

Speciation completion rates have limited impact on macroevolutionary diversification

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Speciation rates vary considerably across lineages at the macroevolutionary scale, but we know little about what causes these variations. In order to better understand the factors that control speciation rates at this scale, we aim to investigate how each step of the speciation process (speciation initiation, survival of incipient species and speciation completion) influences the rate of speciation.

The protracted birth-death (PBD) model of speciation accounts for the fact that speciation takes time

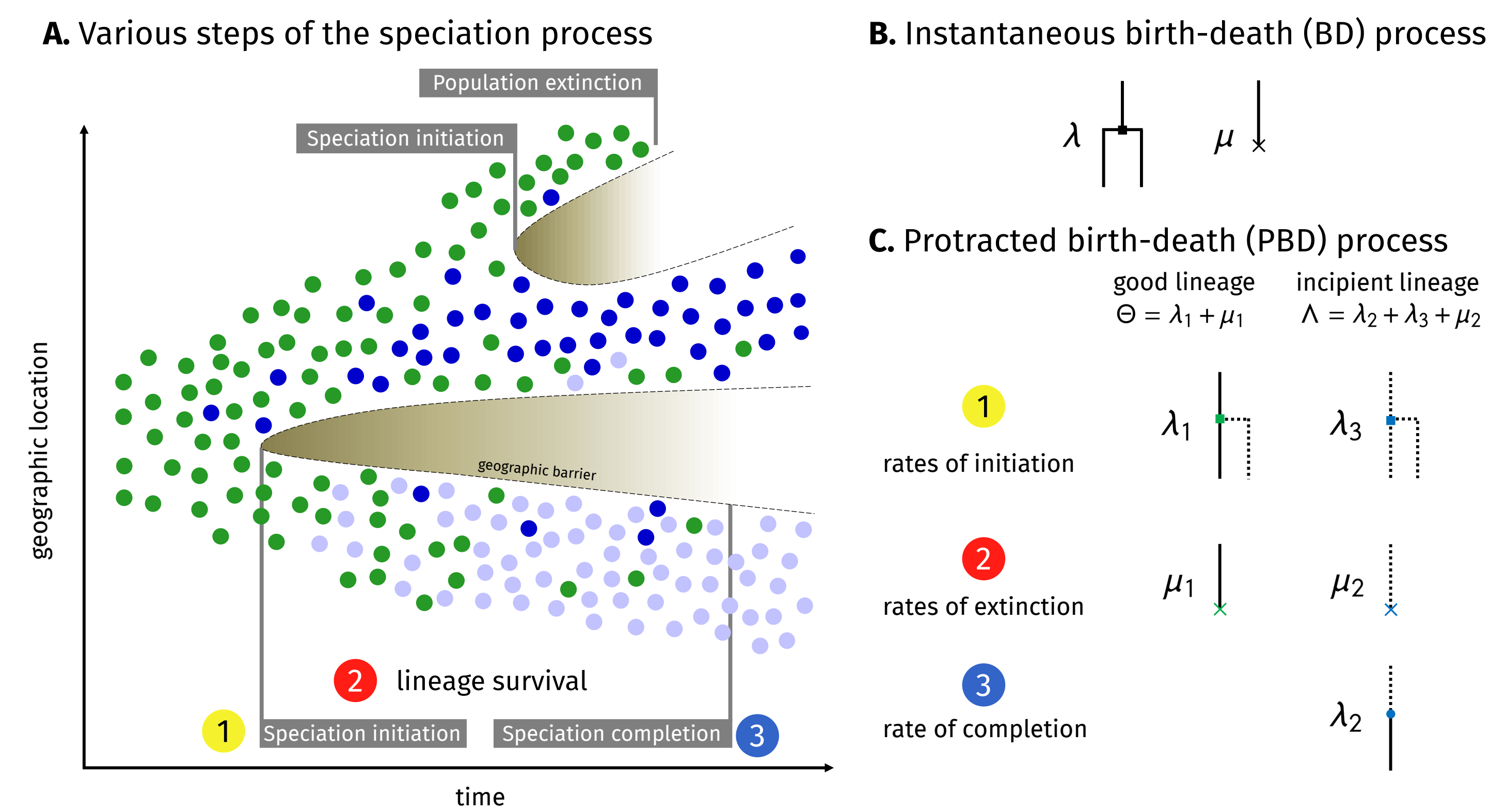


Figure 1. A. Illustration of the multistep speciation process, adapted from ref.¹ B. Instantaneous birth-death rates. C. Protracted birth-death (PBD) process with the rates as defined in ref.²

