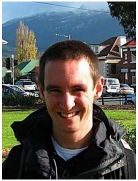
Inferring the ancestral population size under a birth-death process, from a reconstructed phylogenetic tree and a record of occurrences

Groupe de travail Math-Bio et Santé – LJLL – Paris

Marc Manceau, Antoine Zwaans, Jérémy Andréoletti, Ankit Gupta, Tim Vaughan, Rachel Warnock, Tanja Stadler

June 29, 2020



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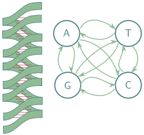
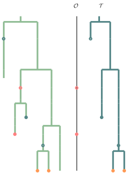
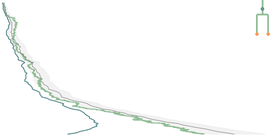
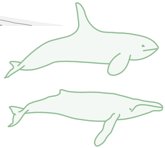
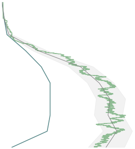
Sketch of the presentation



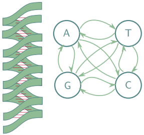








Basics of phylogenetics



The raw data – in macroevolution

- Molecular sequences of extant species
- Morphological traits of extant species
- Morphological traits of fossil species

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G	G	G
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T	T	T
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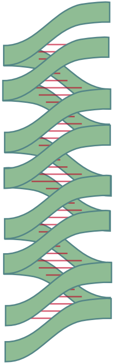

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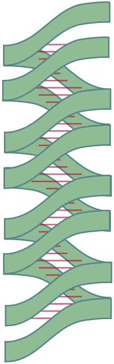

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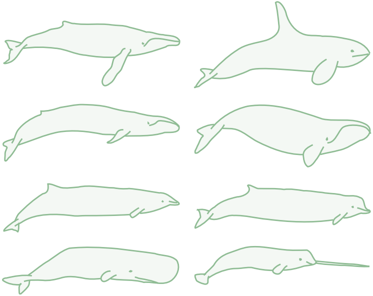

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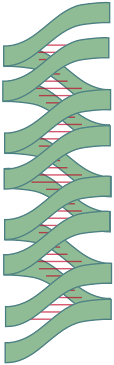

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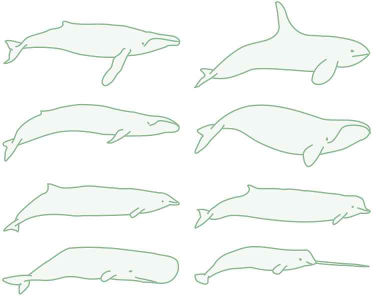

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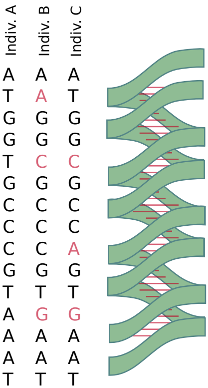

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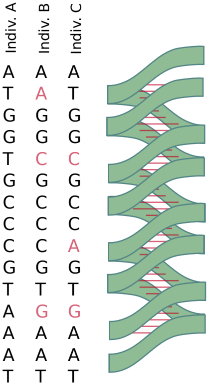

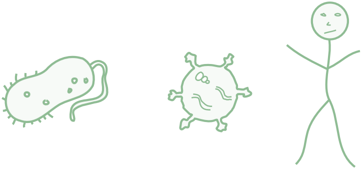

The questions

Macroevolution

1. What is the tempo of diversification ?
2. What are the drivers of trait evolution ?
3. What was the diversity in the past ?

Epidemiology

1. What is the tempo of epidemic spread ?
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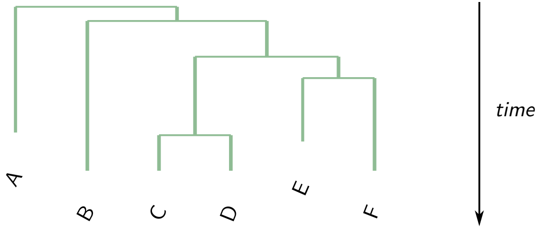

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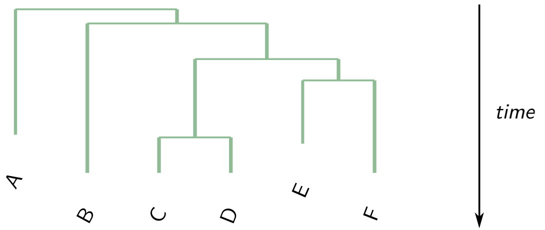

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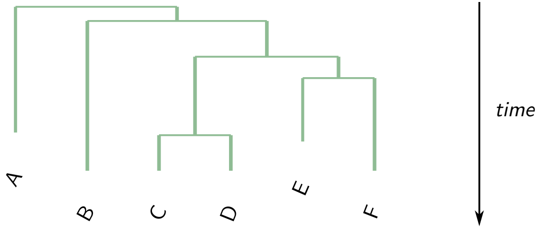

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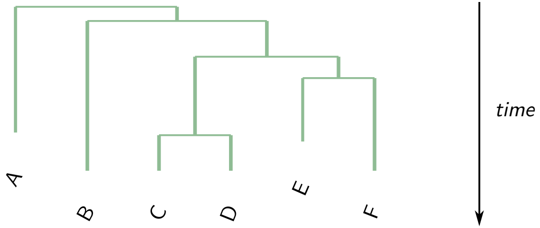

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indiv. D	-	A	G	-	-	-	-	-	...
indiv. E	-	-	G	-	-	-	A	-	...
indiv. F	-	-	G	-	-	-	A	-	...

MODEL

$\mathcal{A}$ = Alignment

$\mathbb{P}(\mathcal{A} \mid \mathcal{T}, \mathcal{R})$

$\mathcal{R}$ = Substitution rate

$\mathbb{P}(\mathcal{R} \mid \mathcal{T})$

$\mathcal{T}$ = Tree

$\mathbb{P}(\mathcal{T})$

$$\mathbb{P}(\mathcal{T}, \mathcal{R} \mid \mathcal{A}) \propto \mathbb{P}(\mathcal{A} \mid \mathcal{R}, \mathcal{T})\, \mathbb{P}(\mathcal{R} \mid \mathcal{T})\, \mathbb{P}(\mathcal{T})$$

RESULT

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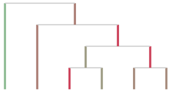

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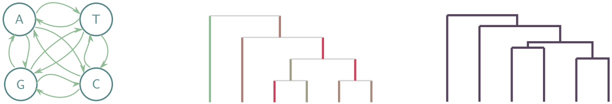

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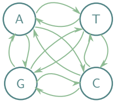

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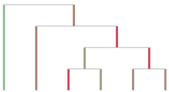

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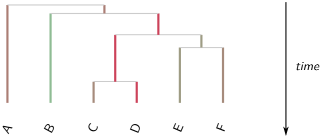
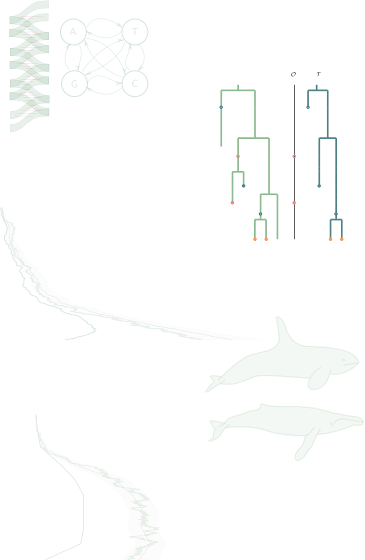


Incorporating occurrences



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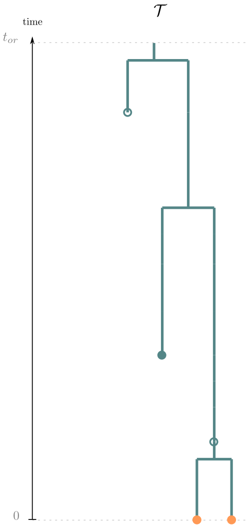

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- In epidemiology, samples are *infected individuals*.
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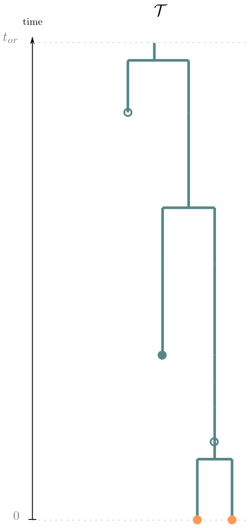

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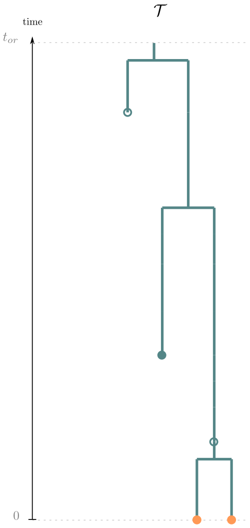

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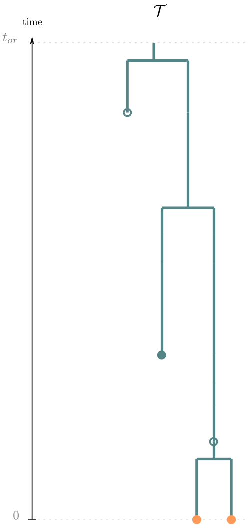

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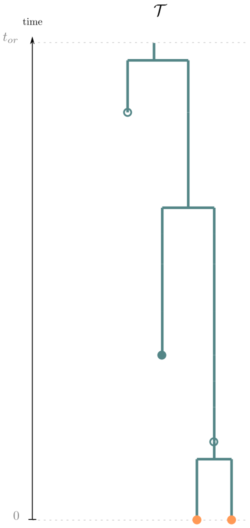

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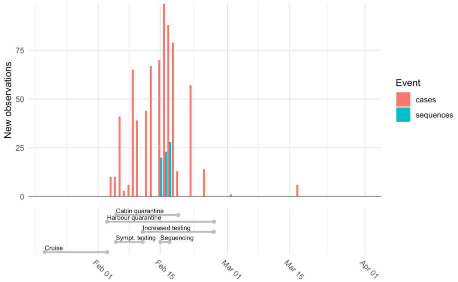

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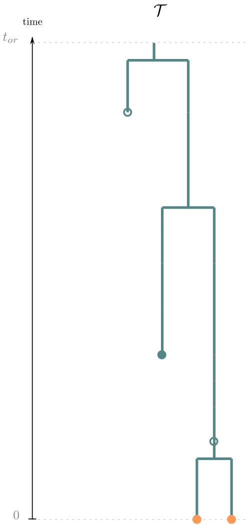

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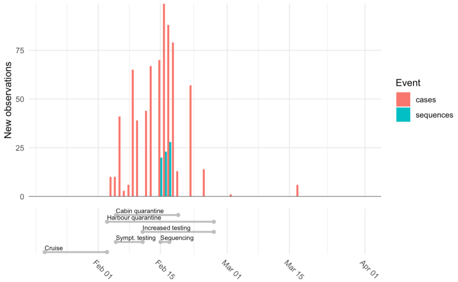

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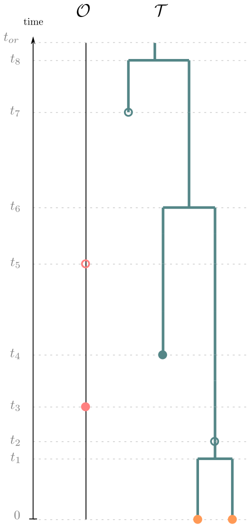

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We call this a record of occurrences $\mathcal{O}$.

