we observe only the seed counts. The model I will describe briefly in the next section is thus called a Hidden Markov Model (HMM): *hidden* because the states are latent, and *Markov* because of the Markovian assumption.

With some parameters θ , the probability of observing some sequences of the two first states is:

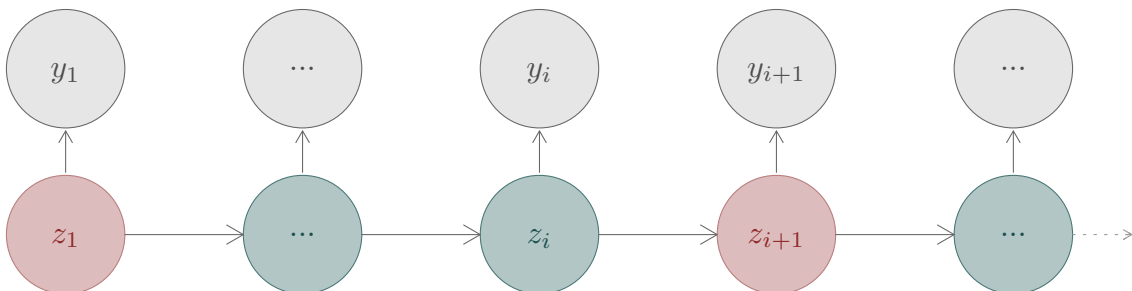
$$p(z_1, z_2 \mid \theta) = p(z_1) \times p(z_2 \mid z_1, \theta)$$

And then, adding the next state:

$$p(z_1, z_2, z_3 \mid \theta) = p(z_1) \times p(z_2 \mid z_1, \theta) \times p(z_3 \mid z_2, \theta)$$

And so on ...

Each observed seed count at each step arises from the state of the tree.



This gives us this likelihood for the two first seed counts:

$$p(y_1, y_2, z_1, z_2 \mid \theta) = p(z_1) p(y_1 \mid z_1, \theta) p(z_2 \mid z_1, \theta) p(y_2 \mid z_2, \theta)$$

And for all observations until $i + 1$:

$$p(y_1, \dots, y_{i+1}, z_1, \dots, z_{i+1} \mid \theta) = p(z_1) p(y_1 \mid z_1, \theta) \prod_{k=2}^{i+1} p(z_k \mid z_{k-1}, \theta) p(y_k \mid z_k, \theta).$$

So, what parameters do we have to estimate?

2.2.1 Transition between states

Let's look at the part which concerns the latent states.

First, we need to infer the initial state probability $p(z_1)$, i.e. the probability that the first year is an **on-year** or an **off-year**. Because we have only two states, $p(z_1 = \text{on}) = 1 - p(z_1 = \text{off})$ —i.e. we have only one parameter to estimate.

We also have to infer the probabilities of transition $p(z_k \mid z_{k-1}, \theta)$. With two states, this corresponds to this transition matrix:

$$M = \begin{bmatrix} p(z_k = \text{on} \mid z_{k-1} = \text{on}, \theta) & p(z_k = \text{off} \mid z_{k-1} = \text{on}, \theta) \\ p(z_k = \text{on} \mid z_{k-1} = \text{off}, \theta) & p(z_k = \text{off} \mid z_{k-1} = \text{off}, \theta) \end{bmatrix}$$

$$M = \begin{bmatrix} \tau_{\text{on} \rightarrow \text{on}} & \tau_{\text{on} \rightarrow \text{off}} \\ \tau_{\text{off} \rightarrow \text{on}} & \tau_{\text{off} \rightarrow \text{off}} \end{bmatrix}$$

The probability of assignment of z_2 to one of the two states is then obtain with the product:

$$\begin{bmatrix} p(z_2 = \text{on}) & p(z_2 = \text{off}) \end{bmatrix} = \begin{bmatrix} p(z_1 = \text{on}) & p(z_1 = \text{off}) \end{bmatrix} \cdot M$$

