The evolutionary potential of “living fossils”

D.J. Bennett, M.D. Sutton and S.T. Turvey

Photo credit: James Field

Who?

Status: Post-doc

Location: Gothenburg, Sweden

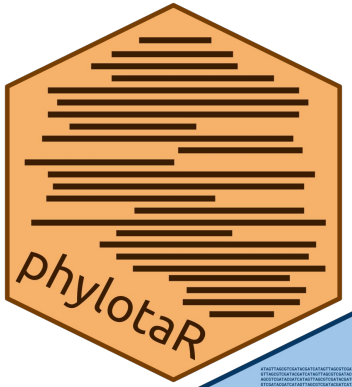
Affiliation(s):

- Antonelli Lab (antonelli-lab.net)
- Gothenburg Global Biodiversity Centre (ggbc.gu.se)

Project: Development of a modular pipeline for generating phylogenetic trees (SUPERSMART now in R *supersmartR*)

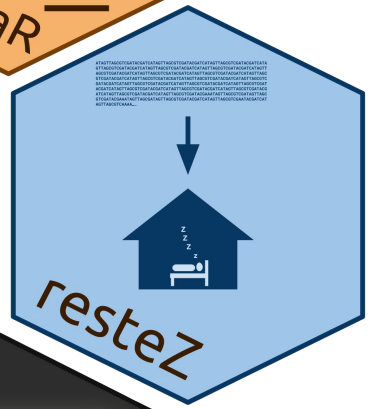
supersmartR

- Modular phylogeny generation pipeline
  - Independent R packages
- See the website: github.com/AntonelliLab/supersmartR



Automated retrieval of orthologous sequence clusters in R

Download and query whole sections of GenBank



Install and launch external command-line programs within R.

PhD Thesis

Title: An appraisal of the “living fossil” concept
Location: London, UK
Years: 2013 - 2017
Key questions:

1. What, if anything, is a living fossil?
2. Is “living fossil” a valid delimiter?
3. What is the evolutionary potential of living fossils?*

Sam Turvey
Institute of Zoology, London

Mark Sutton
Imperial College London

*And what does any of this have to do with conservation biology?

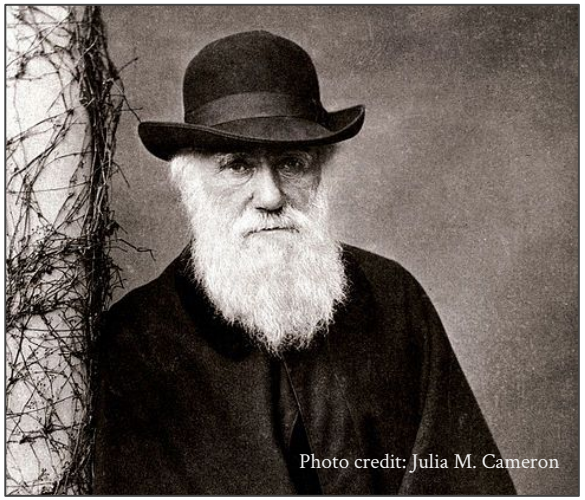
Question I.
What is a living fossil?

Photo credit: James Field

What is a living fossil?

- Nobody knows
  - No strict definition
  - A taxon experiencing little (or no) evolution?
- Coined by Darwin
  - First in 1858 in a letter to Hooker
- Hugely controversial
  - A taxon that has escaped evolution?
  - Reminiscent of *scala naturae*
- Certain taxa are persistently labelled as living fossils

Coelacanth, the most famous "living fossil"



"Species and groups of species, which are called aberrant, and which may fancifully be called **living fossils**, will aid us in forming a picture of the ancient forms of life."

On the Origin of Species, 1859

Discordance

- Range of definitions
  - Lazarus taxon, evolutionary dead-end, phylogenetic relict, bradytelic, evolutionary distinct
- Range of factors
  - Species-poor, primitive features, conserved characteristics, generalist, geographically isolated, surviving for a long time
- Conflicting living fossil examples

Photo credits: U.S. Fish and Wildlife Service, Bernard Spragg, Megan Hansen, Derek Keats, MarAlliance2018

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Photo credits: U.S. Fish and Wildlife Service, Bernard Spragg, Megan Hansen, Derek Keats, MarAlliance2018

A numbers approach

"Living fossils"

Clade	Age (Ma)	Change*	N.
Horseshoe crabs	445	Low	4
Ginkgo	200-300	Low	1
Tuatara	220	Low	6

*Qualitative comparison of observed number of morphological and ecological range and change as determined through the fossil record and living species

A numbers approach

"Living fossils"

"Dying organisms"

Clade	Age (Ma)	Change*	N.
Horseshoe crabs	445	Low	4
Ginkgo	200-300	Low	1
Tuatara	220	Low	6
Passerine birds	82	High	5,739
Flowering plants	125	High	352,000
Aphids	80-150	Med	4,400

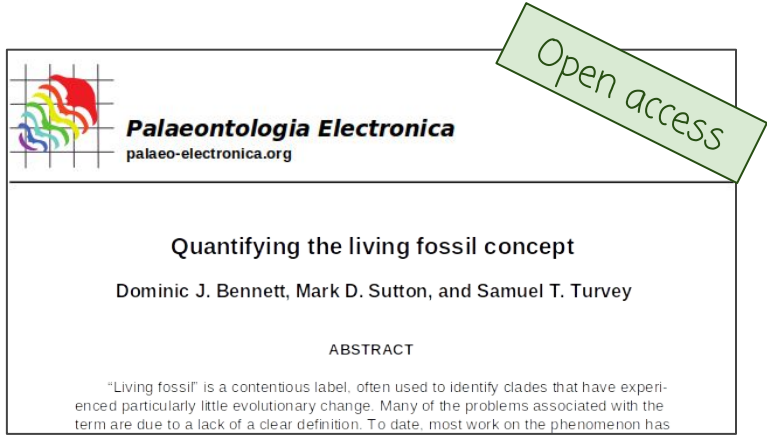
*Qualitative comparison of observed number of morphological and ecological range and change as determined through the fossil record and living species

Quantifying the concept

- *Living-fossil-ness*
- Evolutionary Performance Index (EPI)
  - Success (*S*)
  - Change (*C*)
  - Time (*T*)
- Sister-contrasts

$$EPI = log(\frac{\frac{S_i}{S_j} + \frac{C_i}{C_j}}{T_i})$$

- Calculated for > 24,000 taxa



Citation
Bennett, Dominic J., Sutton, Mark D., and Turvey, Samuel T. 2018. Quantifying the living fossil concept. *Palaeontologia Electronica* 21.1.15A 1-25. https://doi.org/10.26879/750

GitHub: github.com/DomBennett/Project-EPI

Bird and mammal “living fossils” ….

Photo credit: Patrick_K59

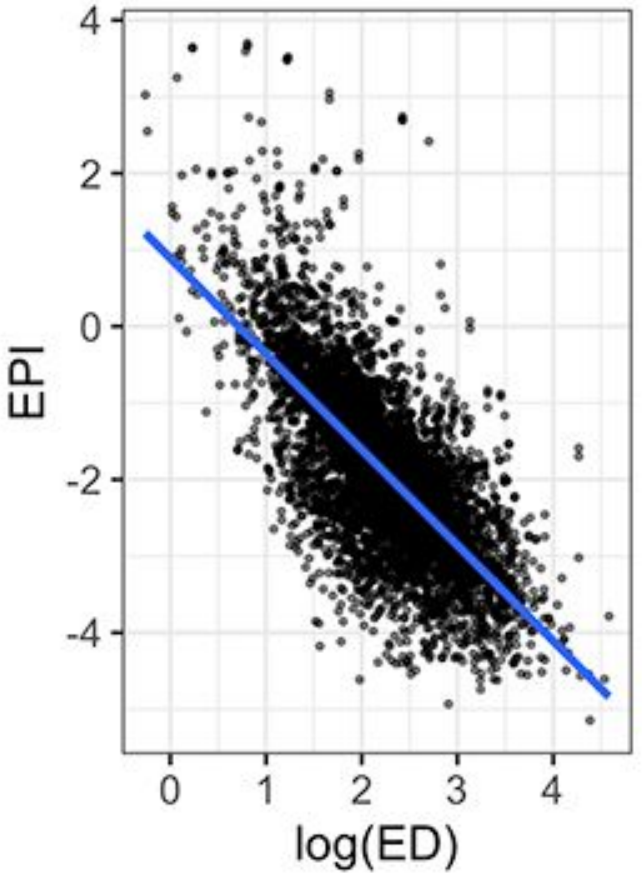
Photo credit: Murray Foubister

Change and success relative to sister taxa

Common name	Scientific name	Change	Success	Time	EPI
Egg-laying mammals	**Monotremata**	**0.97**	**0.000537**	**166.2**	**-5.15**
Marsupials	Metatheria	1	0.0668	147.7	-4.93
Ratites and Tinamous	Palaeognathae	1.01	0.00624	116.75	-4.74
Anteaters, sloths and armadillos	Xenarthra	0.99	0.00692	101.1	-4.62
Afrotherians	Afrotheria	0.98	0.0208	101.3	-4.62
Fowl	Galloanserae	0.97	0.0552	103.54	-4.61
Aardvark	*Orycteropus afer*	0.92	0.00943	93.2	-4.61
Odd-toed ungulates	Perissodactyla	0.86	0.012	87.3	-4.61
Hoatzin	***Opisthocomus hoazin***	**0.76**	**0.000113**	**72.45**	**-4.56**

