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GELIFES
Groningen Institute for Evolutionary Life Sciences

UNIVERSITY of STIRLING

Time-dependent / Diversity-dependent diversification:

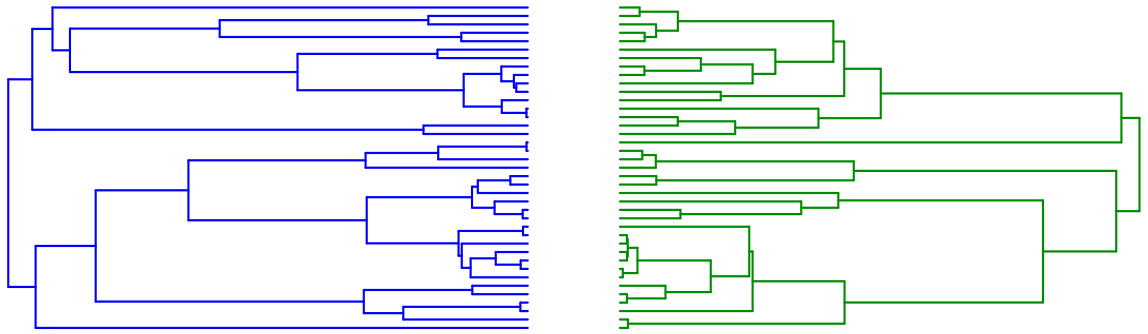
What's the difference?

Théo Pannetier

Supervisors

Rampal S. Etienne

Lynsey Bunnefeld



Macroevolution

STOCHASTIC MODELS OF PHYLOGENY AND THE EVOLUTION OF DIVERSITY[1]

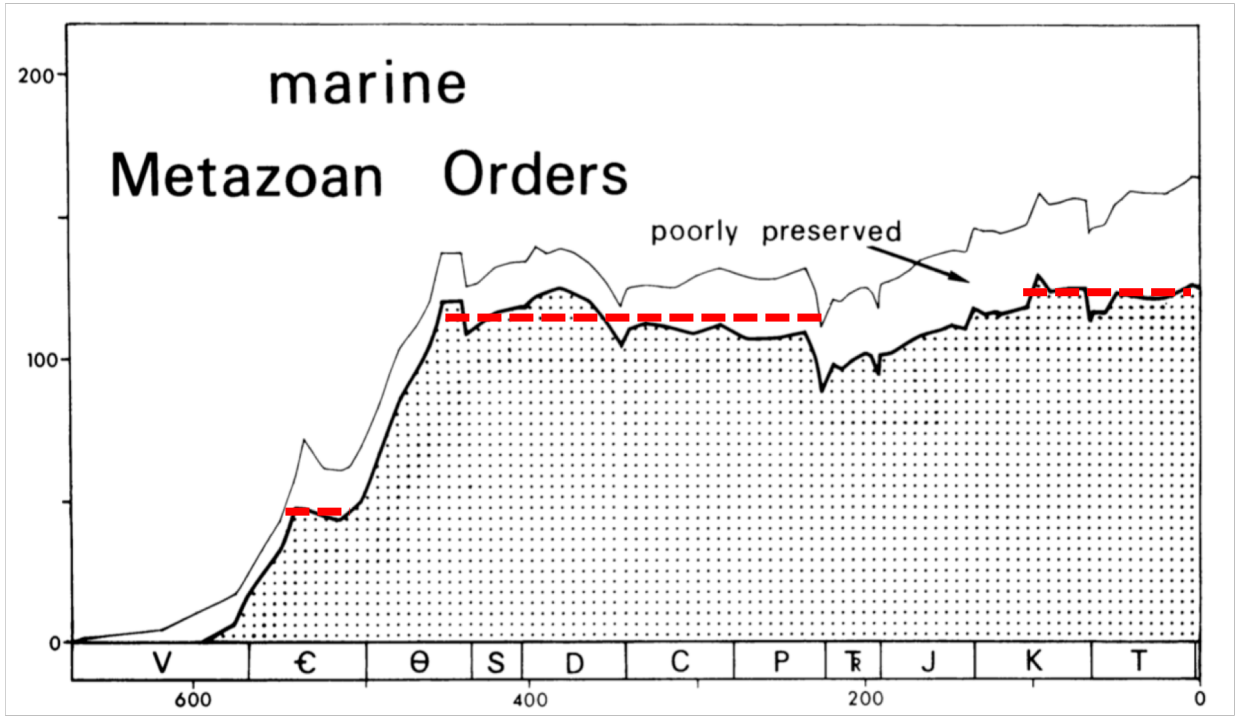
DAVID M. RAUP, STEPHEN JAY GOULD, THOMAS J. M. SCHOPF, AND DANIEL S. SIMBERLOFF

This is the first in a projected series of papers that might bear the general title "nomothetic paleontology." "Nomothetic" is a term used by psychologists, historians, and philosophers to designate an approach to historical science favoring the study of "cases and events as universals, with a view to formulating general laws." The conventional approach, on the other hand, is termed "idiographic": "the study of cases or events as individual units, with a view to understanding each one separately" (Random House Dictionary).

Macroevolution: formulating general laws regarding evolution on large time-scales

Fossil patterns

‘Nomothetic’ paleontology: what does the fossil record tell us about rules of evolution ?



Sepkoski 1978

‘Plateauing’ diversity and rebounds after mass extinctions

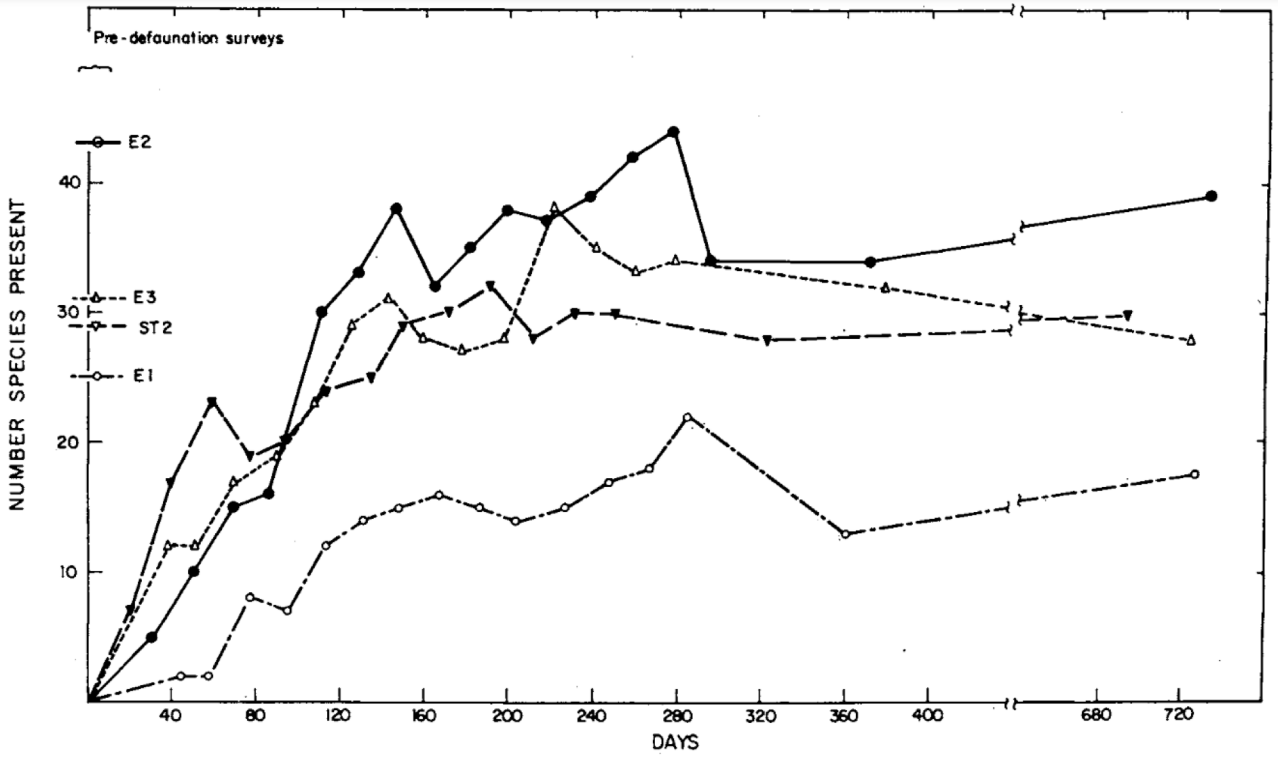
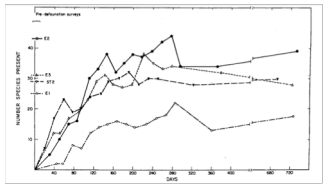
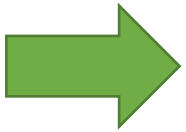


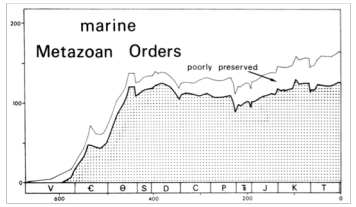
FIG. 1. The colonization curves of four small mangrove islands in the lower Florida Keys whose entire faunas, consisting almost solely of arthropods, were exterminated by methyl bromide fumigation. The figures shown are the estimated numbers of species present, which are the actual numbers seen plus a small fraction not seen but inferred to be present by the criteria utilized by Simberloff and Wilson (1969) and Simberloff (1969). The number of species in an inverse function of the distance of the island to the nearest source of immigrants. This effect was evident in the predefaunation censuses and was preserved when the faunas regained equilibrium after defaunation. Thus, the near island E2 has the most species, the distant island E1 the fewest, and the intermediate islands E3 and ST2 intermediate numbers of species.

