Como se estuda macroevolução?

Precisamos de geralmente duas coisas

Fenótipos

Genealogias (Filogenias)

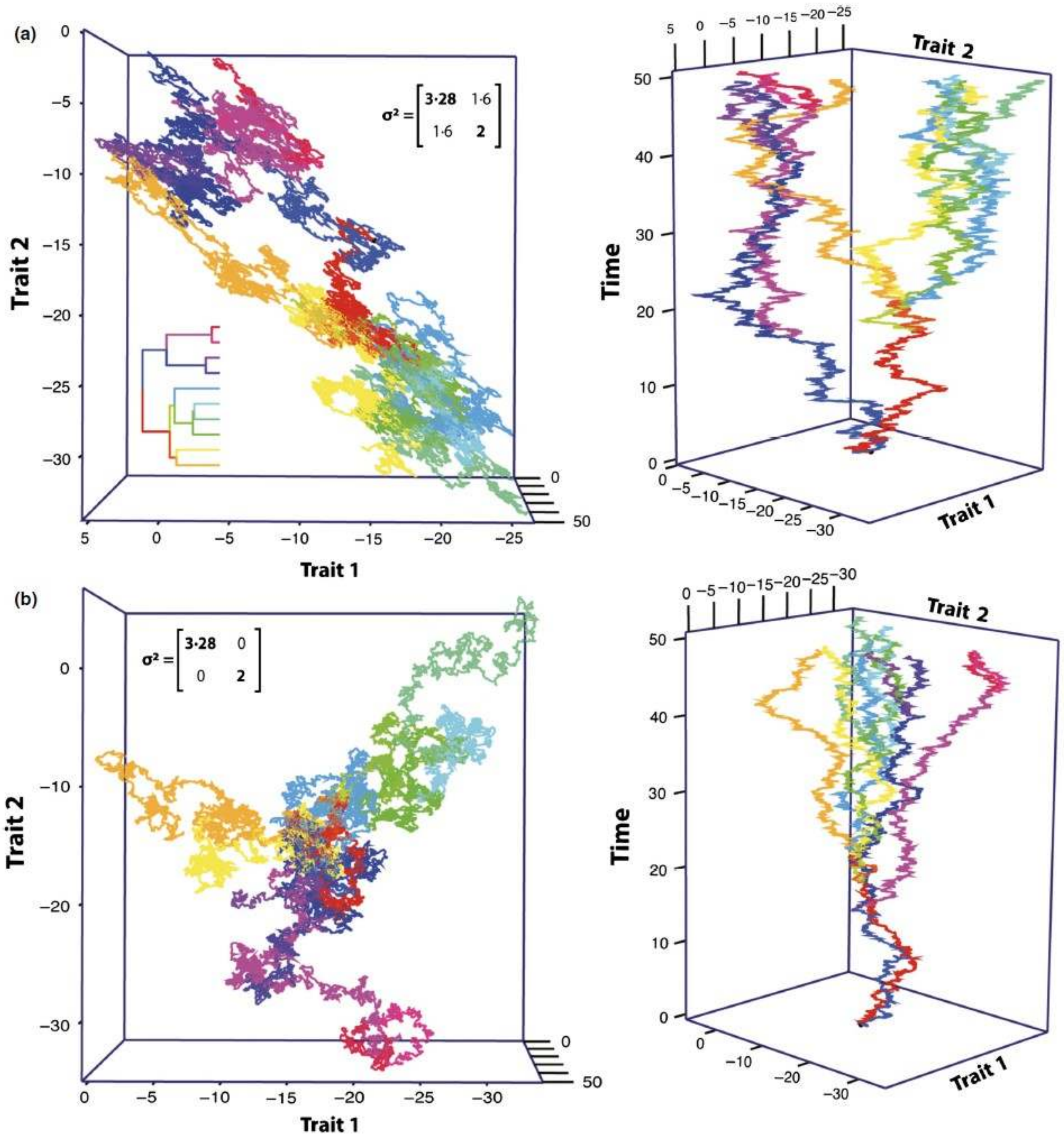
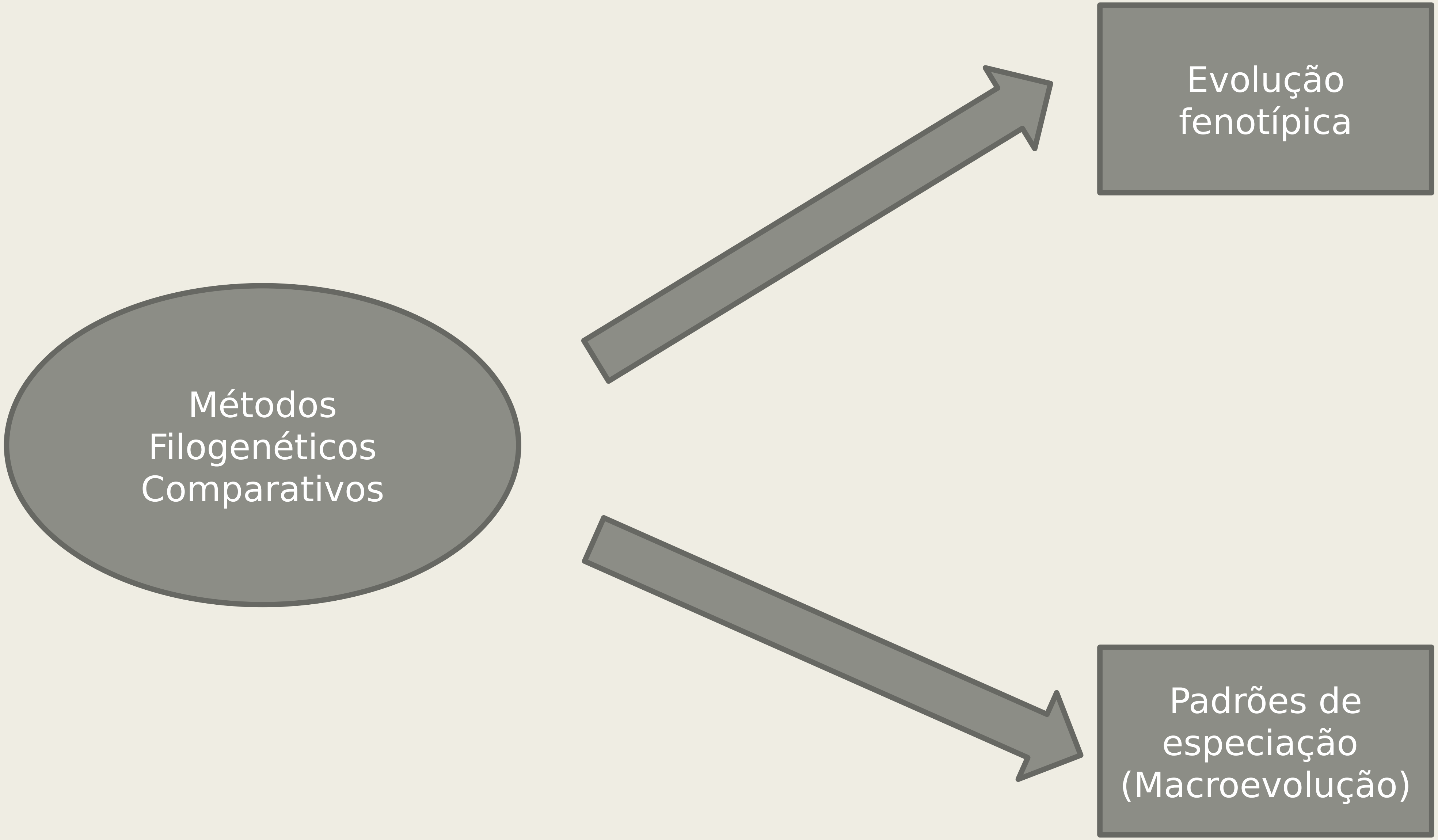


Fig. 2. Examples of two phenotypic traits evolving under a bivariate Brownian motion (BM) process within a 10 species tree [inset in (a)]. In (a), a

O que são Métodos Filogenéticos Comparativos?

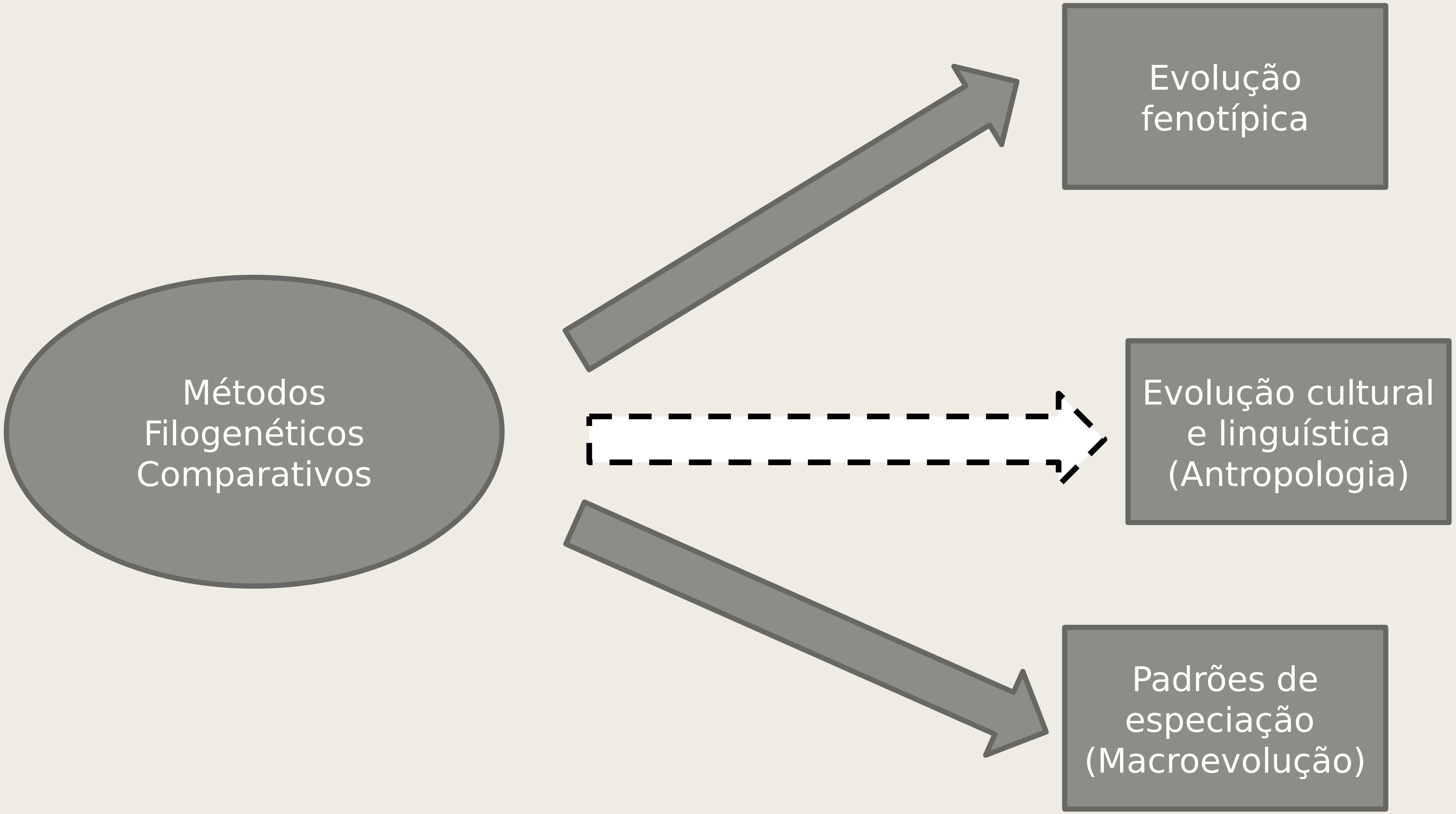
- Conjunto de métodos estatísticos que usam a relação de parentesco entre as espécies para testar hipóteses evolutivas sobre seus atributos
- Interesse surgiu no fim da década de 1970 com a disponibilidade de filogenias
  - *Processo evolutivo deixa ”rastros” no fenótipo das espécies*
    - Espécies mais próximas *tendem* a ser mais parecidas
- Perguntas comuns
  - *Qual o padrão filogenético de uma dada característica das espécies?*
  - *Sob que processo e em que velocidade essa característica evolui?*
  - *Qual a correlação dessa característica com outras ou com a variação ambiental?*



Métodos Filogenéticos Comparativos

Evolução fenotípica

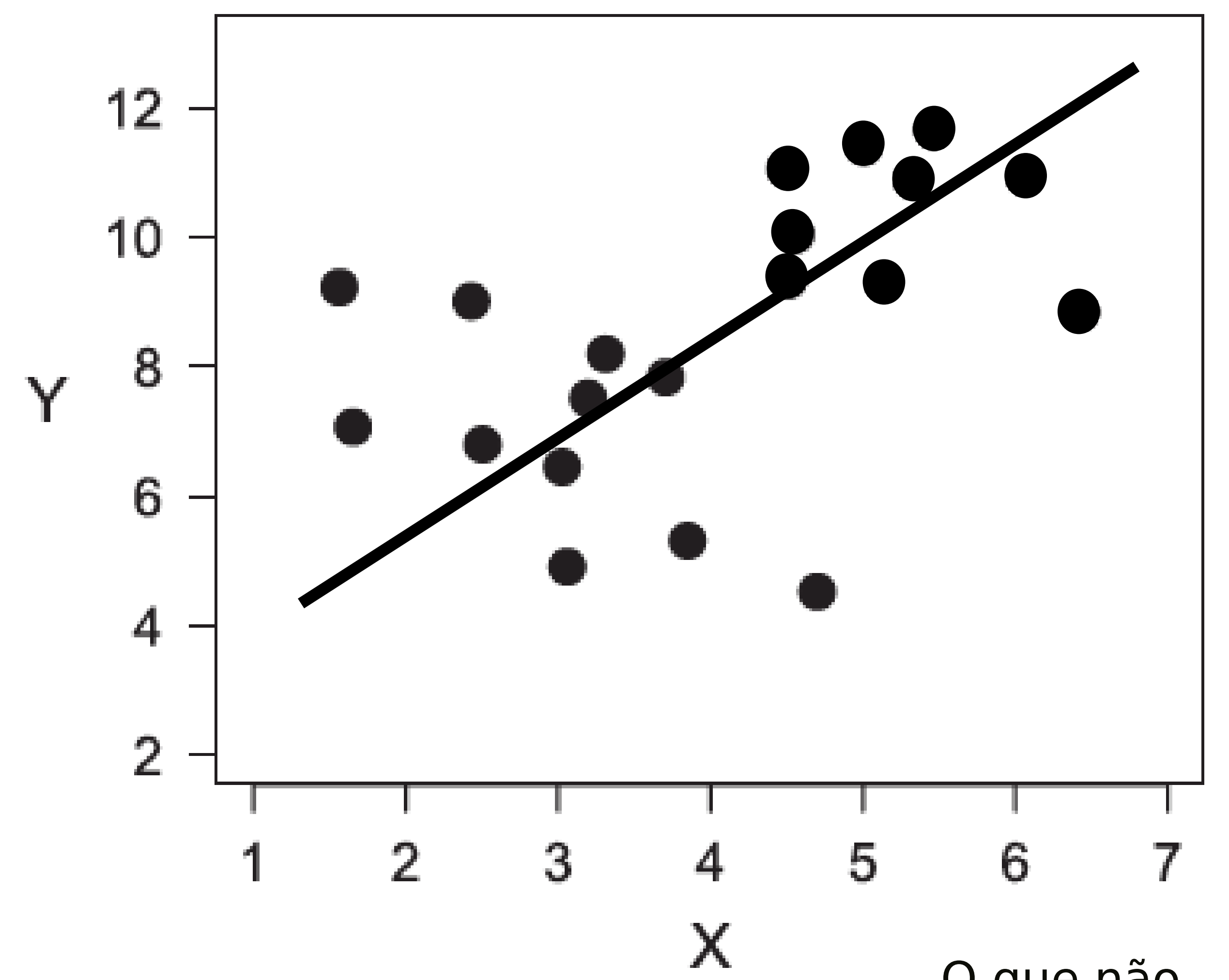
Padrões de especiação (Macroevolução)


Métodos Filogenéticos Comparativos
Evolução fenotípica
Evolução cultural e linguística (Antropologia)
Padrões de especiação (Macroevolução)

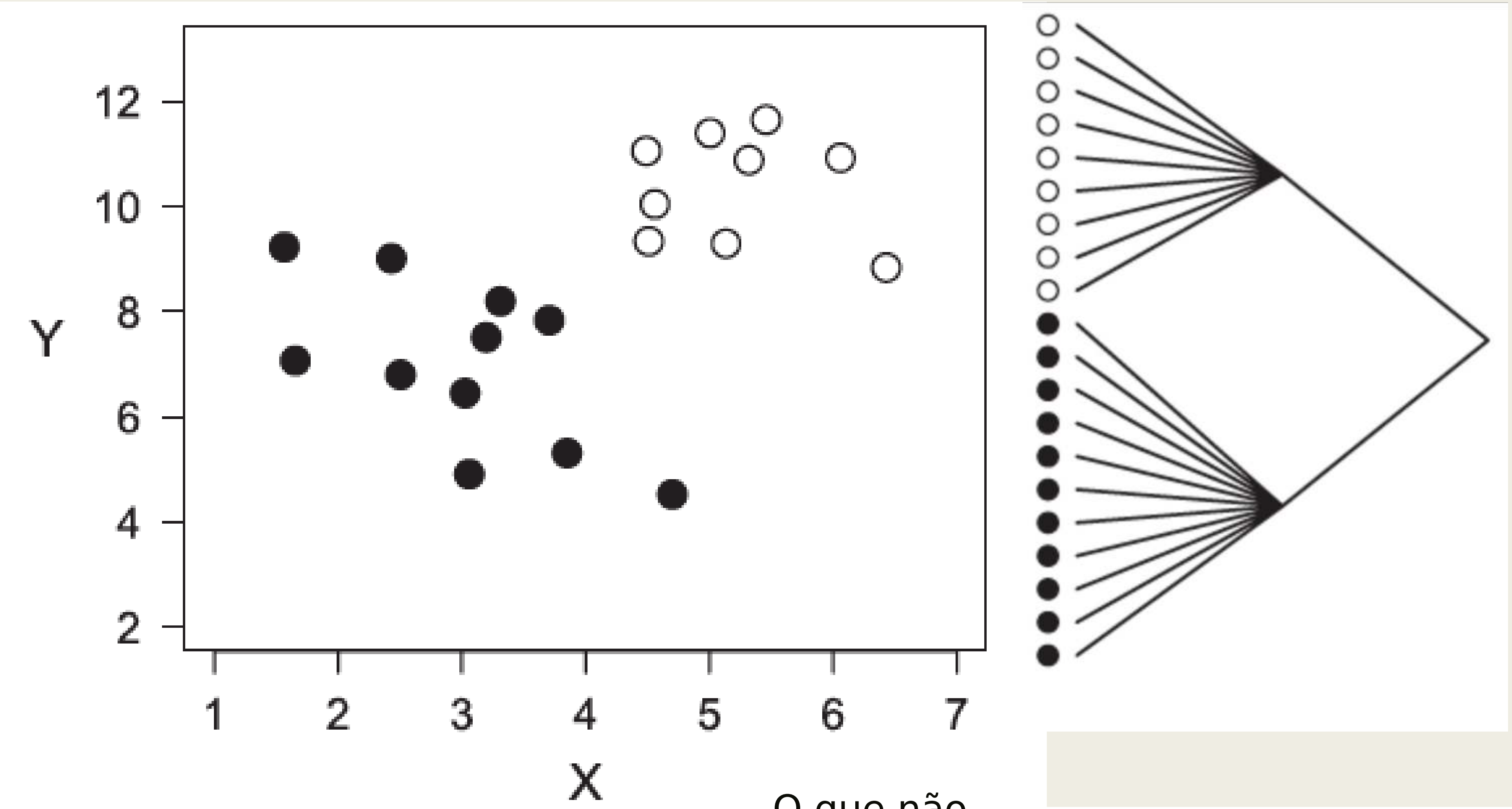
O que são Métodos Filogenéticos Comparativos?