EPI correlates with ED

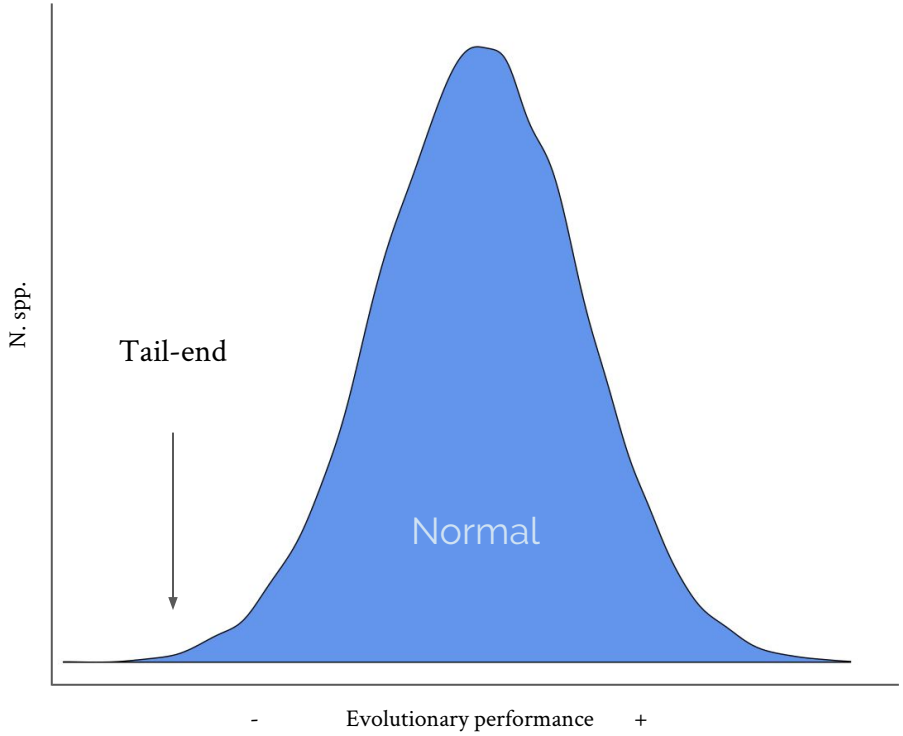
- Evolutionary distinctness (ED) is a measure of phylogenetic isolation:
  - Proportion of branch in a tree uniquely represented by a species
- Correlates with EPI, Pearson's R: **-0.72**
- **ED is a correlate for living-fossil-ness**

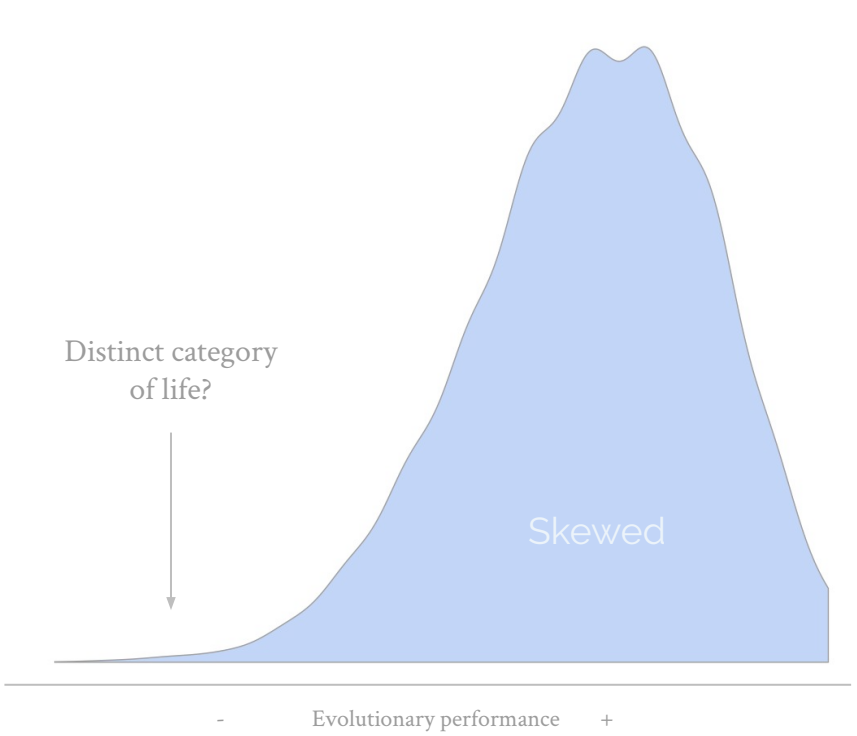


Question II.
Is “living fossil” valid?