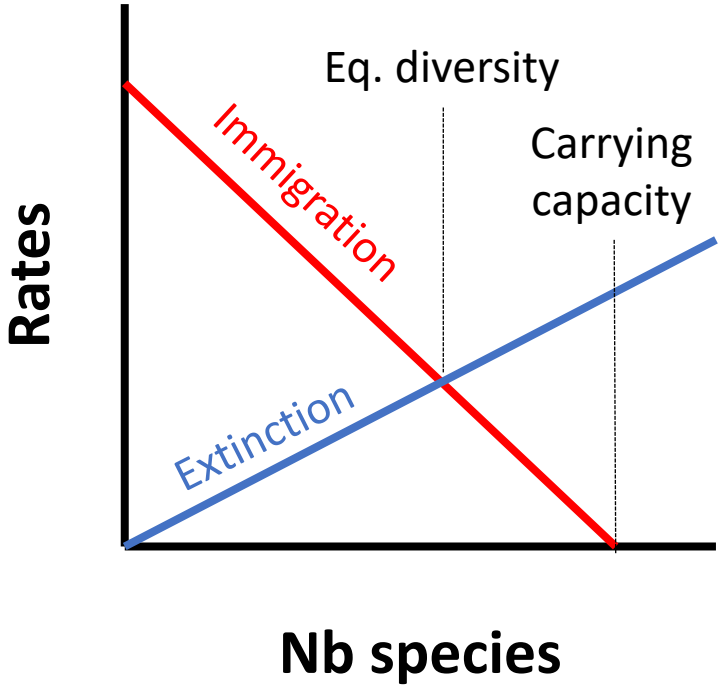
FIG. 2. *Upper:* Island E1, the second smallest island in the experimental series. *Lower:* Island E9, the largest island in the experimental series; note also the presence of supratidal mud.

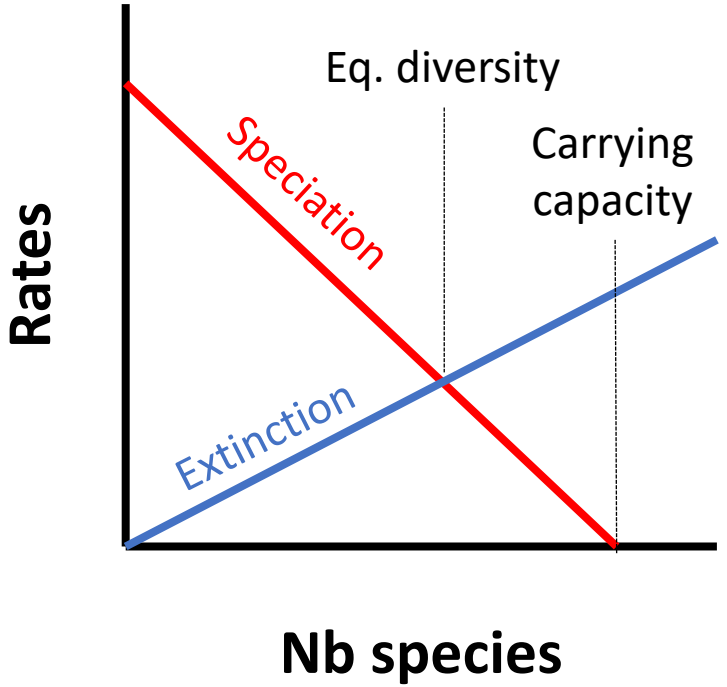
From island biogeography to diversity-dependent diversification



