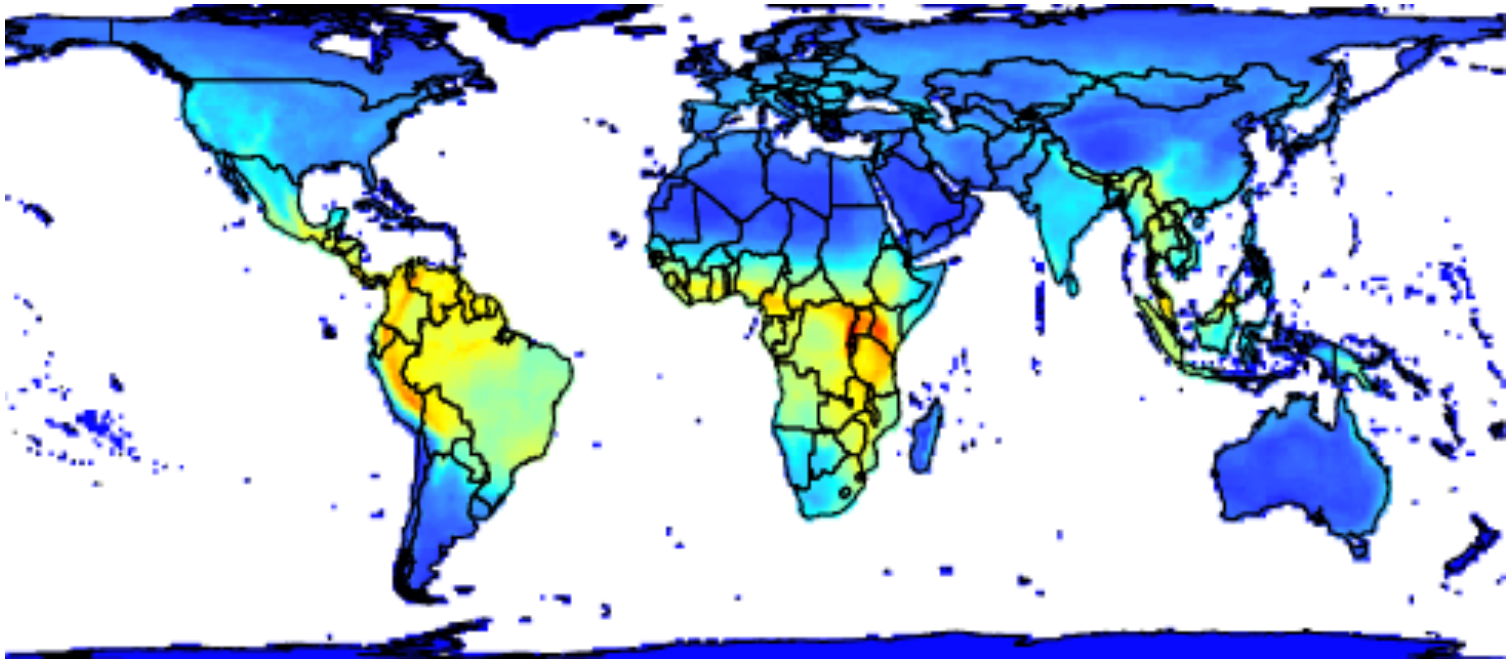
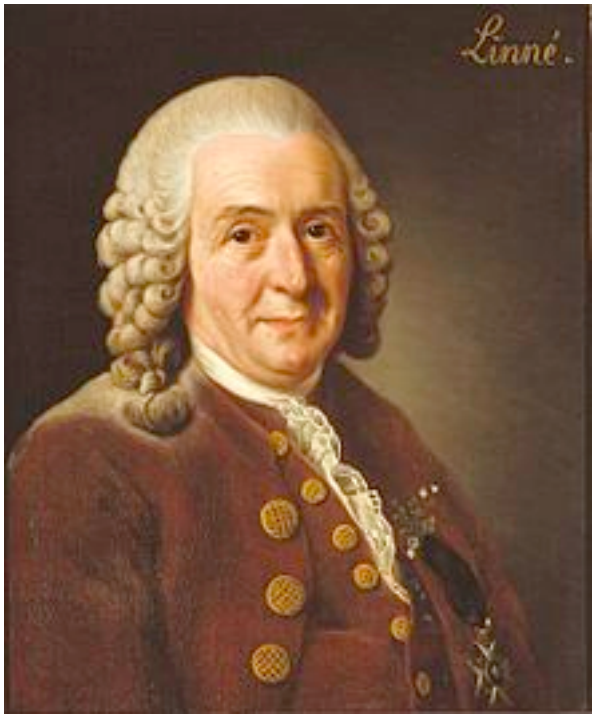
Understanding how biodiversity is distributed in space and time



