

# Diversification slowdowns: can we distinguish diversity-dependence and time-dependence?

Théo Pannetier<sup>1,2</sup>, César Martinez<sup>3</sup>, Lynsey Bunnefeld<sup>2</sup>, Rampal S. Etienne<sup>1</sup>

<sup>1</sup> Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, the Netherlands

<sup>2</sup> Biological & Environmental Sciences, University of Stirling, Scotland

<sup>3</sup> Center for Environmental Economics – Montpellier (CEE-M), France

## Background:

Empirical phylogenies often display a pattern of lineage accumulation that seems to slow down toward the present, suggesting that **diversification within a clade slows down** over time. This is classically interpreted as the result of long-term ecological dynamics, although other explanations have been invoked. Under this scenario, speciation is promoted by free **niche availability**, causing a **decline of speciation rates** as species accumulate in the clade. The central feature of this model is that diversification is controlled by species diversity. Here, we explore whether simulated trees produced under a **diversity-dependent process** can be distinguished from trees simulated under a **time-dependent process**, that show on average an equivalent decline of speciation rate over time.

## Diversity-dependent diversification (DD)

*Adapted from the population biology density-dependent model*

**Speciation rate**  $\lambda_n = \max\left(0, \lambda_0 \left(1 - \frac{n}{K}\right)\right)$

**Extinction rate**  $\mu = \mu_0$

## Time-dependent diversification (TD)

*A 'mimic' of the first model, built to be as close as possible*

**Speciation rate**  $\lambda_t = \mu_0 + \frac{(E(N_{DD}))'(t)}{E(N_{DD})(t)}$

**Extinction rate**  $\mu = \mu_0$

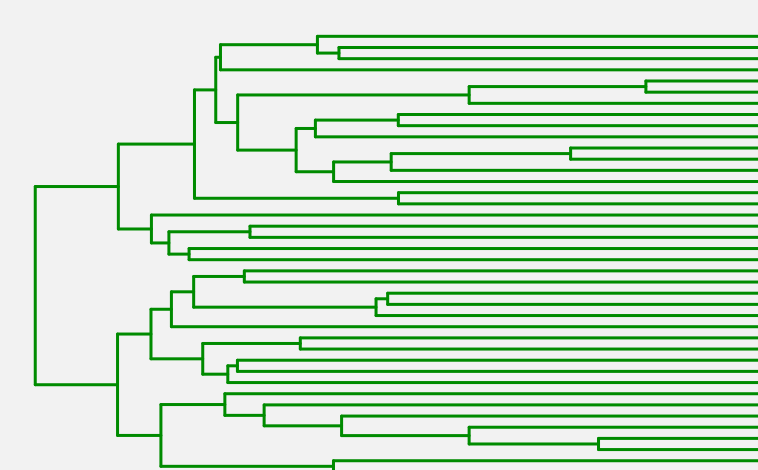
NB : both rates are per-capita

## Simulations

1,000 trees were simulated under variable extinction levels and age (15 Ma here)

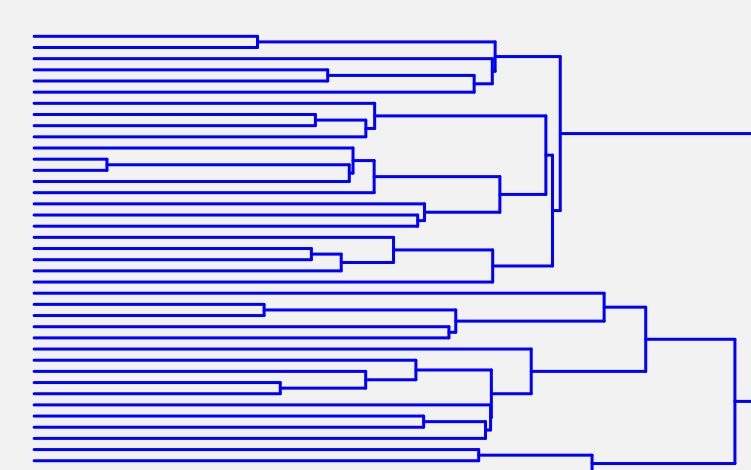
Both models yield very similar trees, but DD tree size distribution is much narrower