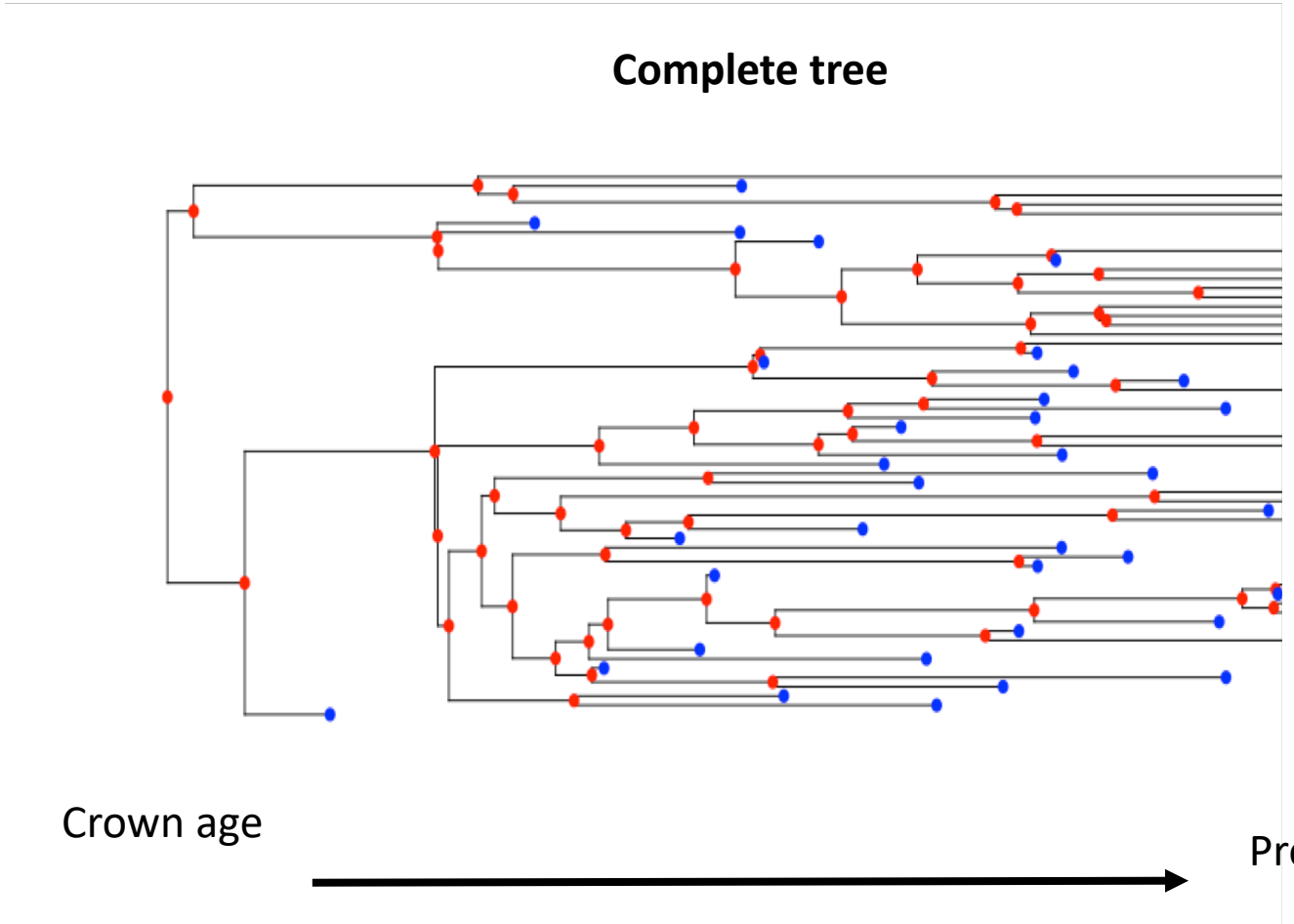








Reconstructed molecular phylogenies

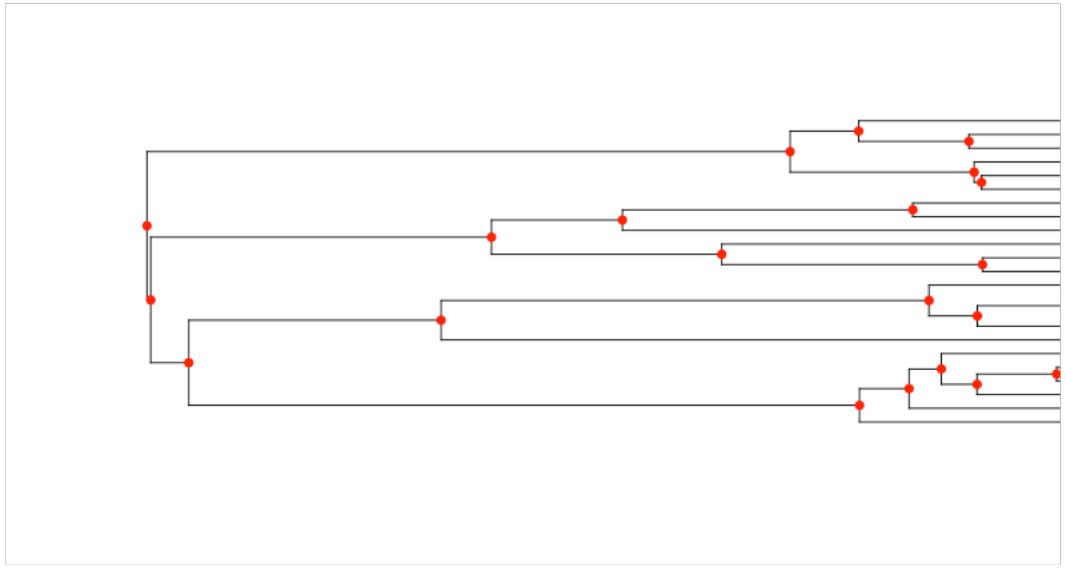


Birth rate (b) = Speciation rate (λ_t)

Death rate (d) = Extinction rate (μ_t)

Reconstructed molecular phylogenies

Reconstructed tree



Crown age → Present

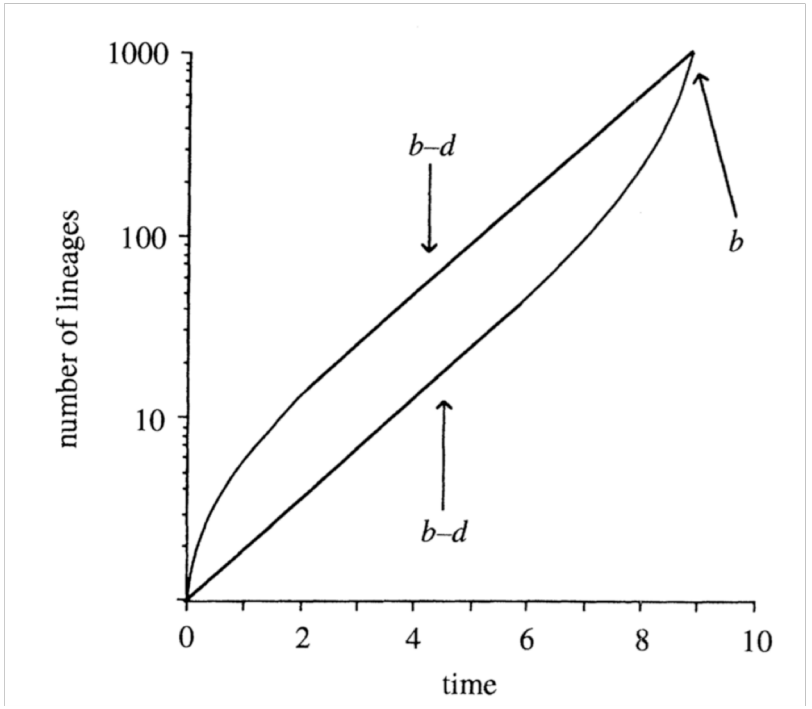
Birth rate (b) = Speciation rate (λ_t)

Death rate (d) = Extinction rate (μ_t)

The reconstructed evolutionary process

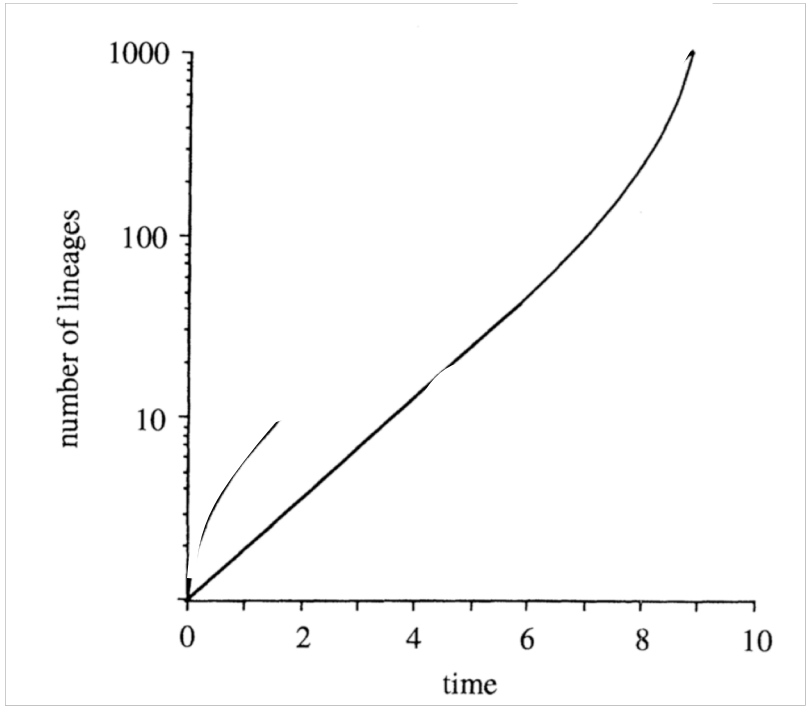
SEAN NEE, ROBERT M. MAY AND PAUL H. HARVEY

A.F.R.C. Unit of Ecology and Behaviour, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.



Empirical patterns: a diversification slowdown ?

Constant-rate diversification
Expectation



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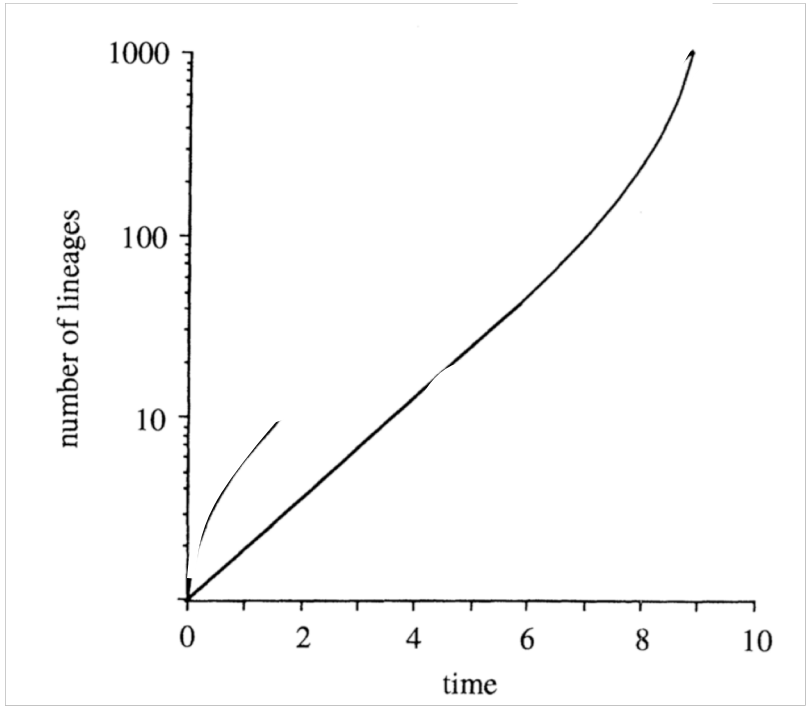
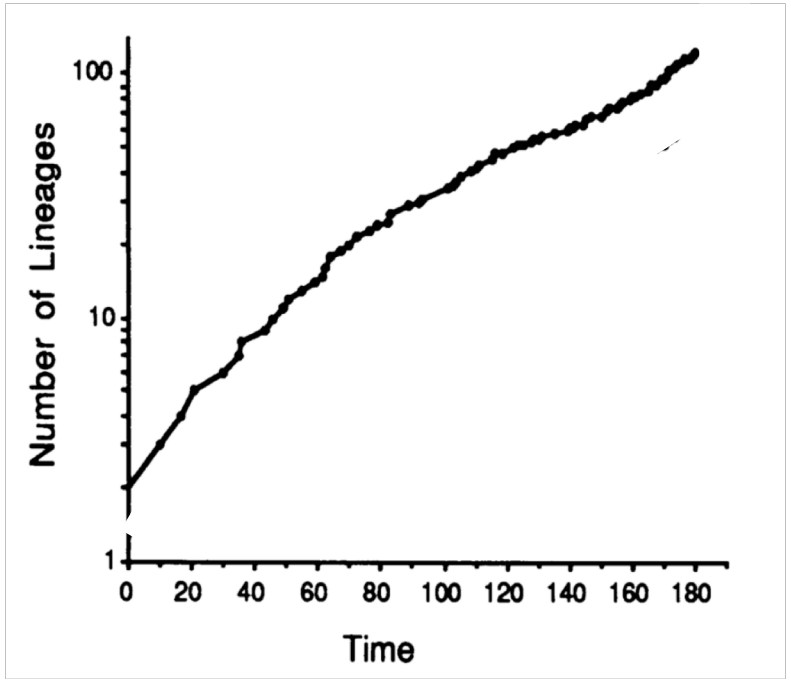