- *Problema da Autocorrelação Filogenética => viola os pressupostos dos métodos ”convencionais”*
- *Necessidade de se incorporar a relação entre as espécies nas análises*

O problema do parentesco comum



O problema do parentesco comum



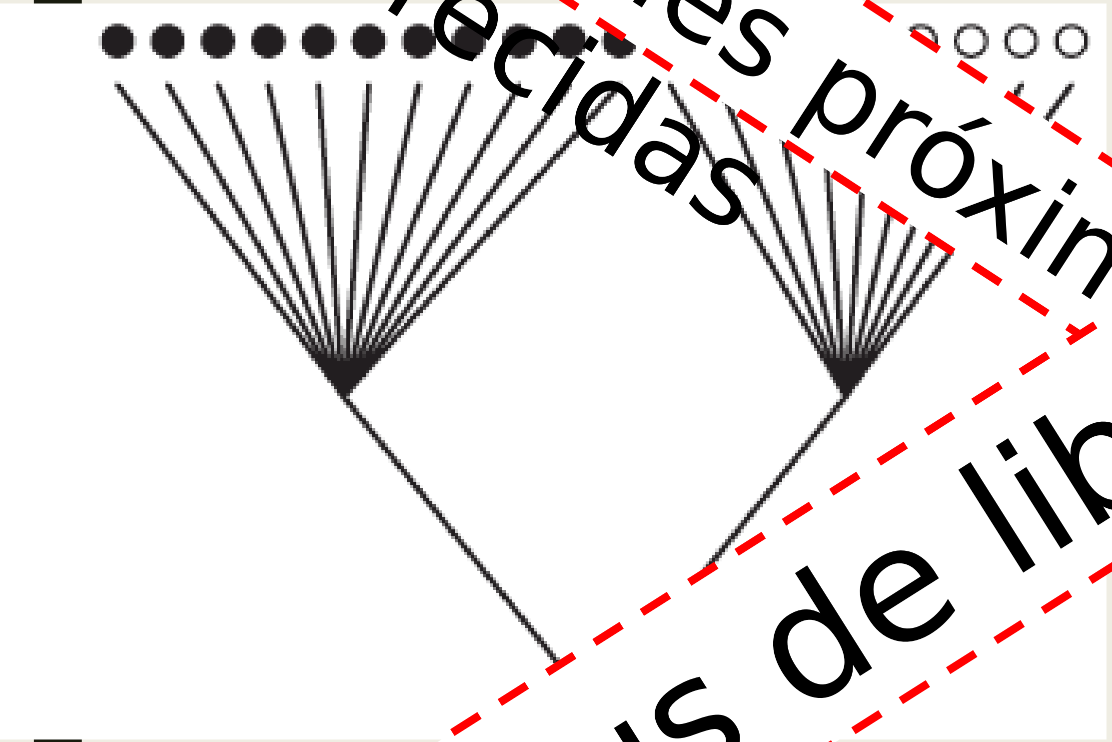
E cies não são independe

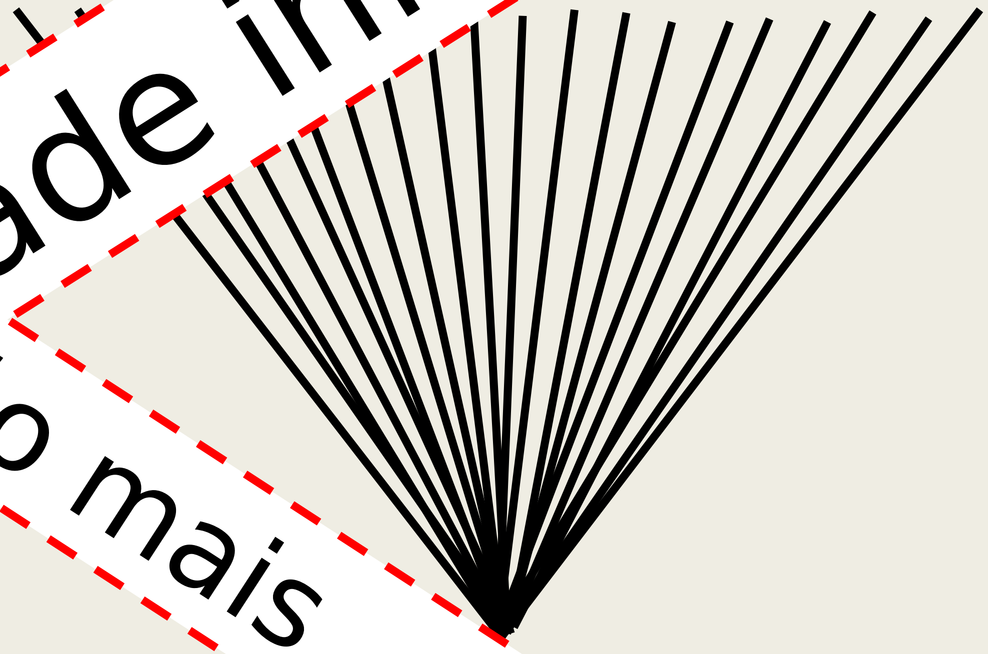
Espécies próxim

parecidas

ão mais

Graus de liberdade inflados





ia

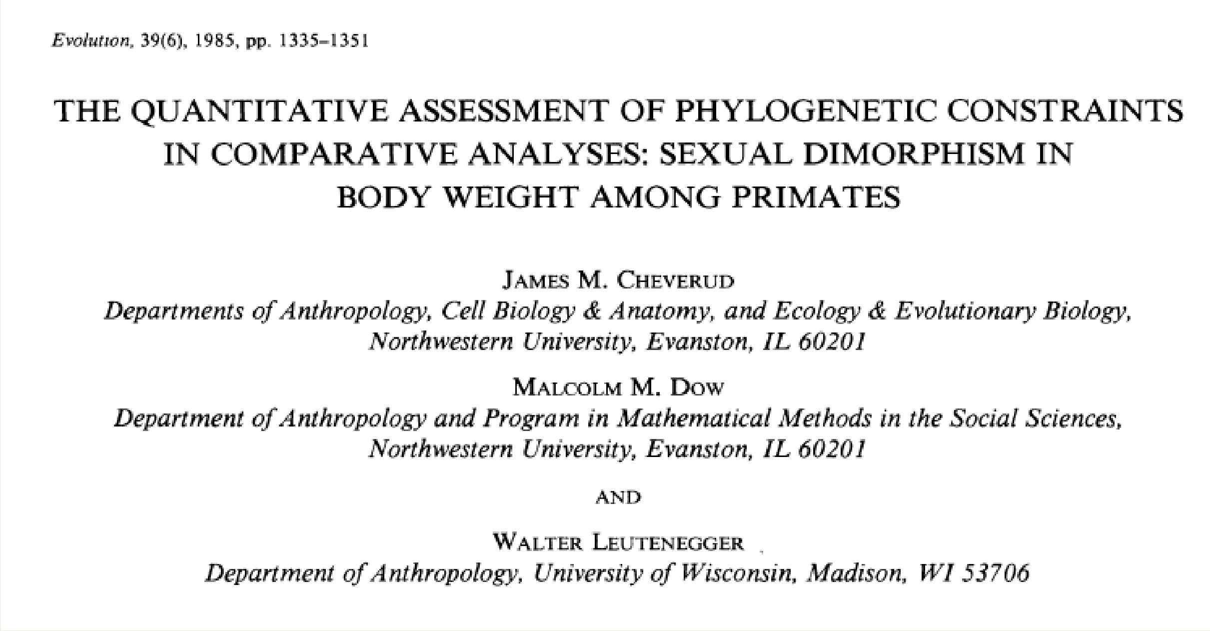
eal”

Filo em

est

> “Phylogenies are fundamental to evolutionary biology, there is no doing it without taking them into account”

Joe Felsenstein (1985)



Evolution, 39(6), 1985, pp. 1335–1351

THE QUANTITATIVE ASSESSMENT OF PHYLOGENETIC CONSTRAINTS IN COMPARATIVE ANALYSES: SEXUAL DIMORPHISM IN BODY WEIGHT AMONG PRIMATES

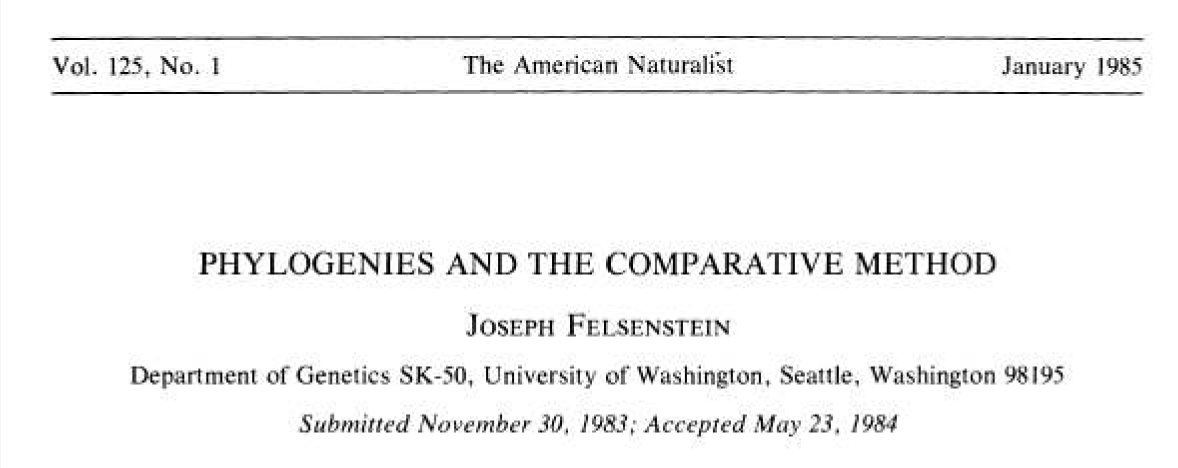
JAMES M. CHEVERUD
Departments of Anthropology, Cell Biology & Anatomy, and Ecology & Evolutionary Biology,
Northwestern University, Evanston, IL 60201

MALCOLM M. DOW
Department of Anthropology and Program in Mathematical Methods in the Social Sciences,
Northwestern University, Evanston, IL 60201

AND

WALTER LEUTENEGGER
Department of Anthropology, University of Wisconsin, Madison, WI 53706

1985



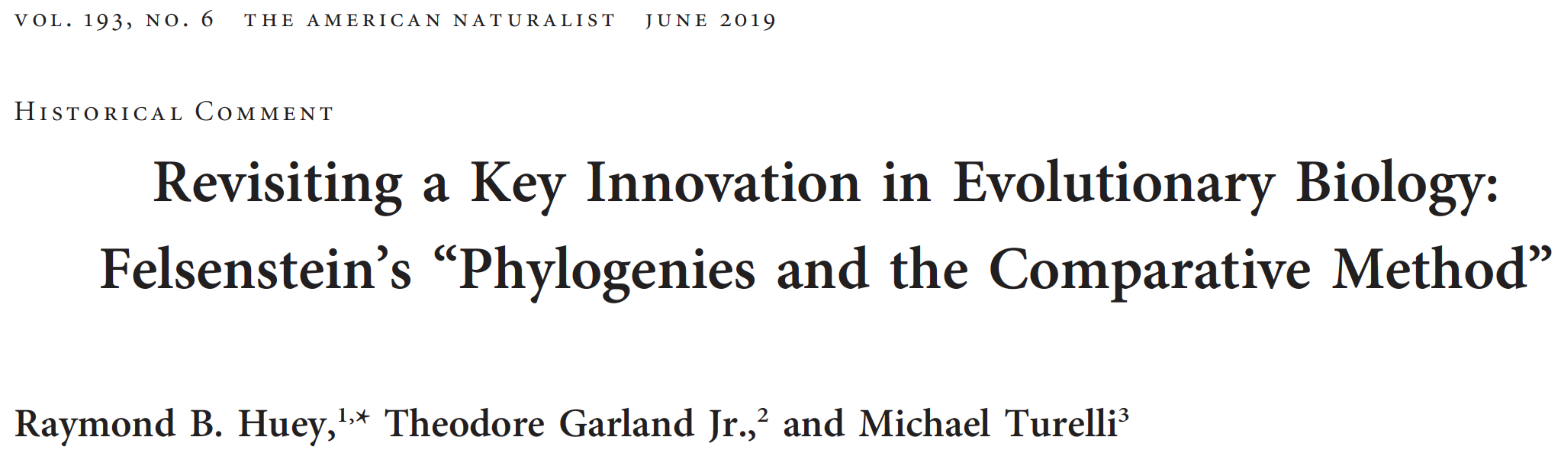
Vol. 125, No. 1 The American Naturalist January 1985

PHYLOGENIES AND THE COMPARATIVE METHOD

JOSEPH FELSENSTEIN

Department of Genetics SK-50, University of Washington, Seattle, Washington 98195

Submitted November 30, 1983; Accepted May 23, 1984

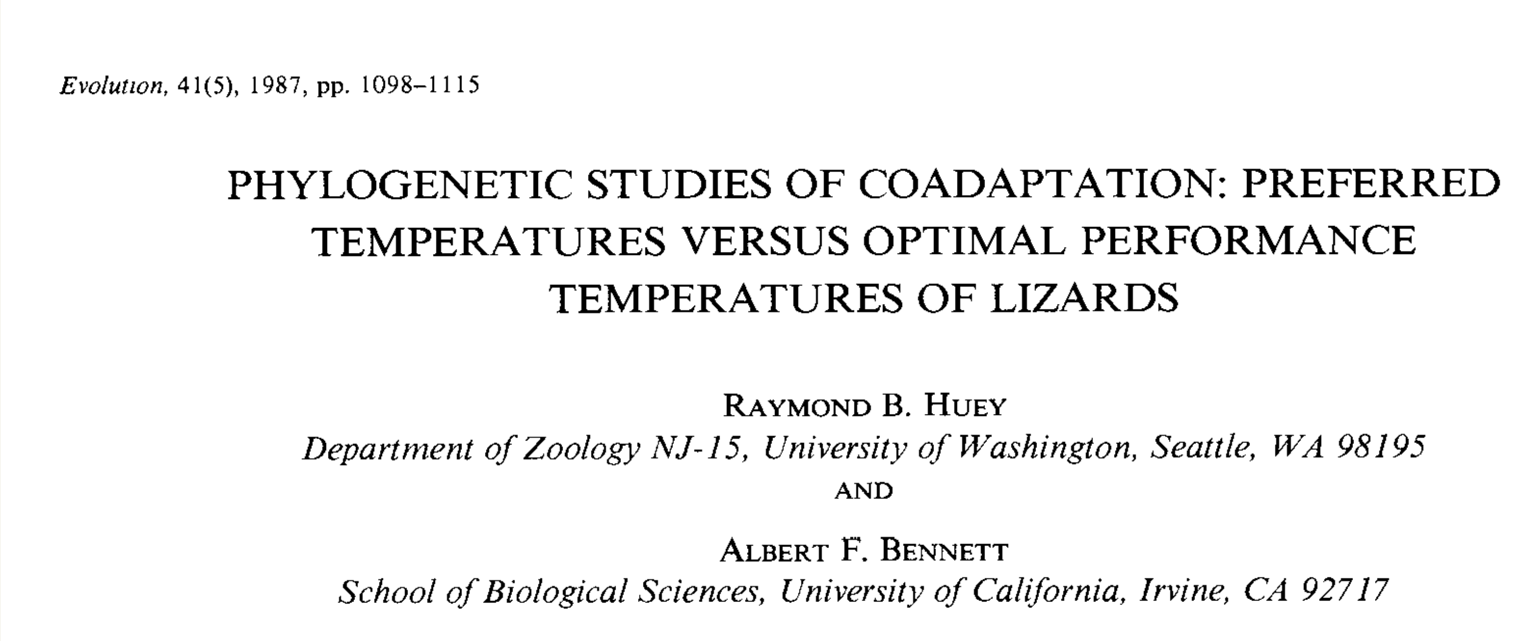


VOL. 193, NO. 6 THE AMERICAN NATURALIST JUNE 2019

HISTORICAL COMMENT

Revisiting a Key Innovation in Evolutionary Biology: Felsenstein's "Phylogenies and the Comparative Method"

Raymond B. Huey,[1,*] Theodore Garland Jr.,[2] and Michael Turelli[3]



Evolution, 41(5), 1987, pp. 1098–1115

PHYLOGENETIC STUDIES OF COADAPTATION: PREFERRED TEMPERATURES VERSUS OPTIMAL PERFORMANCE TEMPERATURES OF LIZARDS

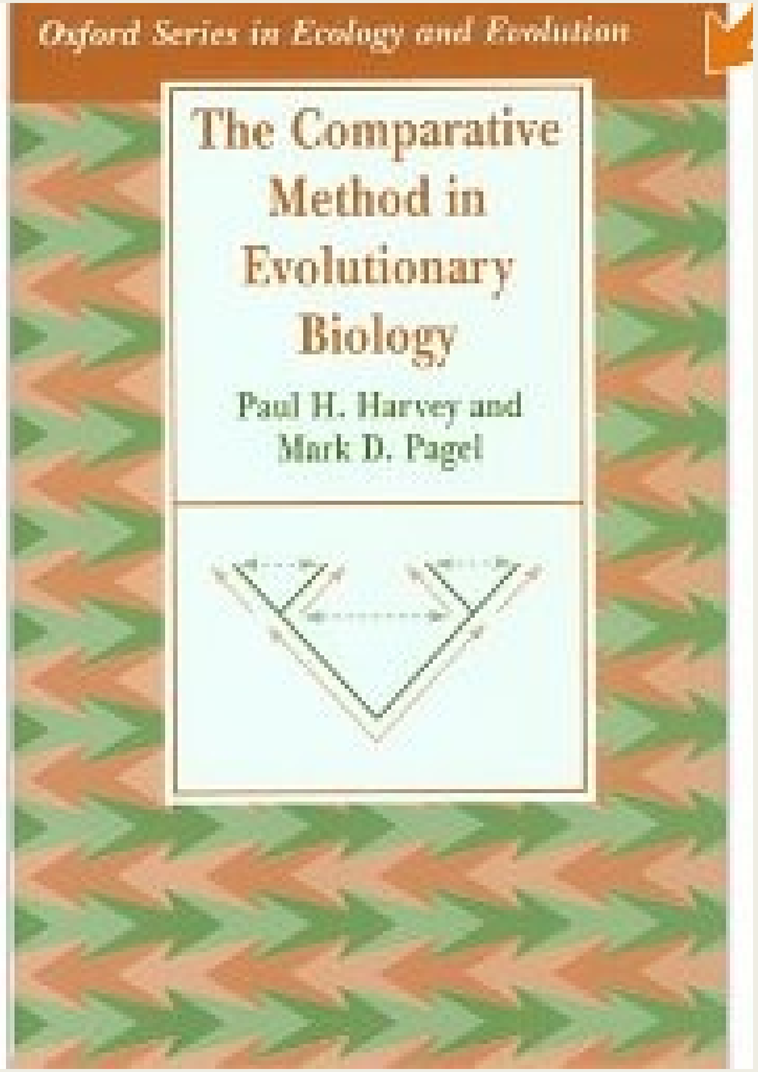
RAYMOND B. HUEY
Department of Zoology NJ-15, University of Washington, Seattle, WA 98195
AND
ALBERT F. BENNETT
School of Biological Sciences, University of California, Irvine, CA 92717

1987

Estimativa de estado ancestral: Squared-change parsimony

Principais métodos/Abordagens

- Estimativa (”reconstrução”) de estado ancestral
- Mensuração e teste de ”sinal” filogenético
- Ajuste de Modelos de Evolução à atributos (BM, OU, EB/LB, trend etc)
- Estimativa de taxas de evolução de atributo(s) ao longo da filogenia
- Estimativa de ótimos/picos/regimes adaptativos ao longo da filogenia
- Evolução correlacionada de atributos contínuos (PGLS, phyloGLM) e categóricos (Pagel’s method)