No extinction ( $\mu_0 = 0$ )



$$\bar{N} = 39.0$$

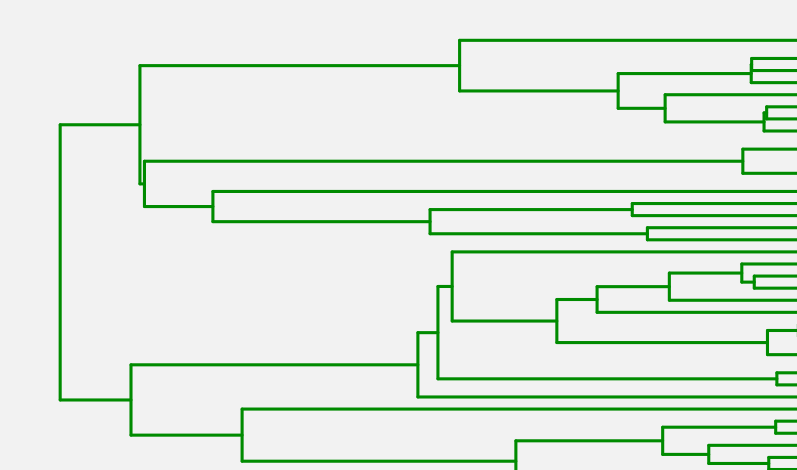
$$\sigma_N = 0.12$$



$$\bar{N} = 37.921$$

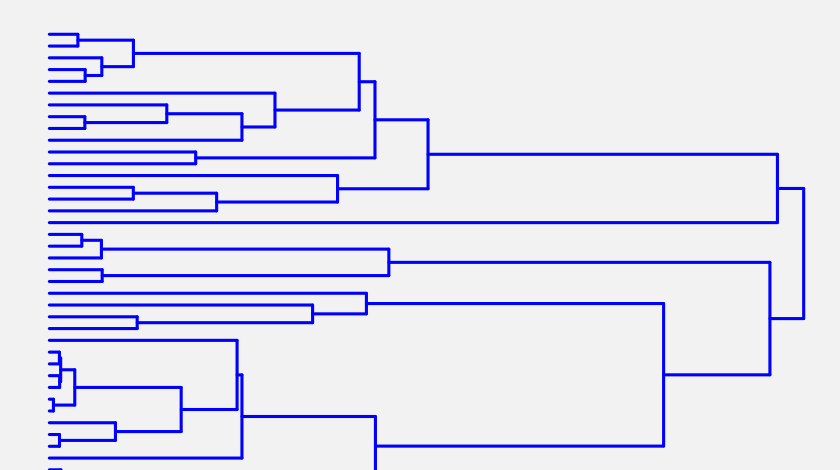
$$\sigma_N = 26.107$$

With extinction ( $\mu_0 = 0.4$ )



$$\bar{N} = 36.6$$

$$\sigma_N = 6.86$$



$$\bar{N} = 60.454$$

$$\sigma_N = 42.620$$

## Model selection

### Akaike information criterion

We fitted both models to the simulated trees using likelihood methods

DD is preferred in both cases. This is due to the narrower tree size distribution, making any individual tree more likely under DD.