[Empirical]
Reality

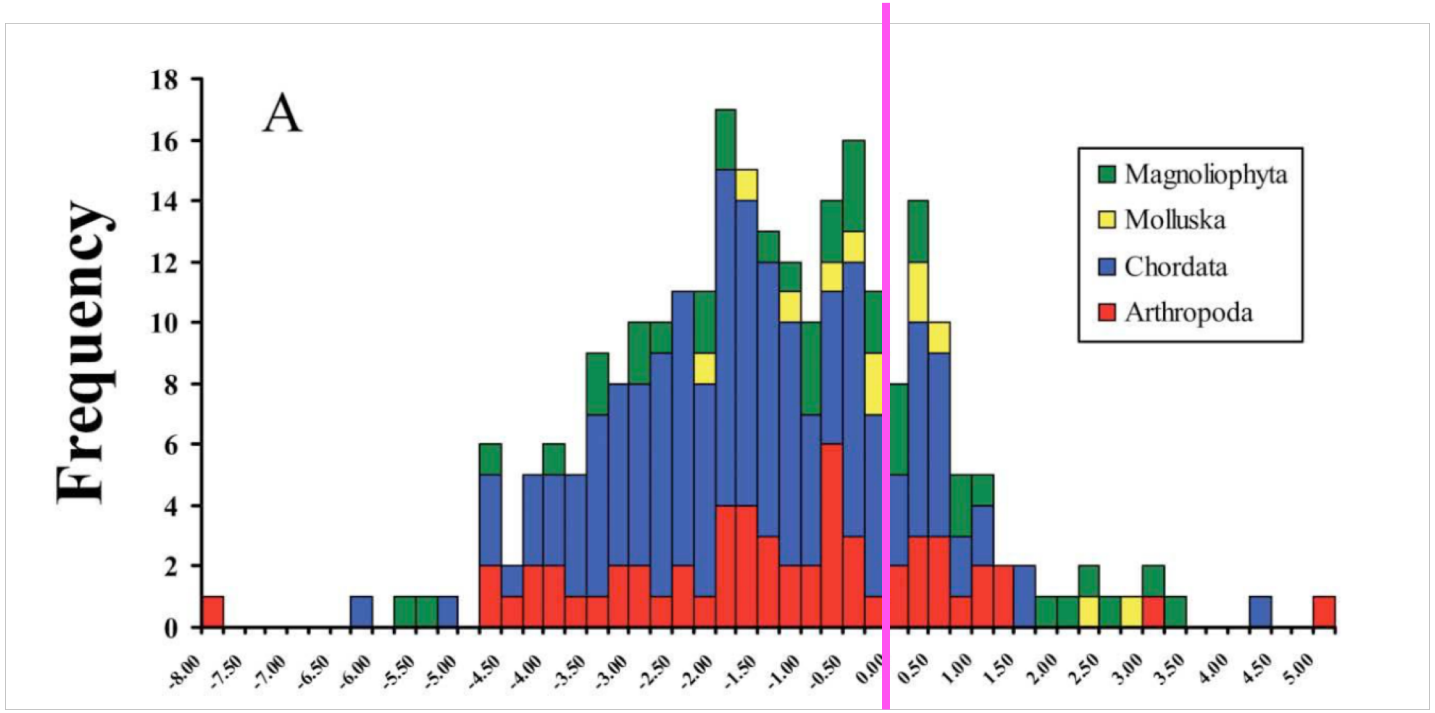


from Nee et al. 1992

Empirical patterns: a diversification slowdown ?

A widespread pattern:

Phillimore & Price (2008) – 13/23 bird genera
McPeek (2008) ≈ 2/3 of phylogenies tested



Gamma

Empirical patterns: a diversification slowdown ?

Biological interpretations

Diversity-dependence - diversification slowing down as niche space available to the clade fills up

Age-dependence - clades become competitively 'obsolescent'

Environment-dependence - Fast diversification driven by environmental factors in the past

Methodological interpretations

Incomplete sampling – missing taxa in the phylogeny

Protracted speciation – Failure to recognize recent speciation events

→ How to distinguish diversity-dependence from other hypotheses?

Question

Can diversity-dependence be distinguished from similar diversity-**independent** models?

Diversity-dependent speciation

$$\lambda = \lambda_0 \left(1 - \frac{n}{K'}\right)$$

Question

Can diversity-dependence be distinguished from similar diversity-**independent** models?

Diversity-dependent speciation

$$\lambda = \lambda_0 \left(1 - \frac{n}{K}\right)$$

Time-dependent decline

$$\lambda = \lambda_0 \left(1 - \frac{t}{K}\right)$$

e.g. Rabosky & Lovette (2008)

Formulation of the time-dependent model

Looking for a time-dependent (TD) model as close as possible to diversity-dependence (DD)

$$E(N_{TD})(t) = E(N_{DD})(t)$$

$$\lambda(t) = \mu_0 + \frac{\left(E(N_{DD})\right)'(t)}{E(N_{DD})(t)}$$

César Martinez

Now at Center for Environmental Economics - Montpellier

Simulations

DD $\{\lambda_0, \mu_0, K\}$ $\lambda = \lambda_0 \left(1 - \frac{n}{K}\right)$

TD $\{\lambda_0, \mu_0, K\}$ $\lambda = \mu_0 + \frac{\left(E(N_{DD})\right)'(t)}{E(N_{DD})(t)}$