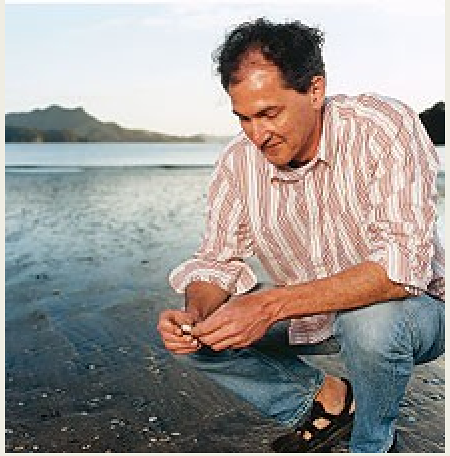
Oxford Series in Ecology and Evolution

The Comparative Method in Evolutionary Biology

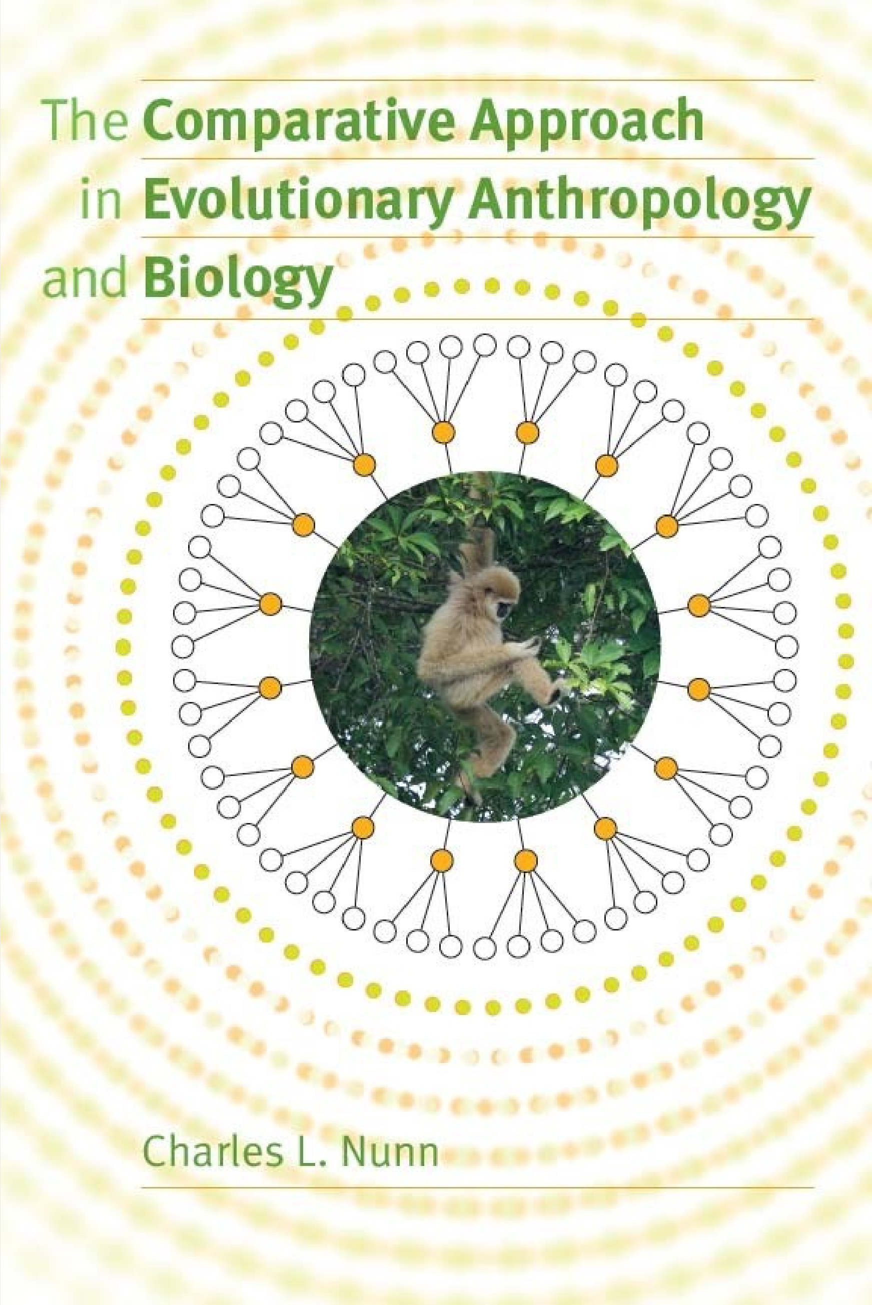
Paul H. Harvey and Mark D. Pagel

1991

Paul Harvey



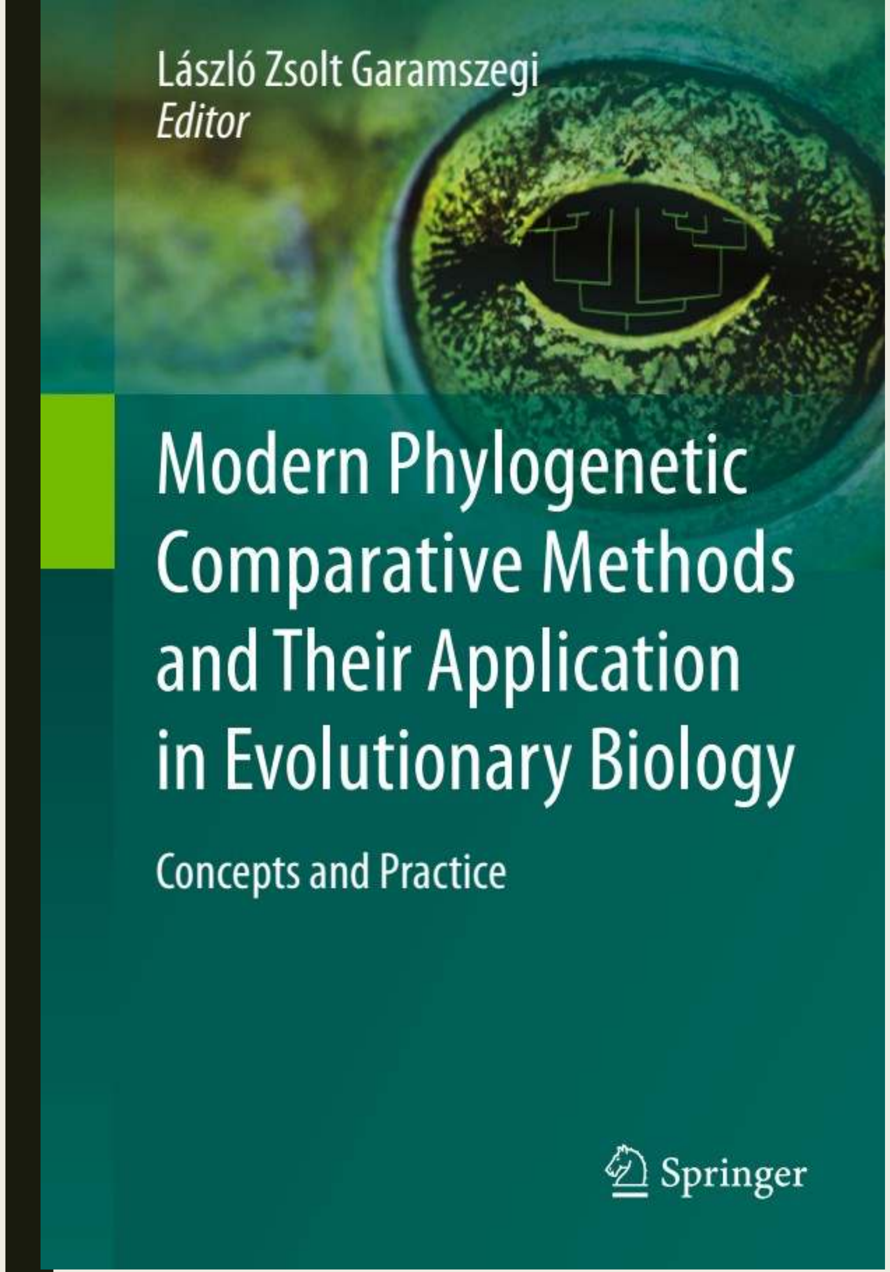
Mark Pagel



2011

Charles Nunn, Duke University

O que não



László Zsolt Garamszegi
Editor

Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology

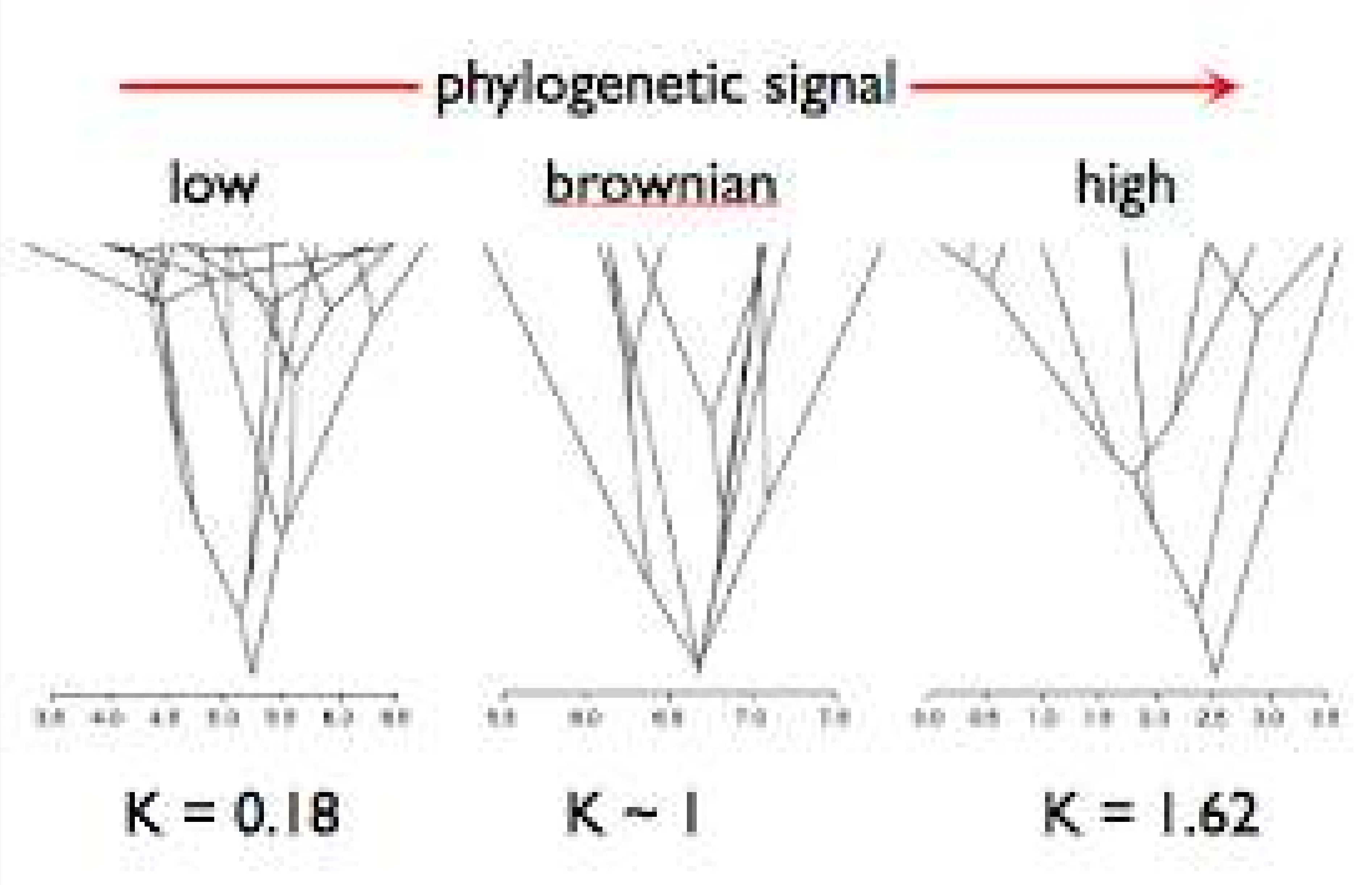
Concepts and Practice

Springer

2015

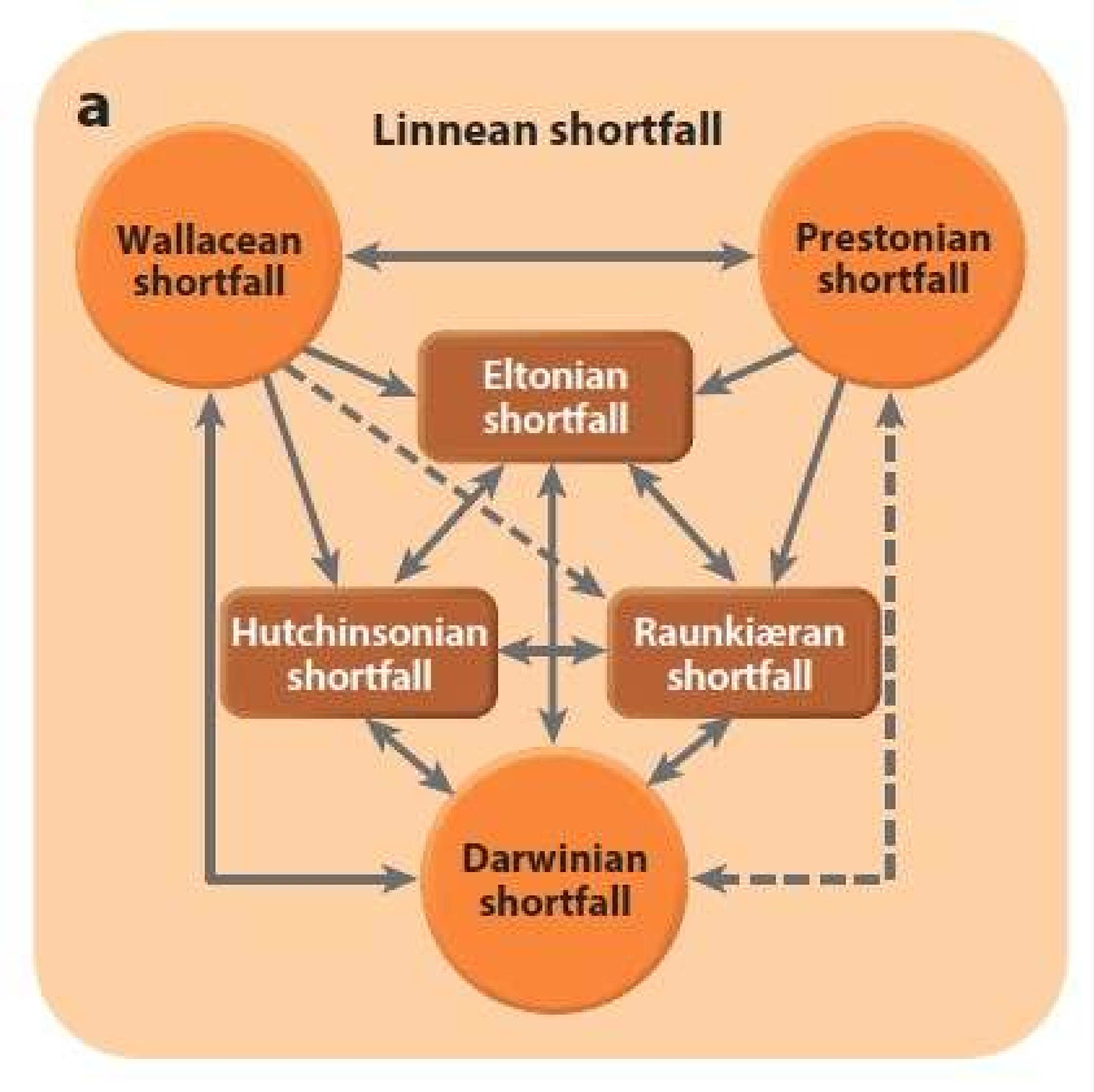
Sevilha, Espanha, Novembro 2014

http://www.mpcm-evolution.org/practice

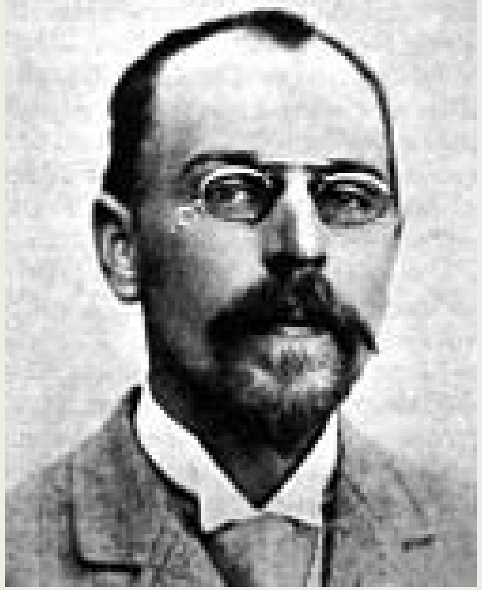

phylogenetic signal
low
brownian
high
3.5 4.0 4.5 5.0 5.5 6.0 6.5
5.5 6.0 6.5 7.0 7.5
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
K = 0.18
K ~ 1
K = 1.62

Problemas mais comuns

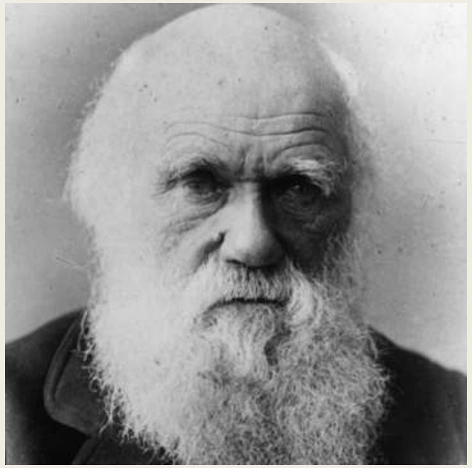
- Falta completa de dados (filogenéticos e traits)
- **Descasamento (*mismatch*) entre disponibilidade de dados de traits e de filogenias**
- Dados existem mas não estão acessíveis
- Déficits de conhecimento sobre biodiversidade: Darwiniano e Raunkiaeriano
  - *Dificultam ganho de conhecimento sobre evolução de atributos*
  - *Impedimento para estudos comparativos*



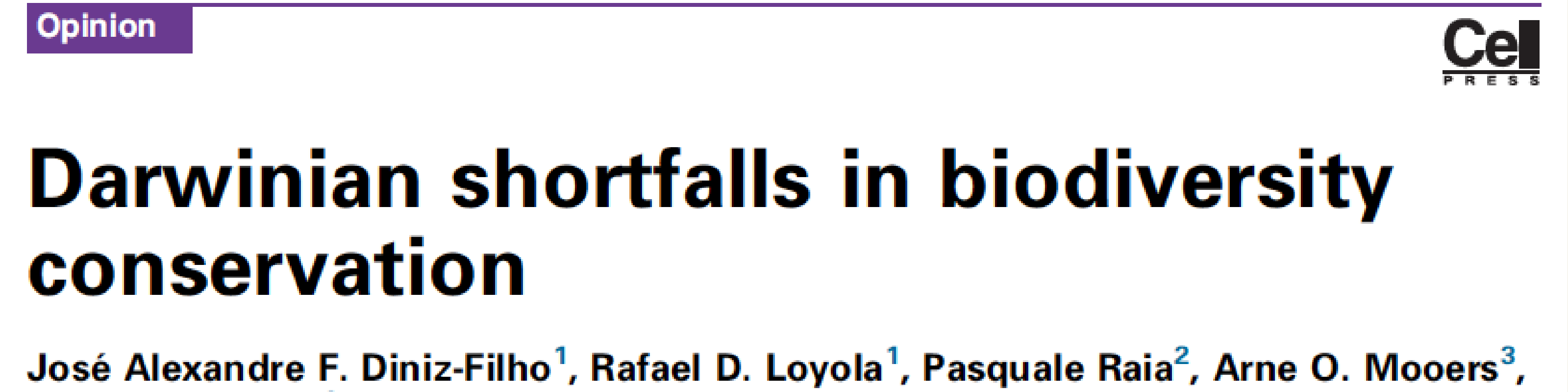
Hortal et al. 2015



Déficit Rauniaeriano
Falta de informações sobre atributos das espécies



Déficit Darwiniano
Falta de informações sobre relações entre espécies

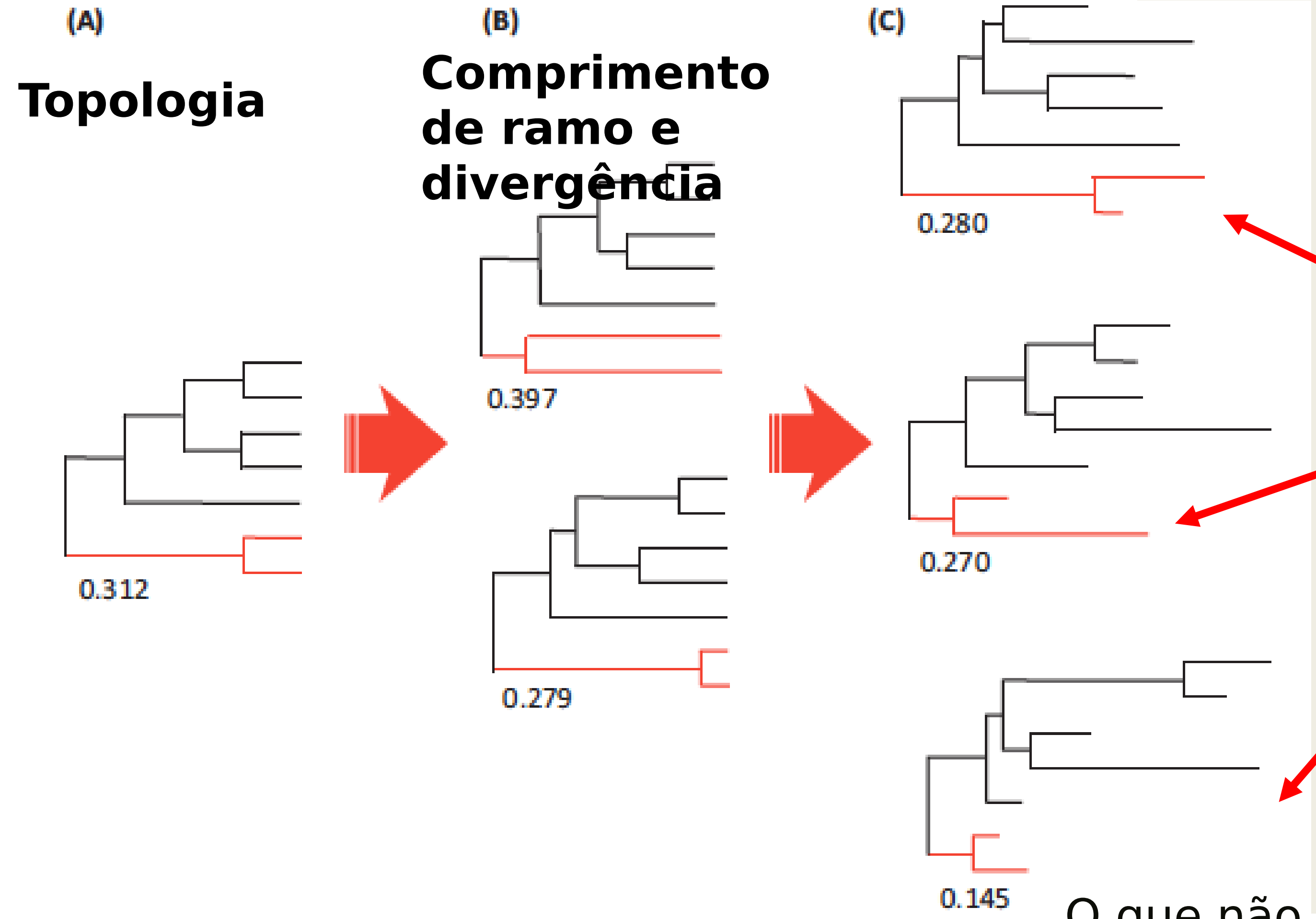


Opinion

Darwinian shortfalls in biodiversity conservation

José Alexandre F. Diniz-Filho[1], Rafael D. Loyola[1], Pasquale Raia[2], Arne O. Mooers[3], and Luis M. Bini[1]

Ignorâncias



Topologia

Comprimento de ramo e divergência

Modelo evolutivo De atributos

Meu deu
agora? Me
cucuia
doutorad
me soco

Pacotes phyndr e taxonlookup

Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2015

doi: 10.1111/2041-210X.12517

APPLICATION

A simple approach for maximizing the overlap of phylogenetic and comparative data

Matthew W. Pennell[1,2†], Richard G. FitzJohn[3†] and William K. Cornwell[4,5†]

- Maximiza a amostragem trocando espécies na árvore, para os quais não há dados de atributos, por espécies ”filogeneticamente equivalentes” sem alterar a estrutura da filogenia
  - Baseado em ranking taxonômico (ou só os nomes dos gêneros) ou uma árvore topológica
  - Alternativa a métodos de aleatorização ou de imputação de dados faltantes

Ecology and Evolution

Open Access

Filling the gap in functional trait databases: use of ecological hypotheses to replace missing data

Simon Taugourdeau[1,2,3], Jean Villerd[1,2], Sylvain Plantureux[1,2], Olivier Huguenin-Elie[3] & Bernard Amiaud[4,5]

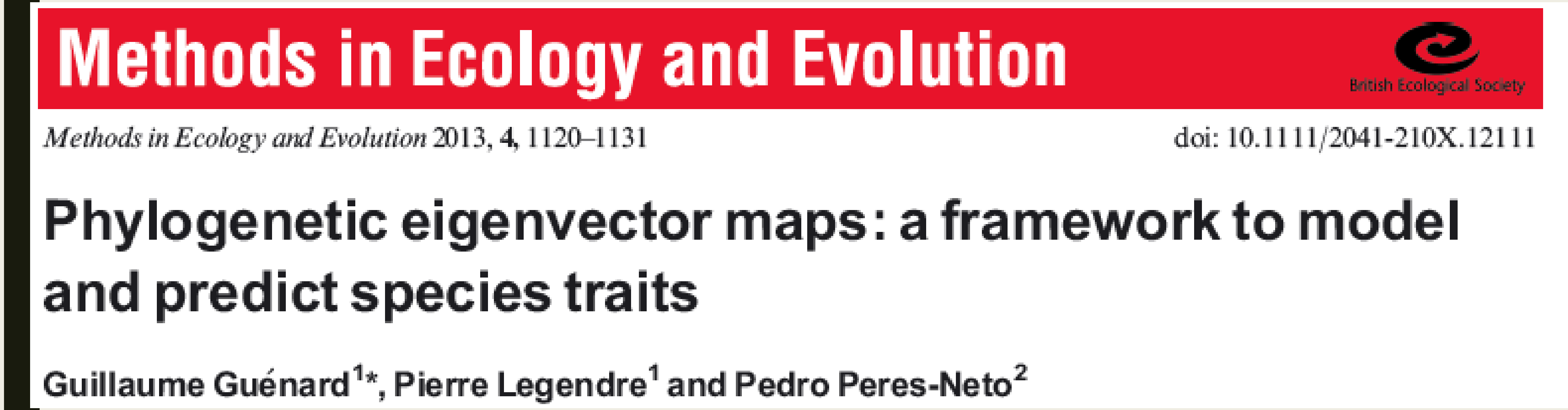
Forum

EDITOR'S CHOICE

Ecography 37: 105–110, 2014
doi: 10.1111/j.1600-0587.2013.00528.x
© 2013 The Author. Ecography © 2013 Nordic Society Oikos
Subject Editor: Nathan J. Sanders. Accepted 26 July 2013