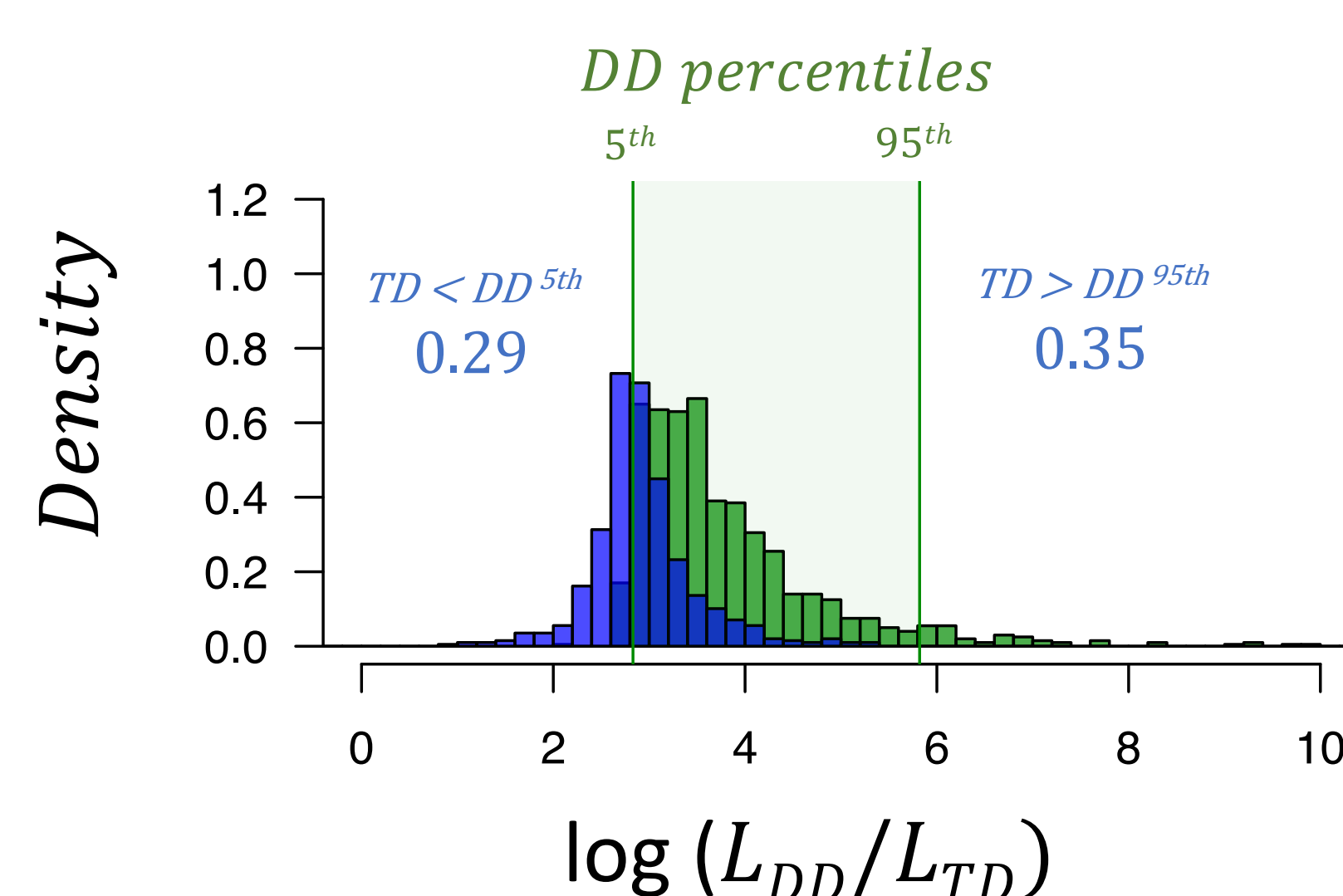