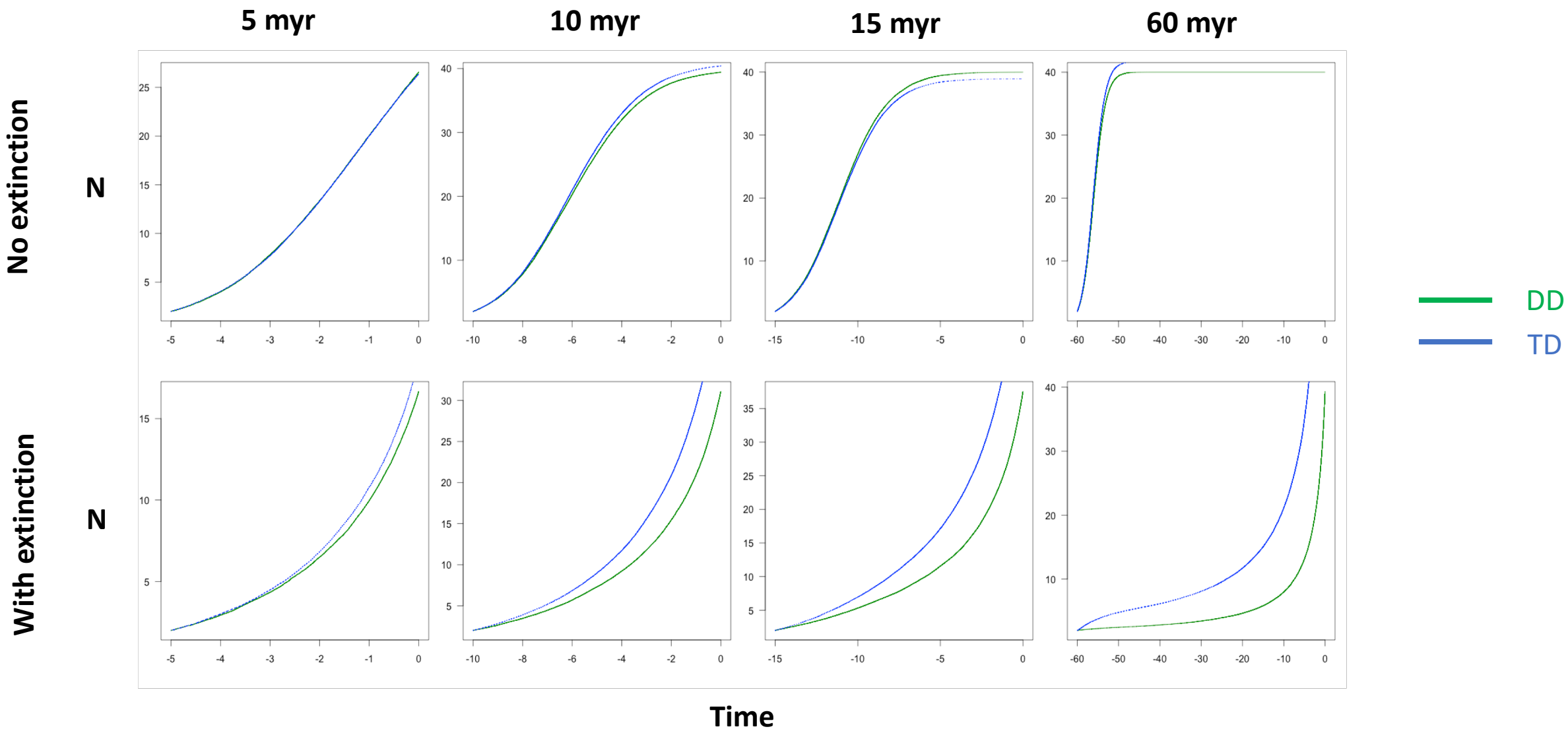
Without / with extinction

$$\mu_0 = \{0 ; 0.4\}$$

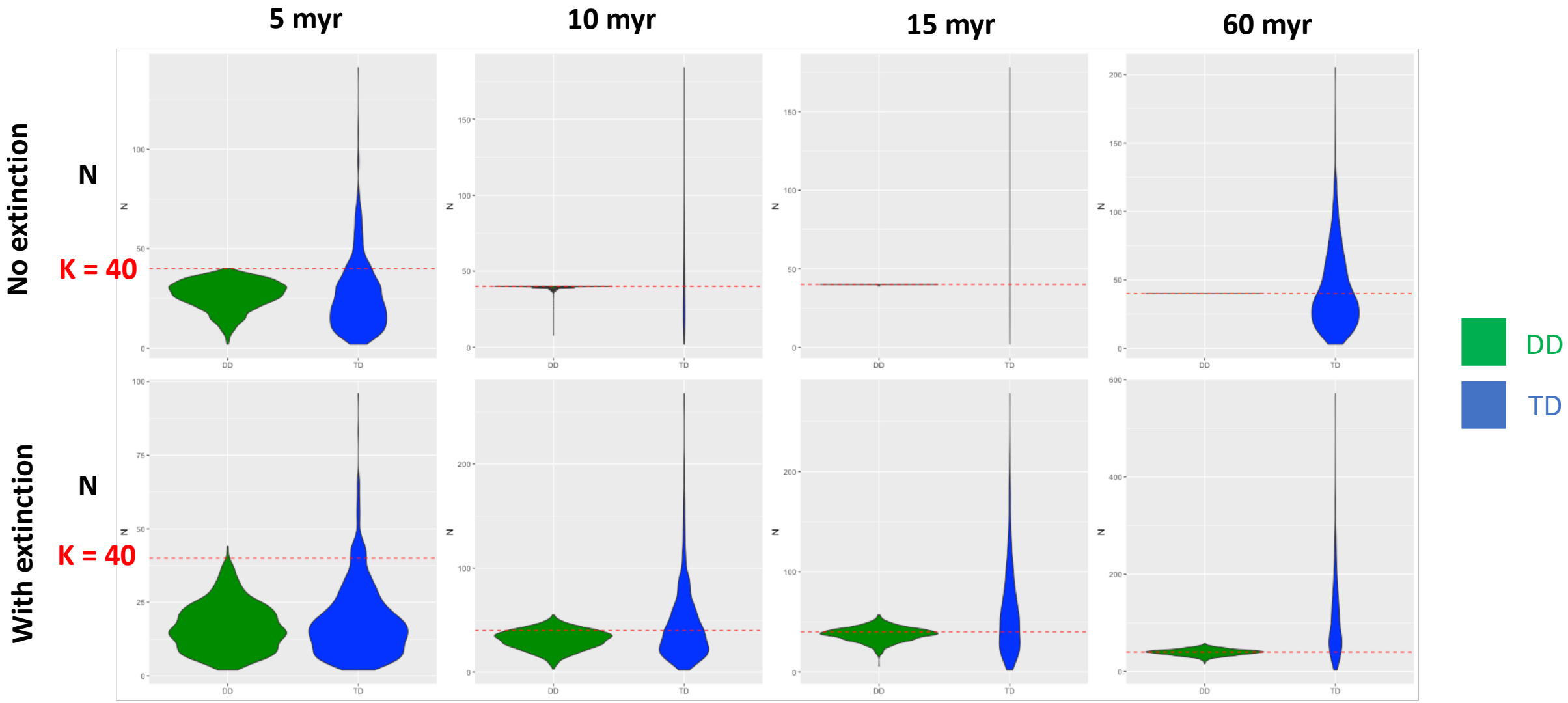
Simulation times

$$Age = \{5 ; 10 ; 15 ; 60\}$$

Simulated trees: lineages-through-time plots



Simulated trees: tree size distribution



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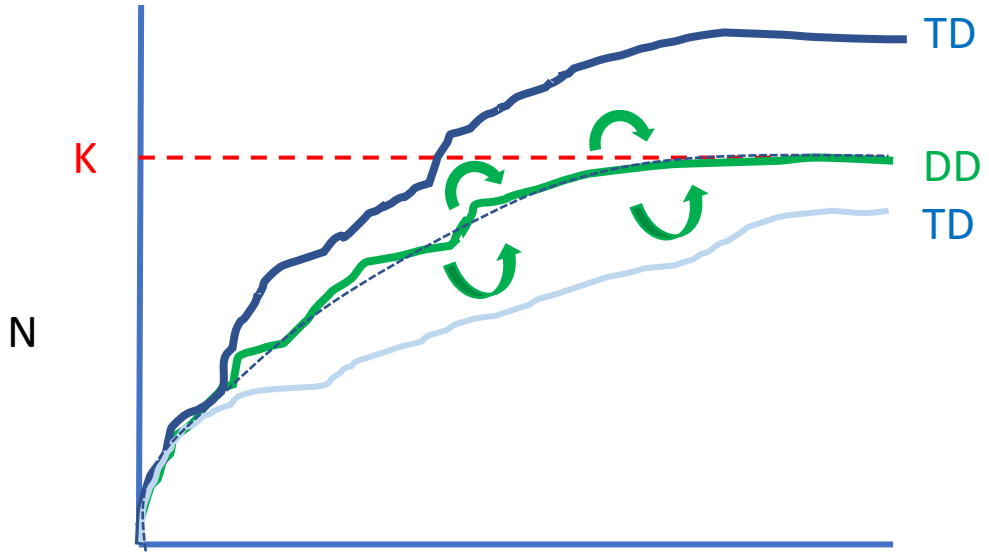
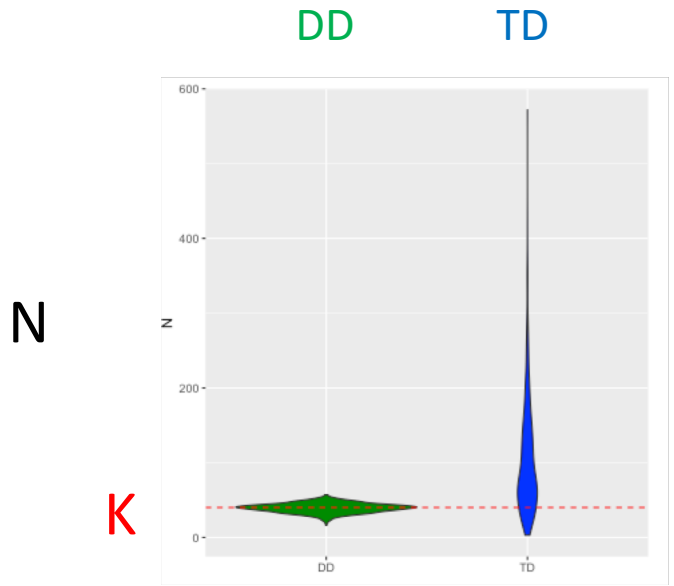