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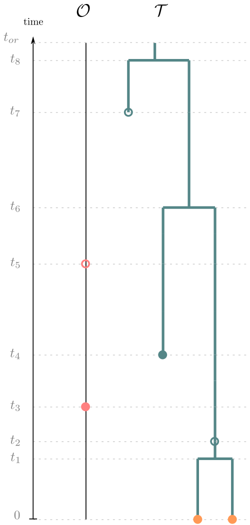

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- In macroevolution, samples are *species*.

But additional signal could come from:

- case count data, i.e. non-sequenced individuals,
- undescribed fossils without any character data attached.

We call this a record of occurrences $\mathcal{O}$.

What is the total number of individuals in the past ?

Model
following Vaughan et al, *MBE*, 2019

t_{or} origin

λ birth

ψ sampling and tree inclusion

μ death

ω sampling for occurrences

r removal at sampling

ρ sampling at present

Model

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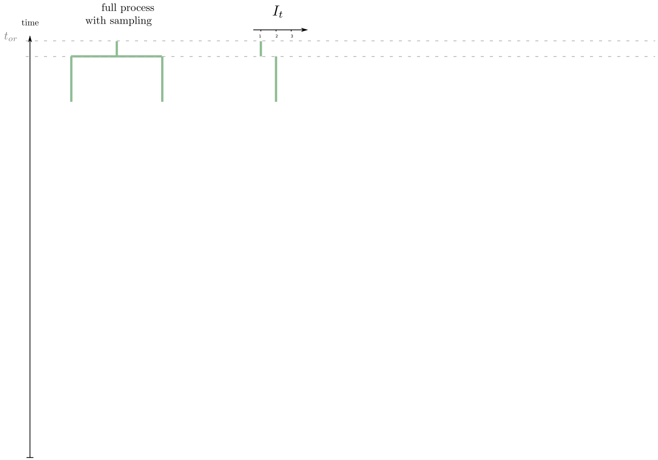

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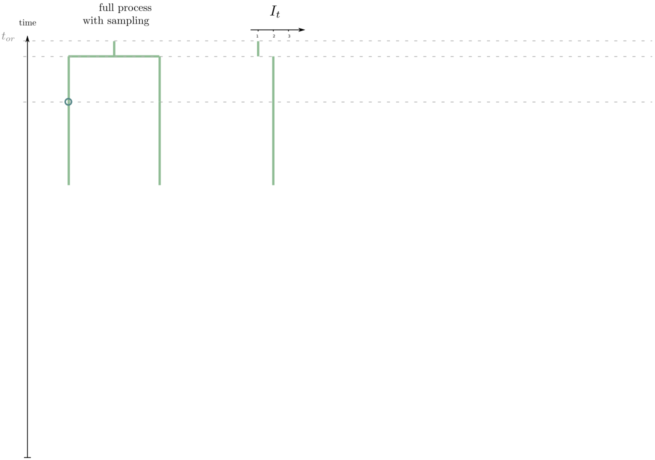

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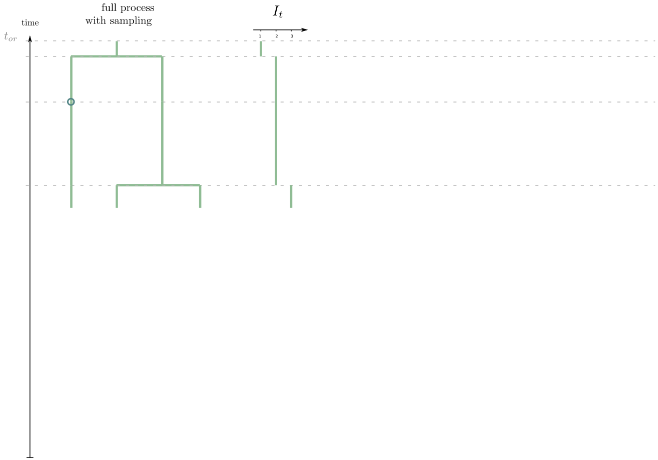

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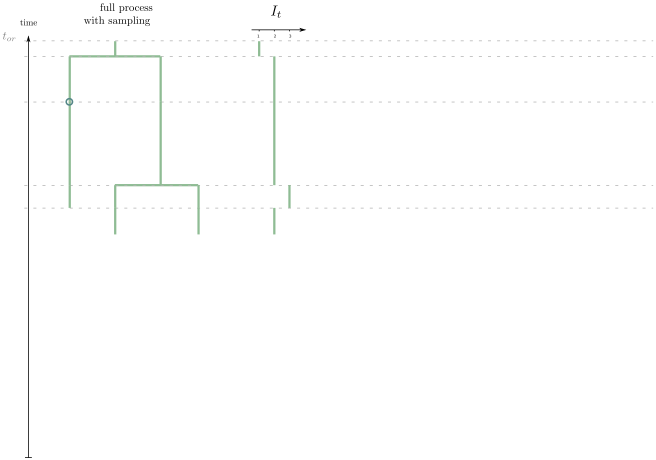

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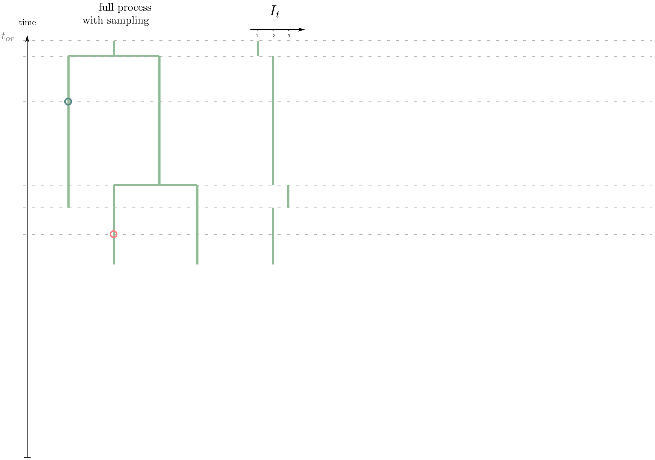

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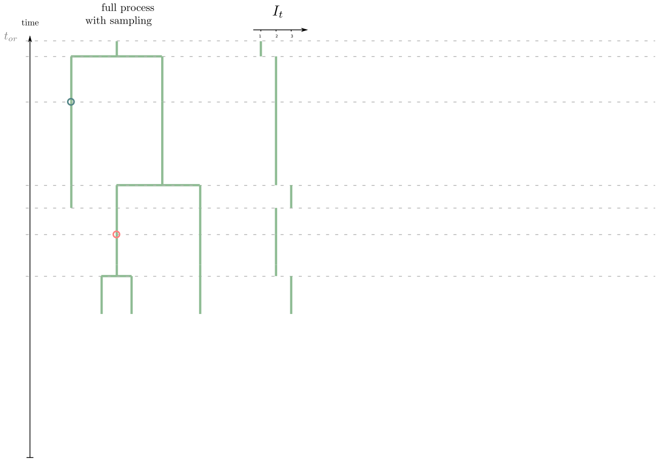

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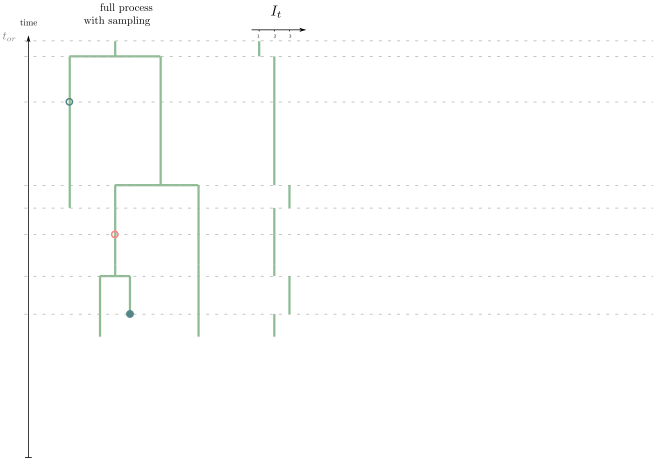

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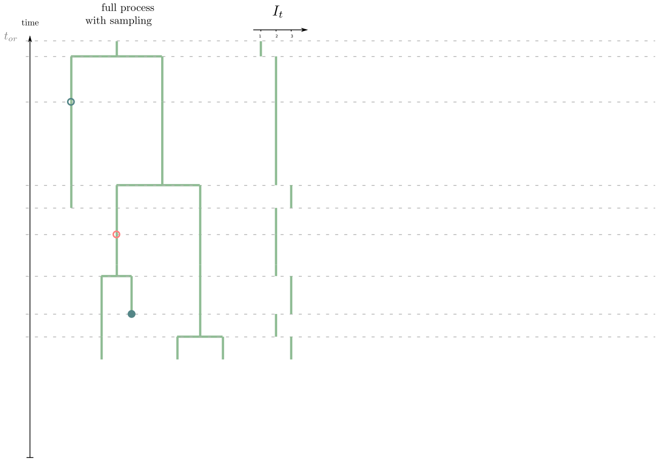

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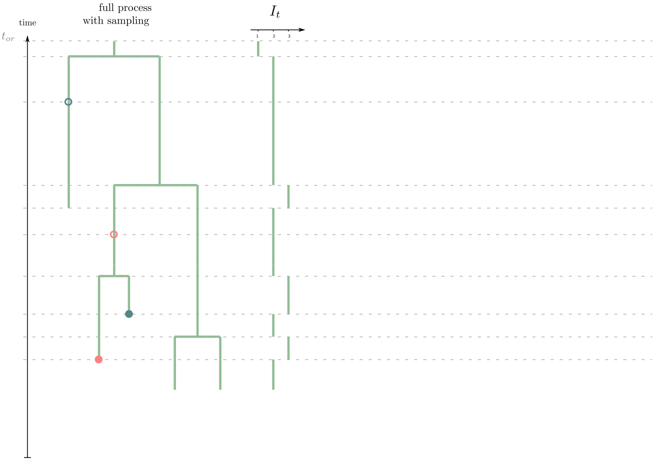