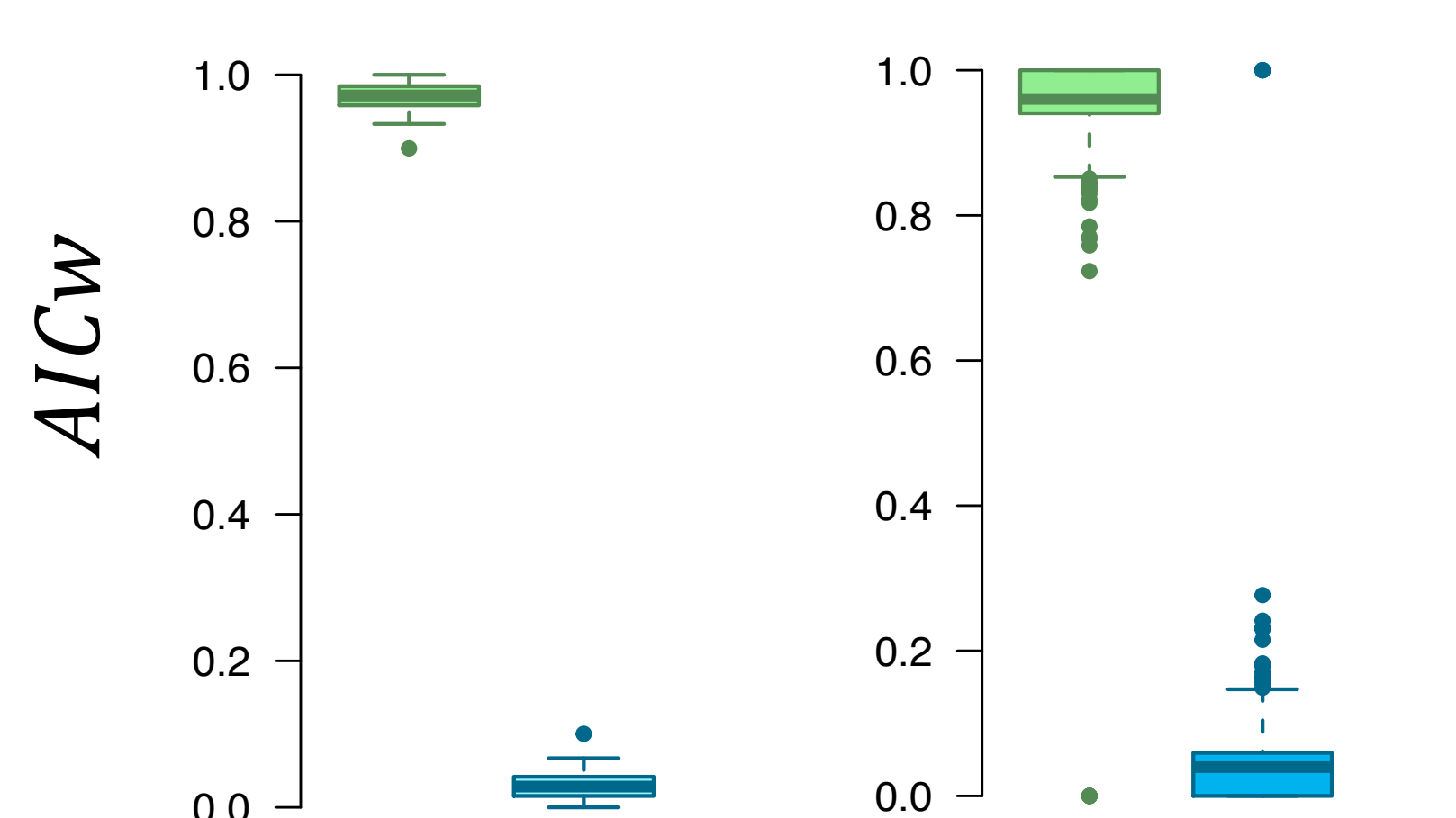
### Bootstrap likelihood ratio test