Equivalent time-dependant birth-death (BD) rates

We define $p_S^G(t)$ and $p_E^G(t)$ the probabilities that a good lineage speciates or goes extinct within a given time t between 0 (start of the process) and T (present; see **figure 2**):

$$p_E^G(t) = \underbrace{\frac{\mu_1}{\Theta}(1 - e^{-\Theta t})}_{(1)} + \underbrace{\int_0^t \lambda_1 e^{-\Theta u} p_E^I(t-u) p_E^G(t-u) du}_{(2)},$$

$$p_S^G(t) = \int_0^t \underbrace{\lambda_1 e^{-\Theta u}}_{(init.)} \times \left(\underbrace{p_C^I(t-u)}_{(3)} + \underbrace{(1 - p_C^I(t-u)) p_S^G(t-u)}_{(4)} \right) du$$

with $p_E^I(t)$ and $p_C^I(t)$ the probabilities of extinction/completion of an incipient lineage within a time t .

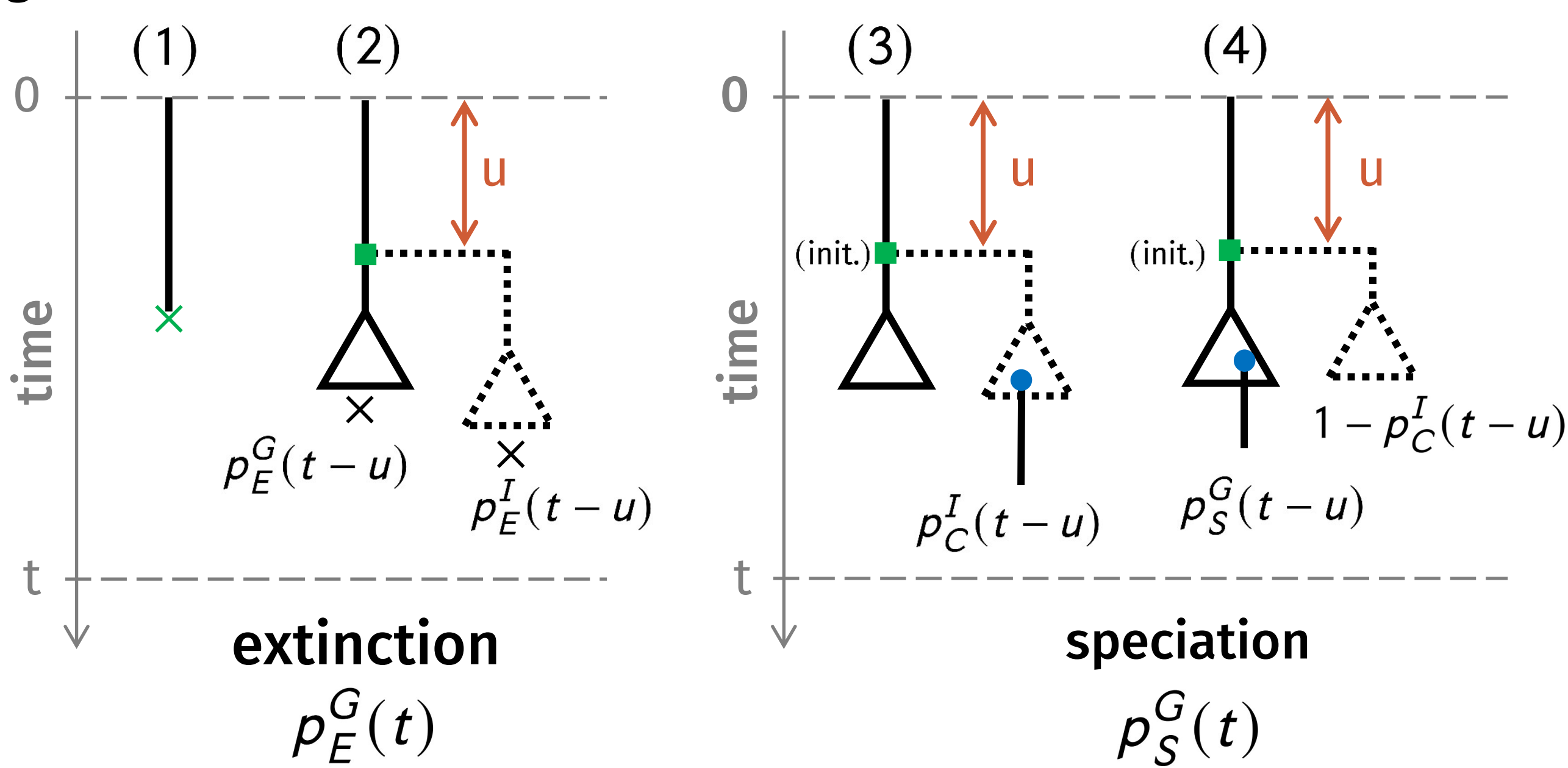


Figure 2. Description of the exclusive ways of extinction (1 and 2) or speciation (3 and 4) for a good lineage. Note that $p_E^G(t) + p_S^G(t) < 1$ because nothing can happen.