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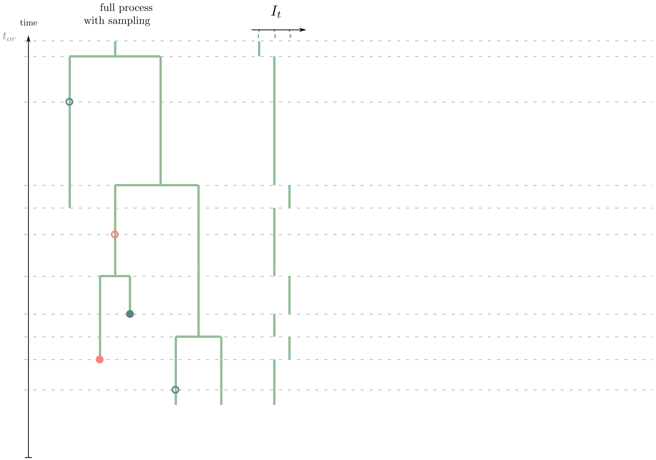

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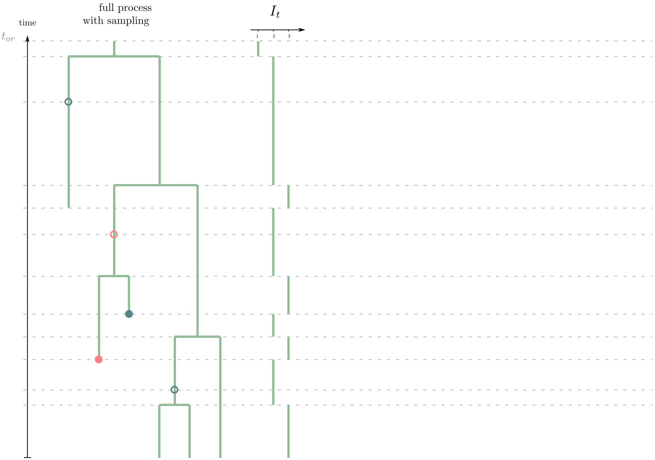

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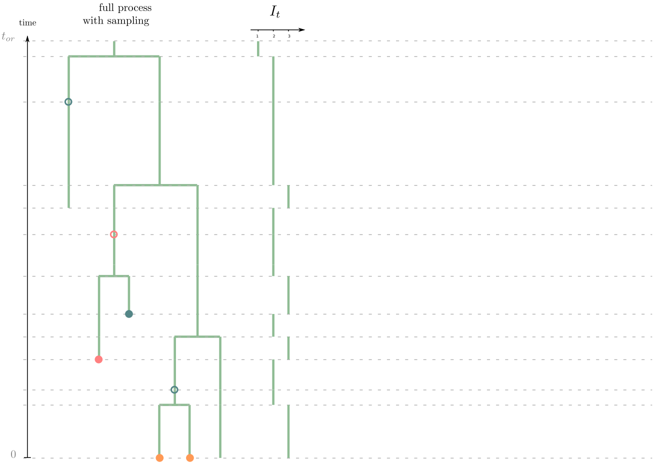

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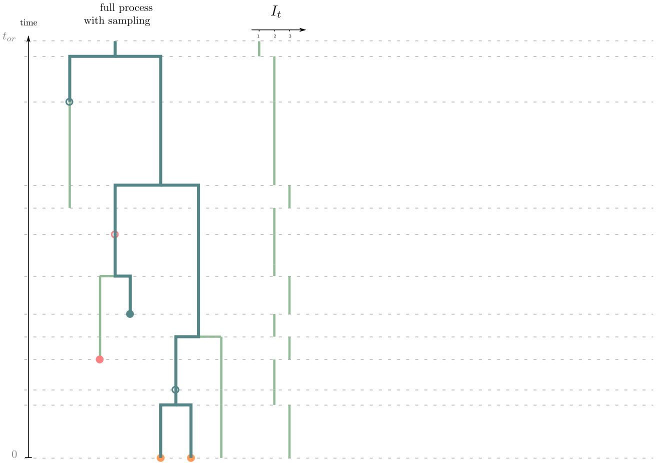

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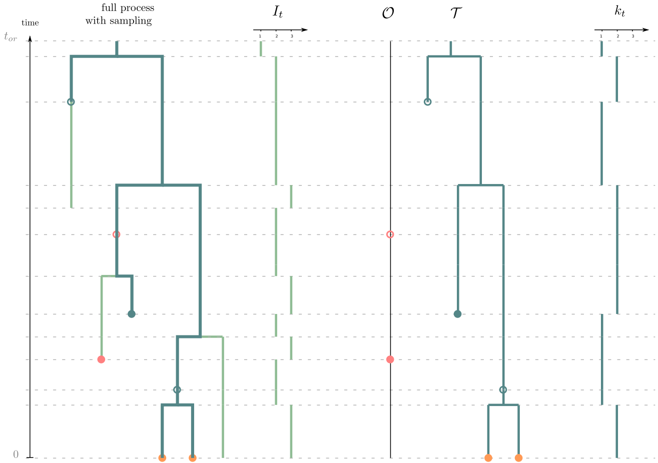

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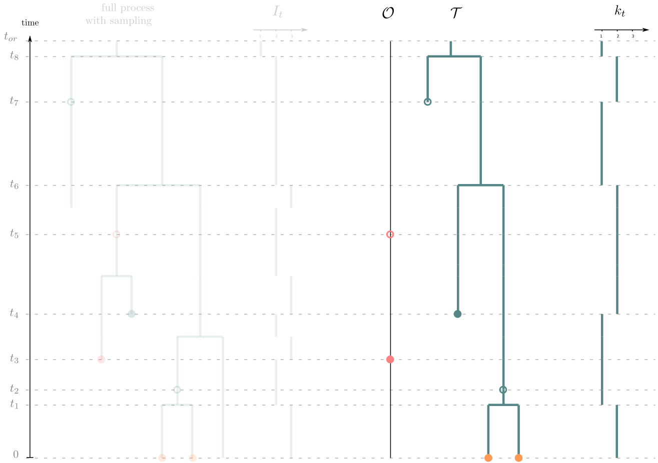
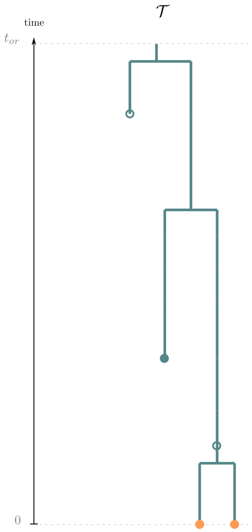


Incorporating occurrences
A bit of context



What is done, without occurrences,

- estimate $\hat{\lambda}, \hat{\mu}$ using the full tree
- compute $\mathbb{E}_{\hat{\lambda},\hat{\mu}}(I_t \mid I_{t_{or}} = 1)$.

Fast, but not accurate

What has been proposed, with occurrences,

- simulate population size trajectories conditioned on the full tree
- to approximate $\mathbb{P}(I_t \mid \mathcal{T}, \mathcal{O})$.

Accurate, but slower

Incorporating occurrences

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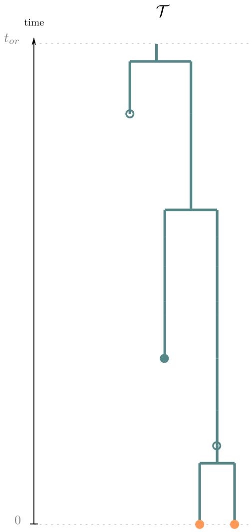

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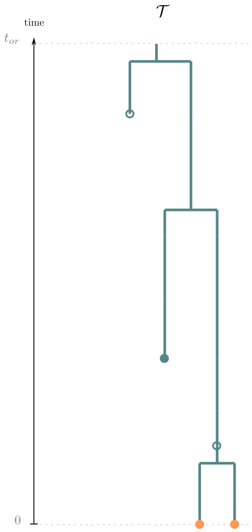

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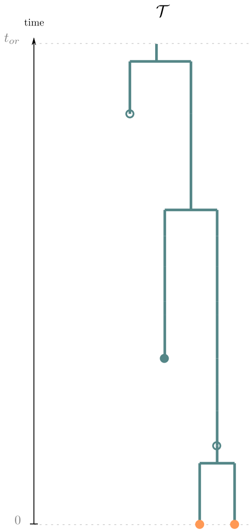

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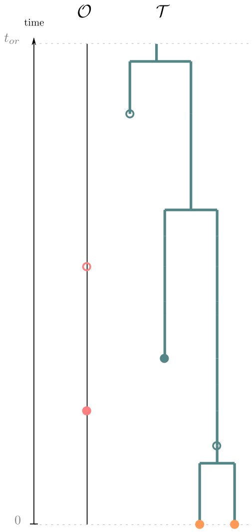

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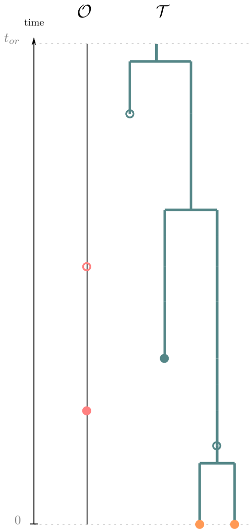

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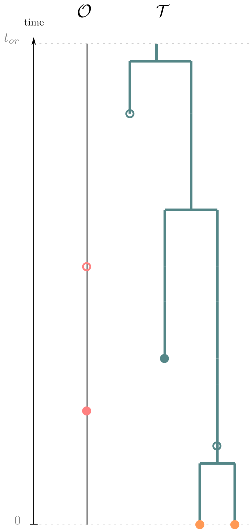

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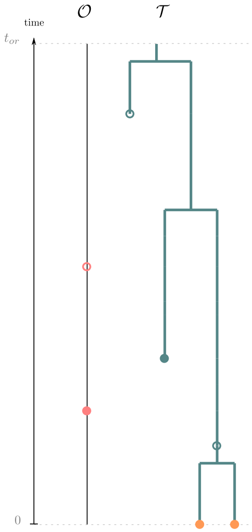

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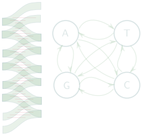
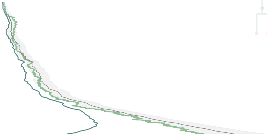
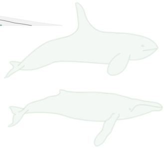
The ancestral population size