Again, because we have only two states, the transition matrix corresponds to only two parameters, for example:

$$M = \begin{bmatrix} \tau_{\text{on} \rightarrow \text{on}} & 1 - \tau_{\text{on} \rightarrow \text{on}} \\ \tau_{\text{off} \rightarrow \text{on}} & 1 - \tau_{\text{off} \rightarrow \text{on}} \end{bmatrix}$$

In summary, we have 3 parameters to infer: the initial probability of masting $\tau_0 = p(z_1 = \text{on})$, the probability of transitioning from an **off-year** to an **on-year** $\tau_{\text{off} \rightarrow \text{on}}$, and the probability of staying into an on-year state $\tau_{\text{on} \rightarrow \text{on}}$.

2.2.2 Seed production parameters

Now, what about the parameters of the observational model that links the latent state to the observed seed count? The seed production depends on the state of the tree. Basically, it's a mixture model between two probability distributions.

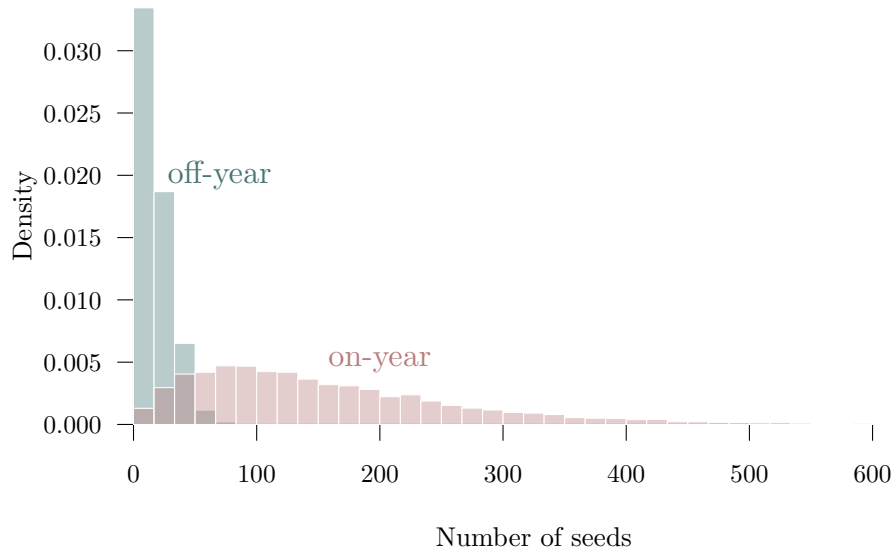
If the tree is in an **off-year**, then we model the (likely low) seed count with a zero-inflated negative binomial distribution:

$$y_i \begin{cases} = 0, & \text{with probability } \theta \\ \sim \text{NegBin}(\mu_{\text{off}}, \phi_{\text{off}}), & \text{with probability } 1 - \theta \end{cases} .$$

If the tree is in an **on-year**, then we model the seed count with a negative binomial distribution:

$$y_i \sim \text{NegBin}(\mu_{\text{on}}, \phi_{\text{on}})$$

This mixture of two probability distributions would look like this:



2.2.3 Adding climate!

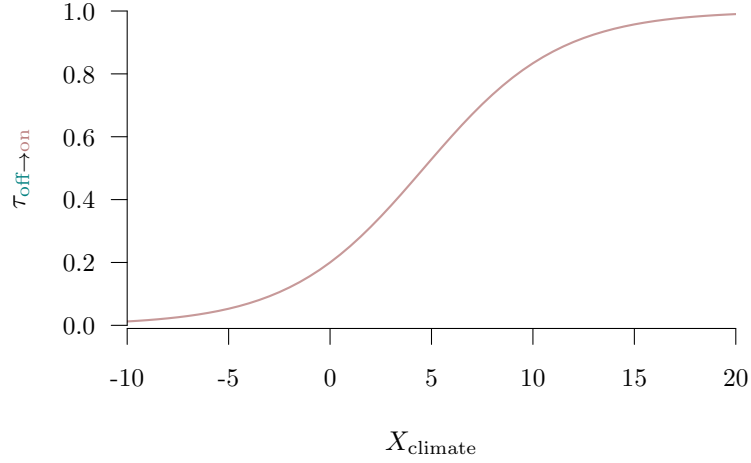
Explicitly modeling reproductive states and the subsequent seed production allows to think more deeply where the different climatic cues should impact the individual reproductive cycles and the population-level masting behavior.