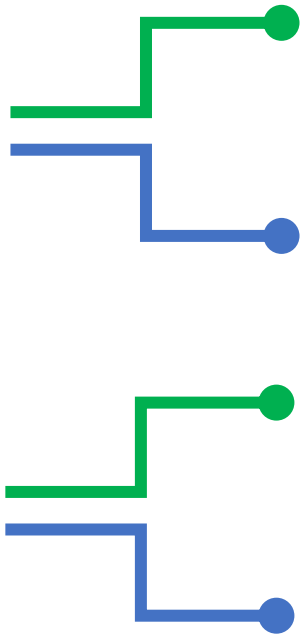


Model comparison

Simulations

DD $\{\lambda_0, \mu_0, K\}$

TD $\{\lambda_0, \mu_0, K\}$



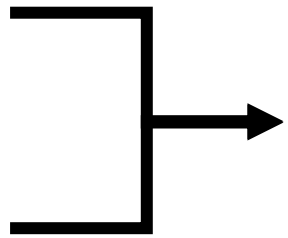
ML optimization

$\mathcal{L}(\mathbf{DD})$

$\mathcal{L}(\mathbf{TD})$

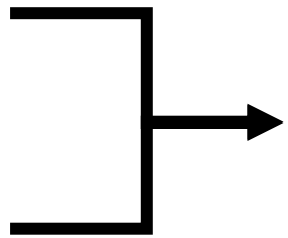
$\mathcal{L}(\mathbf{DD})$

$\mathcal{L}(\mathbf{TD})$



Model selection

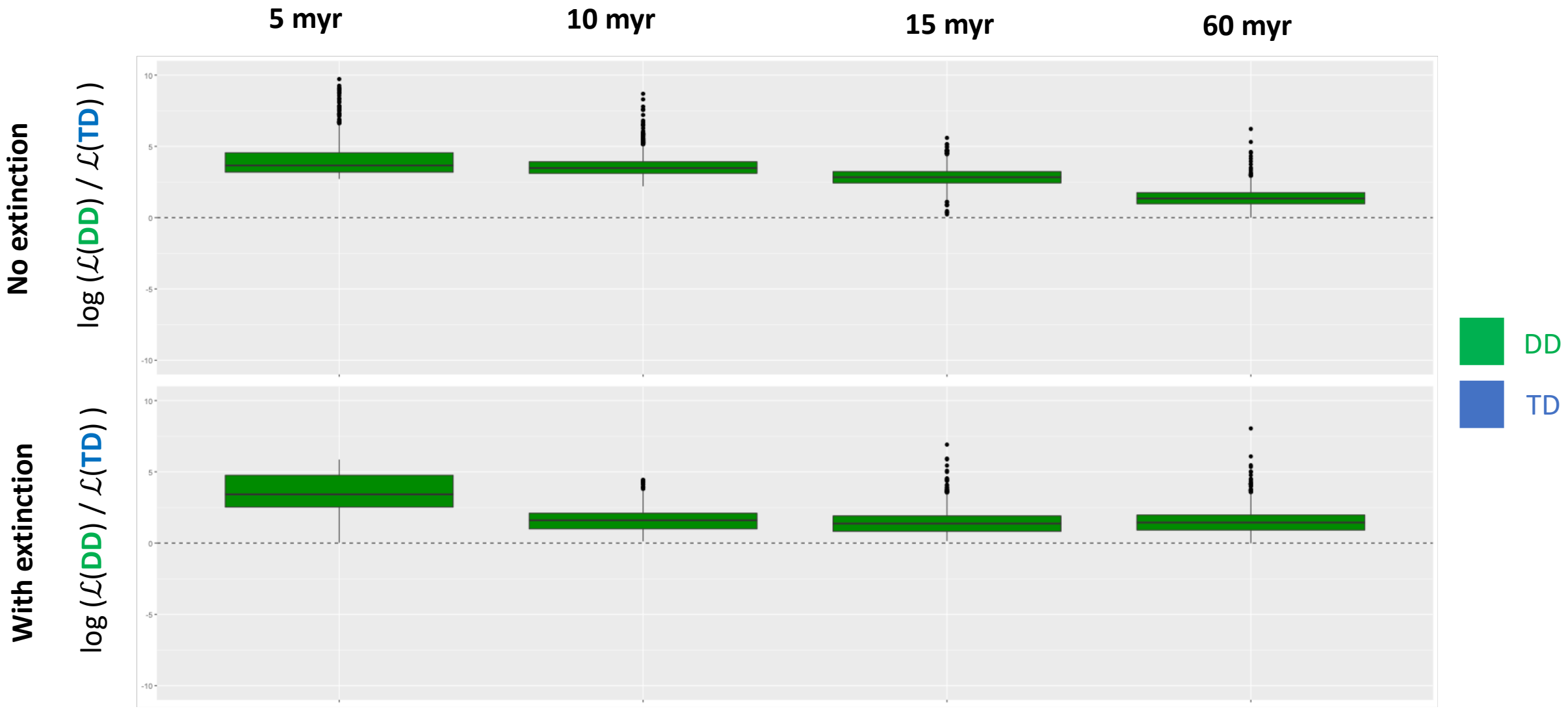
$\log \frac{\mathcal{L}(\mathbf{DD})}{\mathcal{L}(\mathbf{TD})}$



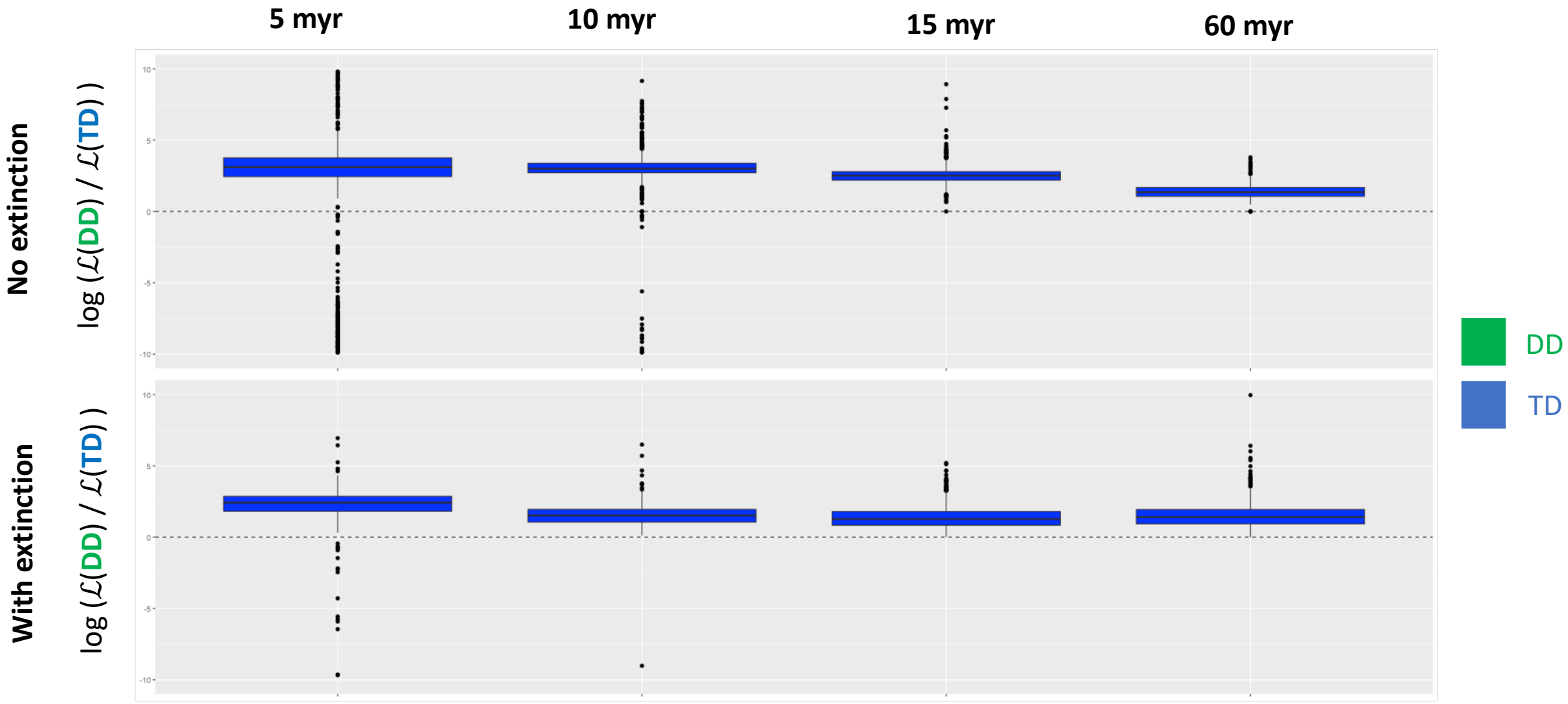
Model selection

$\log \frac{\mathcal{L}(\mathbf{DD})}{\mathcal{L}(\mathbf{TD})}$

Model selection: log-likelihood ratio distribution – DD trees



Model selection: log-likelihood ratio distribution – TD trees



Summary

Can diversity-dependent diversification be distinguished from diversity-independent diversification?