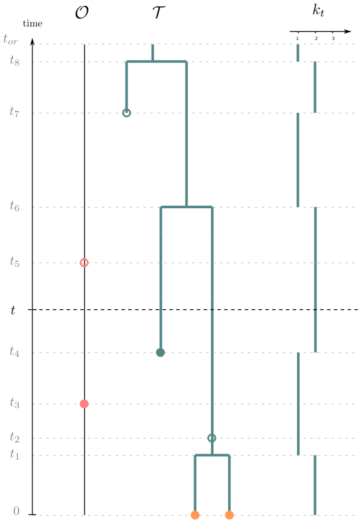






Marc Manceau, Antoine Zwaans, Jérémy Andréoletti, Ankit Gupta, Tim Vaughan, Rachel Warnock, Tanja Stadler

Sketch of the overall strategy



For any time t, we are interested in

$$K_t^{(i)} := \mathbb{P}\left(I_t = k_t + i \mid \mathcal{T}, \mathcal{O}\right)$$

We define

$$M_t^{(i)} := \mathbb{P}\left(T_t^{\uparrow}, \mathcal{O}_t^{\uparrow}, I_t = k_t + i\right)$$

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Then we get

$$\begin{aligned} K_t^{(i)} &\propto \mathbb{P}\left(I_t = k_t + i, T_t^{\uparrow}, \mathcal{O}_t^{\uparrow}, T_t^{\downarrow}, \mathcal{O}_t^{\downarrow}\right) \\ &\propto \mathbb{P}\left(T_t^{\downarrow}, \mathcal{O}_t^{\downarrow} \mid I_t = k_t + i, T_t^{\uparrow}, \mathcal{O}_t^{\uparrow}\right) \\ &\quad \mathbb{P}\left(I_t = k_t + i, T_t^{\uparrow}, \mathcal{O}_t^{\uparrow}\right) \\ &\propto L_t^{(i)} M_t^{(i)} \end{aligned}$$

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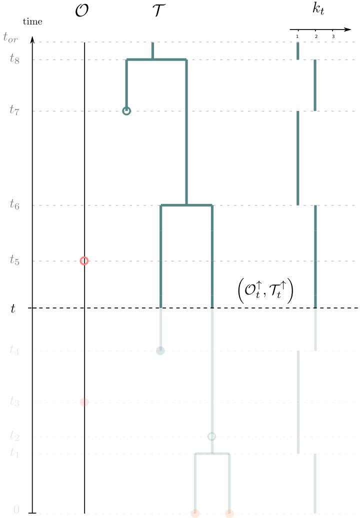

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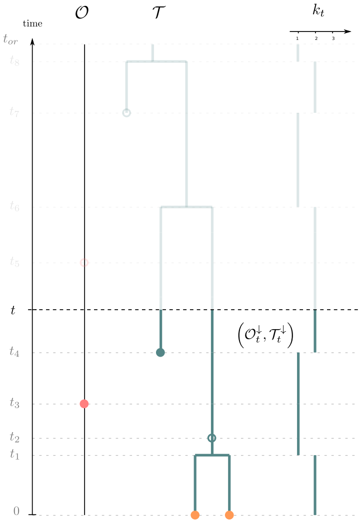

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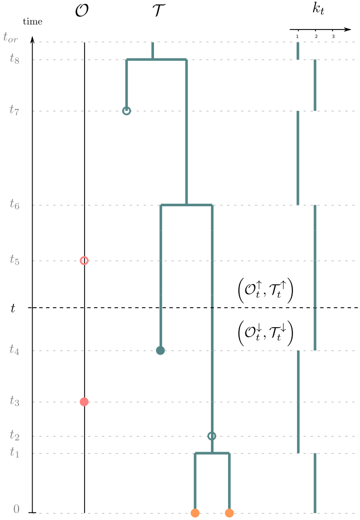

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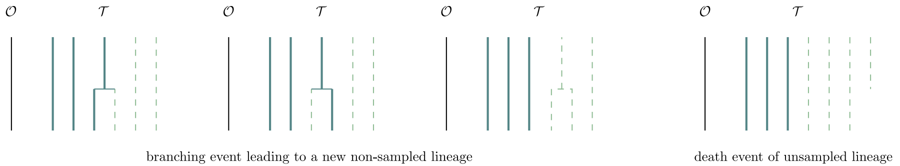
The ancestral population size

Forward-backward traversal of the tree to compute $M_t = \left(\mathbb{P}(T_t^{\uparrow}, \mathcal{O}_t^{\uparrow}, I_t = k_t + i)\right)_{i\geq 0}$



We can write the Master equation, $\forall i \in \mathbb{N}$,

$$M_{t-\delta t}^{(i)} = (1 - (\lambda + \mu + \psi + \omega)(i + k_t)\delta t)\, M_t^{(i)} + \lambda(2k_t + i - 1)\delta t \mathbb{1}_{i>0} M_t^{(i-1)} + \mu(i+1)\delta t M_t^{(i+1)}$$

Leading to a system of ODEs,

$$\frac{dM_t^{(i)}}{dt} = (\lambda + \mu + \psi + \omega)(i + k_t)M_t^{(i)} - \lambda(2k_t + i - 1)\mathbb{1}_{i>0} M_t^{(i-1)} - \mu(i+1)M_t^{(i+1)}$$

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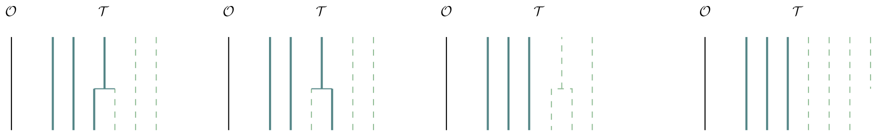

branching event leading to a new non-sampled lineage

death event of unsampled lineage

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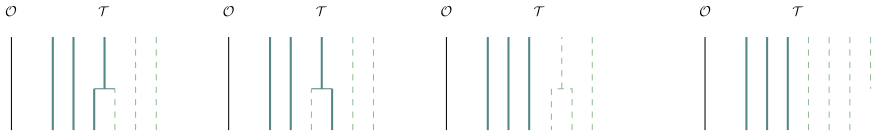

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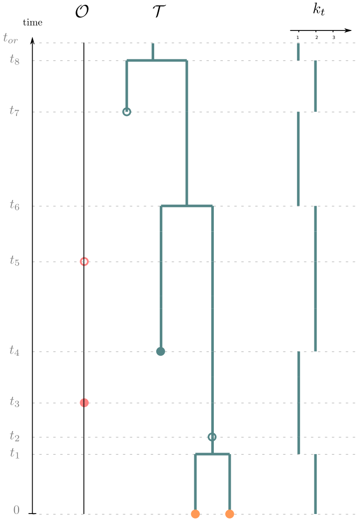
Forward-backward traversal of the tree

A forward breadth-first traversal to compute $M_t = \left(\mathbb{P}(T_t^{\uparrow}, \mathcal{O}_t^{\uparrow}, I_t = k_t + i)\right)_{i \geq 0}$

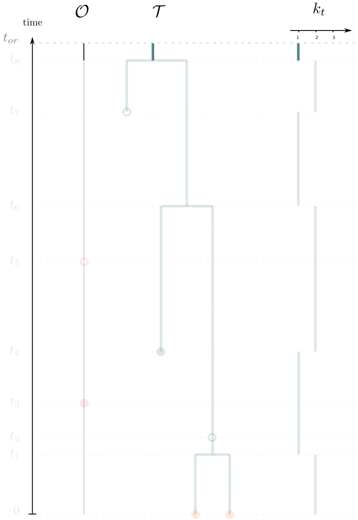


We know how to initialize M_t at the time of origin

$$M_{t_{or}}^{(i)} = \mathbb{P}(I_{t_{or}} = 1 + i) = \mathbb{1}_{i=0}$$

Forward-backward traversal of the tree

A forward breadth-first traversal to compute $M_t = \left(\mathbb{P}(T_t^{\uparrow}, \mathcal{O}_t^{\uparrow}, I_t = k_t + i)\right)_{i \geq 0}$



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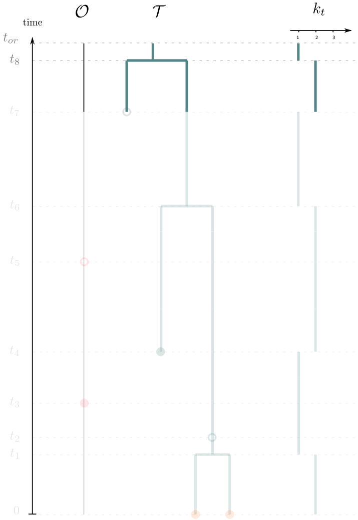

$$M_{t-} = \lambda M_{t+}$$

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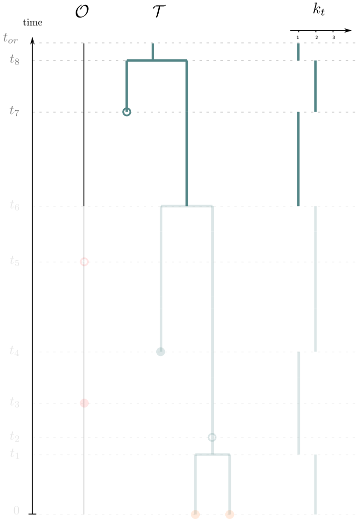

$$M_{t-}^{(i)} = \psi(1-r)\mathbb{1}_{i>0} M_{t+}^{(i-1)}$$

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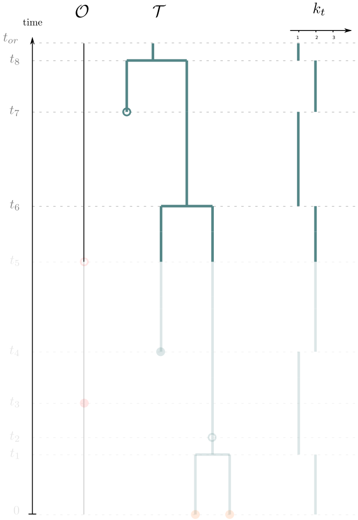

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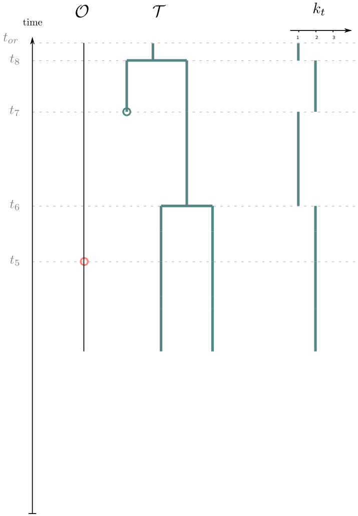