Phylogenetic imputation of plant functional trait databases

Nathan G. Swenson



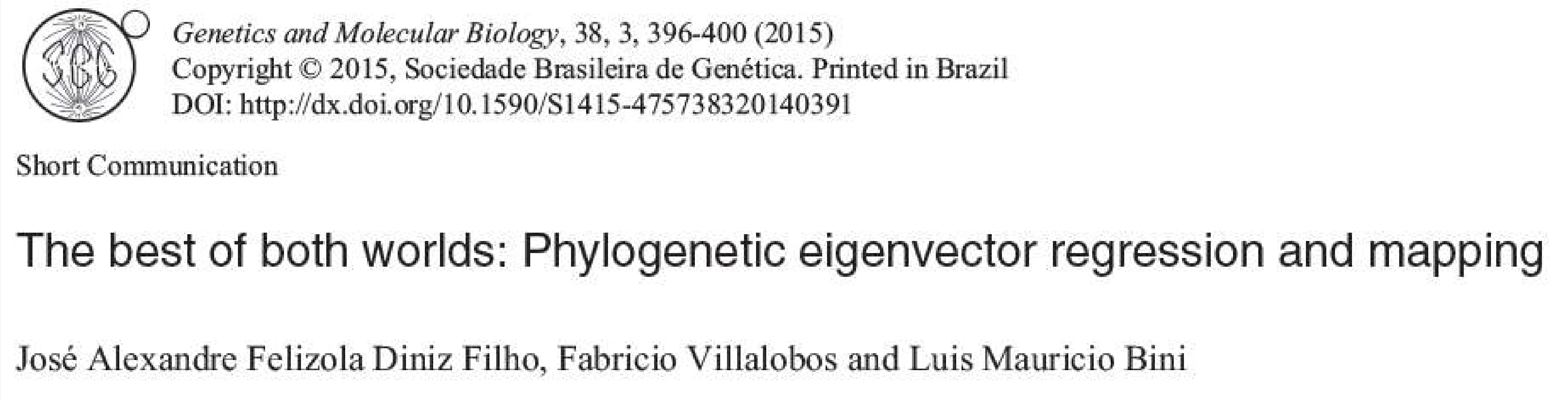
Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2013, 4, 1120–1131 doi: 10.1111/2041-210X.12111

Phylogenetic eigenvector maps: a framework to model and predict species traits

Guillaume Guénard[1]*, Pierre Legendre[1] and Pedro Peres-Neto[2]

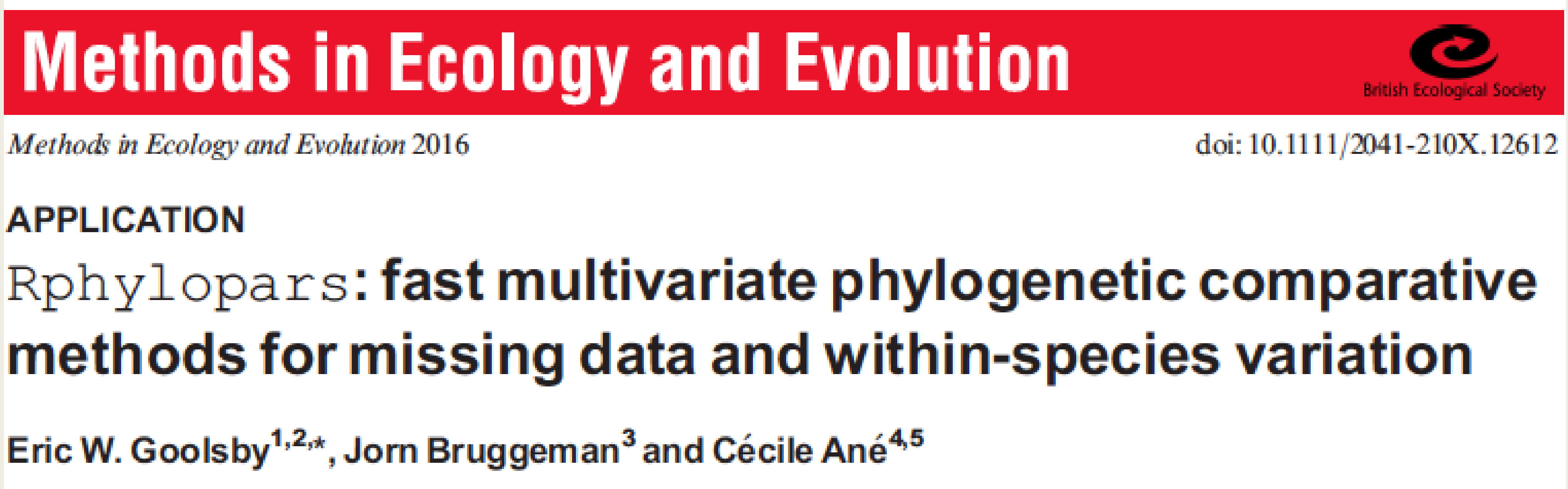


Genetics and Molecular Biology, 38, 3, 396-400 (2015)
Copyright © 2015, Sociedade Brasileira de Genética. Printed in Brazil
DOI: http://dx.doi.org/10.1590/S1415-475738320140391

Short Communication

The best of both worlds: Phylogenetic eigenvector regression and mapping

José Alexandre Felizola Diniz Filho, Fabricio Villalobos and Luis Mauricio Bini



Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2016 doi: 10.1111/2041-210X.12612

APPLICATION

`Rphylopars`: fast multivariate phylogenetic comparative methods for missing data and within-species variation

Eric W. Goolsby[1,2,*], Jorn Bruggeman[3] and Cécile Ané[4,5]

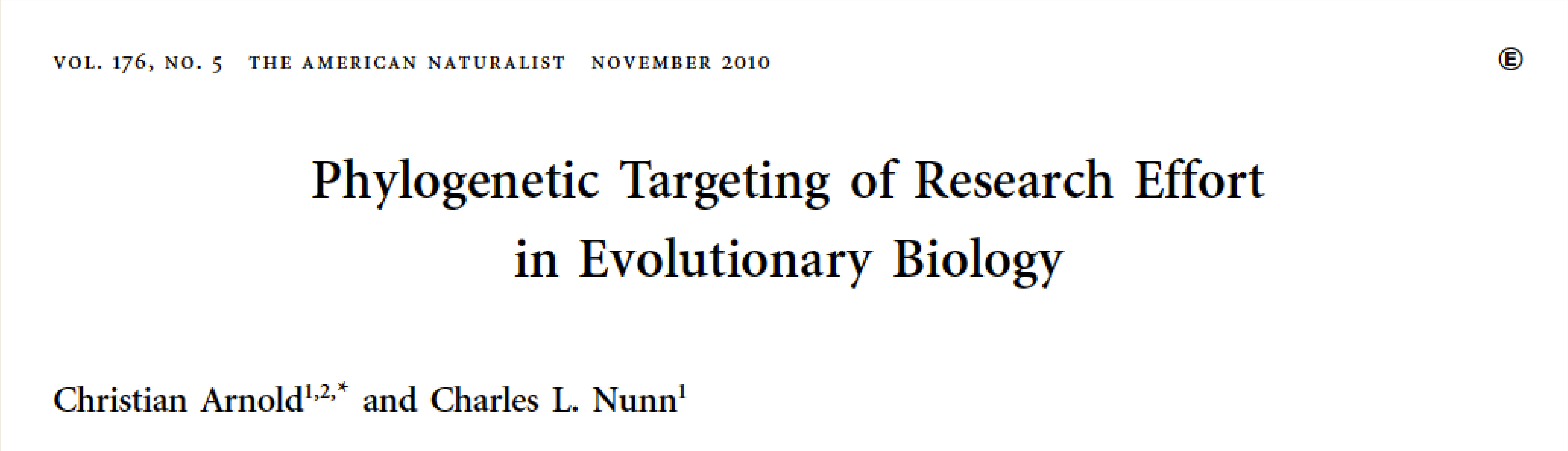
Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2014 doi: 10.1111/2041-210X.12232

Imputation of missing data in life-history trait datasets: which approach performs the best?

Caterina Penone[1*], Ana D. Davidson[2,3], Kevin T. Shoemaker[2], Moreno Di Marco[4], Carlo Rondinini[4], Thomas M. Brooks[5], Bruce E. Young[3], Catherine H. Graham[2] and Gabriel C. Costa[1]



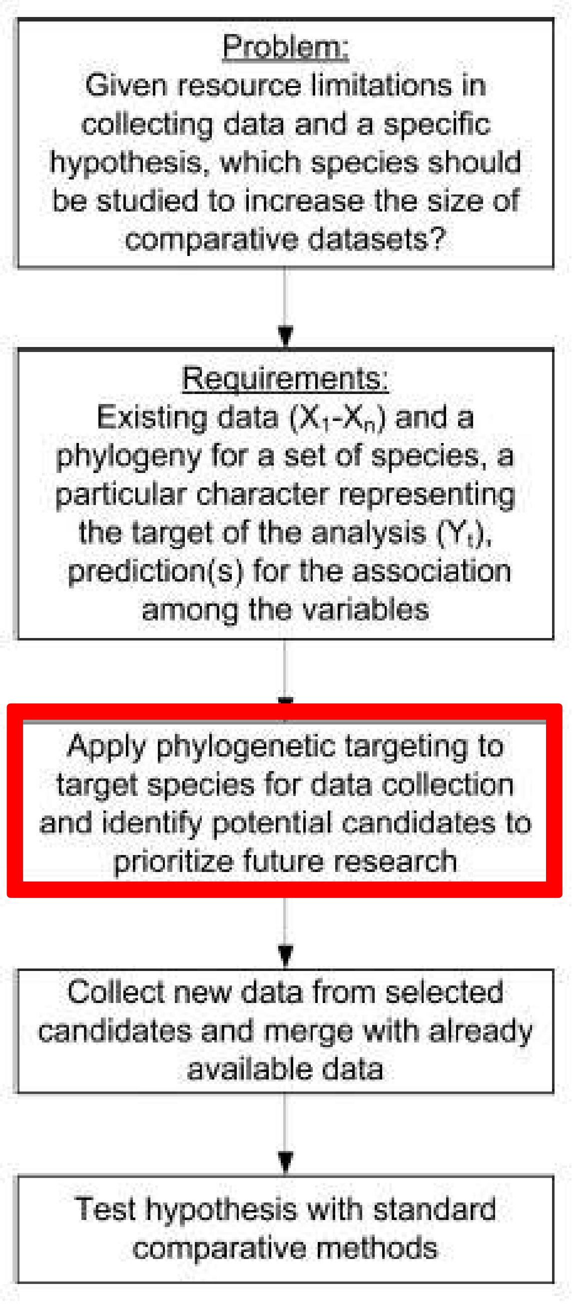
VOL. 176, NO. 5 THE AMERICAN NATURALIST NOVEMBER 2010

Phylogenetic Targeting of Research Effort in Evolutionary Biology

Christian Arnold[1,2,*] and Charles L. Nunn[1]

Workflow PhyloTargeting

3 Atributos contínuos



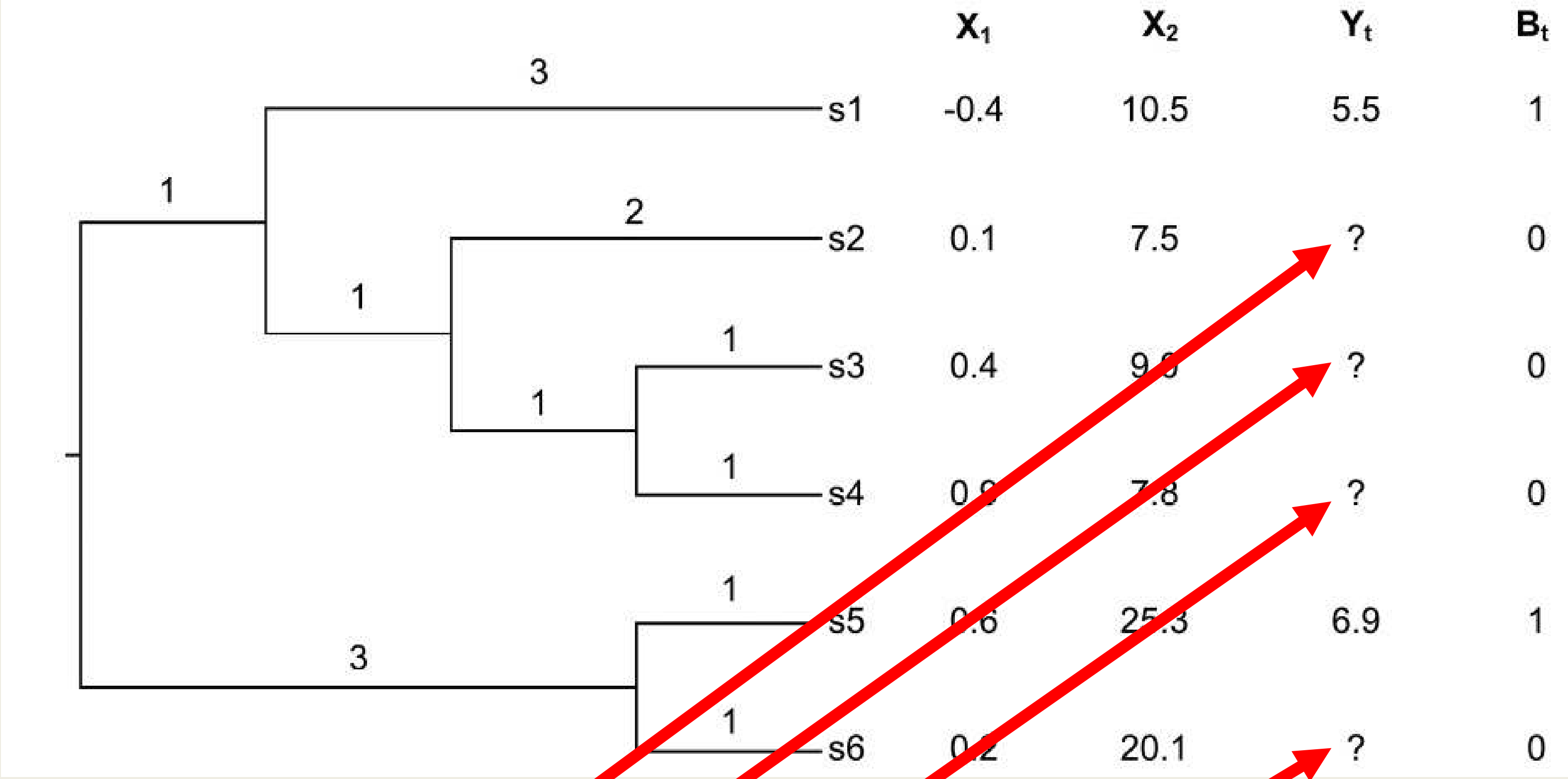
Problem:
Given resource limitations in collecting data and a specific hypothesis, which species should be studied to increase the size of comparative datasets?

Requirements:
Existing data (X_1-X_n) and a phylogeny for a set of species, a particular character representing the target of the analysis (Y_t), prediction(s) for the association among the variables

Apply phylogenetic targeting to target species for data collection and identify potential candidates to prioritize future research

Collect new data from selected candidates and merge with already available data

Test hypothesis with standard comparative methods



	X_1	X_2	Y_t	B_t
s1	-0.4	10.5	5.5	1
s2	0.1	7.5	?	0
s3	0.4	9.0	?	0
s4	0.8	7.8	?	0
s5	0.6	25.3	6.9	1
s6	0.2	20.1	?	0

Espécies com dados faltantes
Para variável resposta

Como otimizar o levantamento de dados?

Limitações de PCMs

VOL. 177, NO. 6 THE AMERICAN NATURALIST JUNE 2011

Seeing the Forest for the Trees: The Limitations of Phylogenies in Comparative Biology

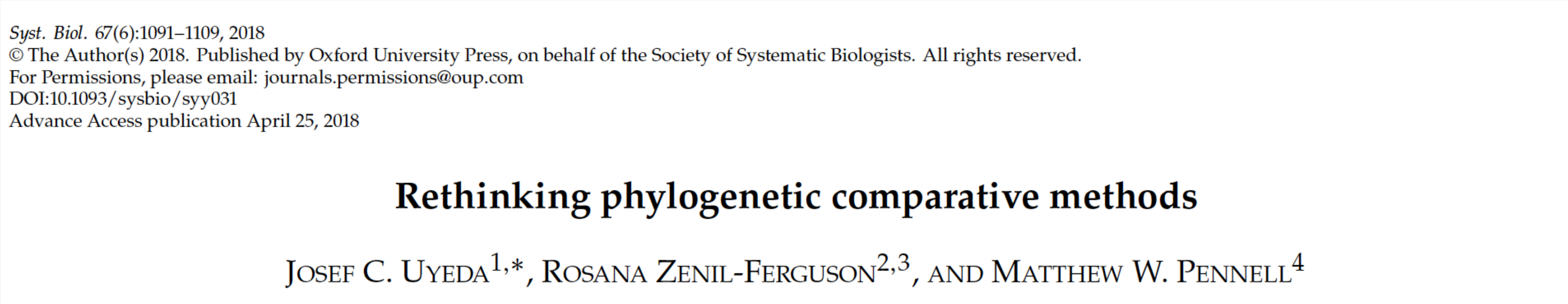
(American Society of Naturalists Address)*

Jonathan B. Losos†

Limitações de PCMs

- Muitos atributos não exibem sinal filogenético, ou seja, tem pouca correlação com a filogenia
  - *Depende da escala filogenética, estatística usada etc*
  - *Convergência (compartilhamento do mesmo regime adaptativo)*
- Estimativas de estados ancestrais tem muita incerteza
  - *Necessidade de incorporar informações de fósseis*
  - *Atributos evoluem sob taxas e modelos diferentes*
- Filogenias são pouco úteis quando há muita variação intraespecífica
- Filogenias ajudam a desvendar padrões, e não processos
  - *Velha história: inferir processos a partir de padrão*
  - *Mesmo padrão pode ser causado por diversos processos*
  - *Evite perguntas dicotômicas: ”efeito relativo da filogenia (ou pior ”história) e ecologia numa característica”*
  - *Filogenias não ”causam” nada, mas sim são maneiras de representar a história evolutiva de um grupo*

> “Phylogenetics is a powerful tool for understanding evolution, but it is not omnipotent.”



Syst. Biol. 67(6):1091–1109, 2018

DOI:10.1093/sysbio/syy031
Advance Access publication April 25, 2018

Rethinking phylogenetic comparative methods

JOSEF C. UYEDA[1,*], ROSANA ZENIL-FERGUSON[2,3], AND MATTHEW W. PENNELL[4]

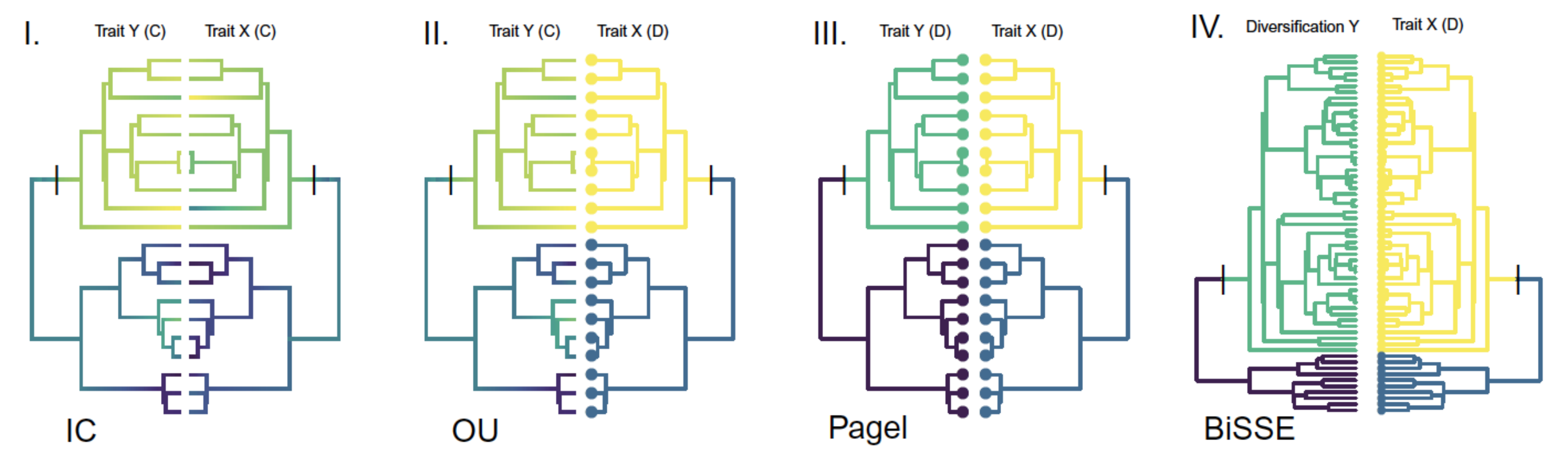
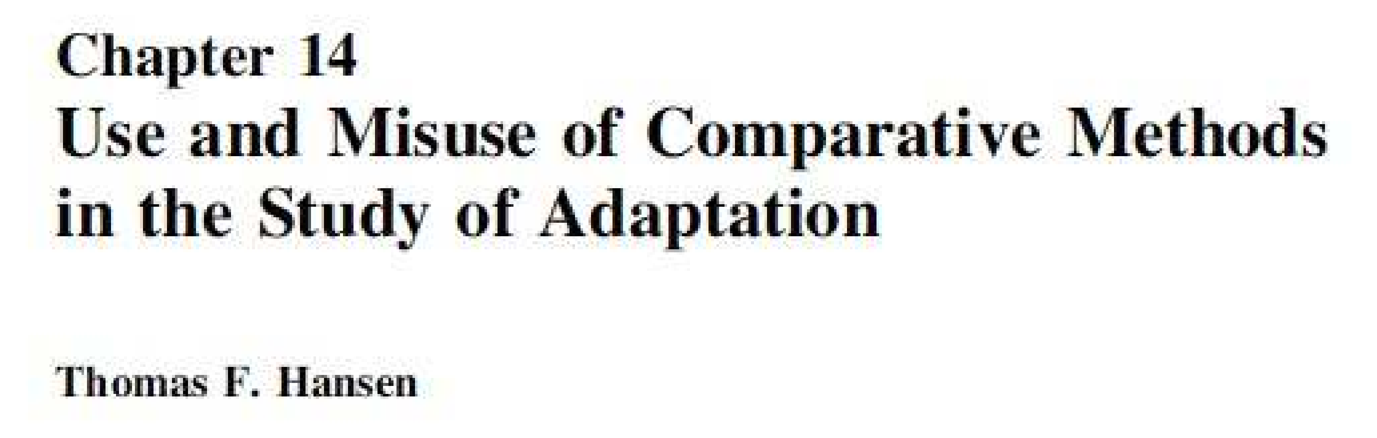


FIGURE 1. Singular, unreplicated events (vertical dashes) can generate apparently significant associations across several types of comparative analyses. Case Studies I–III are indicated in panels I–III, and though we do not consider diversification models such as BiSSE in our examples, they are similarly affected (panel IV). In each case, we map (in some cases, arbitrarily) the dependent variable (*Y*) on the phylogeny on the left and the predictor trait on the same phylogeny to the right (*X*), and indicate whether the trait is a continuous trait (C), a discrete trait (D) or a diversification rate. Colors on the branches indicate the state of the character on the phylogeny—either continuous trait value, discrete character state, or diversification rate regime. Panels I and III correspond to variations of "Felsenstein's worst-case scenario" and "Darwin's scenario," respectively. We also suggest a common method used to analyze such associations: IC = Independent Contrasts (Felsenstein 1985); OU = Ornstein–Uhlenbeck models (Butler and King 2004); Pagel = Pagel's correlation test (Pagel 1994).