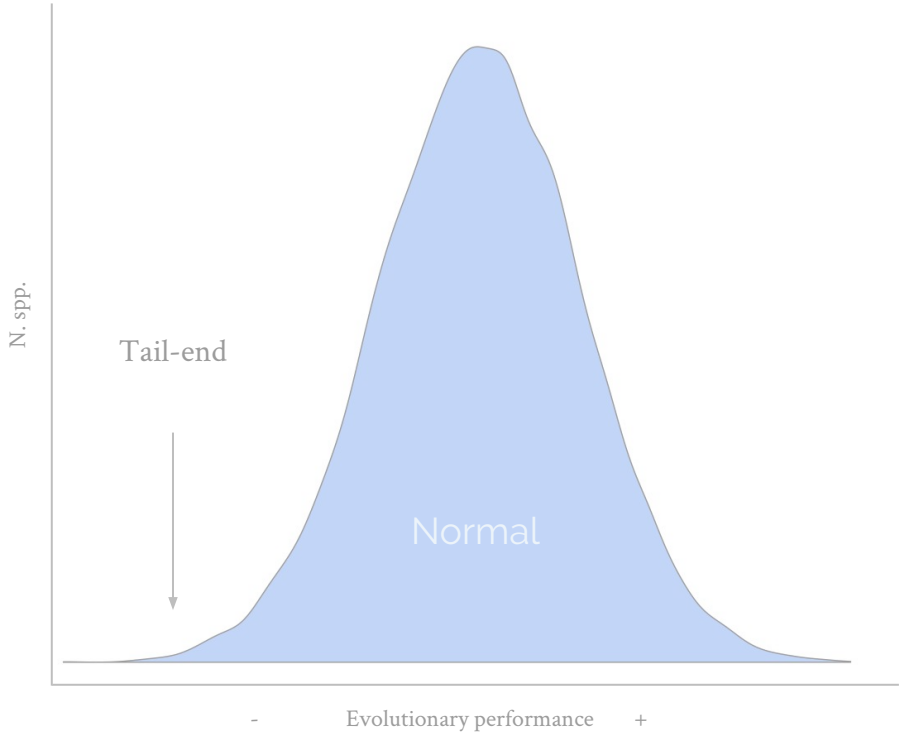
Photo credit: James Field

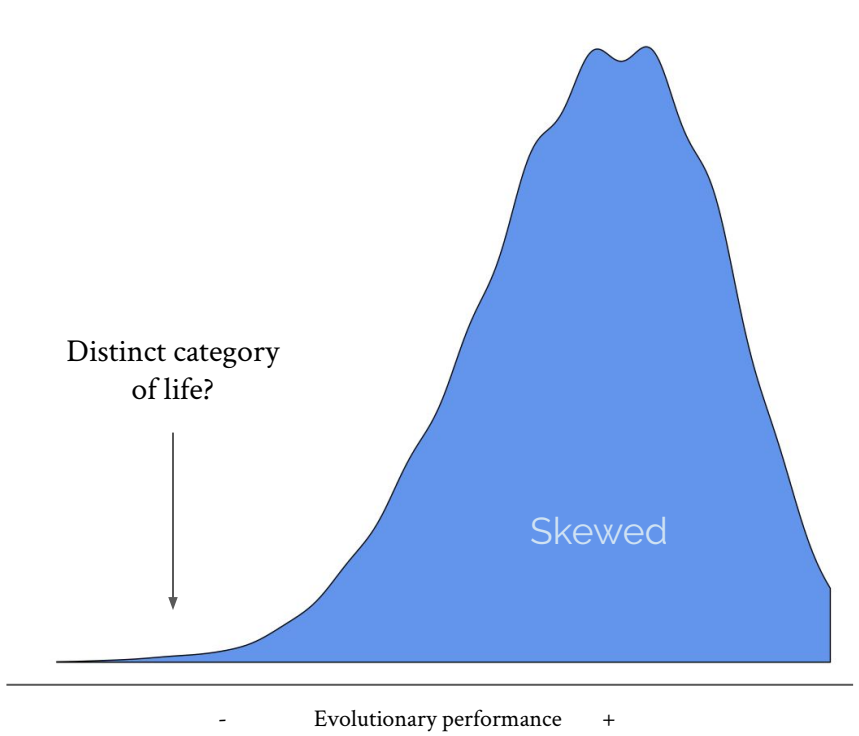
Tail-ends or distinct?





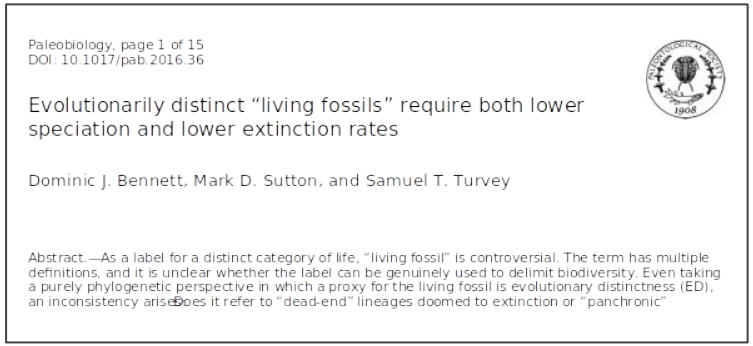
Tail-ends or distinct?





Model tree-growth

- Model scenarios with and without “living fossils”
- Evolutionary distinctness as a proxy for *living-fossil-ness*
  - Proportion of a tree, correlates with EPI
- Compare ‘real’ phylogenetic trees to simulated trees through tree shape



Paleobiology, page 1 of 15
DOI: 10.1017/pab.2016.36

Evolutionarily distinct “living fossils” require both lower speciation and lower extinction rates

Dominic J. Bennett, Mark D. Sutton, and Samuel T. Turvey

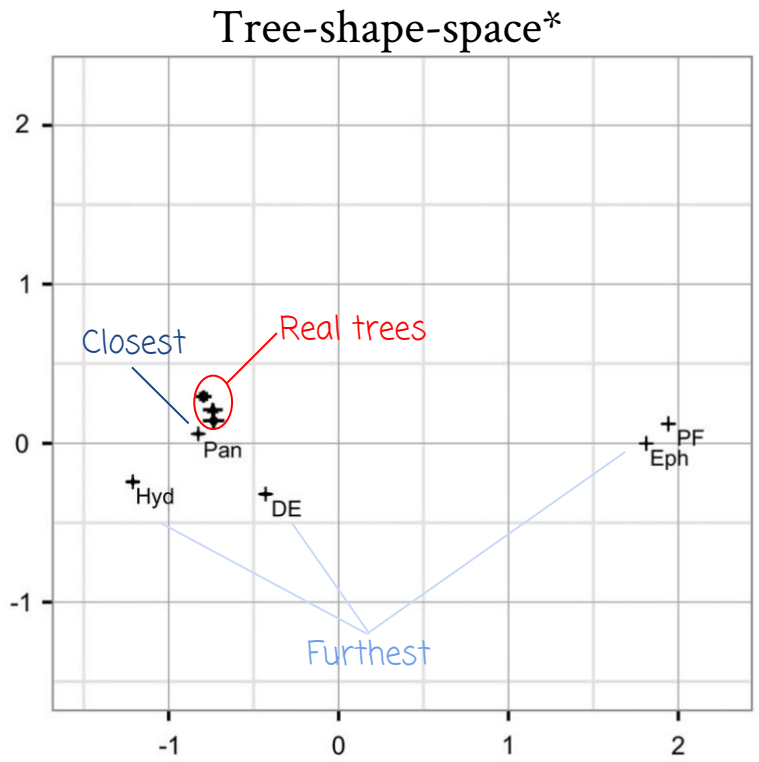
Abstract.—As a label for a distinct category of life, “living fossil” is controversial. The term has multiple definitions, and it is unclear whether the label can be genuinely used to delimit biodiversity. Even taking a purely phylogenetic perspective in which a proxy for the living fossil is evolutionary distinctness (ED), an inconsistency arises: does it refer to “dead-end” lineages doomed to extinction or “panchronic”

Citation
Bennett, D.J., Sutton, M.D. & Turvey, S.T., 2016. Evolutionarily distinct “living fossils” require both lower speciation and lower extinction rates. *Paleobiology*, pp.1–15.

GitHub: https://github.com/DomBennett/Project-EDBMM

Lower rates of extinction and speciation

- Real trees are closest in *tree-shape-space* to the scenario ('Pan') where living fossils have lower speciation and extinction rates
- Conclusions:
  - Not a tail-end
  - A distinct category of biodiversity with a lower diversification rate



* i.e. balance/imbalance, tippiness/branchiness

Question III.
Evolutionary potential of living fossils

Photo credit: James Field

OK, great. But what about conservation?

There are increasing efforts to conserve the "evolutionary distinct." *Why?*

- Distinct features
  - More distance in time from other organisms
  - Distinct features that may be important for ecosystem function
- Evolutionary history
  - Oldest species represent greater history of life
- Evolutionary potential
  - Different traits → Different responses to ecosystem change

Conservation of the **E**volutionarily **D**istinct and **G**lobally **E**ndangered

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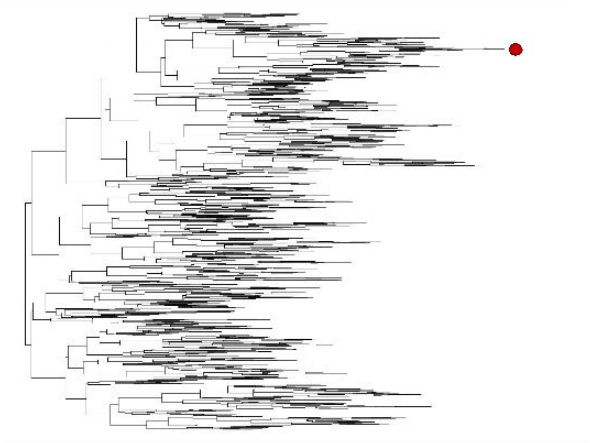
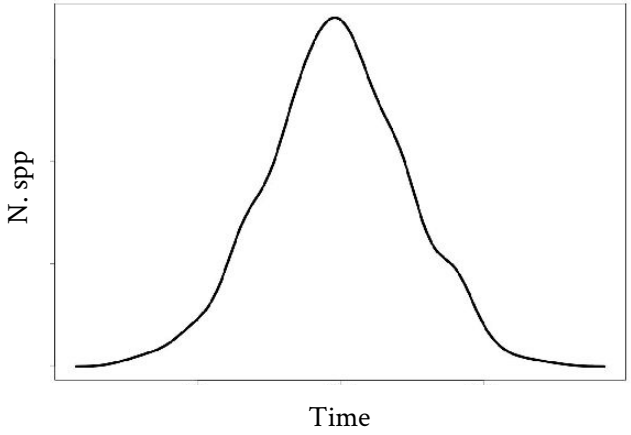
Conservation of the **E**volutionarily **D**istinct and **G**lobally **E**ndangered

Evolutionary relicts?