We looked into possible differences in the fit of DD relative to TD

Models are best distinguished for older trees under a pure birth process (no extinction).

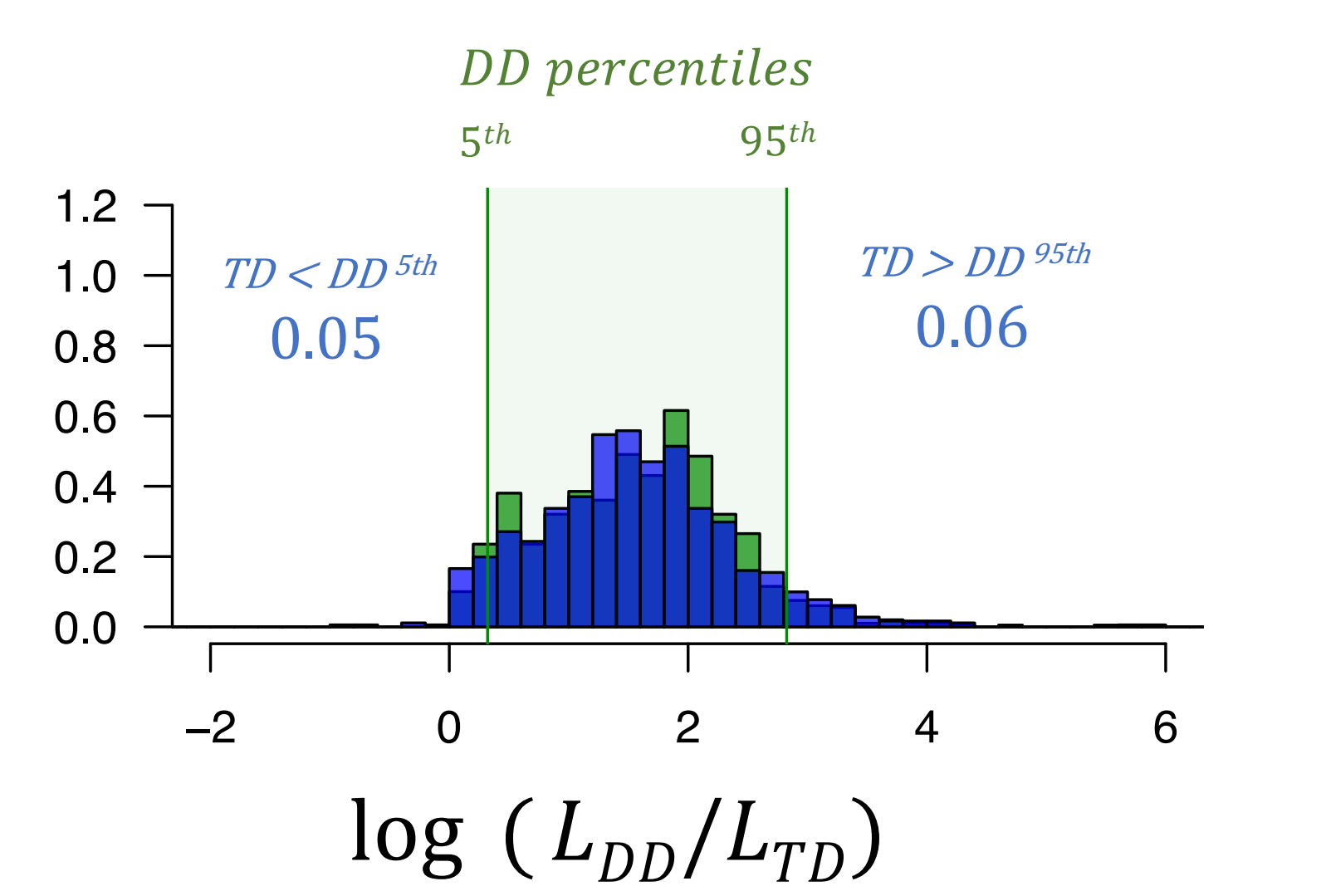
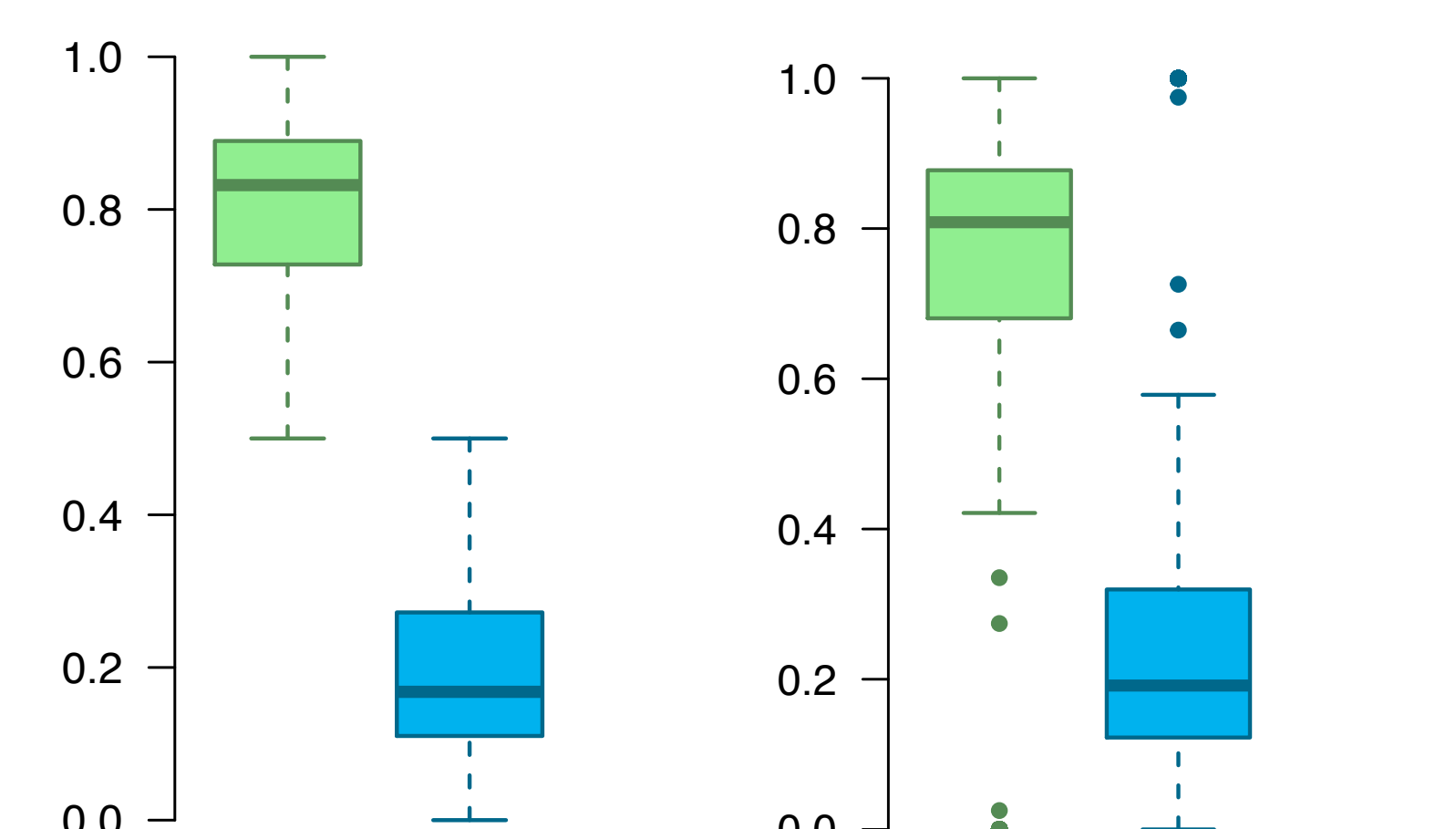
*True model = DD*

*True model = TD*



*True model = DD*

*True model = TD*



## Conclusions:

Time-dependent and diversity-dependent diversification can produce very similar phylogenetic patterns, and the diversity-dependent model often overfits the data.

**Comparing relative likelihood rather than absolute values increases the statistical power of the analysis**, but the power is still unsatisfactory. A development might be to use metrics that capture more finely the distribution of branch lengths, but at the moment, it is not possible to attribute the observed decline in accumulation of species to either intrinsic or extrinsic processes solely on phylogenetic information.