We then define and calculate **equivalent birth and death rates** $\hat{\lambda}(t)$ and $\hat{\mu}(t)$ such that the probabilities of speciation and extinction during an interval $[t - dt, t]$ can be written $\hat{\lambda}(t) dt$ and $\hat{\mu}(t) dt$ for $t \in [0, T]$.

Equivalent constant BD rates

Equivalent BD rates $\tilde{\lambda}, \tilde{\mu}$ satisfy that BD process have the same probability of speciation and expected time for speciation:

$$\tilde{\lambda} = (1 - \pi)\lambda_1 \quad \text{and} \quad \tilde{\mu} = \mu_1$$

with $\pi = \Lambda(1 - \sqrt{1 - 4\lambda_3\mu_2\Lambda^{-2}})/2\lambda_3$ the probability of non-completion of an incipient lineage. The equivalent constant BD rates correspond to the asymptotic equivalent time-dependent rates in the past (see **figure 4**).

The time-dependant equivalent BD process reproduces the protracted speciation process

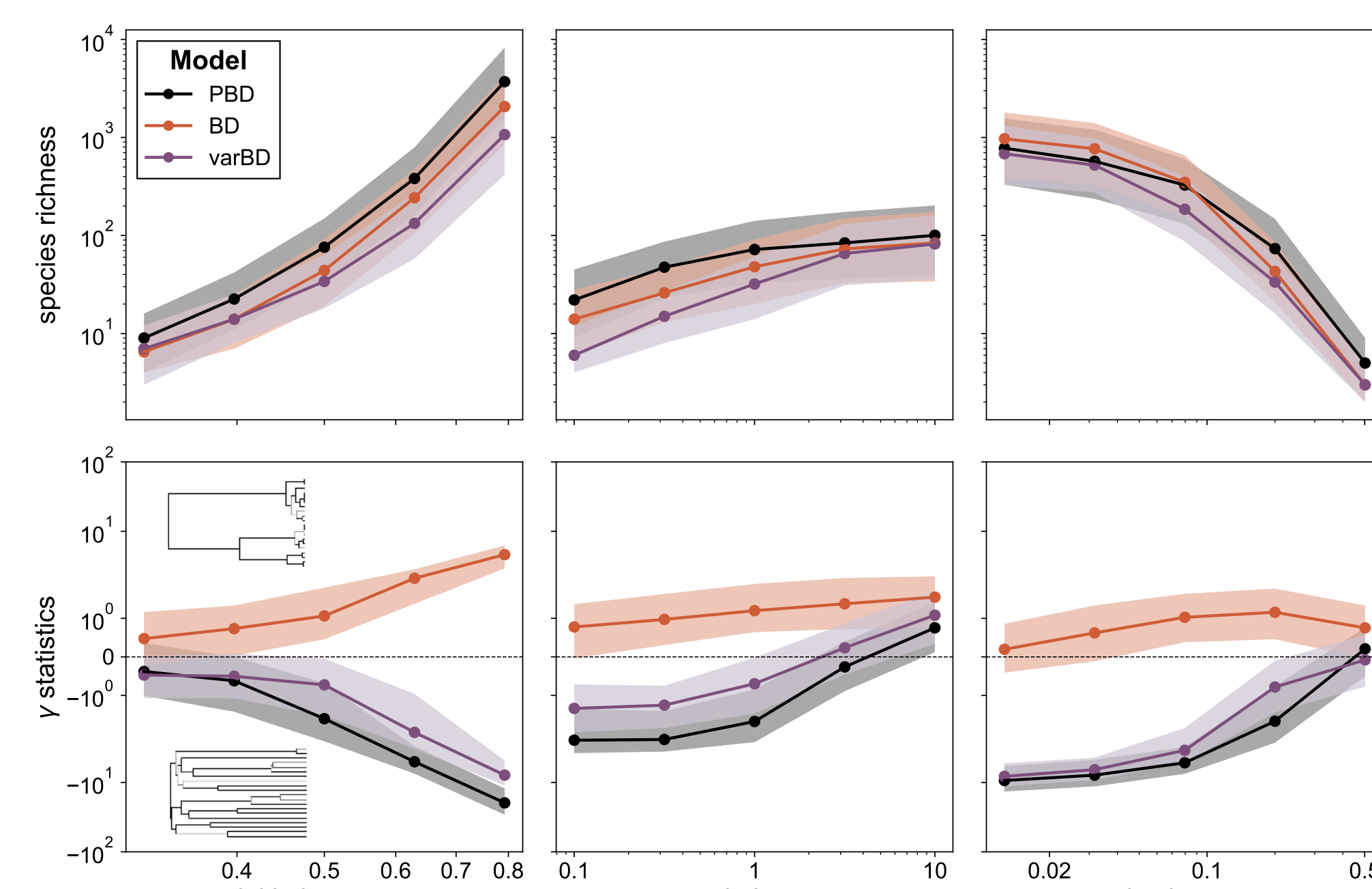