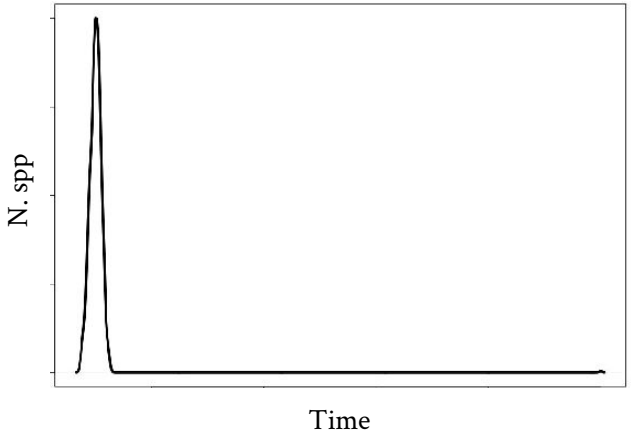
- “Living fossils” are simply the leftovers of a once large radiation
- Conservation implications
  - Independently of humans, more likely to go extinct
  - Less reason to conserve



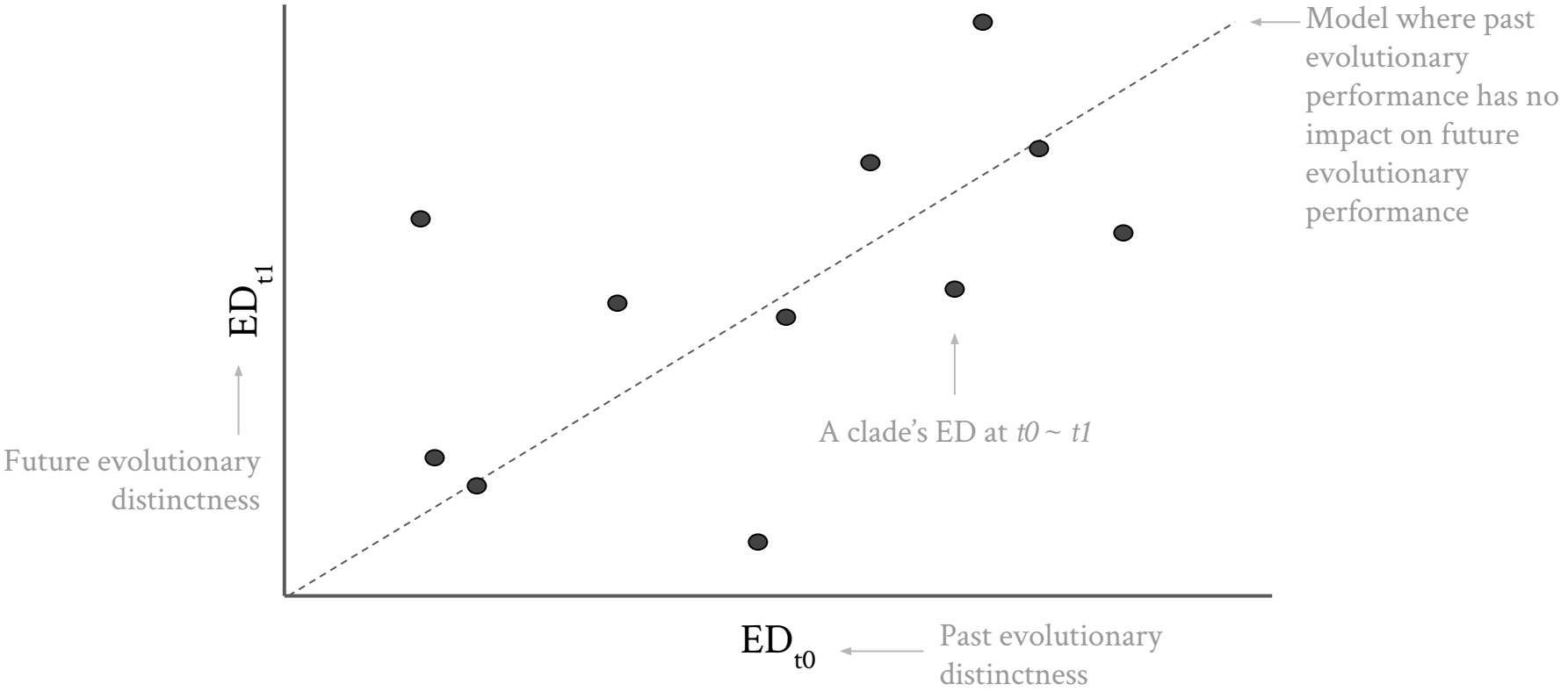


Panchronic forms?

- “Living fossils” are able to persist for long periods of time
- Conservation implications
  - Independently of humans, not likely to go extinct
  - Valid to conserve



Past and future performance



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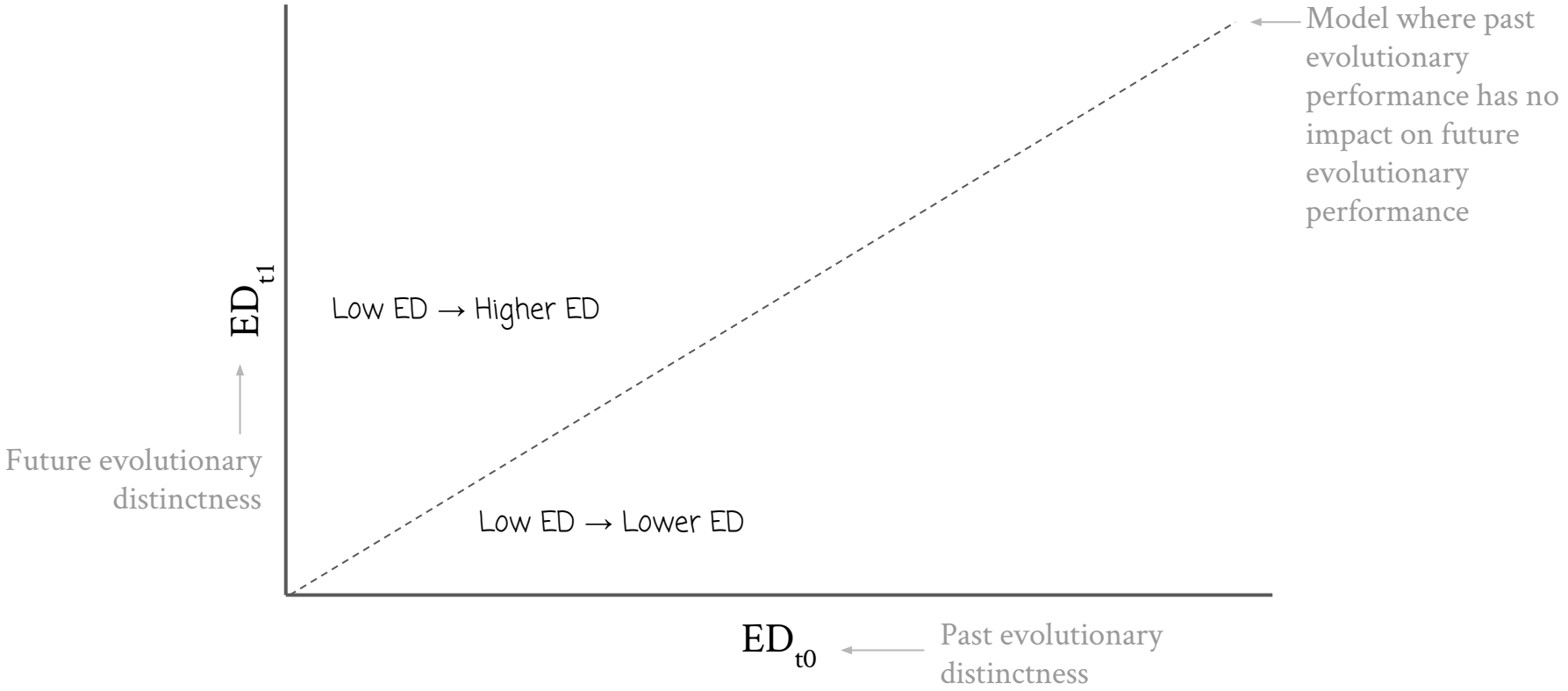