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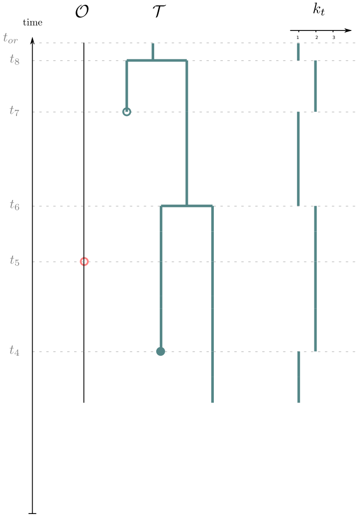

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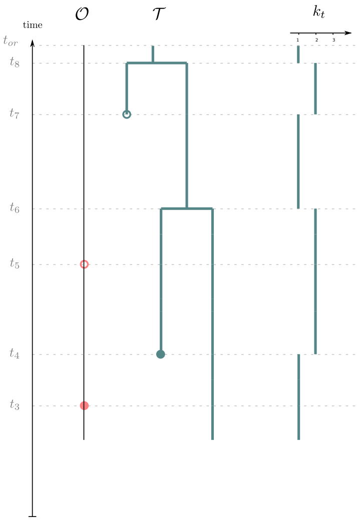

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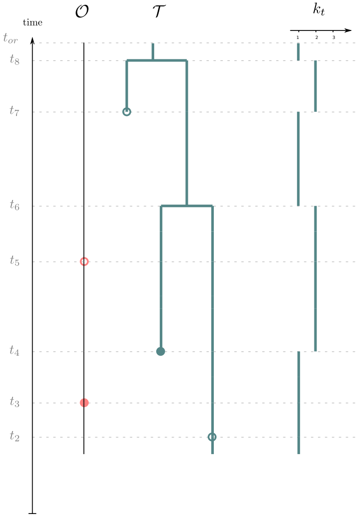

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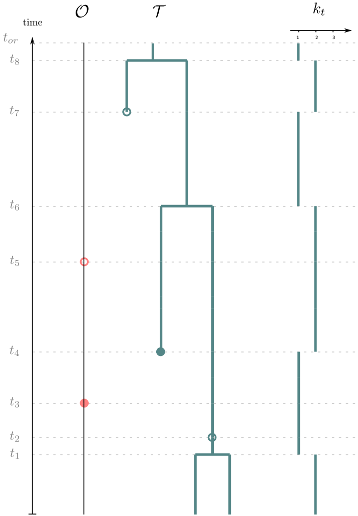

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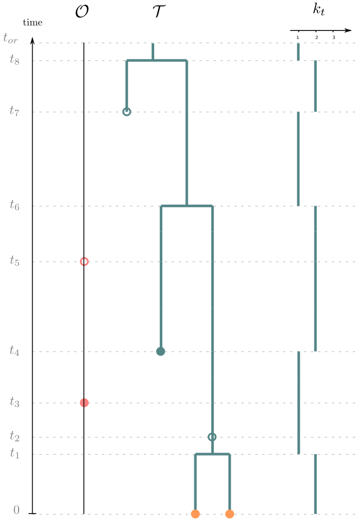

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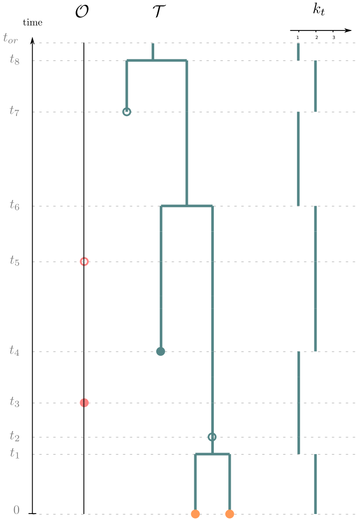

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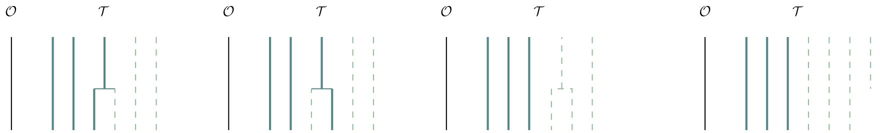
The ancestral population size

Forward-backward traversal of the tree to compute $L_t = \left(\mathbb{P}(T_t^{\downarrow}, \mathcal{O}_t^{\downarrow} \mid I_t = k_t + i)\right)_{i \geq 0}$



branching event leading to a new non-sampled lineage

death event of unsampled lineage

We can write the Master equation, $\forall i \in \mathbb{N}$,

$$L_{t+\delta t}^{(i)} = (1 - (\lambda + \mu + \psi + \omega)(k_t + i)\delta t)\, L_t^{(i)} + \lambda(2k_t + i)\delta t L_t^{(i+1)} + \mu i \delta t L_t^{(i-1)}$$

Leading to a system of ODEs,

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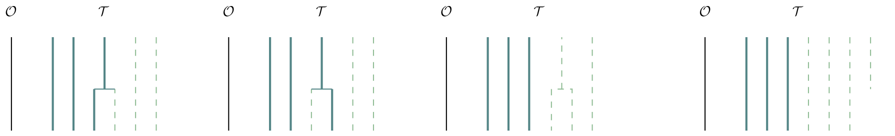

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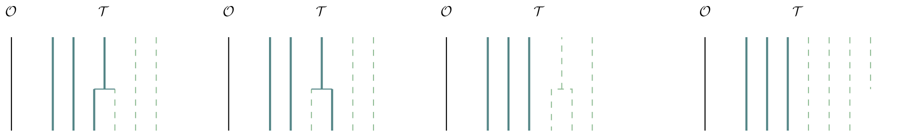

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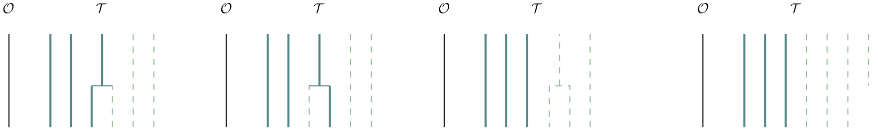

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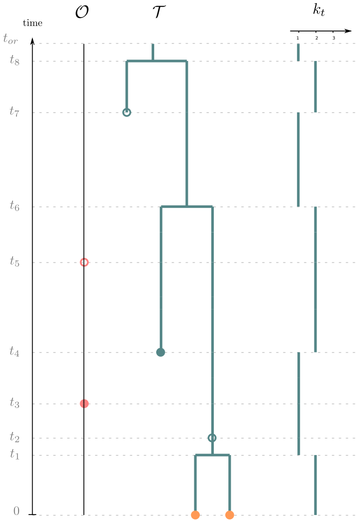

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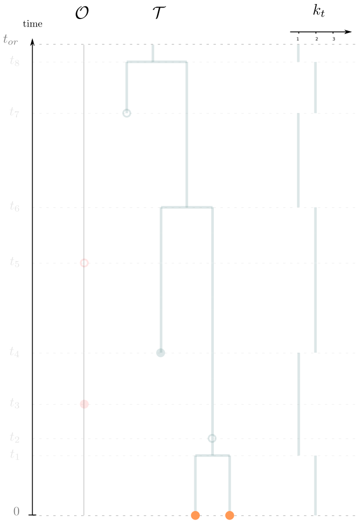

We know how to initialize L_t at present.

$$L_0^{(i)} = \rho^{k_0}(1-\rho)^i$$

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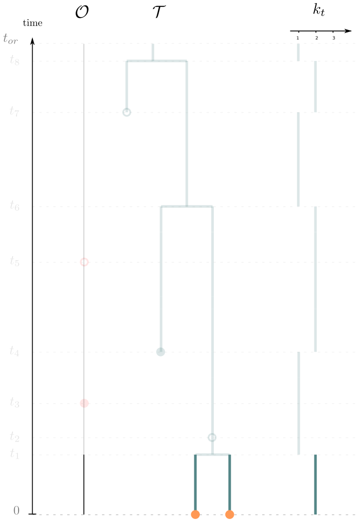

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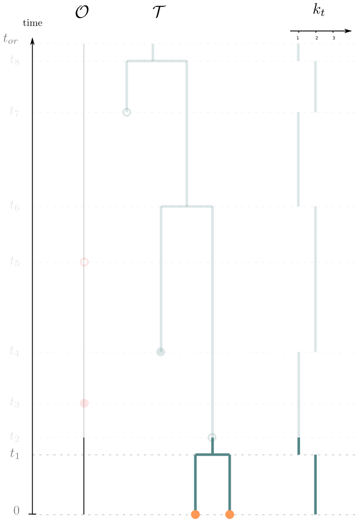

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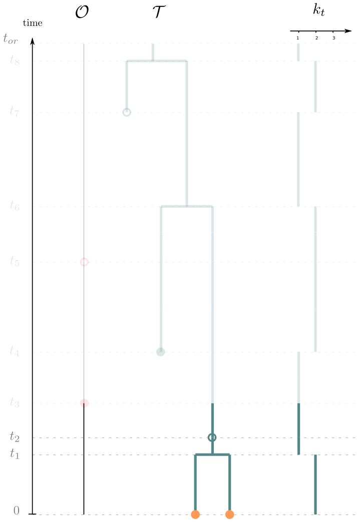

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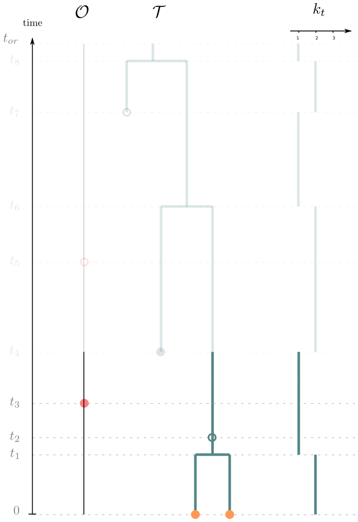

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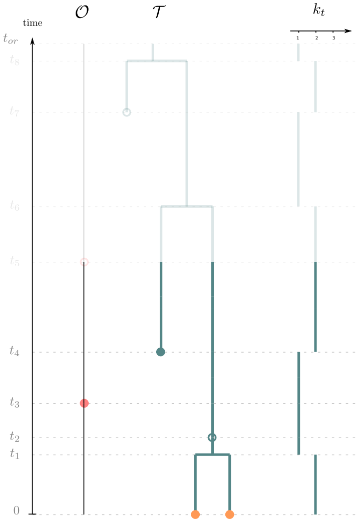