Figure 3. Statistics of trees generated under the PBD process and its equivalent (constant BD and time dependant varBD) BD processes (by row: species richness, γ shape index), for varying initiation, completion and extinction rates.

The completion rate influences the decay of the equivalent birth rate close to the present

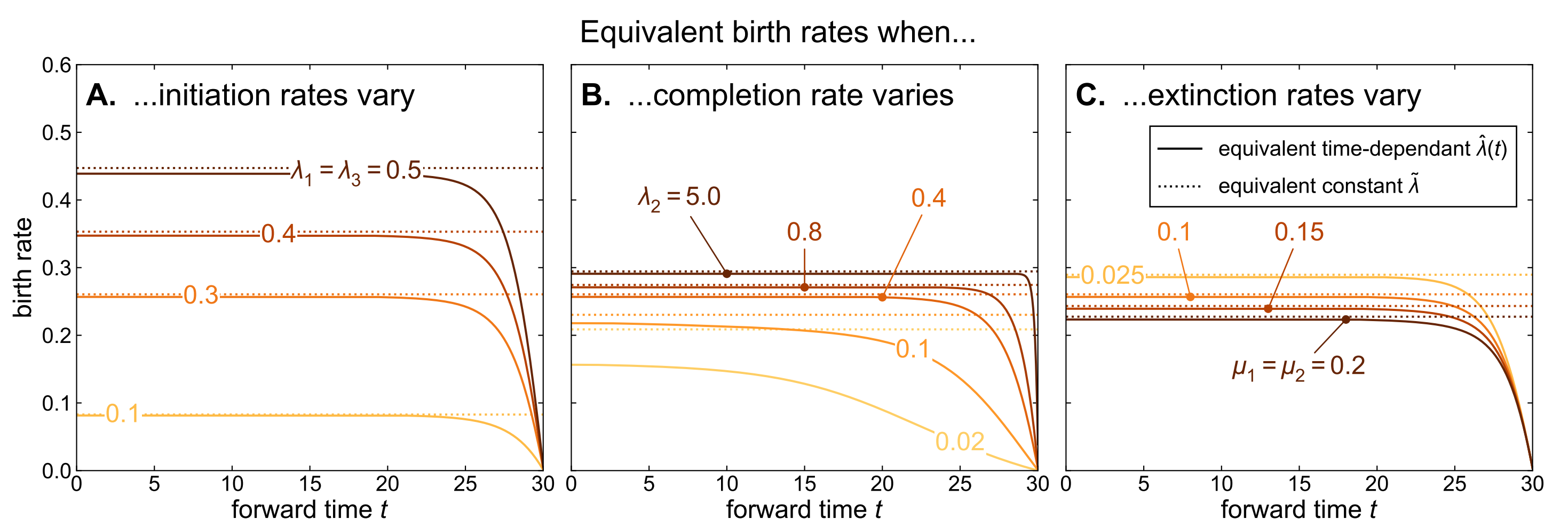


Figure 4. Influence of the parameters of the PBD process on equivalent birth rates.

The birth rate is least affected by the completion rate

With $b := \lambda_1 = \lambda_3$ the initiation rate and $e := \mu_1 = \mu_2$ the extinction rate, we define (\bullet being b, λ_2 or e):

$$\text{relative influence}(\bullet) = \frac{\left| \frac{\partial \tilde{\lambda}}{\partial \bullet} \right|}{\left| \frac{\partial \tilde{\lambda}}{\partial b} \right| + \left| \frac{\partial \tilde{\lambda}}{\partial \lambda_2} \right| + \left| \frac{\partial \tilde{\lambda}}{\partial e} \right|}$$