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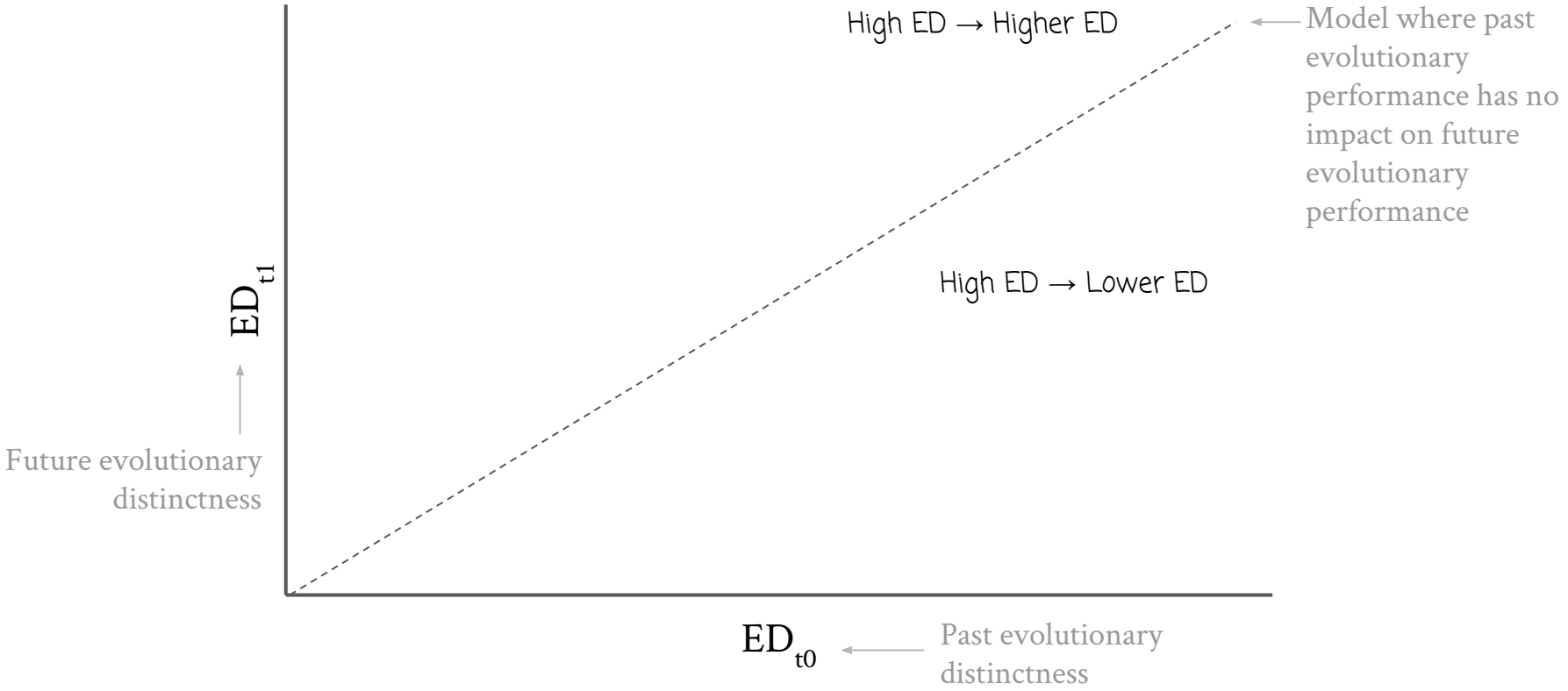
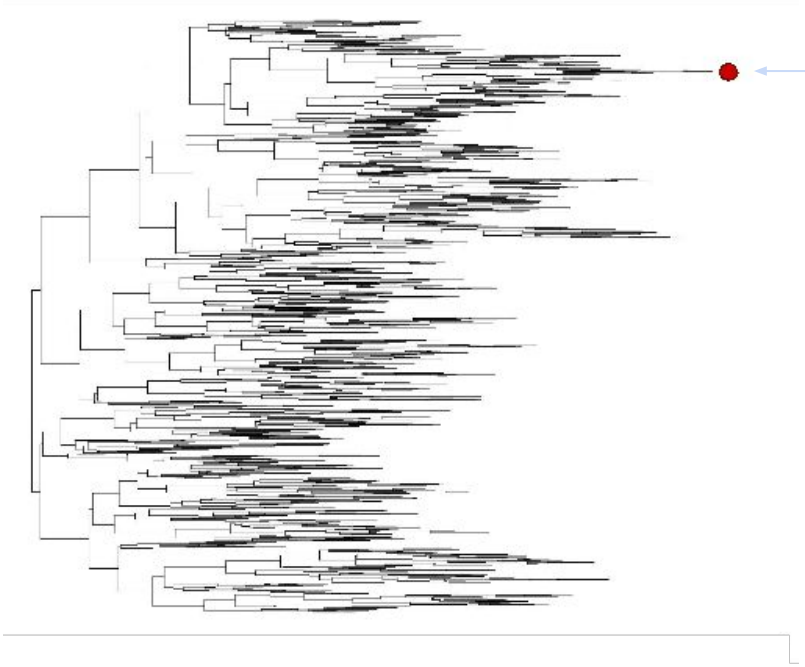
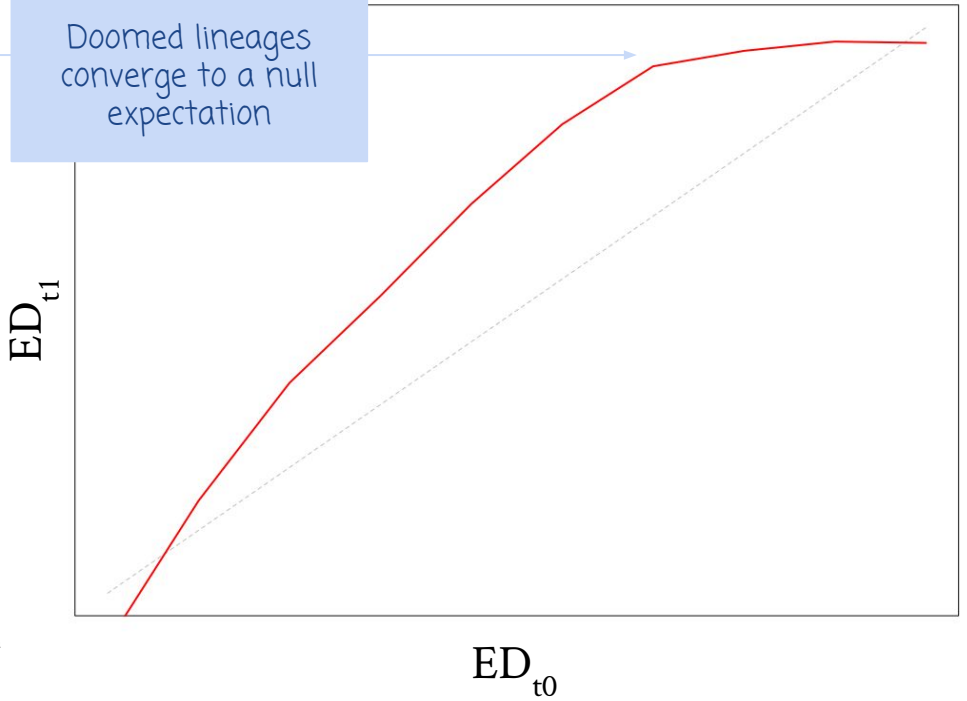