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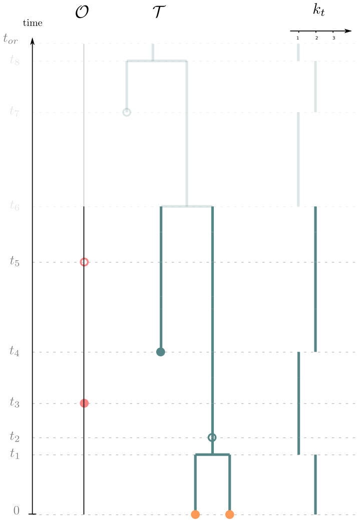

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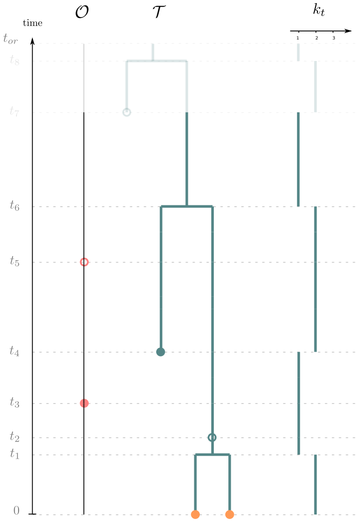

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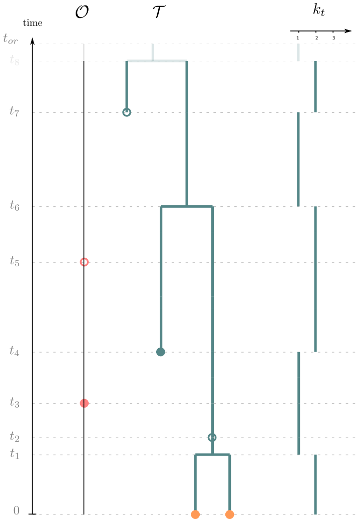

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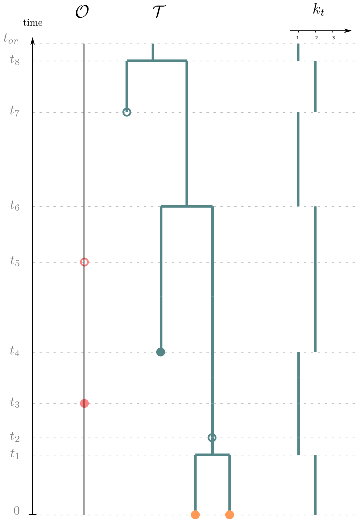

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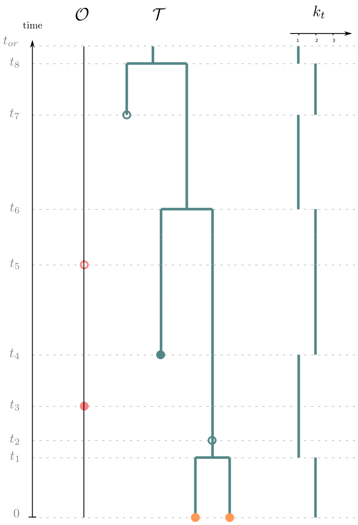

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The ancestral population size

Known corrolaries

Recall that M_t verifies:

$$\frac{dM_t^{(i)}}{dt} = \gamma(i+k)M_t^{(i)} - \lambda(2k+i-1)\mathbb{1}_{i>0}M_t^{(i-1)} - \mu(i+1)M_t^{(i+1)}$$
$$M_{t_{or}}^{(i)} = \mathbb{1}_{i=0}$$

We introduce the corresponding probability generating function:

$$\hat{M}(t,z) = \sum_{i=0}^{\infty} z^i M_t^{(i)}$$

The initial condition translates as $\forall z, \quad \hat{M}(t_{or}, z) = 1$
And the ODE translates as the following PDE:

$$\partial_t \hat{M} = -k(2\lambda z - \gamma)\hat{M} - (\lambda z^2 - \gamma z + \mu)\partial_z \hat{M}$$

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I need to consider the parameter space

I want to compute

	$\omega = 0$	$r = 1$	$\omega \neq 0$ and $r \neq 1$
$\mathbb{P}(\mathcal{T}, \mathcal{O})$	Corollary 3.2	Proposition 3.3	Algorithm 1' or Algorithm 2'
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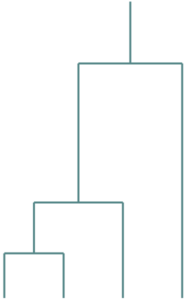
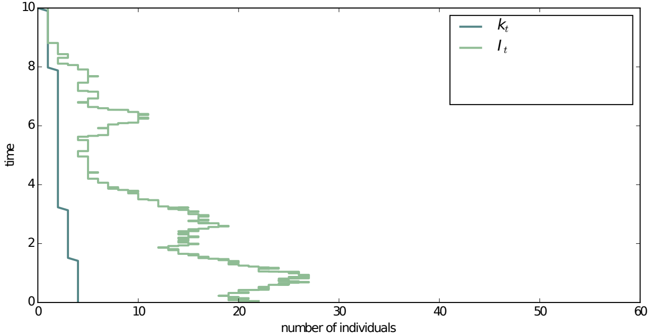
Reconstructing past population size

- With only ρ-sampling ($\psi, \omega = 0, 0$).
- With ρ and ψ-sampling ($\omega = 0$).
- With ρ, ψ, and ω-sampling.





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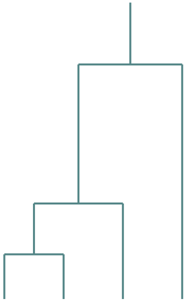

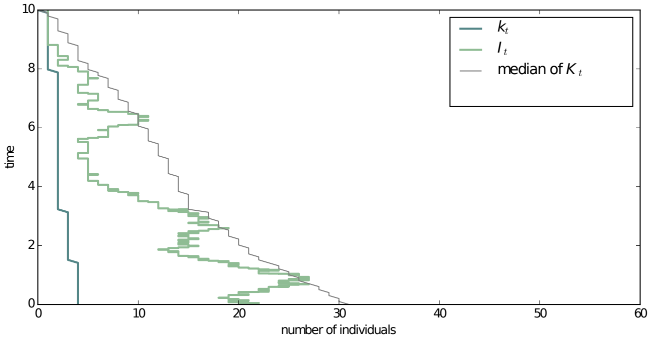

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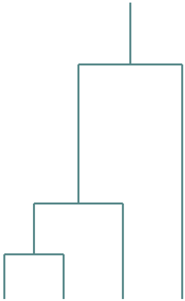

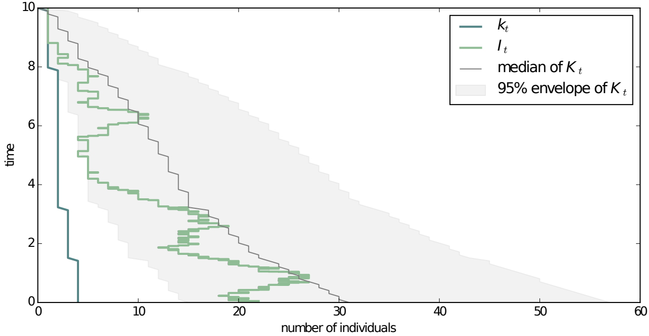

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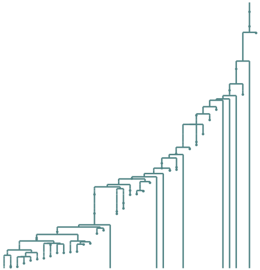

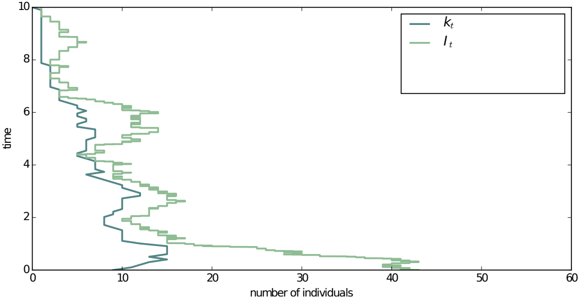

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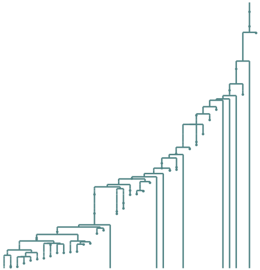

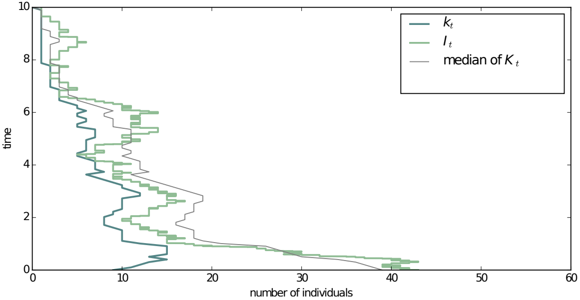

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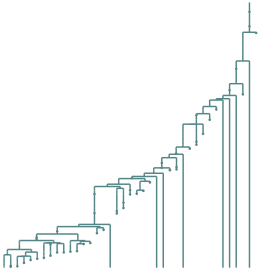

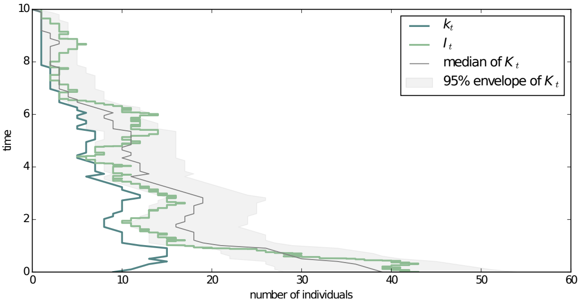

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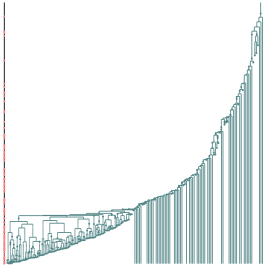

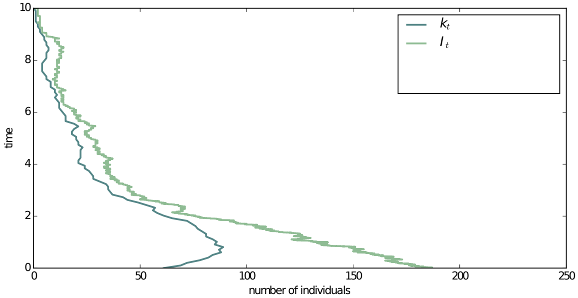

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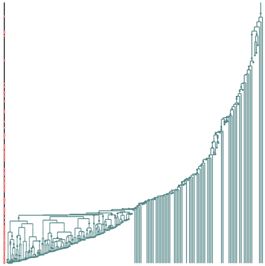