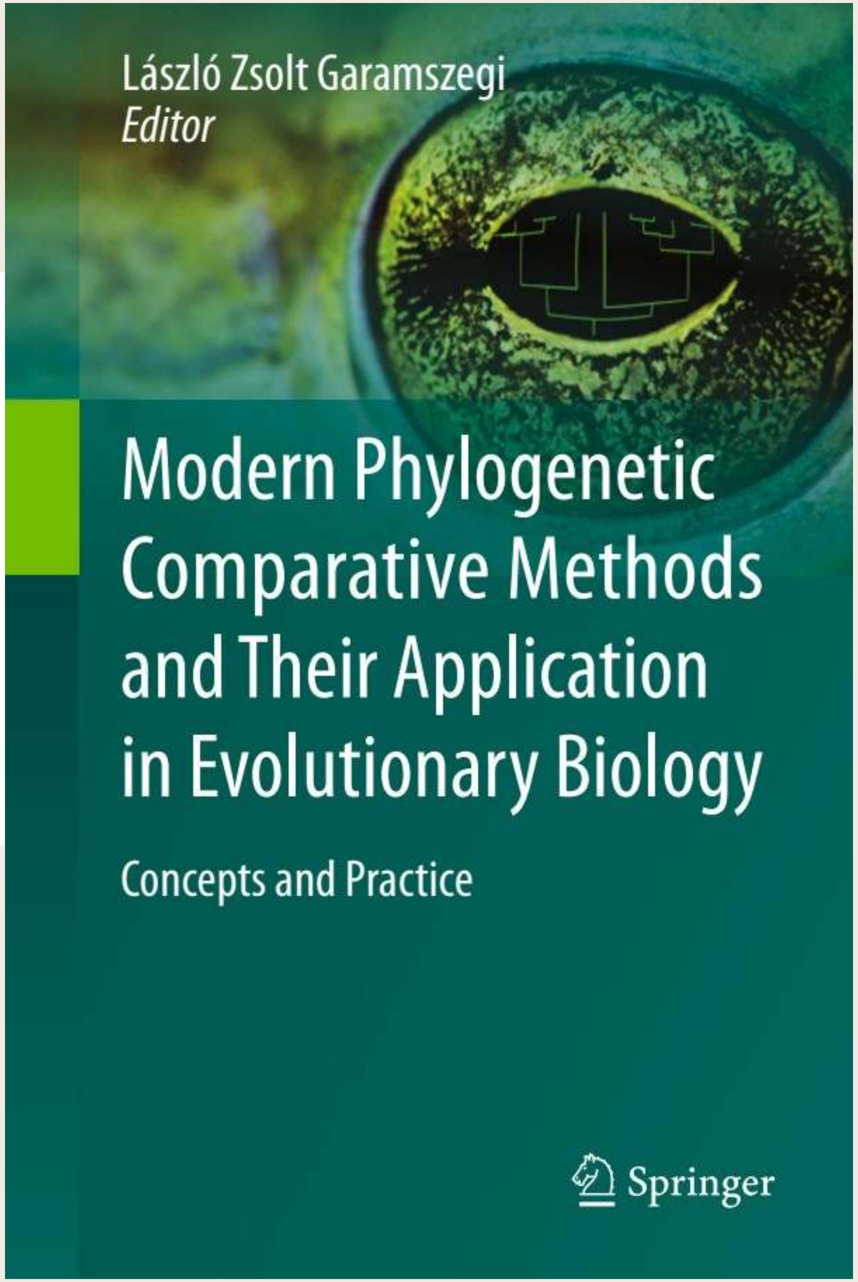
Desusos de Métodos Comparativos



Chapter 14

Use and Misuse of Comparative Methods in the Study of Adaptation

Thomas F. Hansen

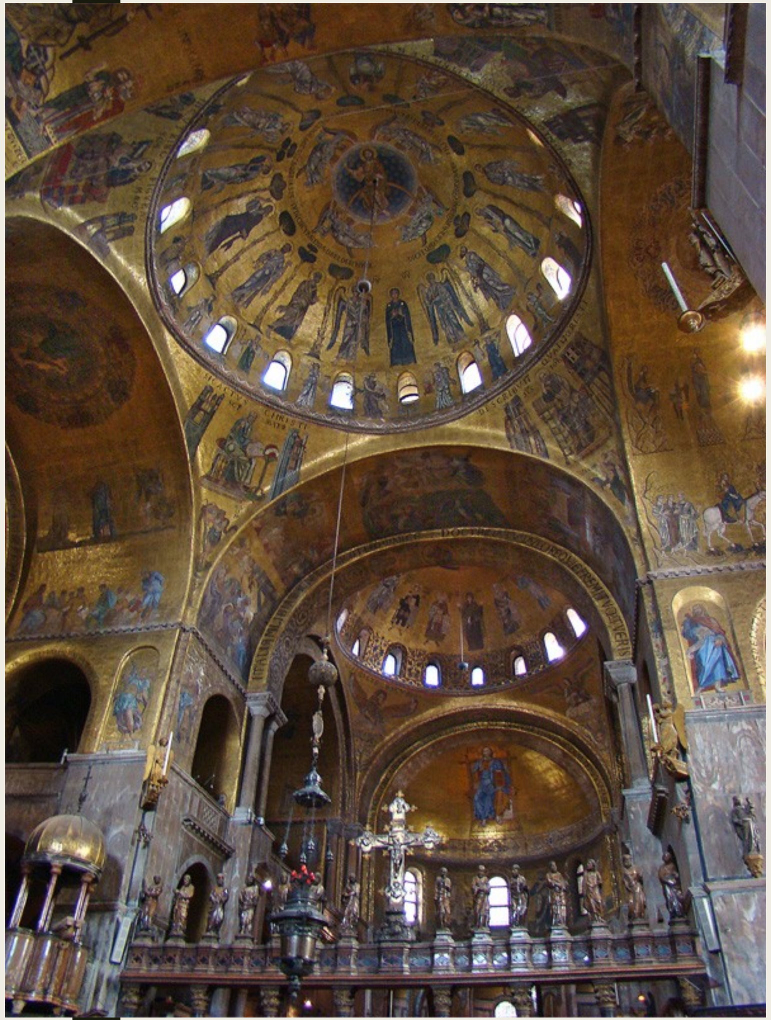


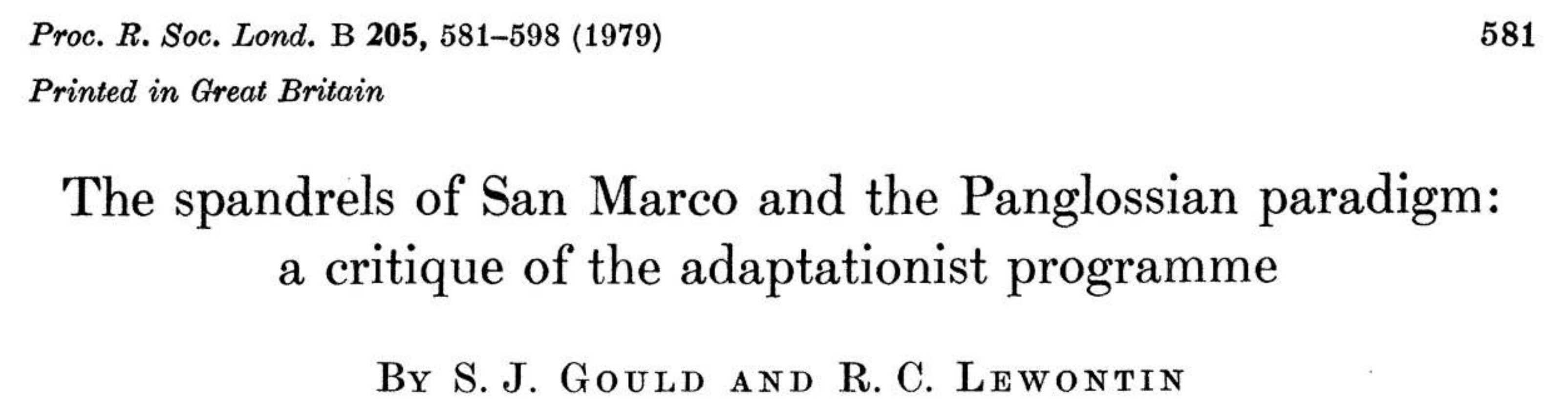
László Zsolt Garamszegi
Editor

Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology

Concepts and Practice

Springer





Proc. R. Soc. Lond. B **205,** 581–598 (1979) **581**
Printed in Great Britain

The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme

BY S. J. GOULD AND R. C. LEWONTIN

Interpretação de evidências de adaptação

- Um padrão pode ser gerado por vários processos
- Só uma boa conexão entre a pergunta e o processo de interesse junto com avaliação de hipóteses alternativas permite inferir adaptação
  - *Sempre levar em conta relações alométricas (com tamanho do corpo)*
- Importância de se usar modelos evolutivos adequados (e.g., OU)
- Toda adaptação é fruto de seleção, mas nem toda leva à adaptação.
  - *Correlação entre atributos, um estado de um atributo pode surgir como correlação a um outro e não como resposta a uma pressão evolutiva*
  - *Levar em conta o contexto ambiental (ou social se for o caso)*

doi:10.1111/j.1420-9101.2009.01757.x

REVIEW

The seven deadly sins of comparative analysis

R. P. FRECKLETON

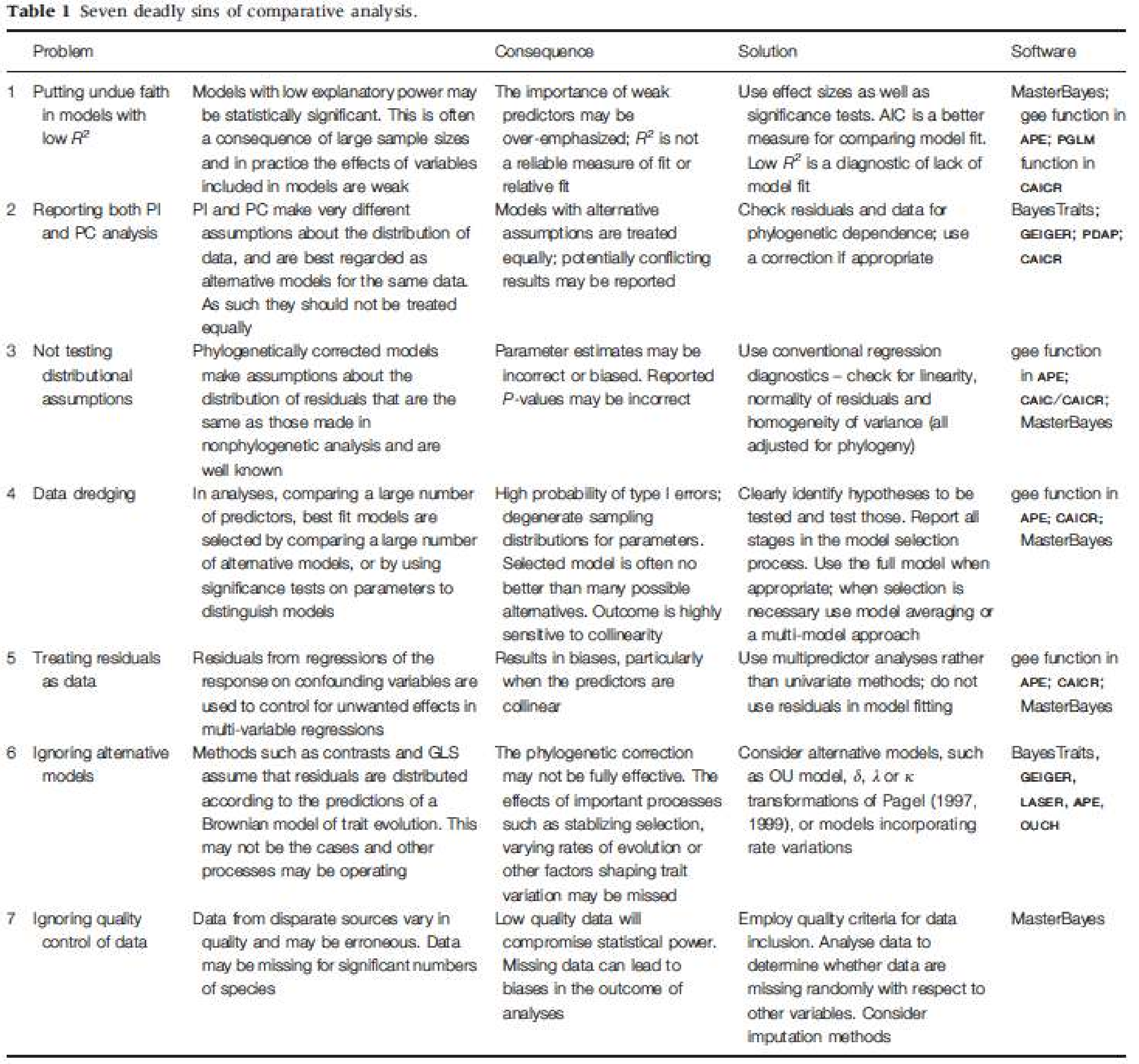


Table 1 Seven deadly sins of comparative analysis.

	Problem		Consequence	Solution	Software
1	Putting undue faith in models with low R^2	Models with low explanatory power may be statistically significant. This is often a consequence of large sample sizes and in practice the effects of variables included in models are weak	The importance of weak predictors may be over-emphasized; R^2 is not a reliable measure of fit or relative fit	Use effect sizes as well as significance tests. AIC is a better measure for comparing model fit. Low R^2 is a diagnostic of lack of model fit	MasterBayes; gee function in APE; PGLM function in CAICR
2	Reporting both PI and PC analysis	PI and PC make very different assumptions about the distribution of data, and are best regarded as alternative models for the same data. As such they should not be treated equally	Models with alternative assumptions are treated equally; potentially conflicting results may be reported	Check residuals and data for phylogenetic dependence; use a correction if appropriate	BayesTraits; GEIGER; PDAP; CAICR
3	Not testing distributional assumptions	Phylogenetically corrected models make assumptions about the distribution of residuals that are the same as those made in nonphylogenetic analysis and are well known	Parameter estimates may be incorrect or biased. Reported *P*-values may be incorrect	Use conventional regression diagnostics – check for linearity, normality of residuals and homogeneity of variance (all adjusted for phylogeny)	gee function in APE; CAIC/CAICR; MasterBayes
4	Data dredging	In analyses, comparing a large number of predictors, best fit models are selected by comparing a large number of alternative models, or by using significance tests on parameters to distinguish models	High probability of type I errors; degenerate sampling distributions for parameters. Selected model is often no better than many possible alternatives. Outcome is highly sensitive to collinearity	Clearly identify hypotheses to be tested and test those. Report all stages in the model selection process. Use the full model when appropriate; when selection is necessary use model averaging or a multi-model approach	gee function in APE; CAICR; MasterBayes
5	Treating residuals as data	Residuals from regressions of the response on confounding variables are used to control for unwanted effects in multi-variable regressions	Results in biases, particularly when the predictors are collinear	Use multipredictor analyses rather than univariate methods; do not use residuals in model fitting	gee function in APE; CAICR; MasterBayes
6	Ignoring alternative models	Methods such as contrasts and GLS assume that residuals are distributed according to the predictions of a Brownian model of trait evolution. This may not be the cases and other processes may be operating	The phylogenetic correction may not be fully effective. The effects of important processes such as stablizing selection, varying rates of evolution or other factors shaping trait variation may be missed	Consider alternative models, such as OU model, δ, λ or κ transformations of Pagel (1997, 1999), or models incorporating rate variations	BayesTraits, GEIGER, LASER, APE, OUCH
7	Ignoring quality control of data	Data from disparate sources vary in quality and may be erroneous. Data may be missing for significant numbers of species	Low quality data will compromise statistical power. Missing data can lead to biases in the outcome of analyses	Employ quality criteria for data inclusion. Analyse data to determine whether data are missing randomly with respect to other variables. Consider imputation methods	MasterBayes

Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2016, 7, 693–699

doi: 10.1111/2041-210X.12533

SPECIAL FEATURE: 5TH ANNIVERSARY OF *METHODS IN ECOLOGY AND EVOLUTION*

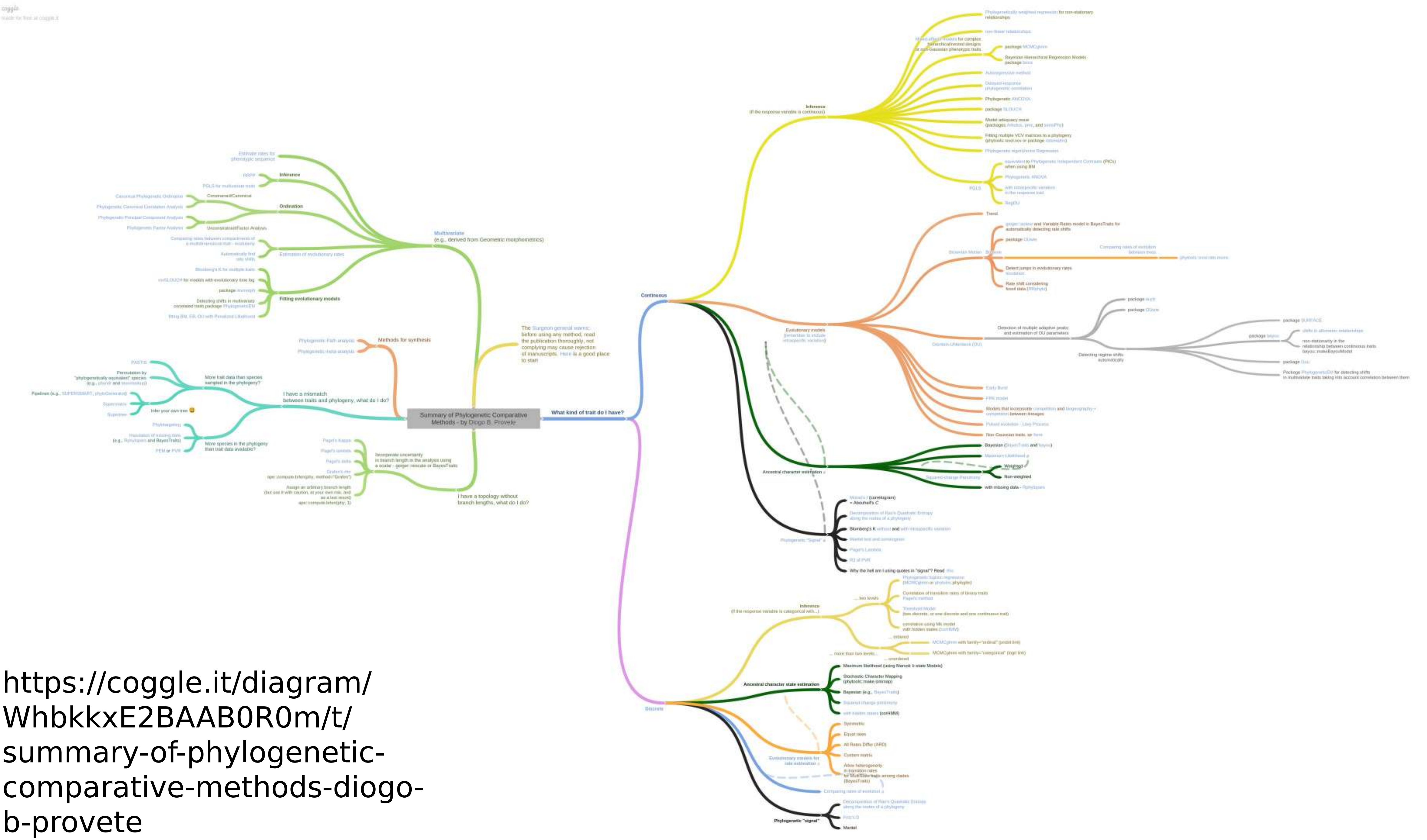
Shedding light on the 'dark side' of phylogenetic comparative methods

Natalie Cooper[1,2*], Gavin H. Thomas[3] and Richard G. FitzJohn[4]

- Leitura cuidadosa antes de utilizar os métodos no R
- Sempre ser crítico sobre os resultados
- Importância de se reportar as análises utilizando ferramentas de reprodutibilidade (R Markdown, LaTeX etc)

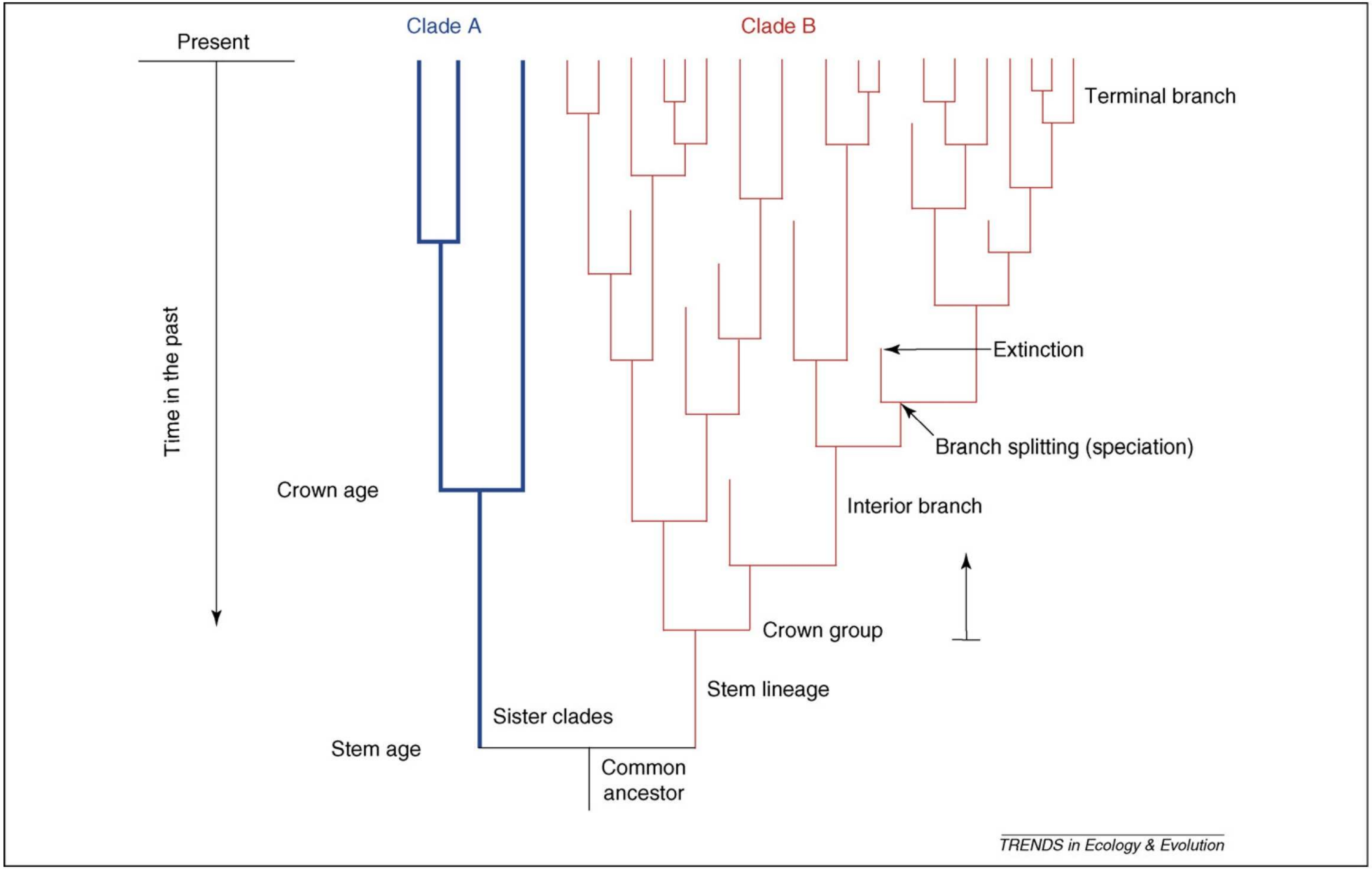
Onde encontrar mais informações sobre PCMs?