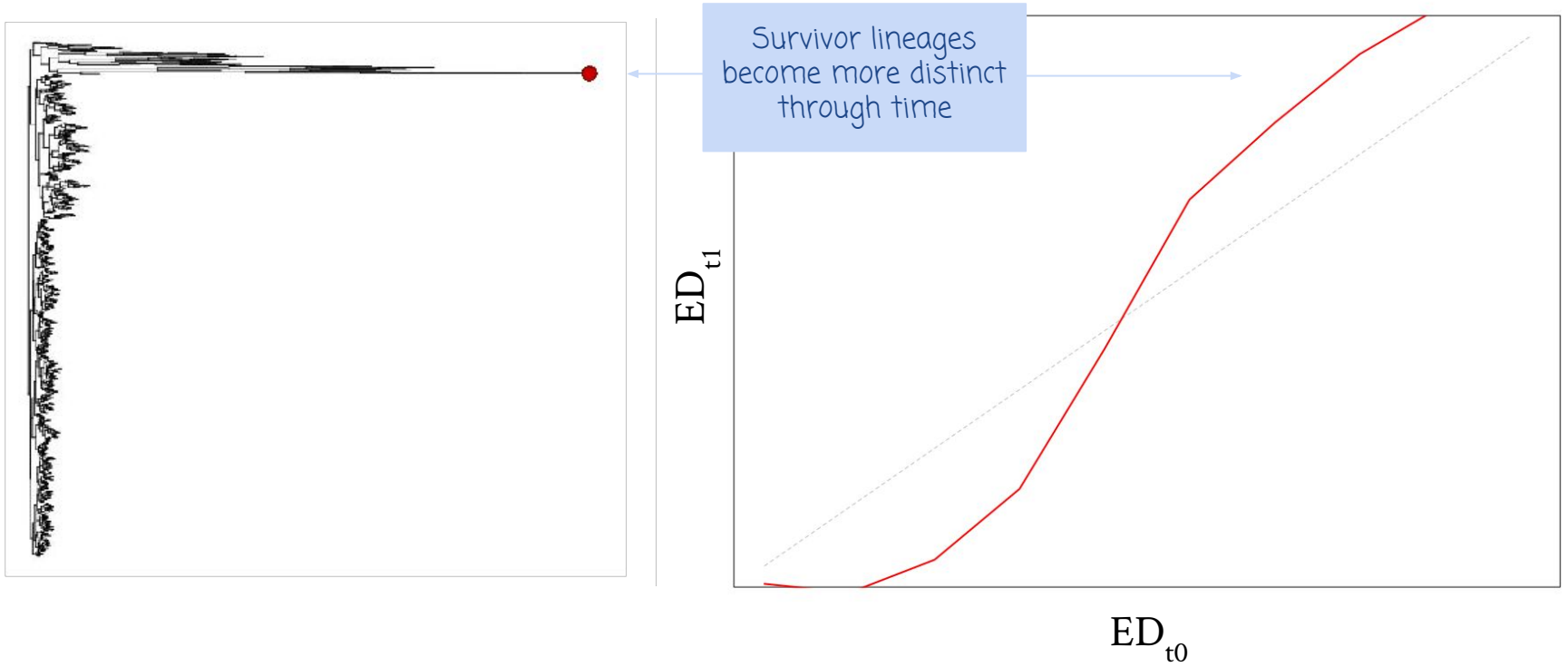
A model for *evolutionary relict*



Doomed lineages converge to a null expectation

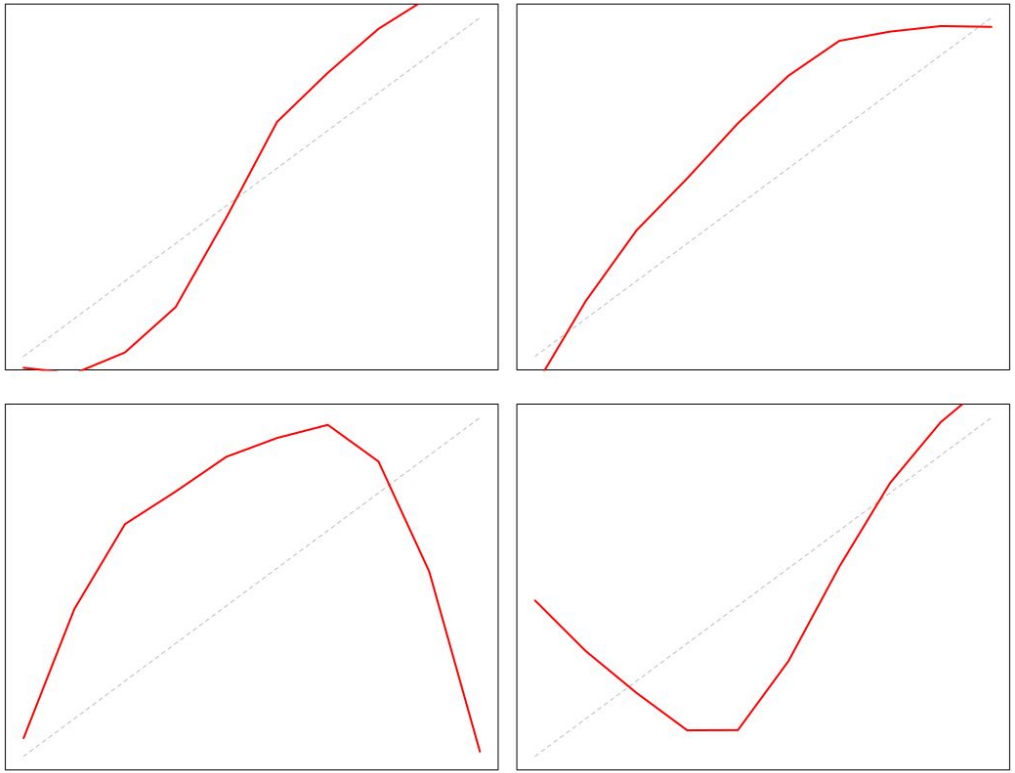


A model for *panchronic*



A range of possible curves

- A complex range of testable models
- Which is the closest to what is observed in the fossil record?



Manuscript for submission

Aim: Model ED_{t0} ~ ED_{t1} to determine which scenario best matches reality

Study group: Mammalia

Data source: Mammalian supertree and mammalian fossil record

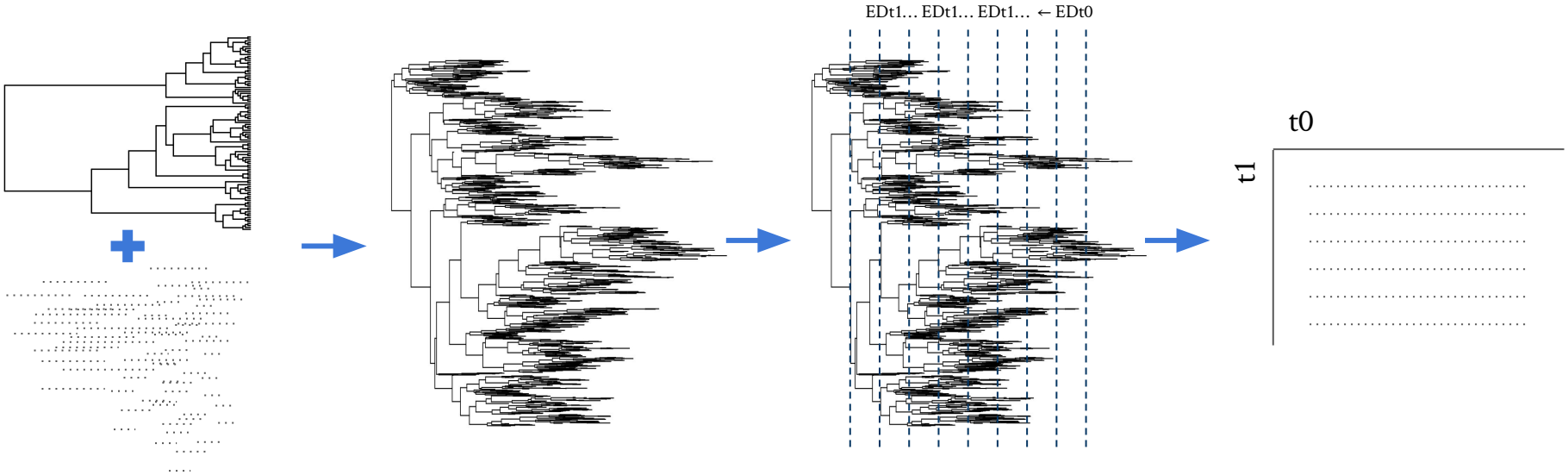
Method: Stochastic fossil pinning and linear modelling

Authors: Bennett, Sutton and Turvey

GitHub [DomBennett/Project-karenina]

Photo credit: Patrick_K59

Data generation



Pin fossils to mammalian supertree

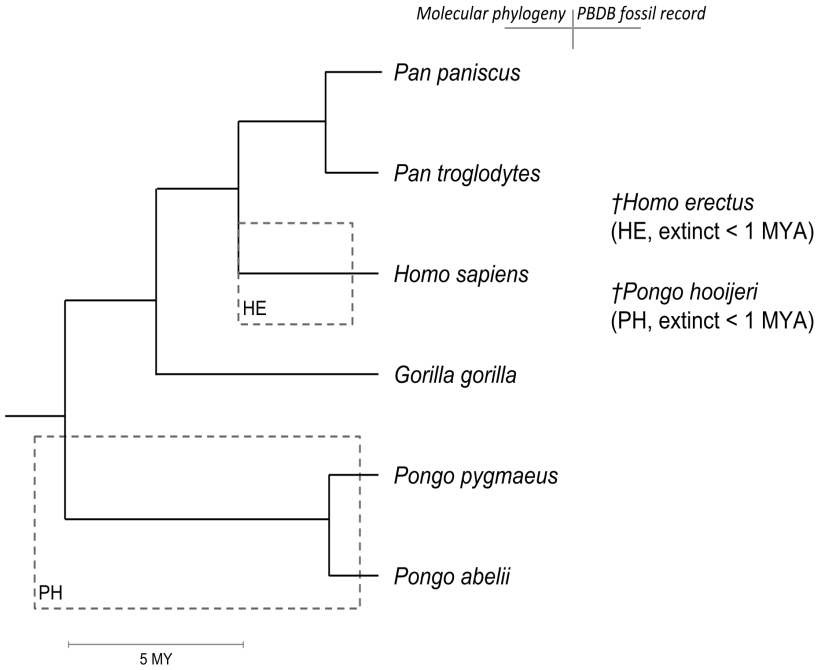
Calculate ED at different time slices

ED at epoch midpoints converted to *t1* and *t0* dataset

Data sources:
Bininda-Emonds et al. *Nature*, 446(7135), 507-12
https://paleobiodb.org/