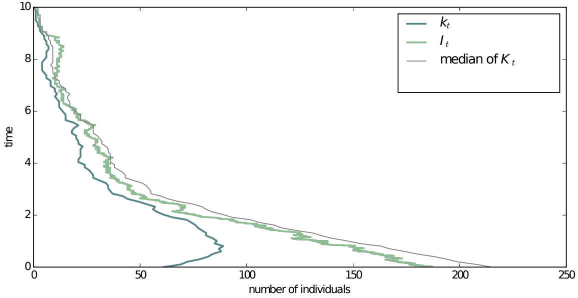

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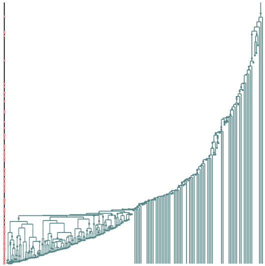
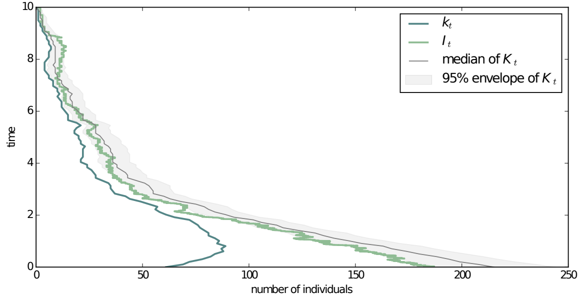
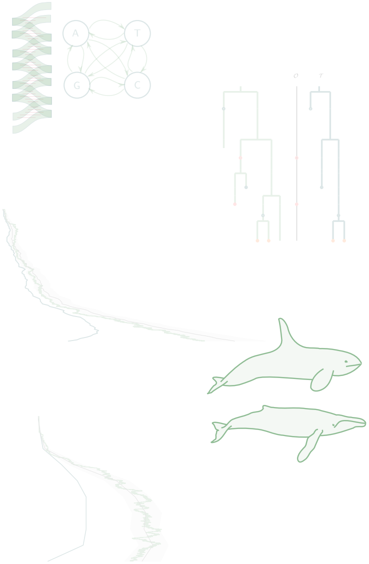




Empirical case studies



Overview of the project
With Antoine Zwaans and Jérémy Andréoletti

Goals:

1. Work with piecewise-constant parameters.
2. Implement the method to compute $\mathbb{P}(\mathcal{T}, \mathcal{O})$.
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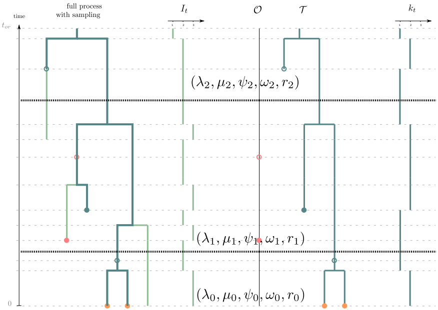

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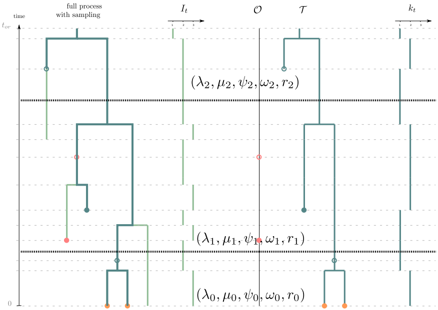

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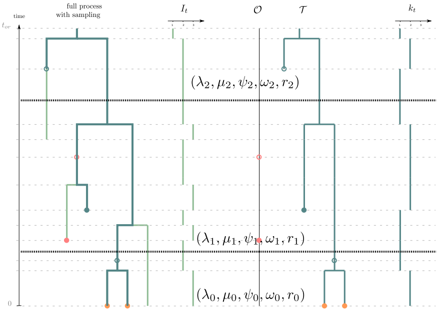

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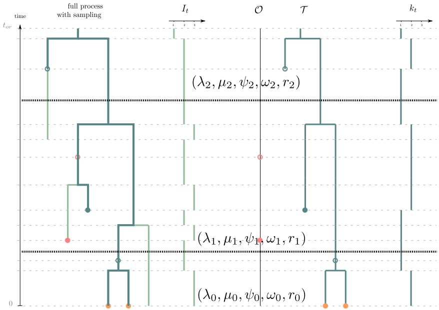

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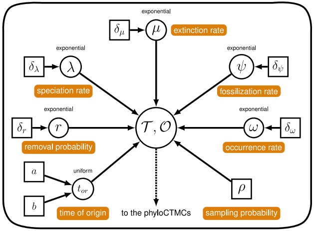

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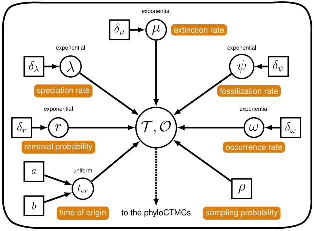
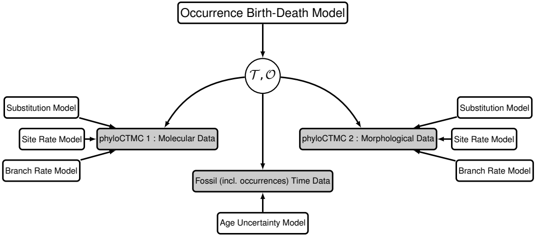
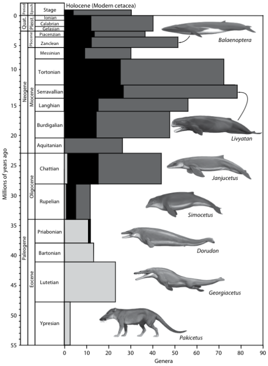




Cetacean diversity

After Marx et al. (2016) and the Paleobiology database

- Generic diversity
- Bias 1: Uneven sampling of time periods/localities,
- Bias 2: Species abundances,



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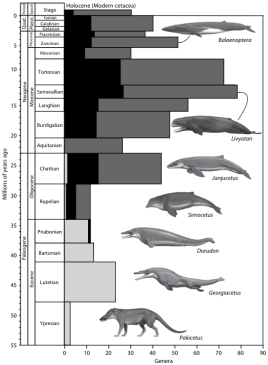

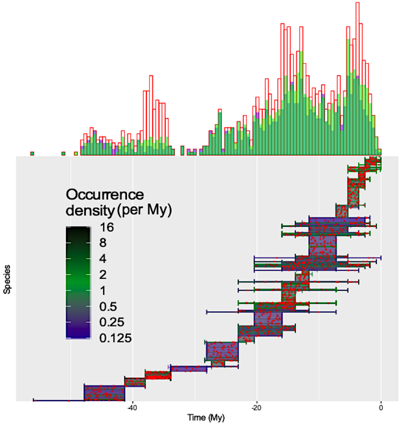

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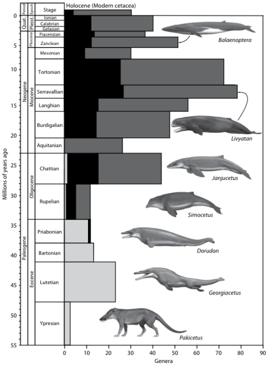

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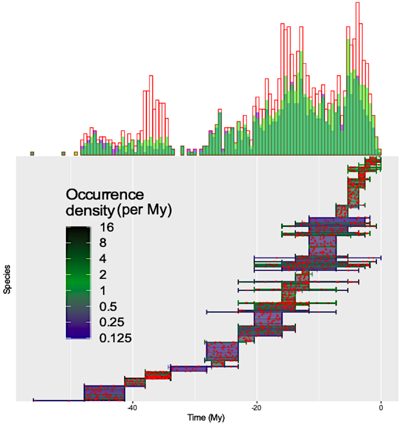

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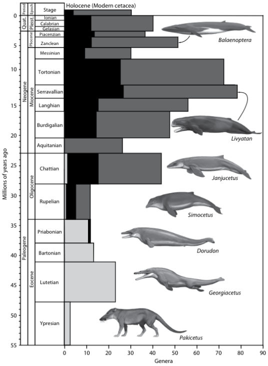

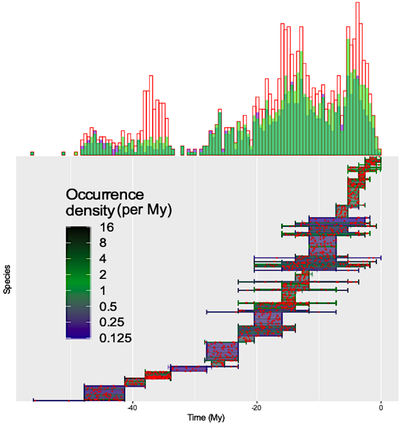

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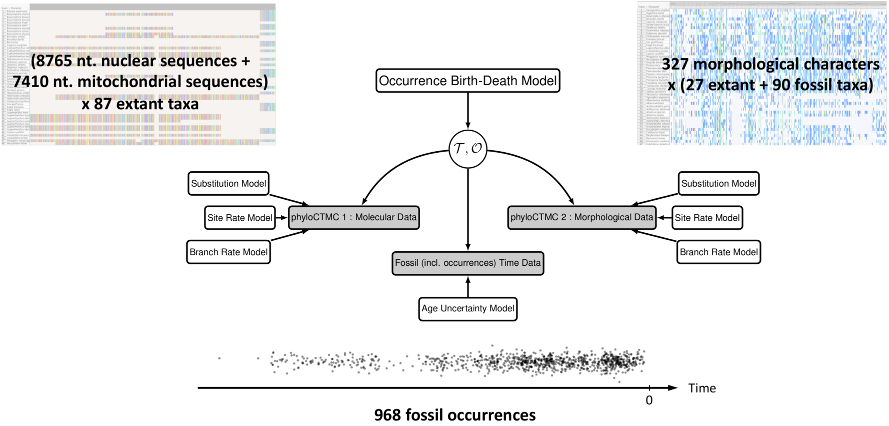
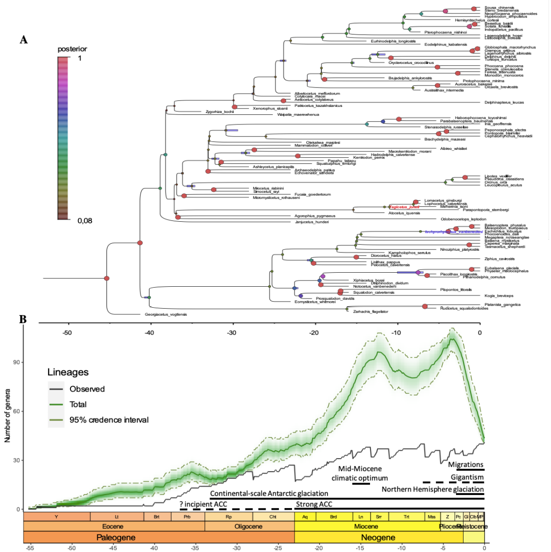


Cetacean diversity
Preliminary results



Covid-19 prevalence on the Diamond princess

- Diamond princess cruise ship,
- Very close to the model assumptions,
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Can we recover the known prevalence ?