- Canais do YouTube
  - *Evolution 2015, 2016 (Vídeos com palestras do congresso)*
  - *PhyloMeth (Curso online sobre métodos comparativos)*
  - *NMBios (cursos sobre genética quantitativa e métodos comparativos*
  - *Phyloseminar (ciclo de palestras online sobre diversos temas em ecologia e evolução)*
- Listas de email (R-SIG-PHYLO) e foruns (stackoverflow.com)
- Cursos do Liam Revell e Luke Harmon (disponíveis no GitHub)
- Companion sites de livros do Charles Nunn e Garamszegi



https://coggle.it/diagram/WhbkkxE2BAAB0R0m/t/summary-of-phylogenetic-comparative-methods-diogo-b-provete

Métodos para inferir dinâmica de diversificação de linhagens

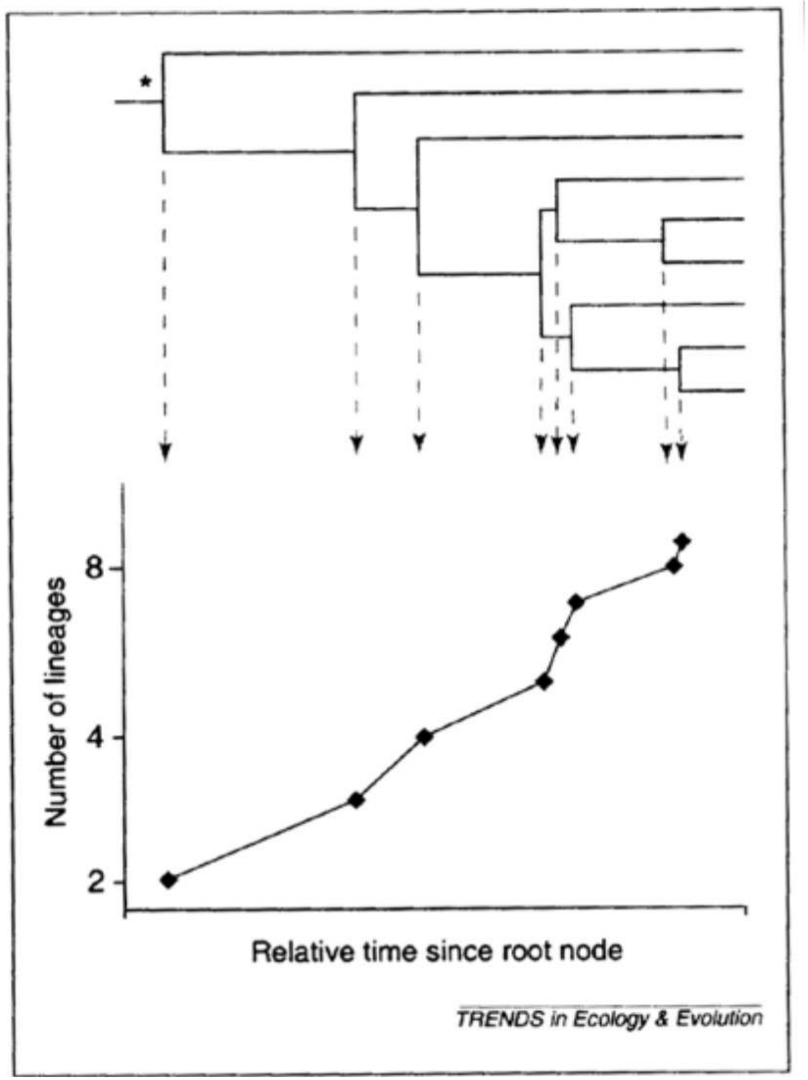


TRENDS in Ecology & Evolution

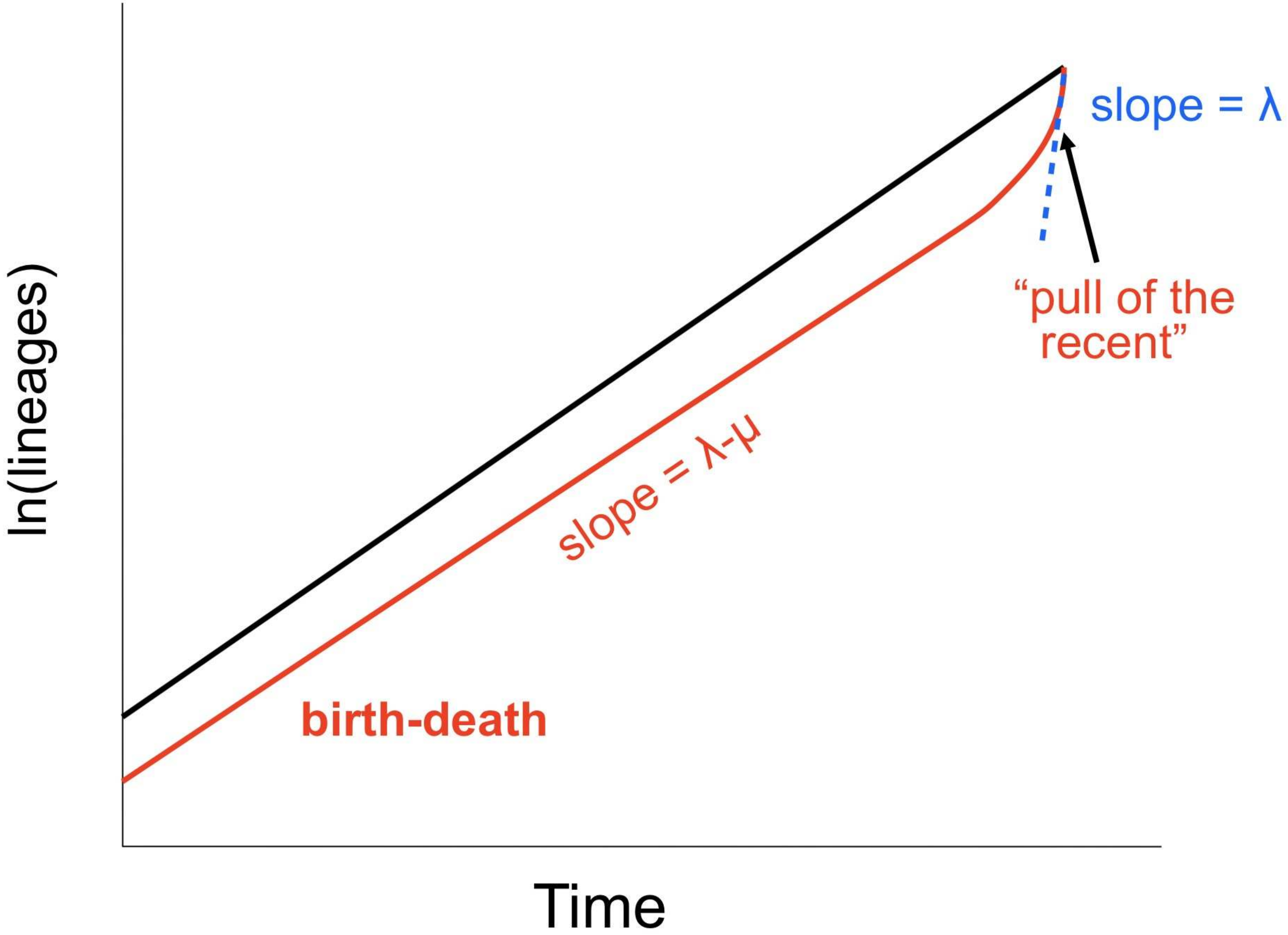
Figure 1. Terms pertaining to phylogenetic trees. Sister clades A and B have a common ancestor at the base of the phylogeny from which the stem lineage (i.e. common ancestor) of each clade descends. At any one time, a clade consists of two or more independently evolving lineages, which are branches of the tree. The stem age of a clade

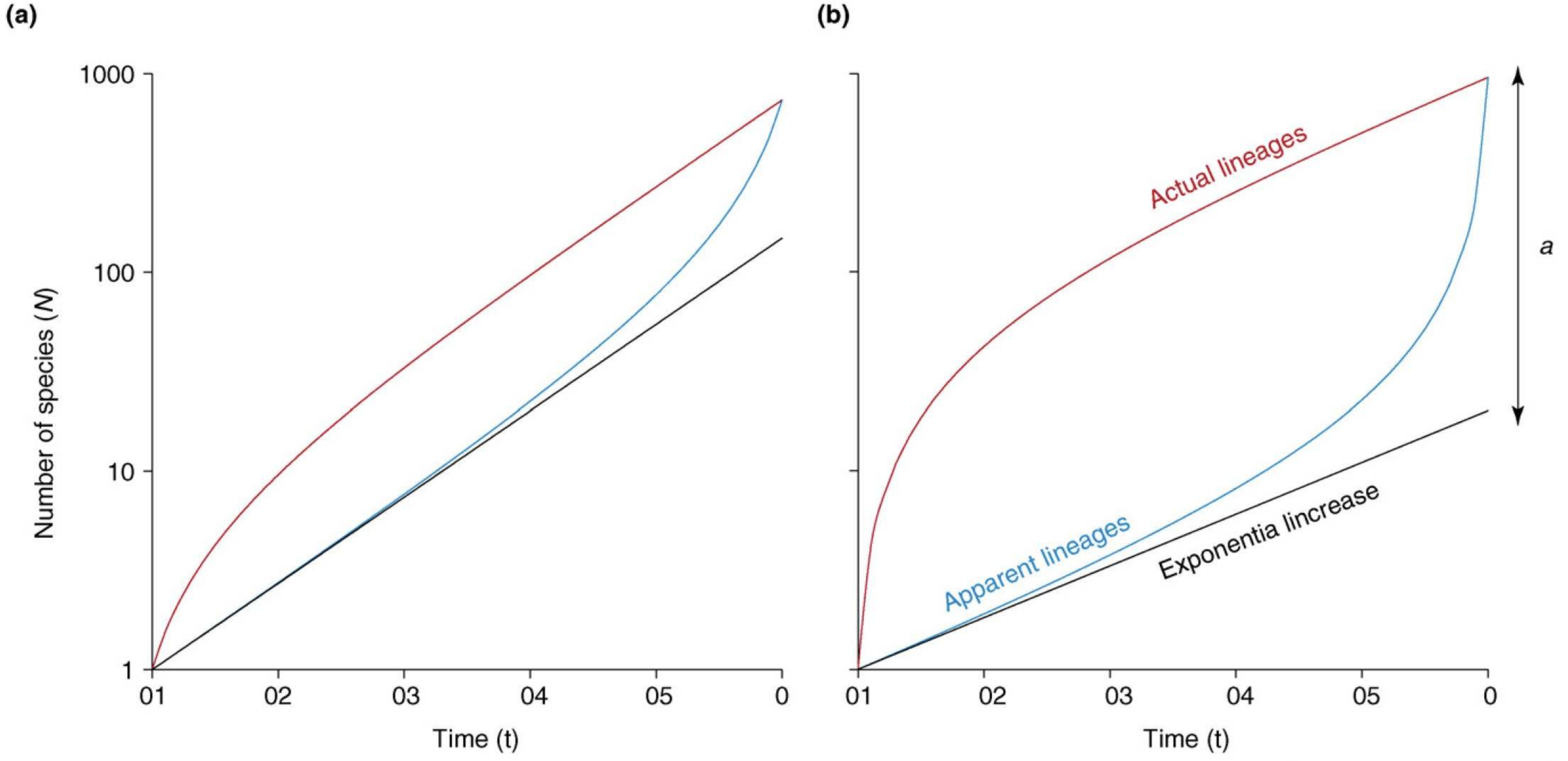
Ricklefs 200

Lineage-through-time



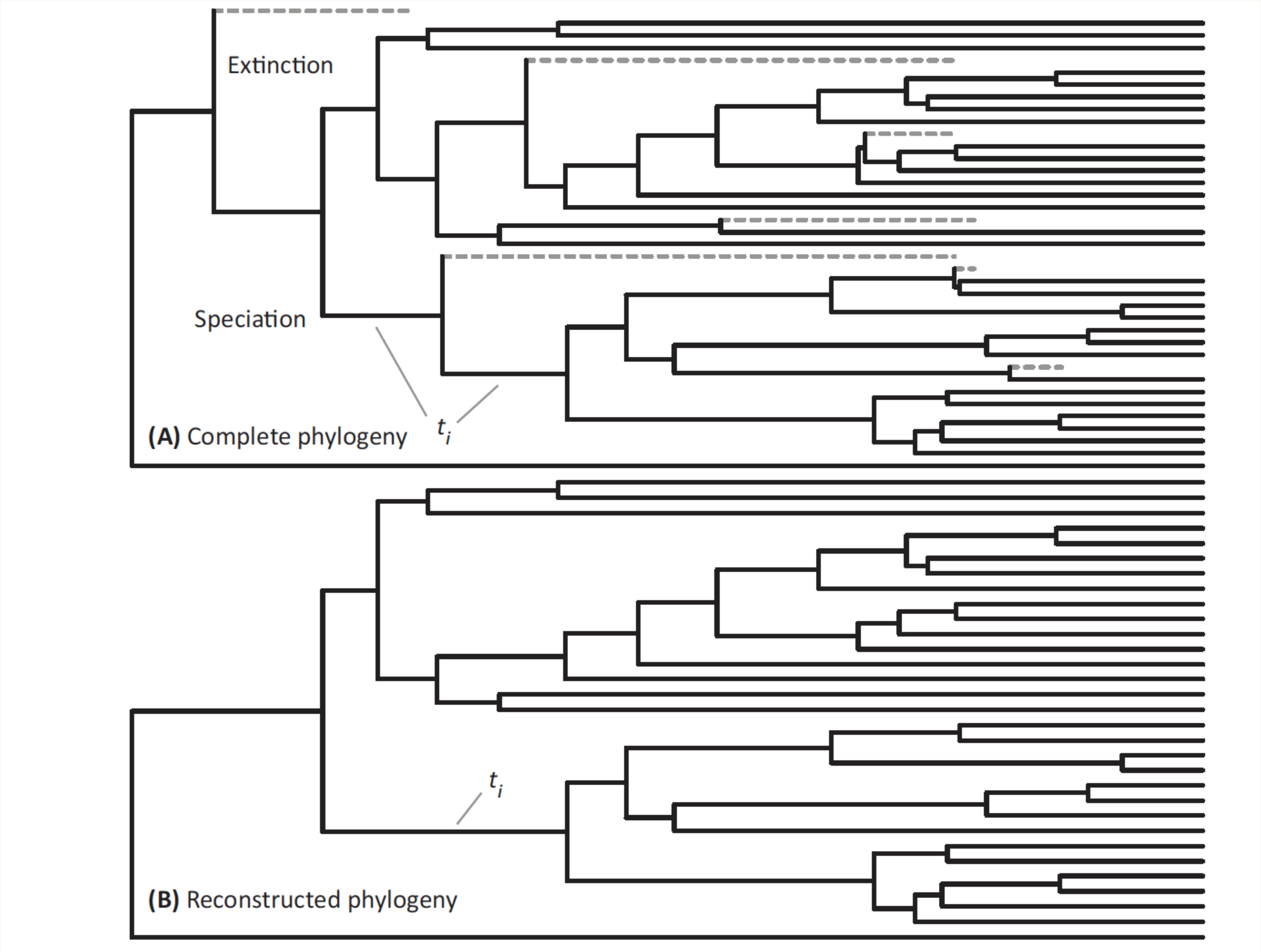
Barraclough T.G., Nee S. 2001. Phylogenetics and speciation. Trends Ecol. Evol. 16:391–399.


slope = λ
"pull of the recent"
slope = λ-μ
birth-death
ln(lineages)
Time

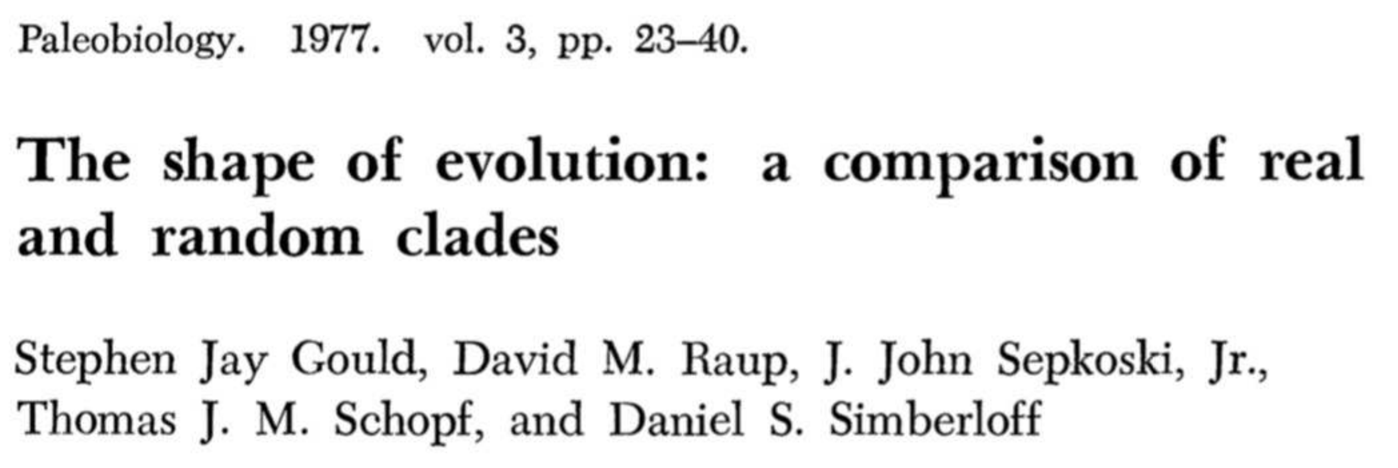


TRENDS in Ecology & Evolution

Figure I. LTT plots for the average number of extant (actual) lineages (N) (red lines) and the average number of apparent lineages (i.e. ancestral to living species) (N_A)



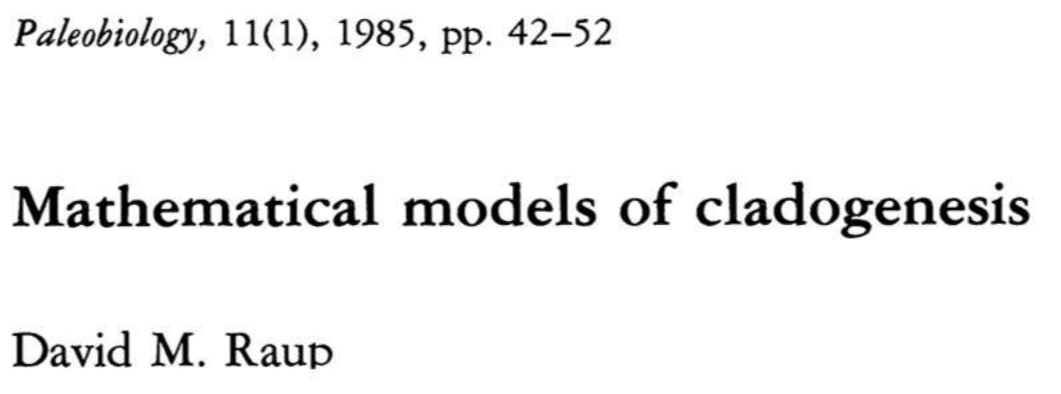
Pyron & Burbrunk



Paleobiology. 1977. vol. 3, pp. 23–40.