The states explicitly encode the developmental constraints, i.e. the temporal overlap between floral bud initiation and fruit development, that explain the alternate bearing at the individual level. The transition between the states are controlled by the matrix transition. If the transition matrix stays constant across time, we would have an **homogeneous** HMM. But what if climate controls the transition between the states?

It's quite easy to include some variations in the transition matrix M , to have an **heterogeneous** HMM. For example, rather than having a constant probability $\tau_{\text{off} \rightarrow \text{on}}$, this probability could vary with the local climate:

$$\text{logit}(\tau_{\text{off} \rightarrow \text{on}}\{t\}) = \text{logit}(\tau_0) + \beta \cdot X_{\text{climate}}\{t\}$$

This would give us this kind of functional form, here with $\beta > 0$:

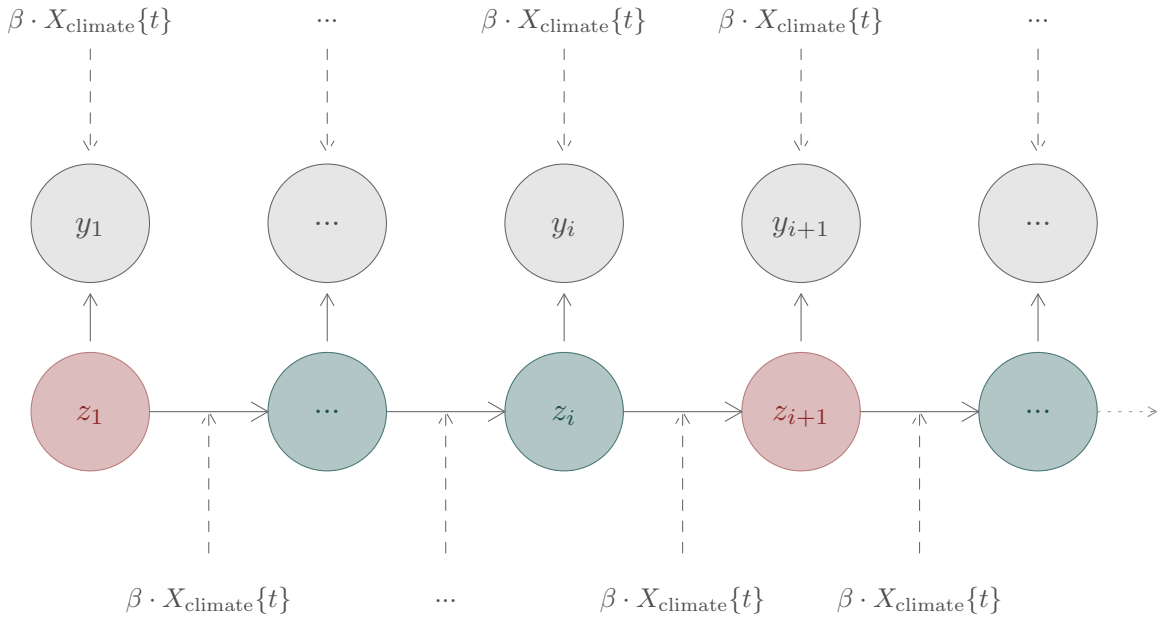


Once the tree is assigned to a state, climate may also impact seed production. The number of seeds in a **off-year** could be seen as a “background noise”, and we would thus prioritize adding some climatic predictors on the seed production of an **on-year**. A simple approach would be to modify the location parameter μ_{on} of the negative binomial like:

$$\mu_{\text{on}}\{t\} = \mu_0 + \beta \cdot X_{\text{climate}}\{t\}$$

Obviously, the covariates X_{climate} could be different for the transition probabilities and the seed production.

In summary, we could schematize the model as follow:



3 The case of beech masting dynamics