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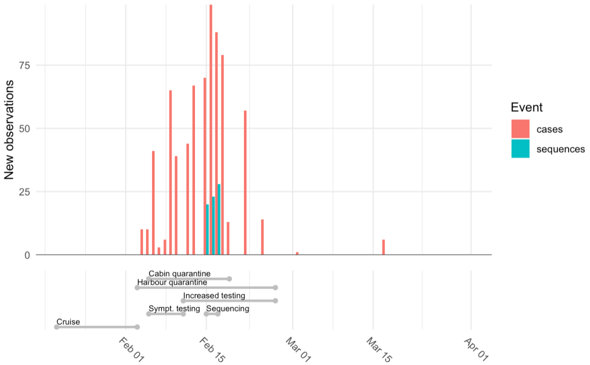

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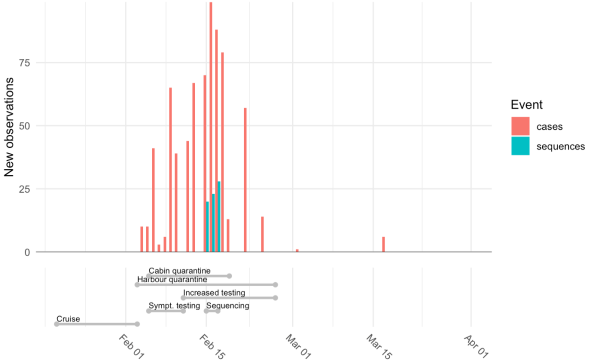

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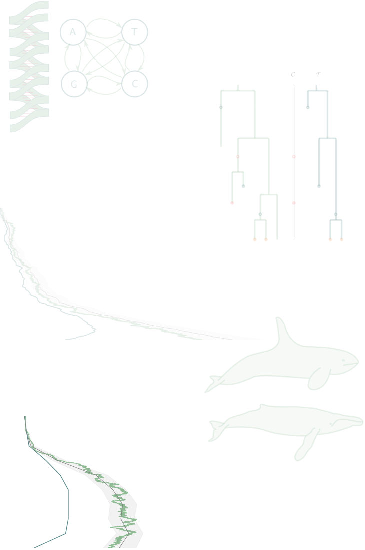
Conclusion



Perspectives
Diversity-dependent diversification

Work in progress

- extension to logistic birth-death processes, with per-capita rates either:

$$\lambda_i = \lambda - \alpha i \quad \text{or} \quad \mu_i = \mu + \beta i$$

- design methods to test hypotheses regarding diversification scenarios,
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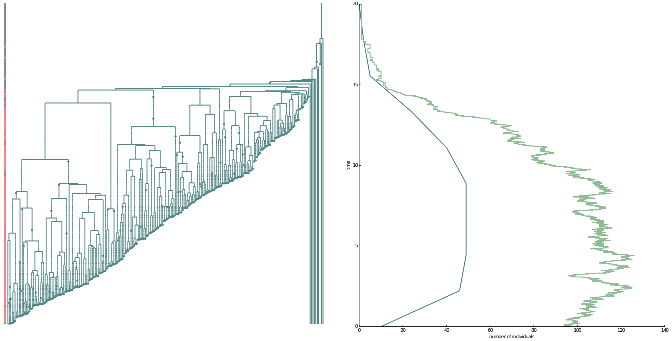

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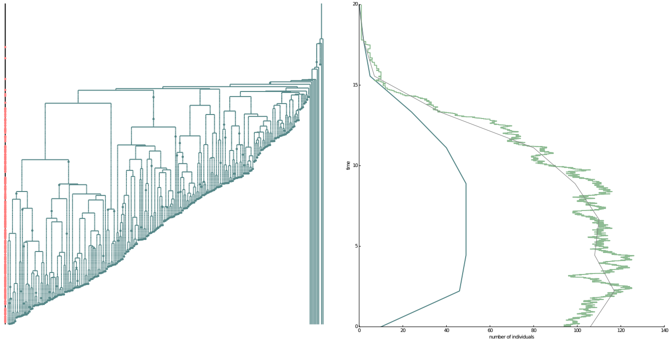

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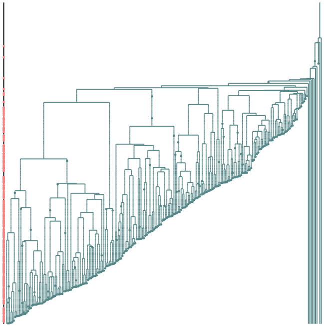

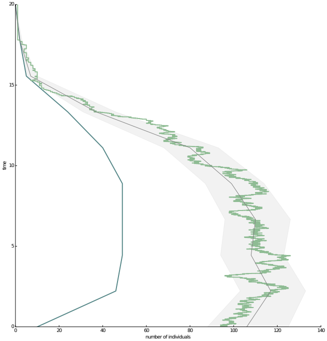

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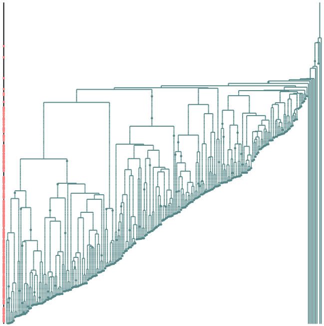

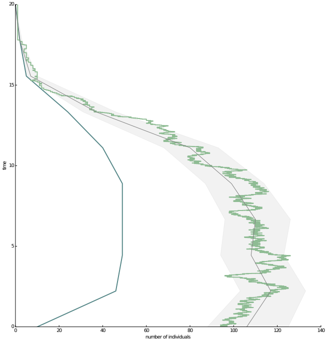

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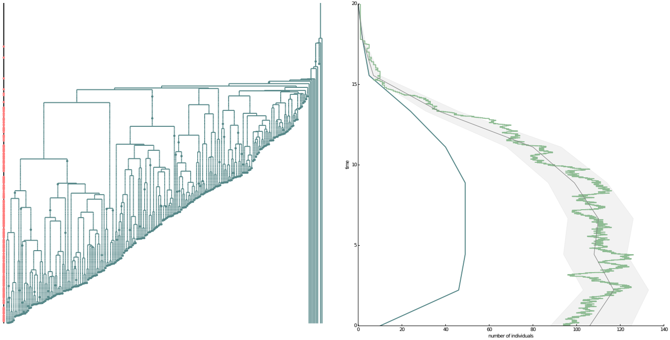

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Illustration on macroevolution and epidemiology datasets.

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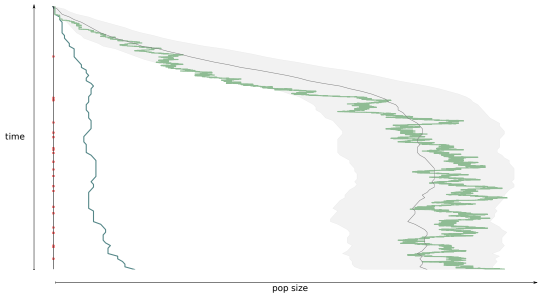

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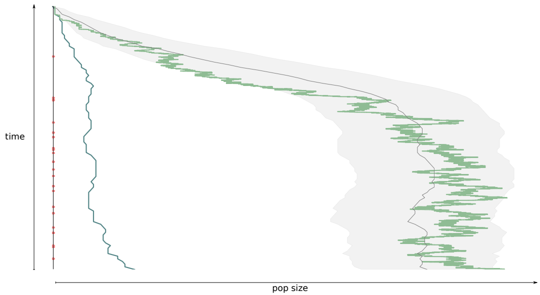

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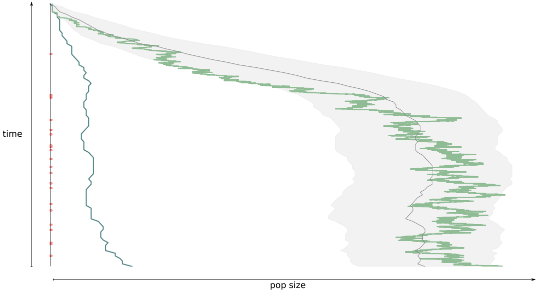

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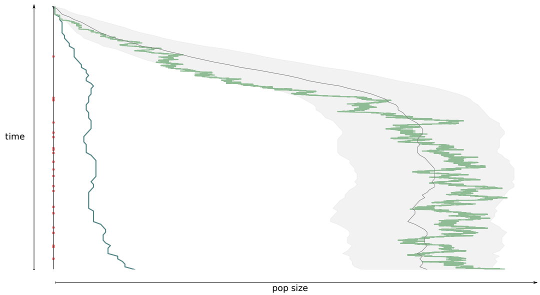

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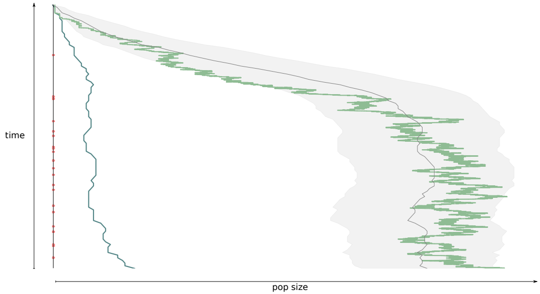

References

Etienne et al. (2012) used backward Kolmogorov equations to compute the likelihood of trees, under a logistic birth-death process.

Leventhal et al. (2013) used the forward Kolmogorov equations to compute the likelihood of trees, under a logistic birth-death process.

Vaughan et al. (2018) introduced the model and a Monte-Carlo method to get $\mathbb{P}\left(I_t \mid \mathcal{O}, \mathcal{T}\right)$.

Laudanno et al. (2019) did something similar to our analytical work on $\hat{M}$.

Gupta et al. (2020) analytical development to compute $\mathbb{P}(\mathcal{T}, \mathcal{O})$ when $r = 1$.

Manceau et al. (submitted) combining the forward and backward traversals to get the ancestral population size.

Andréoletti, Zwaans et al. (in prep) implementation in a Bayesian framework and application on empirical datasets.