Hélène Morlon
Ecole Normale Supérieure

Discovering, classifying, naming, and counting species on Earth

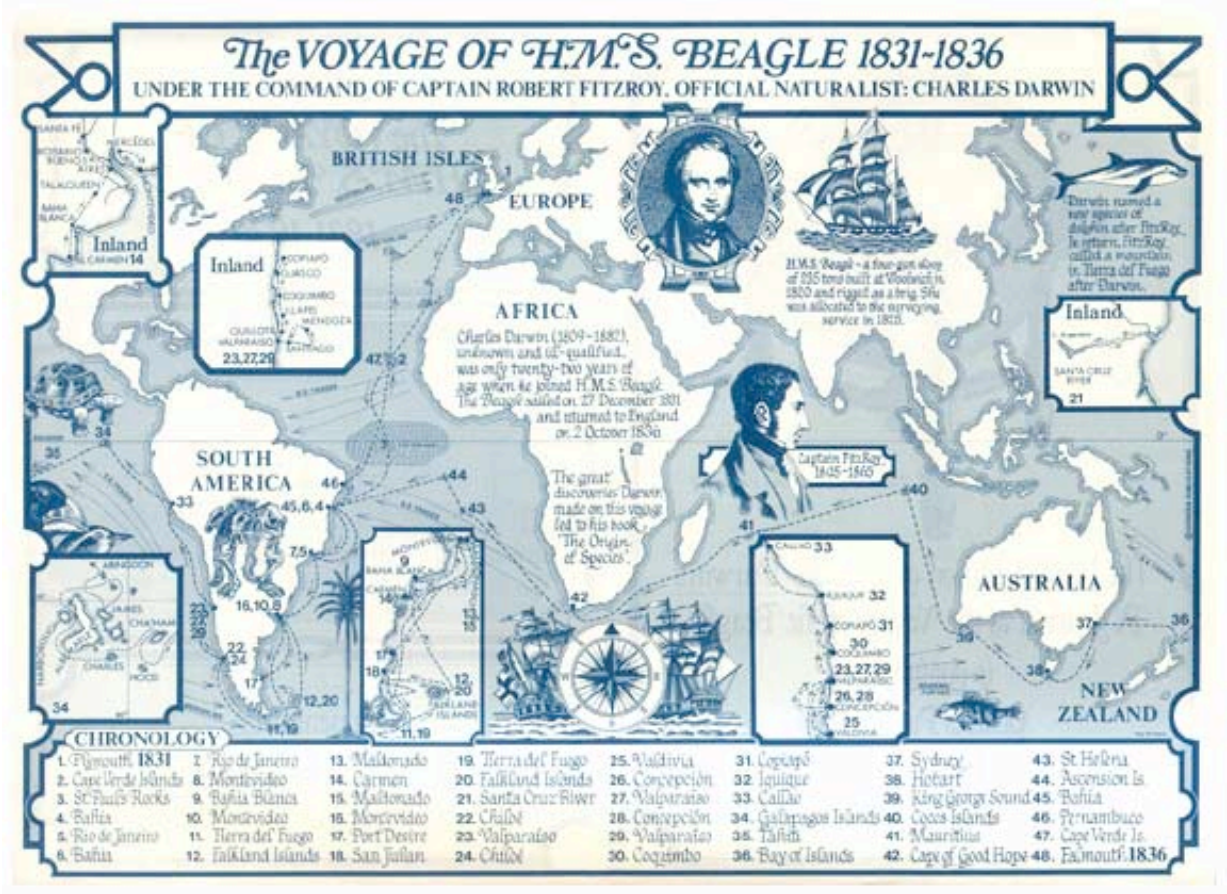


Carl von Linné (1707 – 1778)
Leclerc, Buffon, Von Humbolt

Discovering, classifying, naming, and counting species in the fossil record

Georges Cuvier (1769 – 1832)