- **AIC/Likelihood ratios** always select DD over TD regardless of which is the true model.

  → DD overfits the data!

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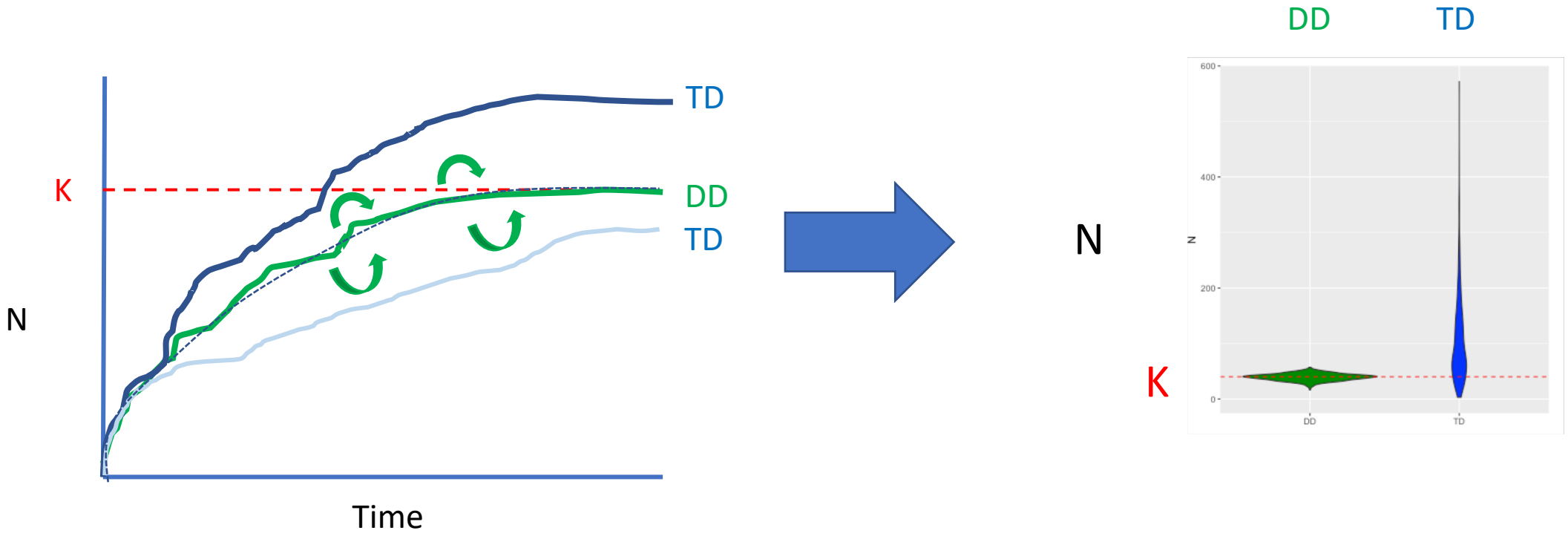

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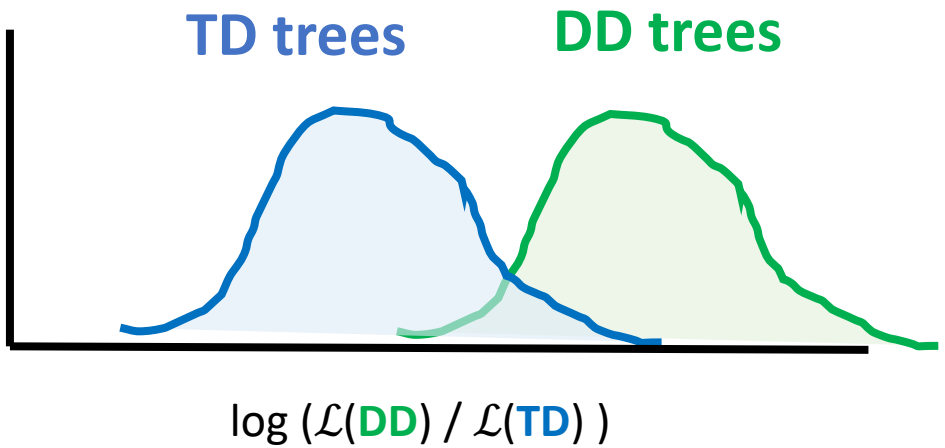
Can diversity-dependent diversification be distinguished from diversity-independent diversification?

Solutions to the overfitting problem ?

- Use the distribution of $\mathcal{L}$(**DD**) / $\mathcal{L}$(**TD**) as a statistic



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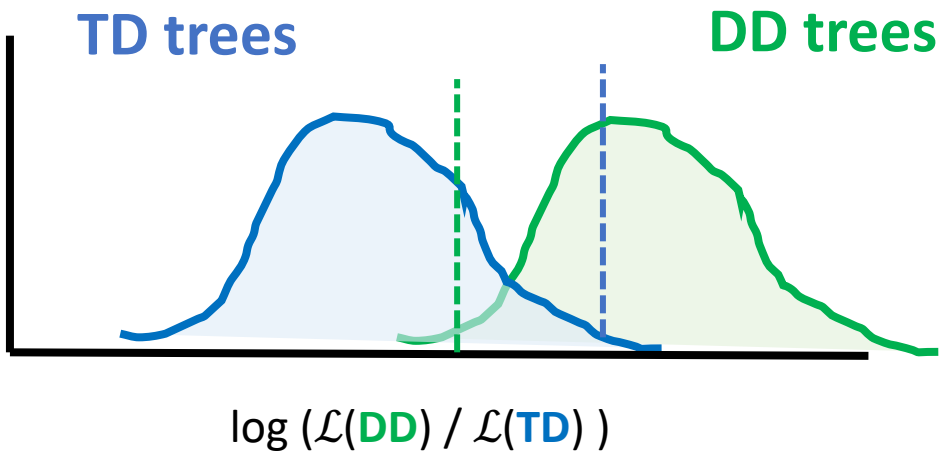
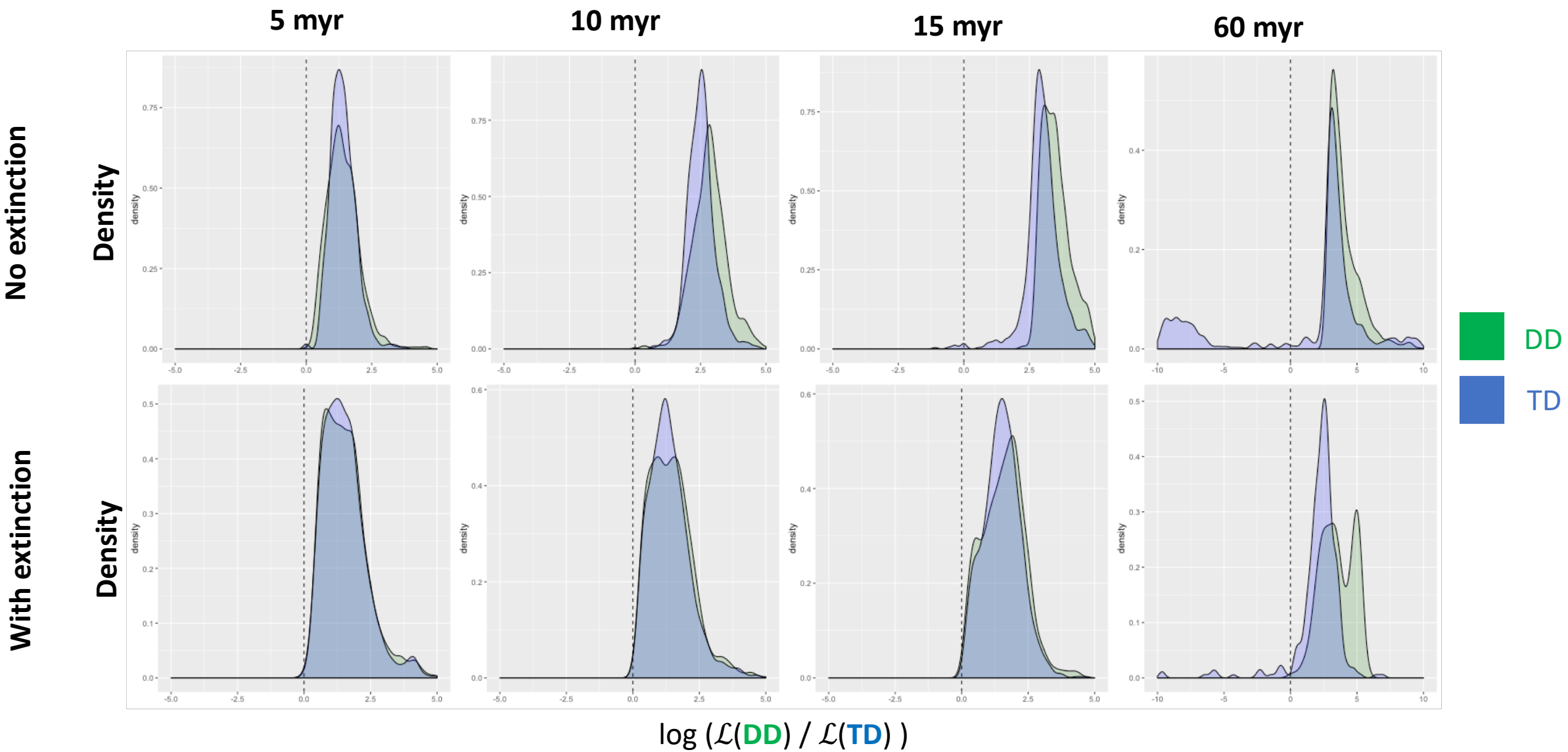