The shape of evolution: a comparison of real and random clades

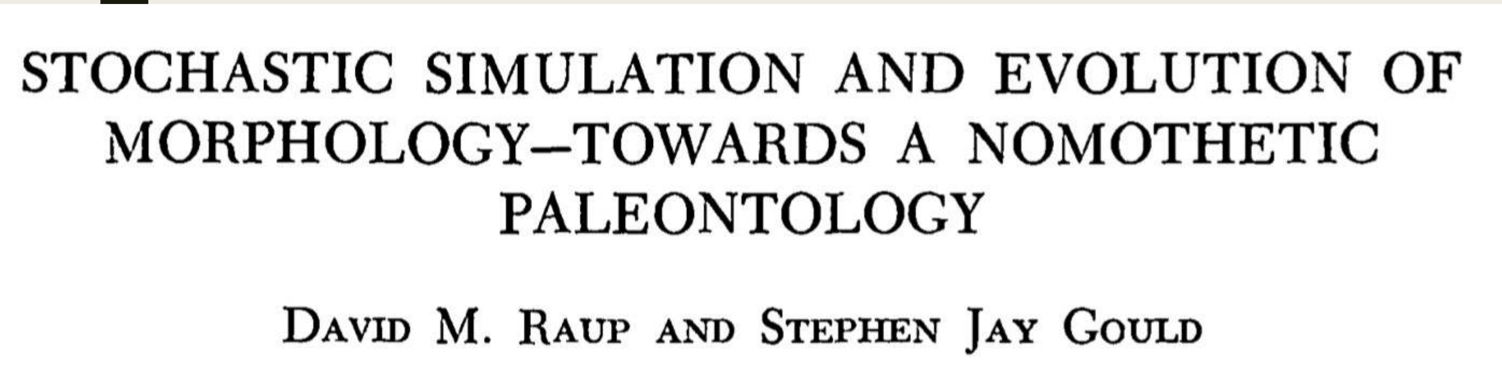
Stephen Jay Gould, David M. Raup, J. John Sepkoski, Jr.,
Thomas J. M. Schopf, and Daniel S. Simberloff



Paleobiology, 11(1), 1985, pp. 42–52

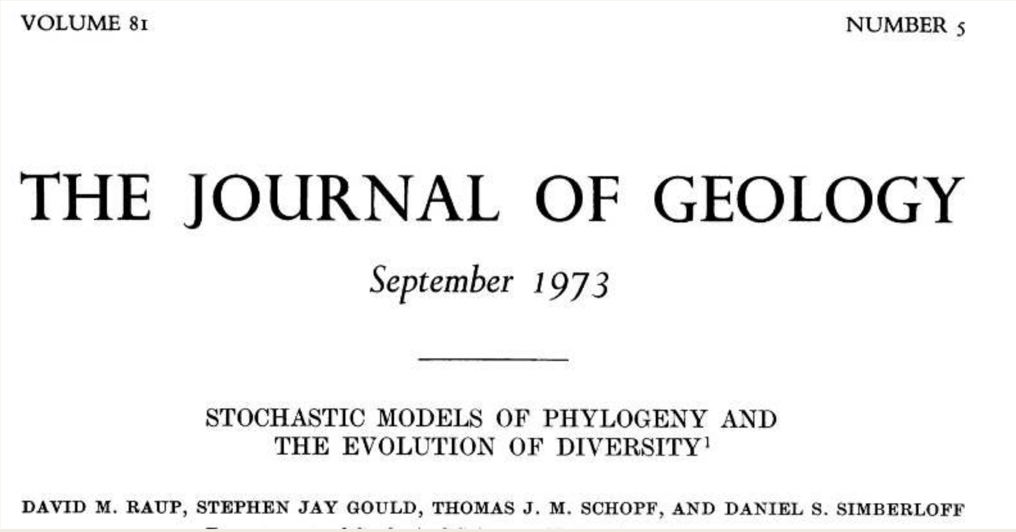
Mathematical models of cladogenesis

David M. Raup



STOCHASTIC SIMULATION AND EVOLUTION OF MORPHOLOGY—TOWARDS A NOMOTHETIC PALEONTOLOGY

David M. Raup and Stephen Jay Gould



VOLUME 81 NUMBER 5

THE JOURNAL OF GEOLOGY

September 1973

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

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

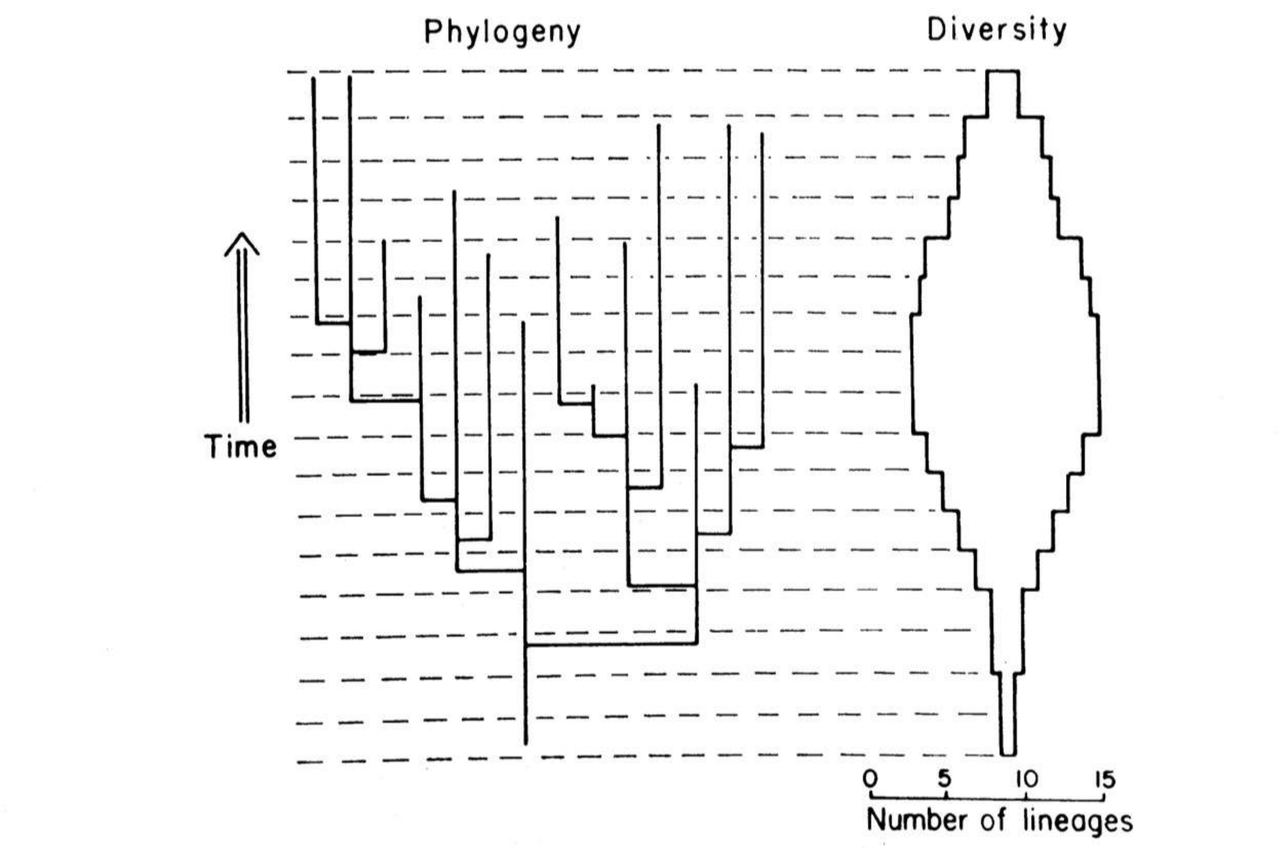


Fig. 1.—Hypothetical phylogeny (*left*) and the pattern of change in number of lineages thro
time (*right*).

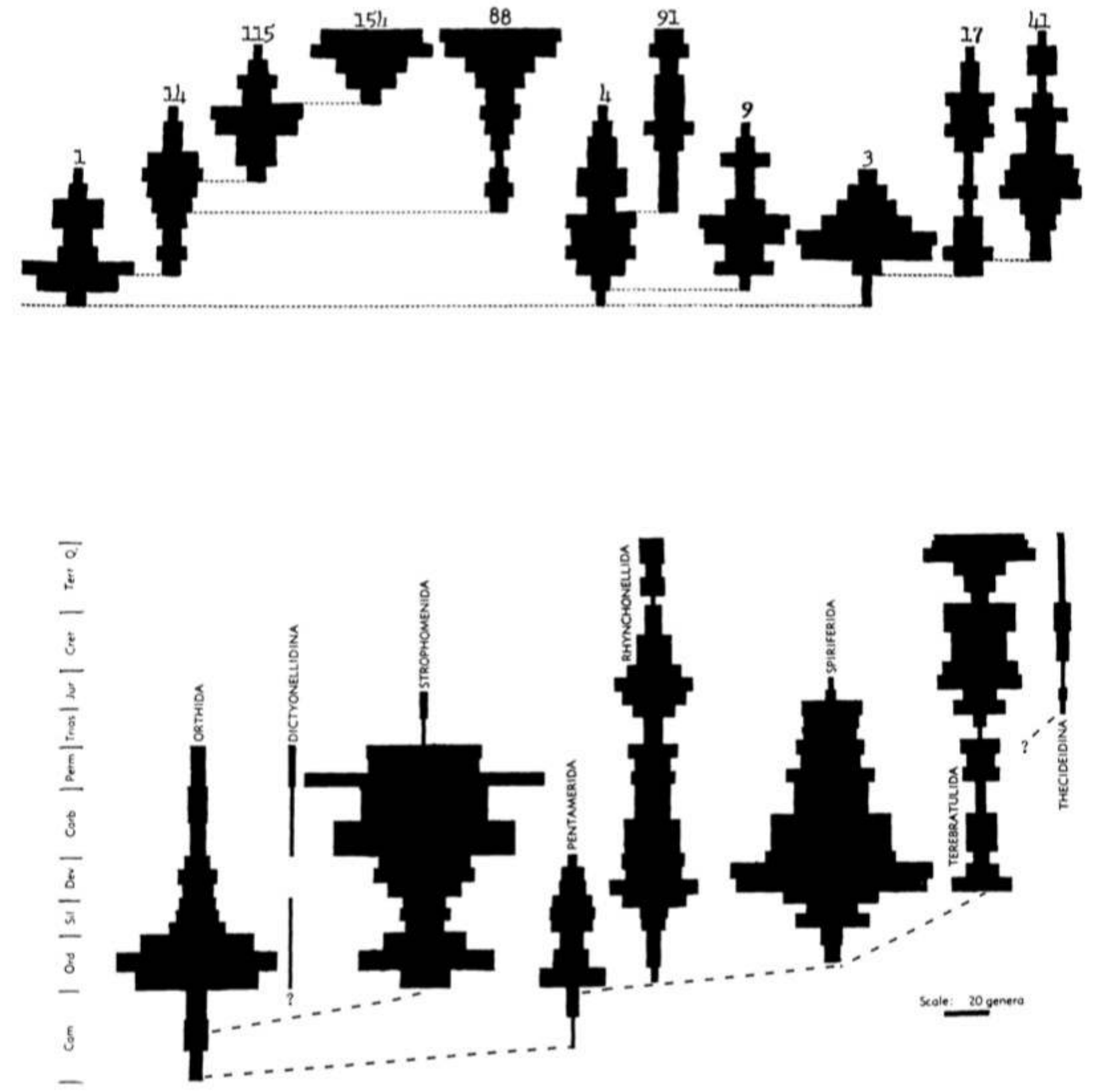
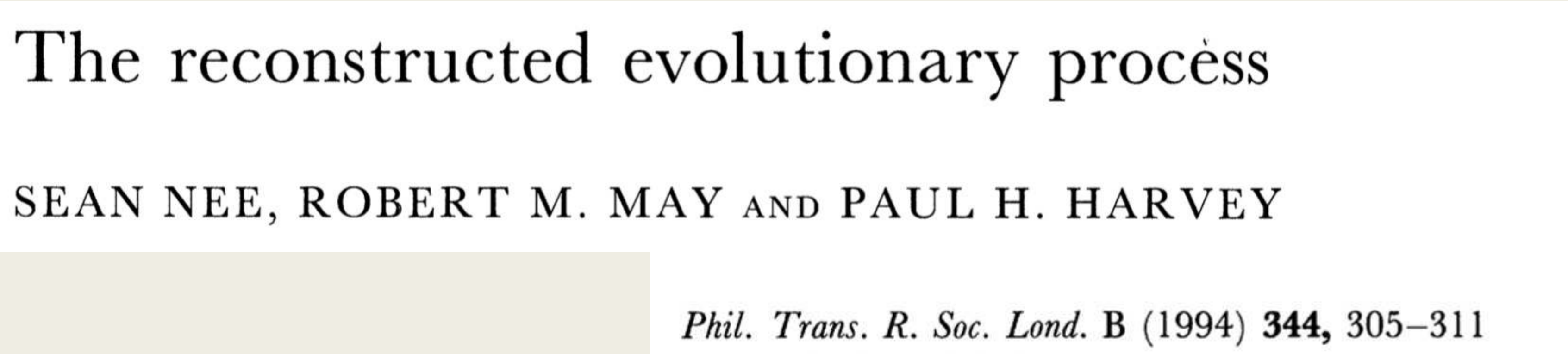


Figure 1. Comparison of random with real clades. Top: clades for one run of the MBL program at branching and extinction probabilities of 0.1. Bottom: real clades for genera within orders of brachiopods, from



The reconstructed evolutionary process

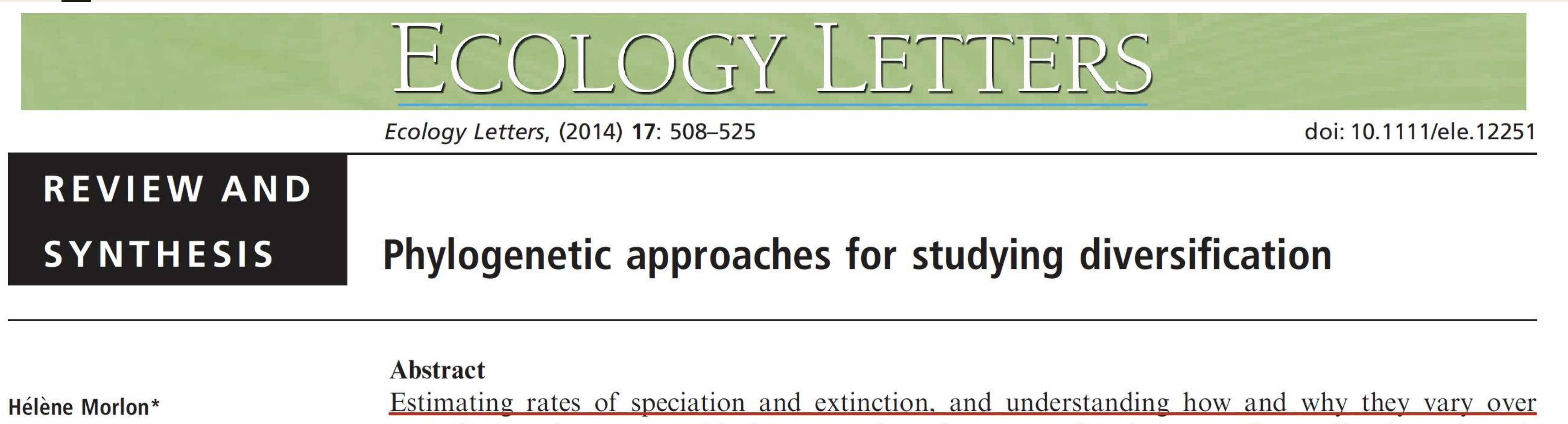
SEAN NEE, ROBERT M. MAY AND PAUL H. HARVEY

Phil. Trans. R. Soc. Lond. B (1994) **344,** 305–311

Proc. Natl. Acad. Sci. USA
Vol. 89, pp. 8322–8326, September 1992
Evolution

Tempo and mode of evolution revealed from molecular phylogenies

SEAN NEE*, ARNE Ø. MOOERS*, AND PAUL H. HARVEY*†



ECOLOGY LETTERS

Ecology Letters, (2014) **17**: 508–525 doi: 10.1111/ele.12251

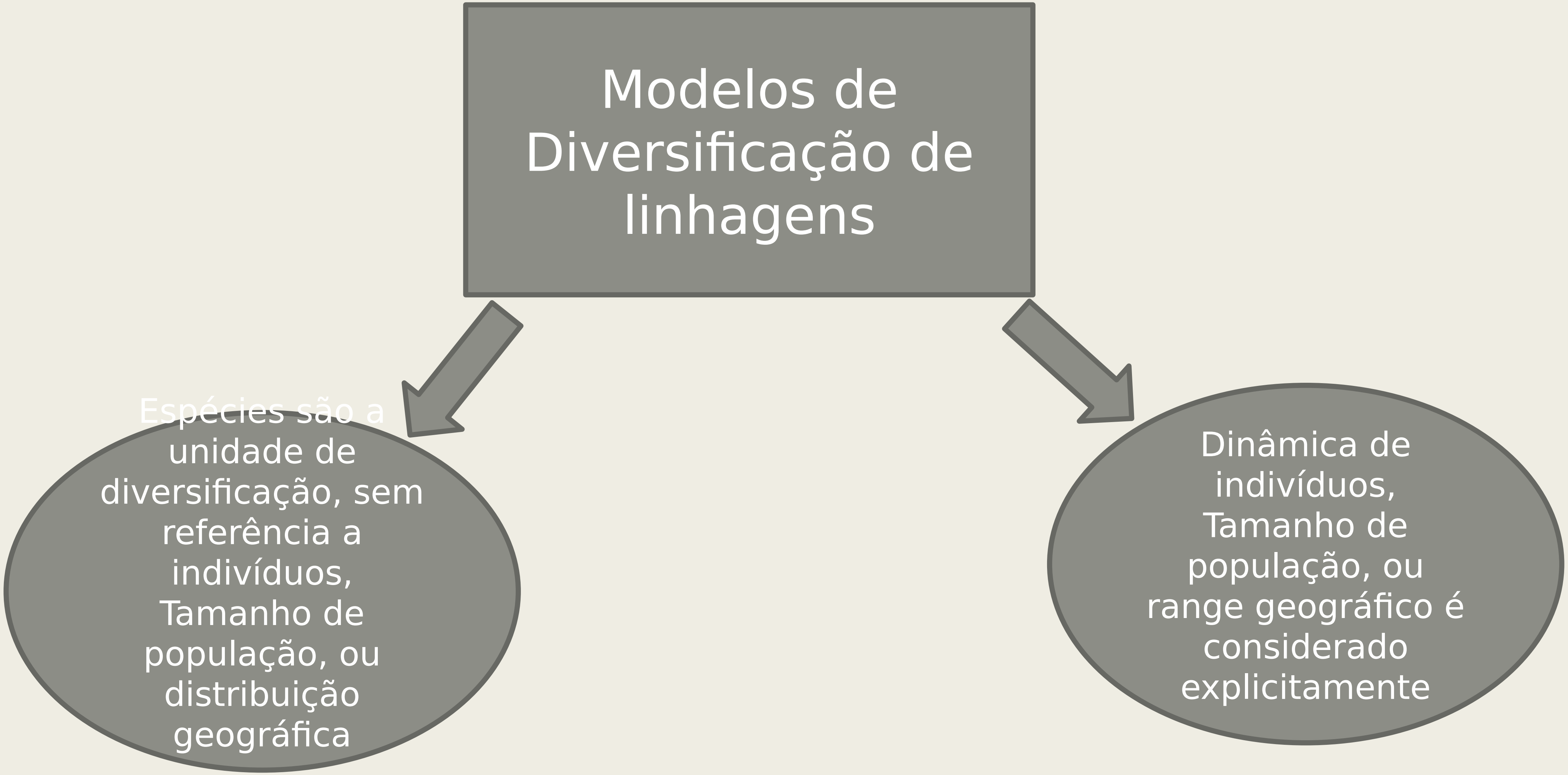
REVIEW AND SYNTHESIS

Phylogenetic approaches for studying diversification

Hélène Morlon*

Abstract

Estimating rates of speciation and extinction, and understanding how and why they vary over

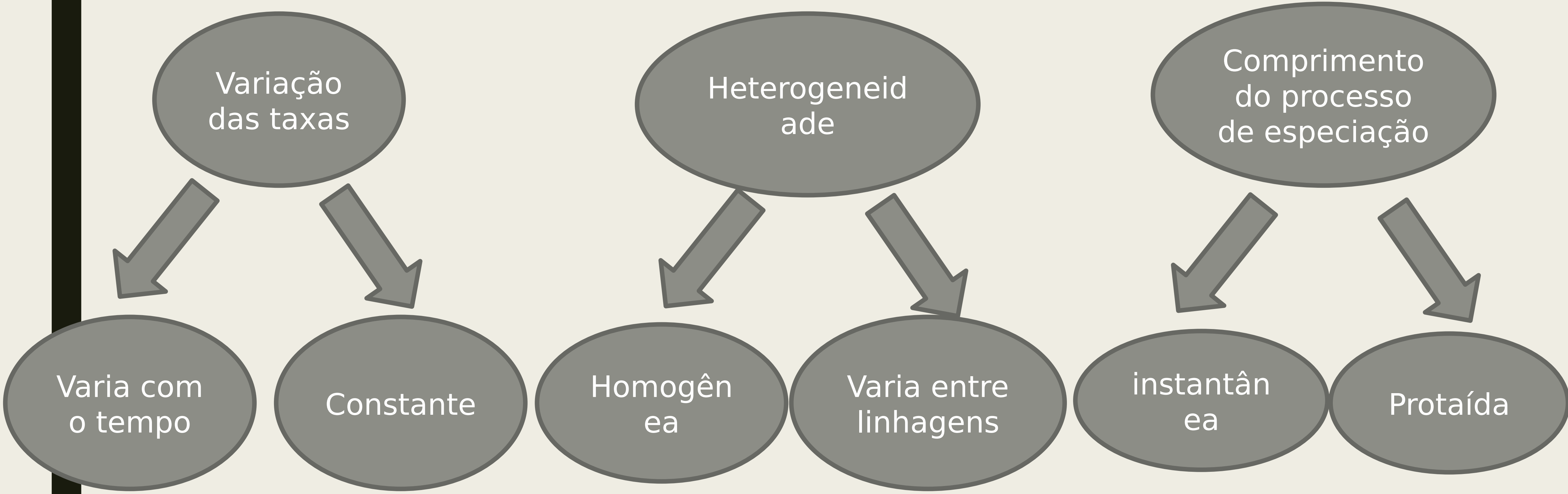


Modelos de Diversificação de linhagens

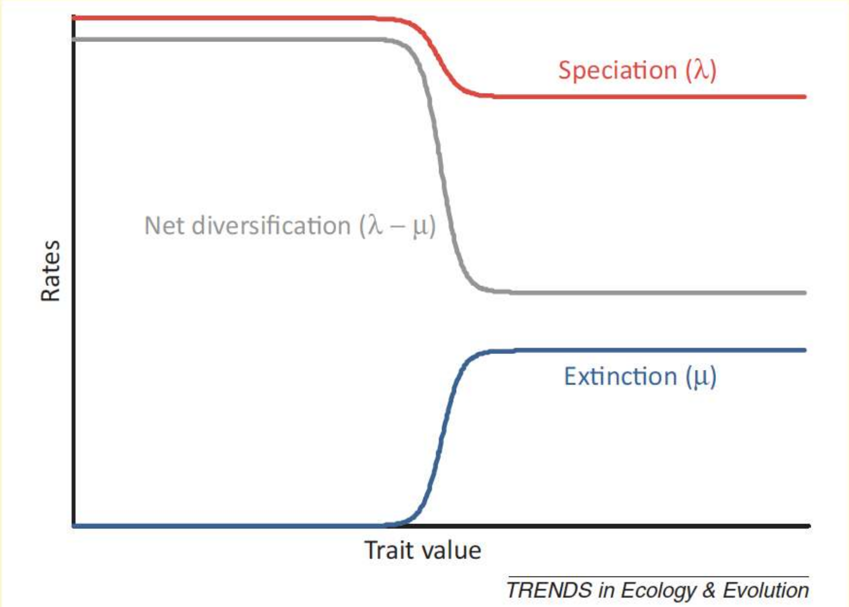
Espécies são a unidade de diversificação, sem referência a indivíduos, Tamanho de população, ou distribuição geográfica

Dinâmica de indivíduos, Tamanho de população, ou range geográfico é considerado explicitamente

Pressupostos dos modelos de diversificação

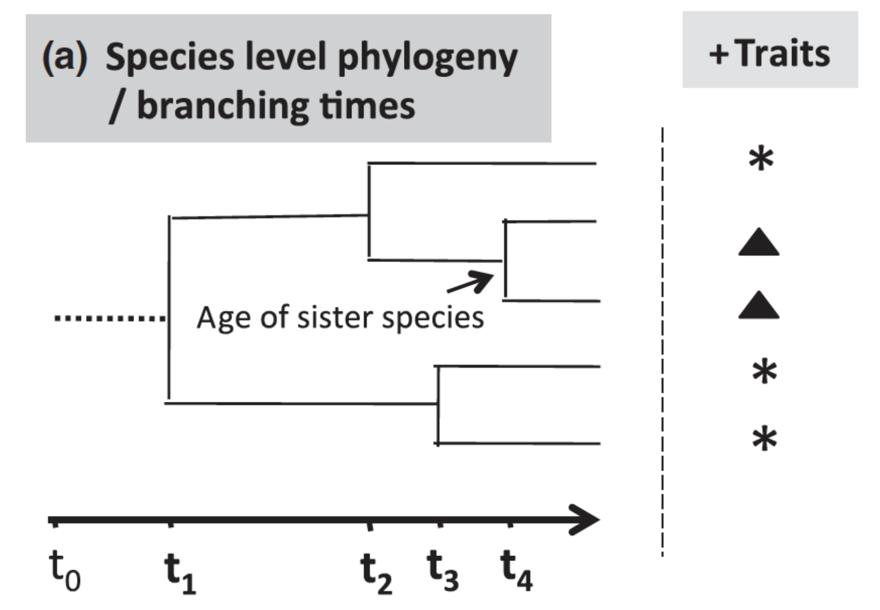


- Variação das taxas
  - Varia com o tempo
  - Constante
- Heterogeneidade
  - Homogênea
  - Varia entre linhagens
- Comprimento do processo de especiação
  - instantânea
  - Protaída



TRENDS in Ecology & Evolution

Figure I. Example of a sigmoidal relation between speciation (negative) and extinction (positive) and a continuously valued trait (e.g., body size), resulting in greater diversification of clades that have lower values of that trait due to their higher net diversification rate.