Stochastic fossil pinning

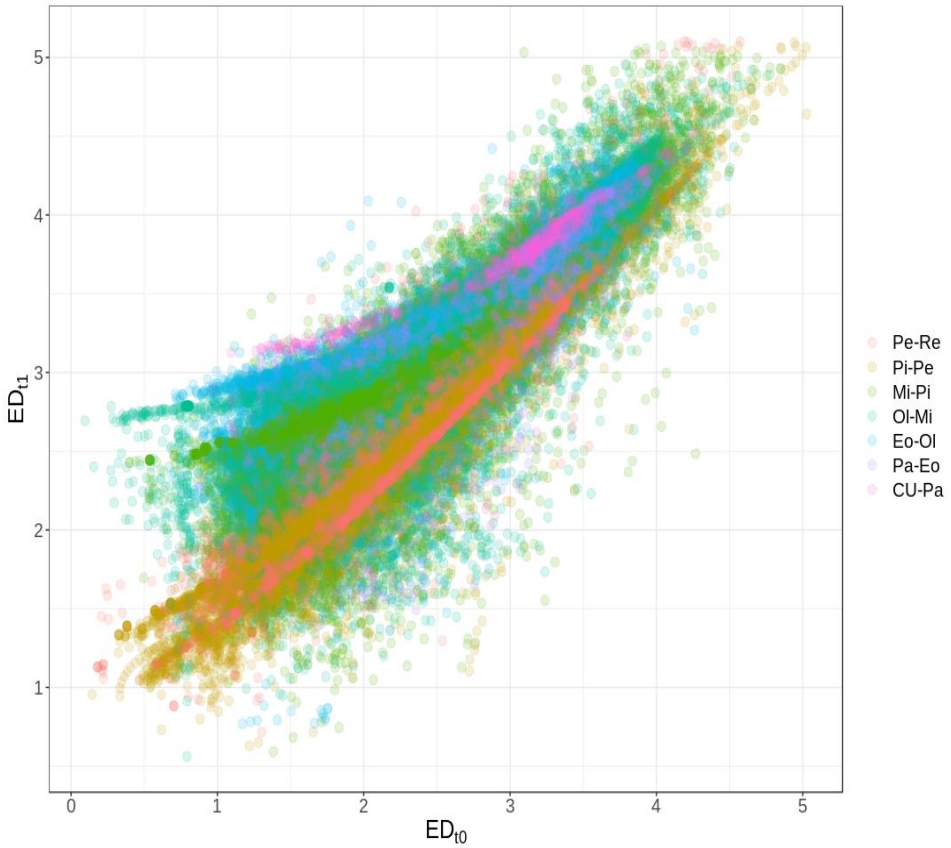
- Performed with *treeman*'s *pinTips*() in R
- 100 different permutations
- Fossil records are stochastically added to the phylogenetic tree with three constraints:
  - Must be within shared lowest taxonomic group
  - Origin of the branch must be before estimated age range
  - Extinction of the branch must be within the the estimated age range



Bennett, D.J., Sutton, M.D. & Turvey, S.T., 2017. treeman: an R package for efficient and intuitive manipulation of phylogenetic trees. *BMC Research Notes*, 10(1), p.30.

Linear modelling

- Linear Mixed Effects Models
  - Accounting for: non-independence between epochs, different size and ages of epochal trees, time differences between epochs, different taxonomic groups
- Three key models
  - Expected linear model (*exp*)
  - Best fitting linear model (*obs1*)
  - Best fitting nonlinear model (*obs2*)
- Two key questions:
  - Does the observed data best fit a linear or a nonlinear model?
  - How does the best model compare to the expected linear model?



Natural log scale: *1, 3, 7, 20, 55 and 148 MYA*

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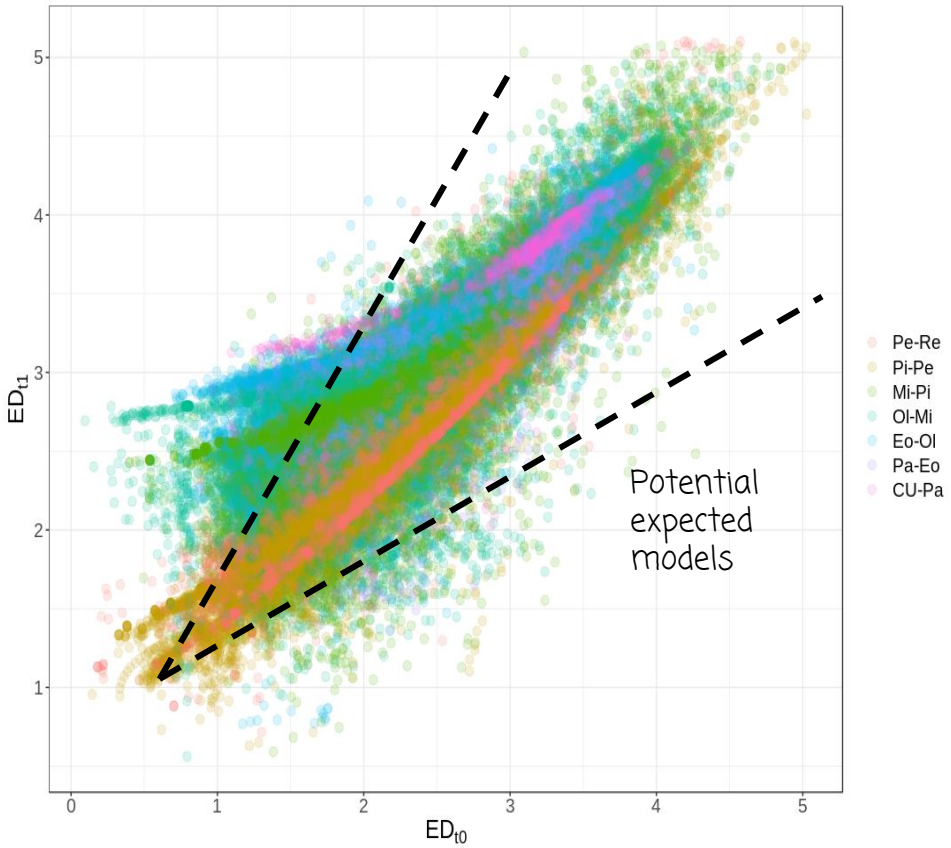