Model selection: log-likelihood ratio distribution



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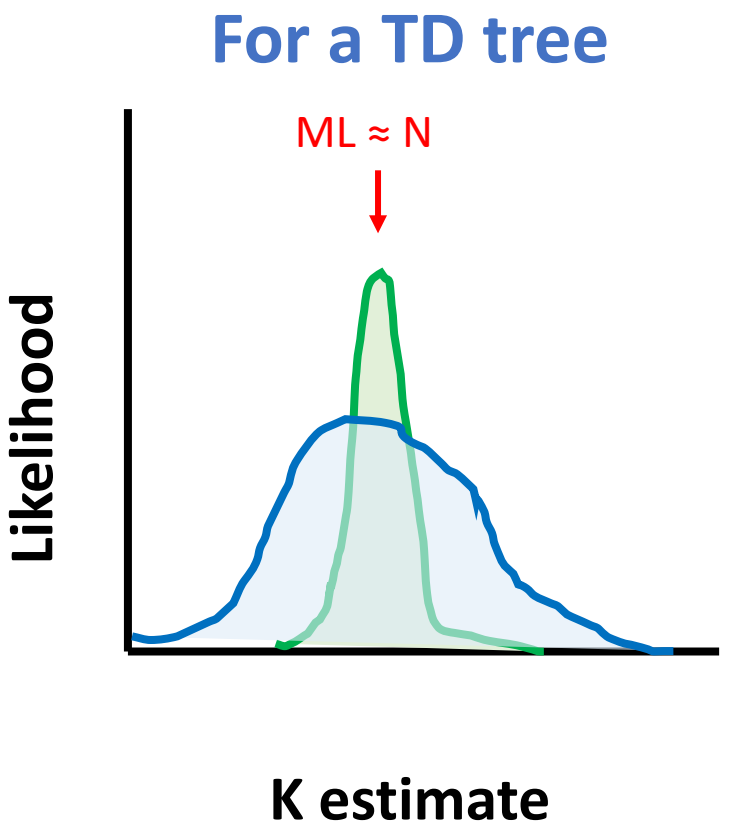
- Use marginalized likelihoods ?



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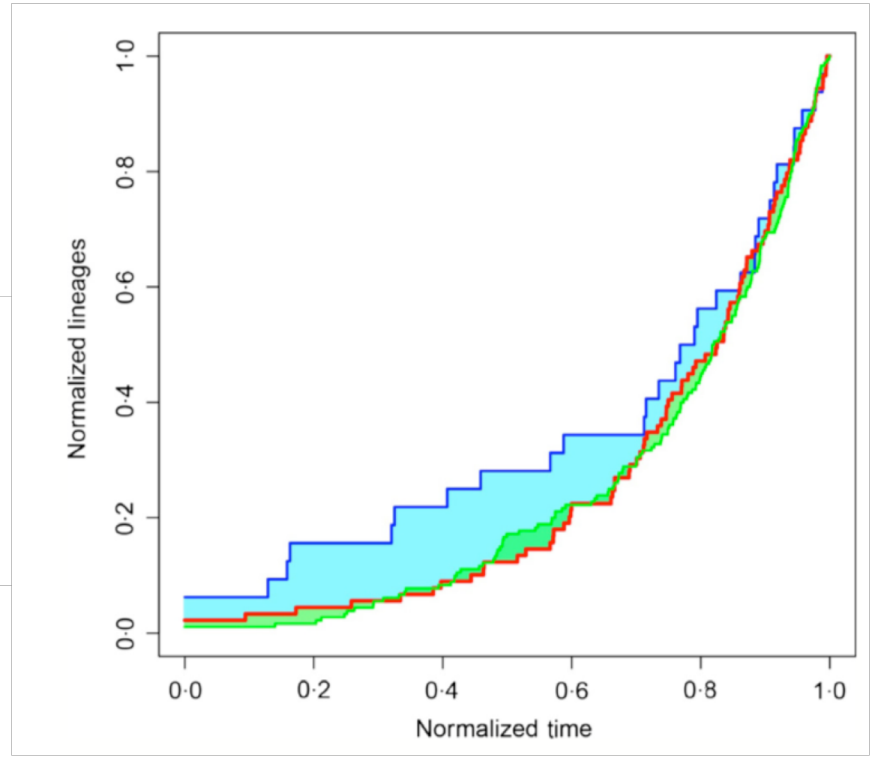
Can diversity-dependent diversification be distinguished from diversity-independent diversification?

Solutions to the overfitting problem ?

- Use the distribution of $\mathcal{L}$(**DD**) / $\mathcal{L}$(**TD**) as a statistic
- Use marginalized likelihoods ?
- Likelihood-free methods e.g. **ABC**

Approximate Bayesian Computation of diversification rates from molecular phylogenies: introducing a new efficient summary statistic, the nLTT

Thijs Janzen[1]*, Sebastian Höhna[2] and Rampal S. Etienne[1]



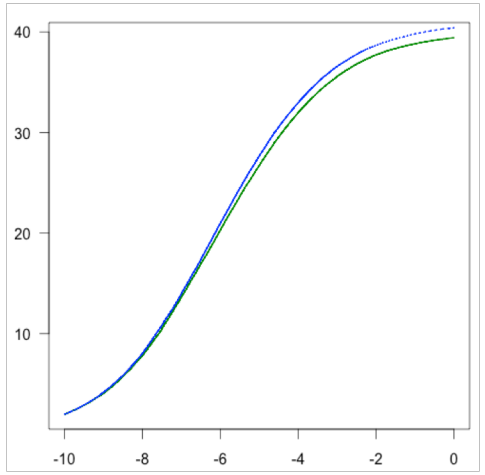
Summary

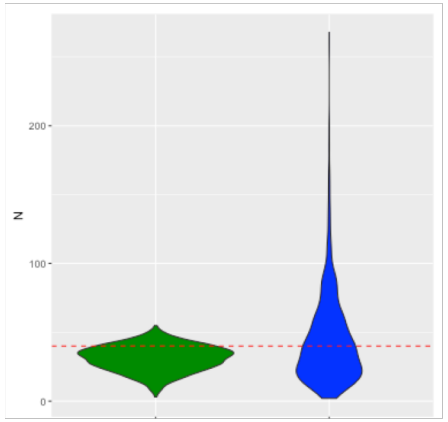
Can diversity-dependent diversification be distinguished from diversity-independent diversification?

Beyond the overfitting problem:

There does not seem to be an imprint of the feedback mechanism of DD on branching patterns

N





→ **Diversity-dependence cannot be reliably inferred from branching patterns alone**

Corroborate branching patterns with predictions for other data, e.g. morphology, range evolution?