Modelos que estimam a diversificação dependente de um atributo

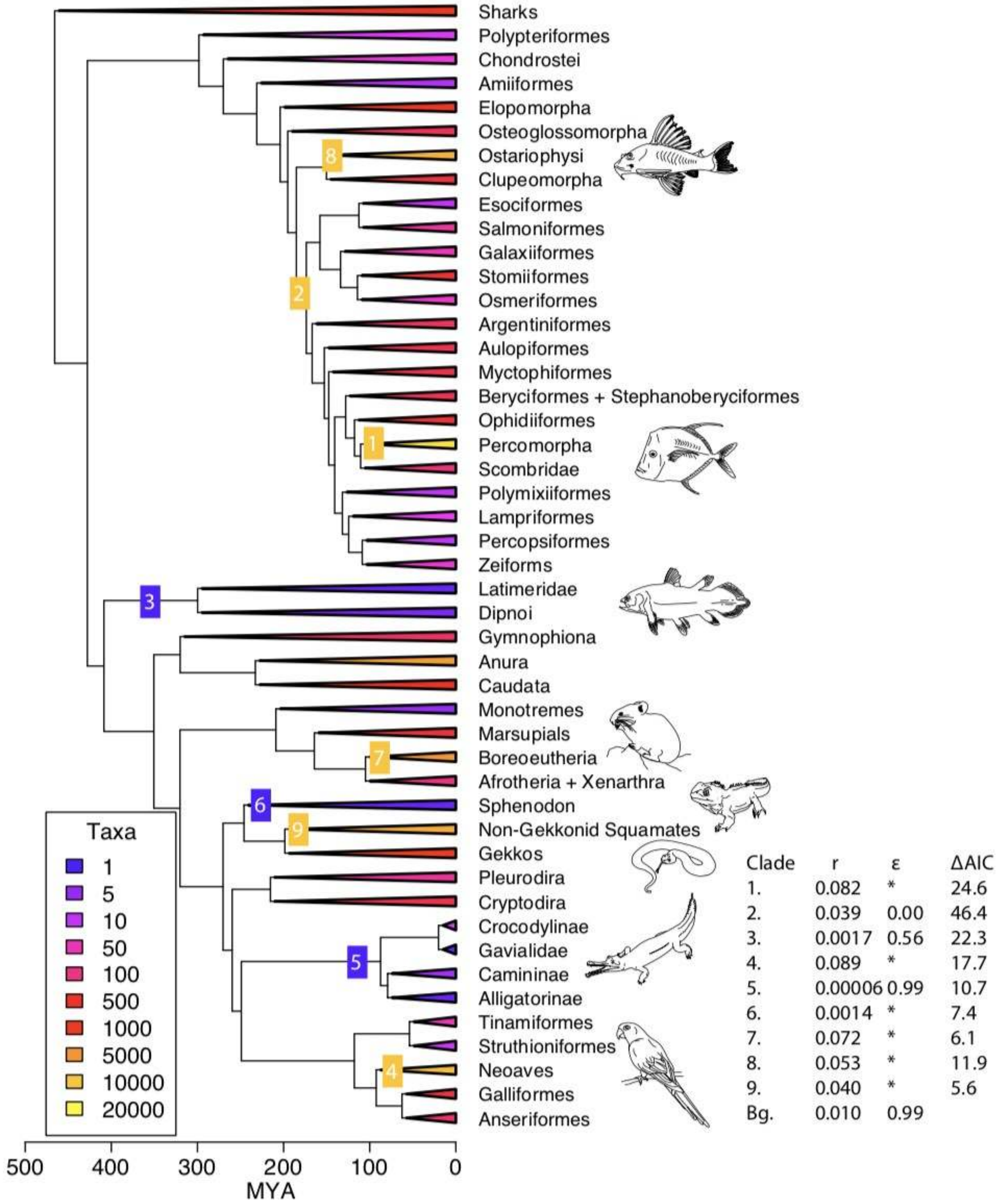
Família de modelos xxSSE

BiSSE, MuSSE, QuaSSE, GeoSSE, BiSSEnes

Hidden States (Semi-paramétricos)

Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates

Michael E. Alfaro[a,1], Francesco Santini[a], Chad Brock[b], Hugo Alamillo[b], Alex Dornburg[c], Daniel L. Rabosky[d,e], Giorgio Carnevale[f], and Luke J. Harmon[g]



Clade	r	ε	ΔAIC
1.	0.082	*	24.6
2.	0.039	0.00	46.4
3.	0.0017	0.56	22.3
4.	0.089	*	17.7
5.	0.00006	0.99	10.7
6.	0.0014	*	7.4
7.	0.072	*	6.1
8.	0.053	*	11.9
9.	0.040	*	5.6
Bg.	0.010	0.99	

Methods in Ecology and Evolution

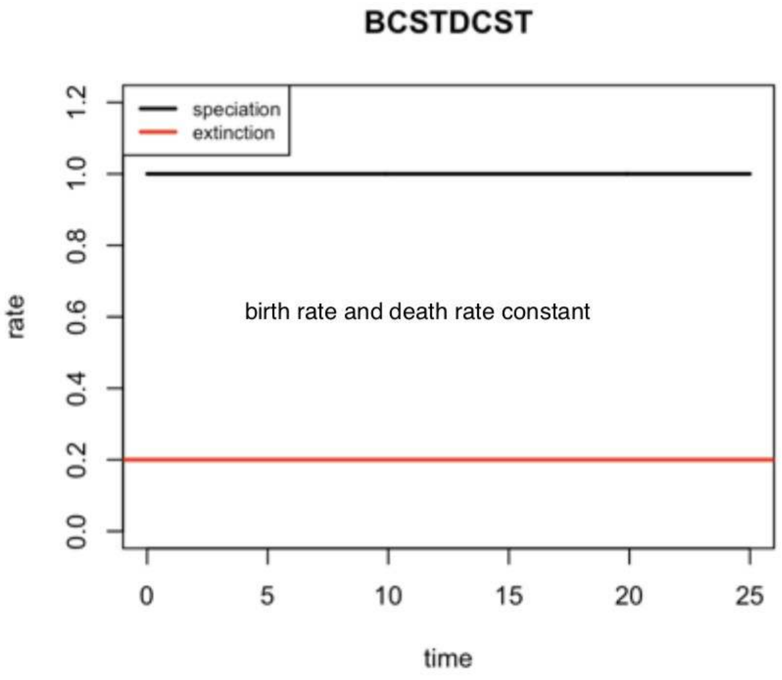
British Ecological Society

Methods in Ecology and Evolution 2016, **7,** 589–597 doi: 10.1111/2041-210X.12526

APPLICATION

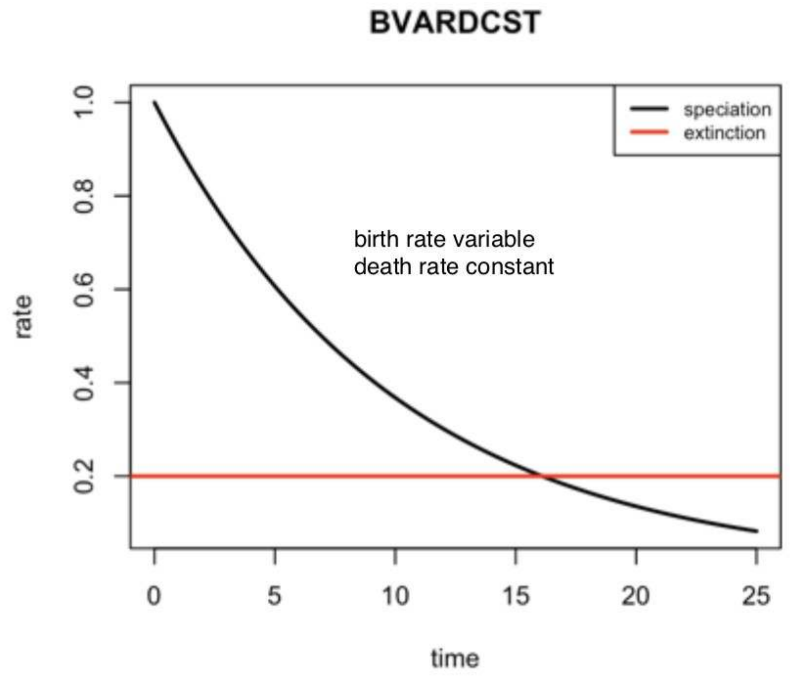
RPANDA: an R package for macroevolutionary analyses on phylogenetic trees

Hélène Morlon[1]*, Eric Lewitus[1], Fabien L. Condamine[2], Marc Manceau[1], Julien Clavel[1] and Jonathan Drury[1]



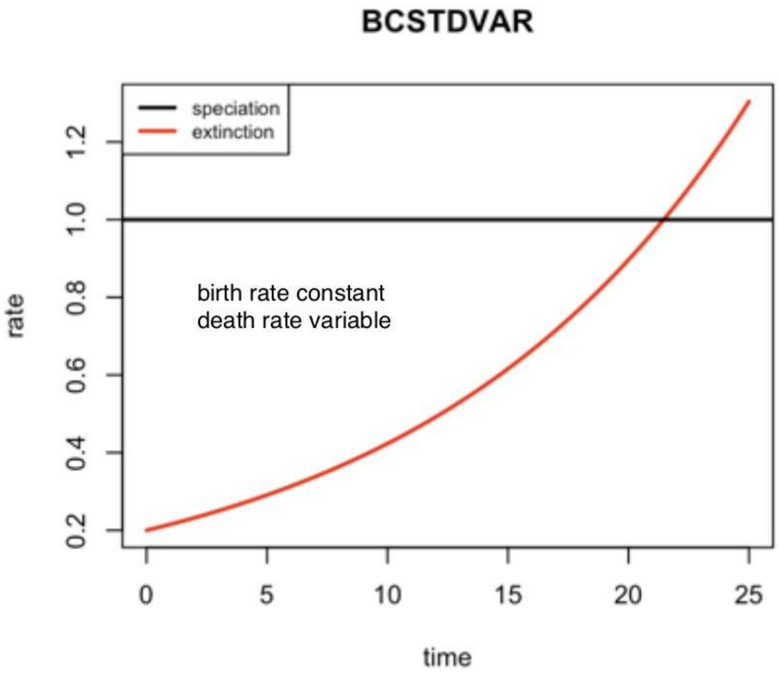
BCSTDCST

birth rate and death rate constant



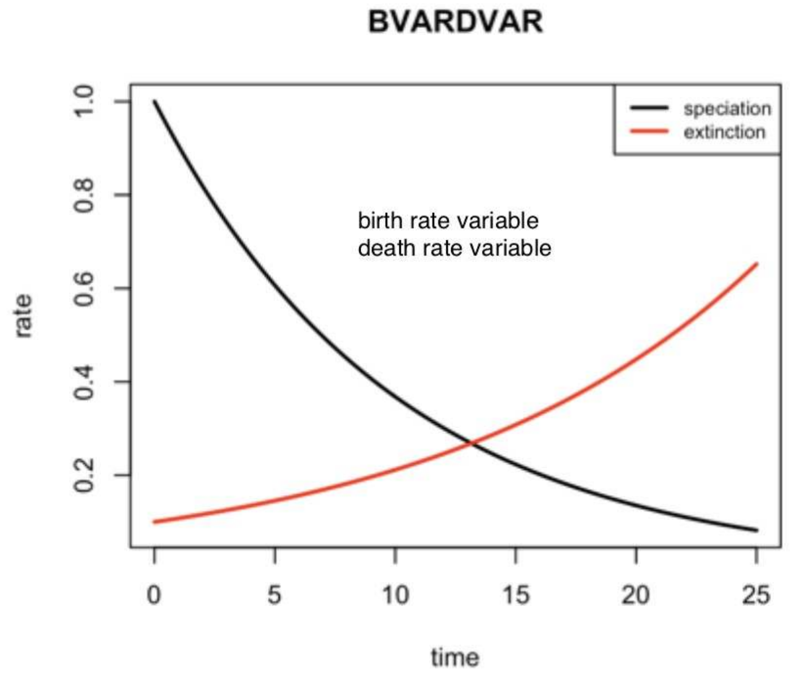
BVARDCST

birth rate variable
death rate constant



BCSTDVAR

birth rate constant
death rate variable



BVARDVAR

birth rate variable
death rate variable

OPEN ACCESS Freely available online

PLOS ONE

Automatic Detection of Key Innovations, Rate Shifts, and Diversity-Dependence on Phylogenetic Trees

Daniel L. Rabosky*

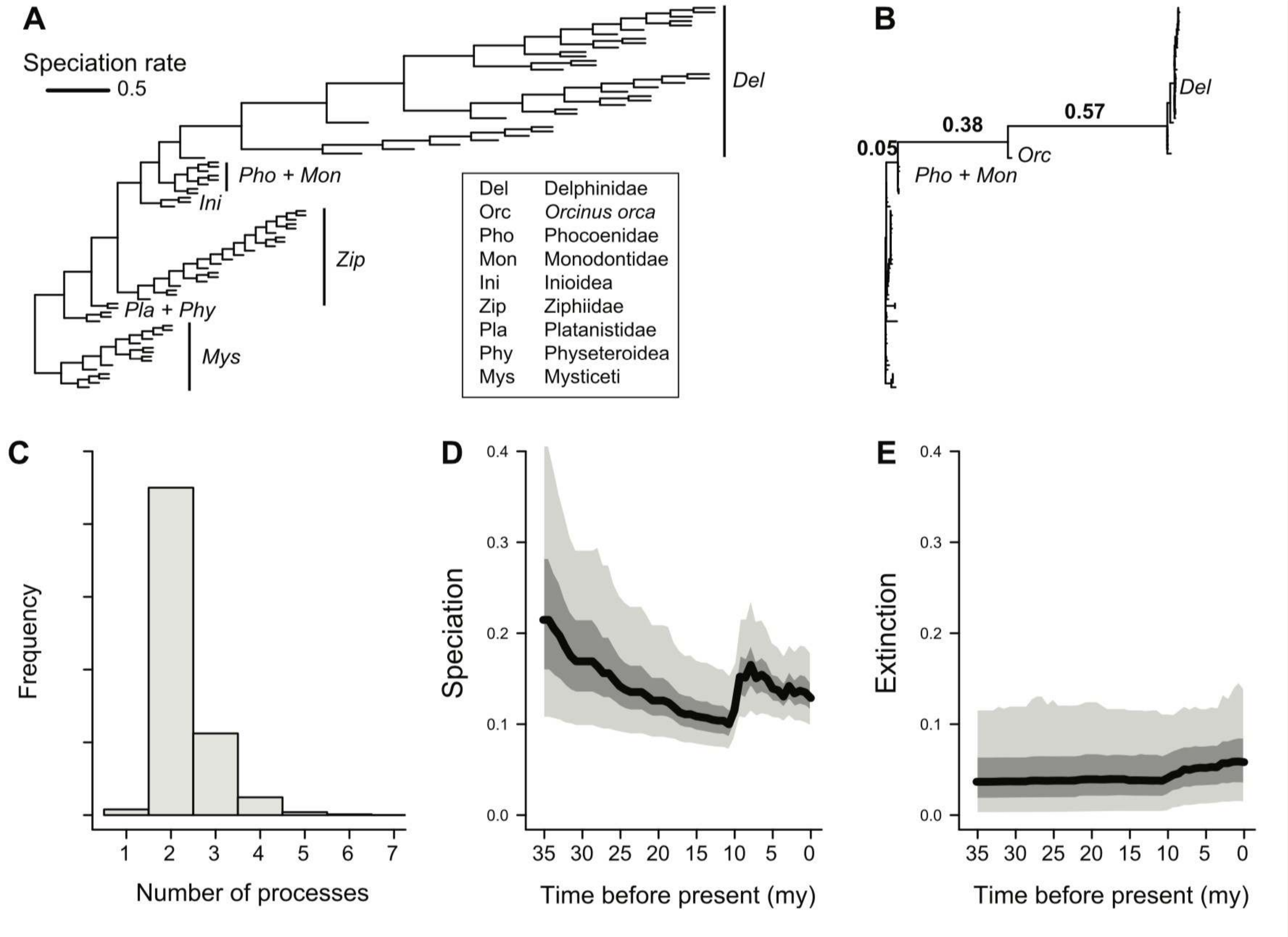
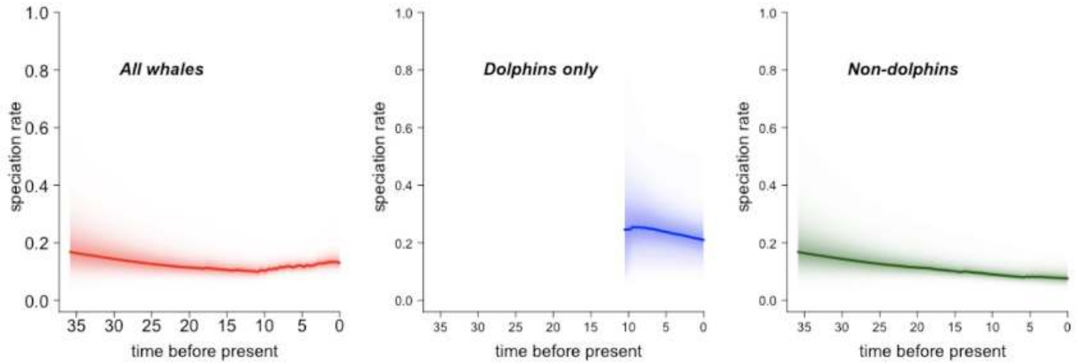
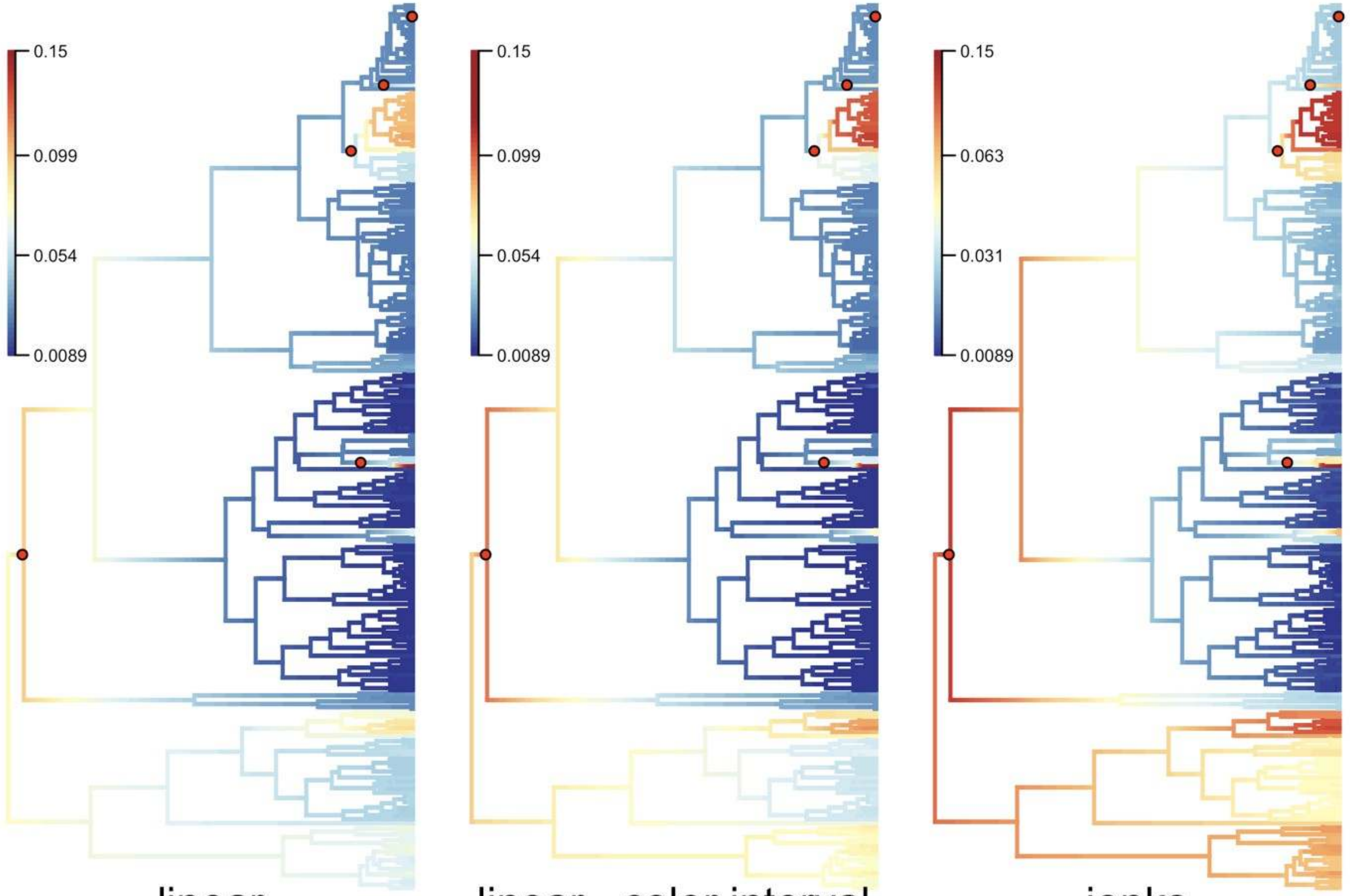


Figure 9. Dynamics of cetacean diversification through time as revealed by BAMM analysis. (A) Phylogeny of cetaceans [51], with branch

3.6. Rate variation through time: color density plot





linear

linear - color.interval

jenks

Fim da Parte 2

Perguntas?


Be Happy
'Cause
Its
Lunch
Time
KeepCalmAndPosters.com