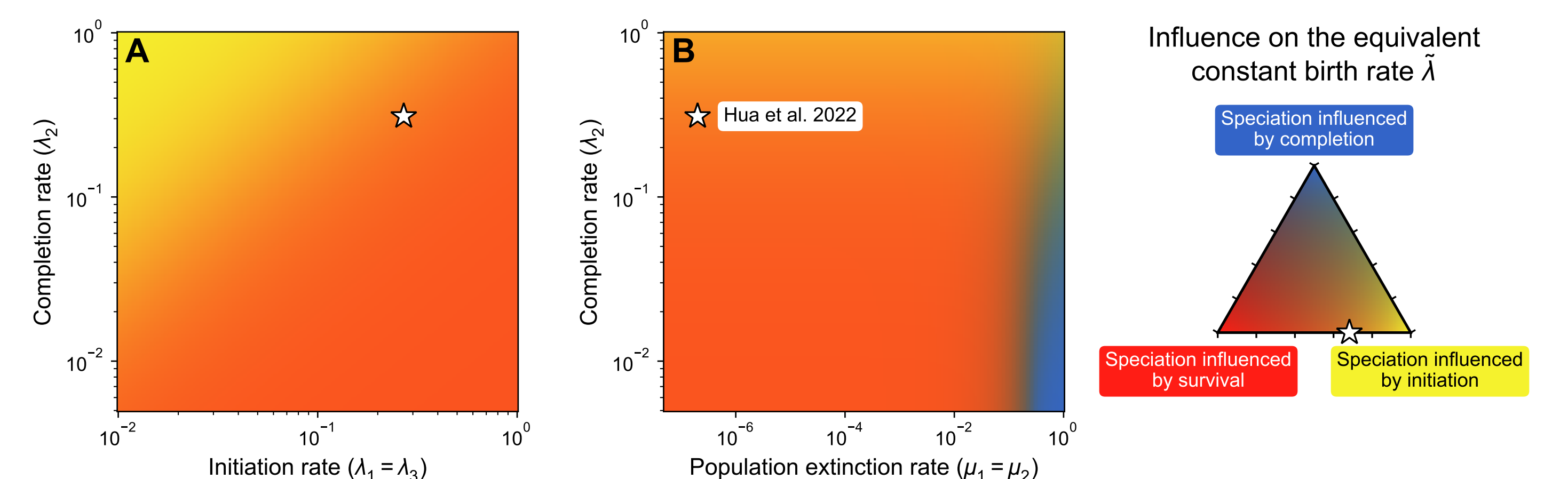
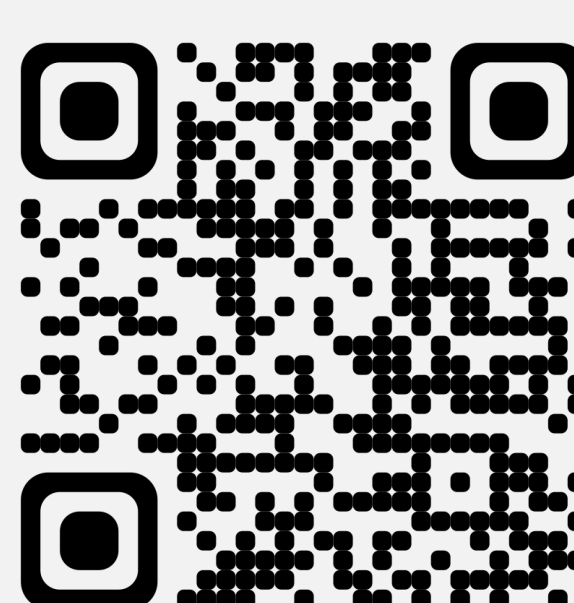


Figure 5. Relative influence of the parameters of the PBD model on the equivalent constant birth rate, with the values fitted on the phylogeny of Australian Rainbow Skinks in ref.³ Image: *Carlia rostralis*, © Graham Winterlood, iNaturalist. CC BY-SA.

Conclusion



See our publication⁴.

- Speciation takes time and the PBD process allows to take this into account.
- The PBD process can be approached with BD process with equivalent rates.
- The completion rate influences the decay of birth rate close to the present but less in the past.
- Speciation initiation and population survival play a larger role than the time it takes for speciation to complete to explain speciation rates.

References ¹Morlon et al., *Annu Rev Ecol Evol Syst* **55**, 1–21 (2024). • ²Etienne et al., *Syst Biol* **61**, 204–213 (2012). • ³Hua et al., *Syst Biol* **71**, 1362–1377 (2022). • ⁴Veron et al., *Philos Trans R Soc B Biol Sci* **380**, 20230317 (2025). •