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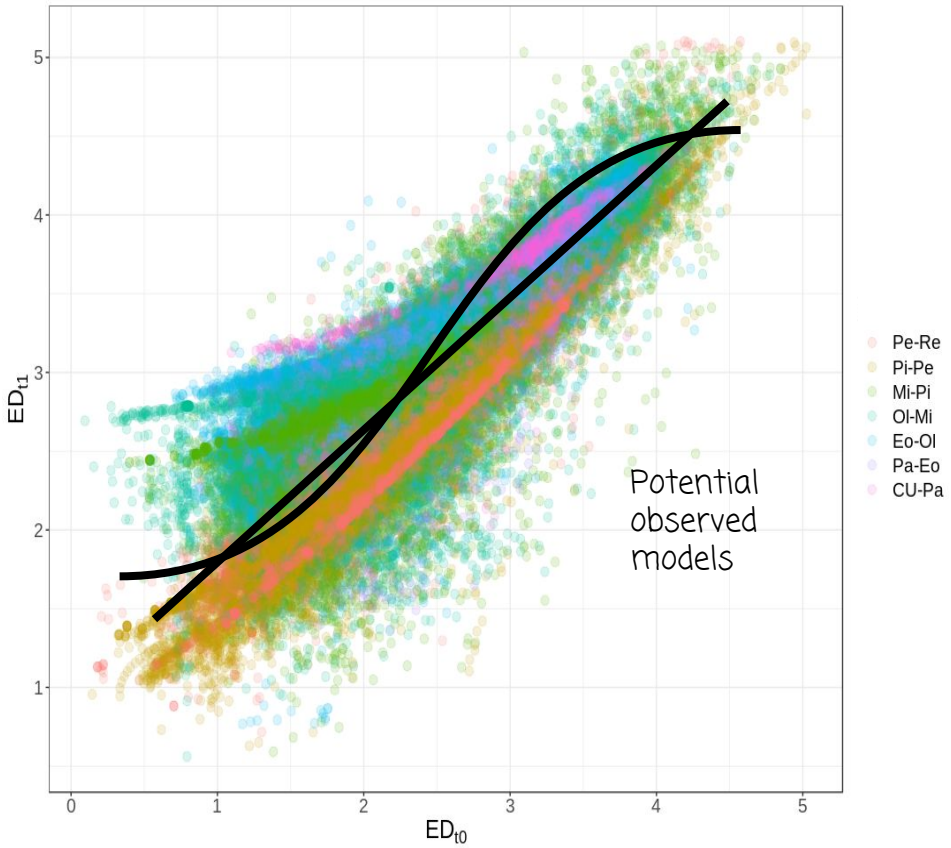
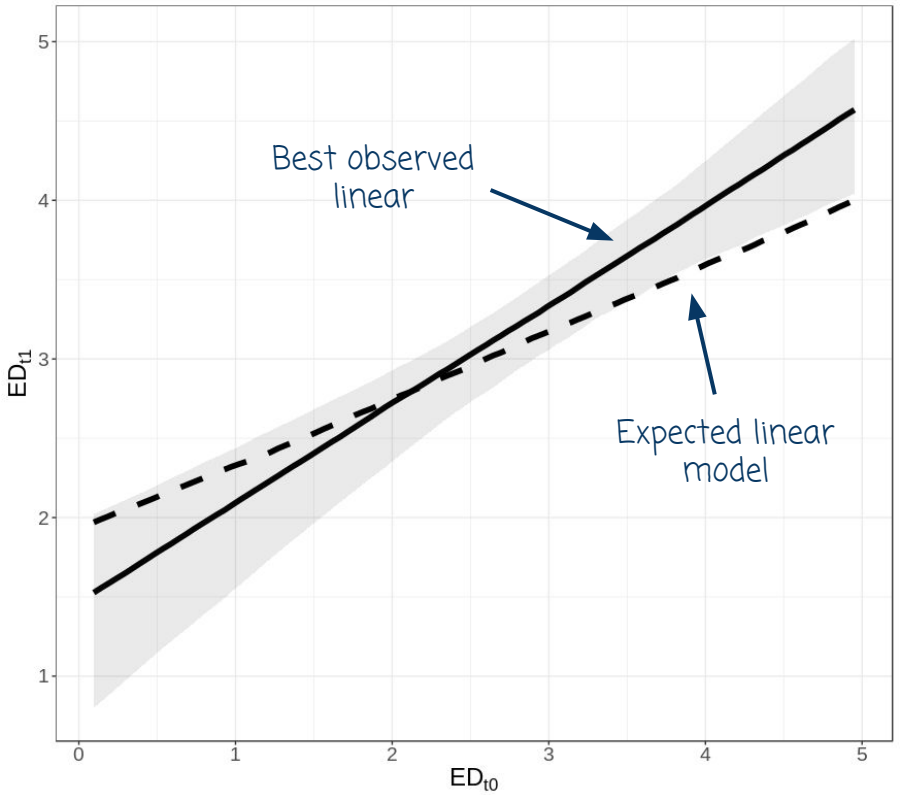


Natural log scale: *1, 3, 7, 20, 55 and 148 MYA*

Results

- Linear or nonlinear?
  - The best non-linear polynomial explained significantly more variation than the best linear
  - **Past performance does impact future performance**
- Expected and best observed
  - Best observed showed higher ED for high EDt0 than expected
  - **High ED leads to higher ED**

Best observed linear model. AIC: **7255**



Formula: $ED_{t1} \sim ED_{t0} + (ED_{t0} | epoch) + (ED_{t0} | genus)$

Results

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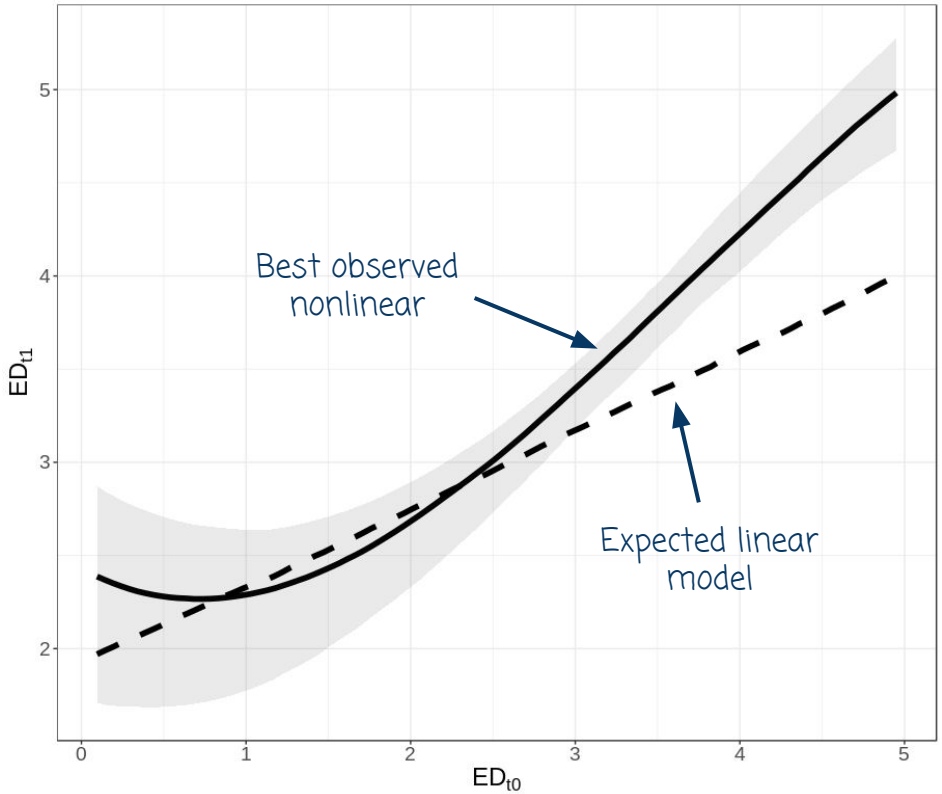
Best observed nonlinear model. AIC: **4710**



Formula: $ED_{t1} \sim poly(ED_{t0}, 3) + (ED_{t0} | epoch) + (ED_{t0} | genus)$

Conclusions

Photo credit: James Field

Messages

- “Living fossils” are a definable entity
- “Living fossils” represent a distinct section of biodiversity
- “Living fossils” experience low rates of both speciation and extinction
- Conserving “living fossils” is **not** a waste of time

Not doomed.

Not the future.

Just unique.

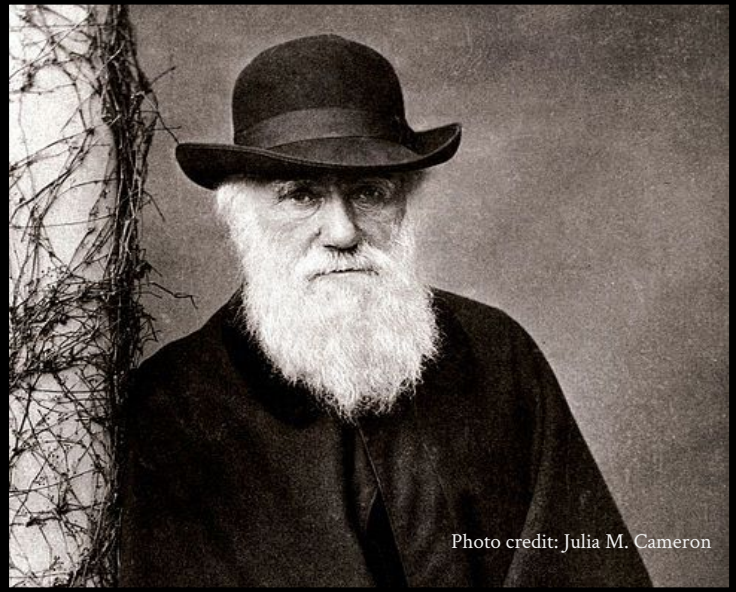


Photo credit: Julia M. Cameron

"I daresay you will think all [*this living fossil thesis*] is utter bosh; but I believe it to be solid truth!"

Darwin, letter to Hooker, 24th December 1858

Darwin Correspondence Project. Letter number: *DCP-LETT-2384*