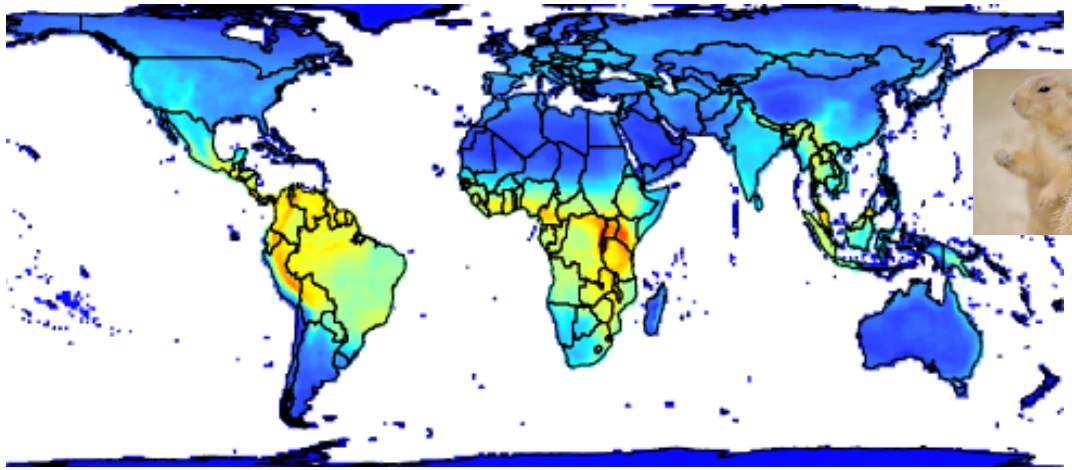
The XIXe century: a century of exploration

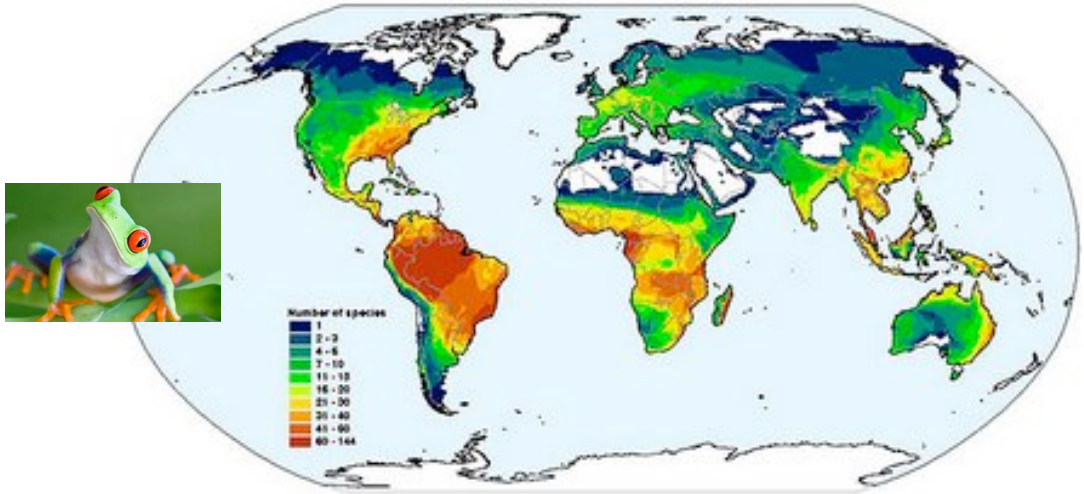


Agassiz, Darwin, Wallace, Watson …

General biodiversity laws

The number of species decreases from the tropics to the poles





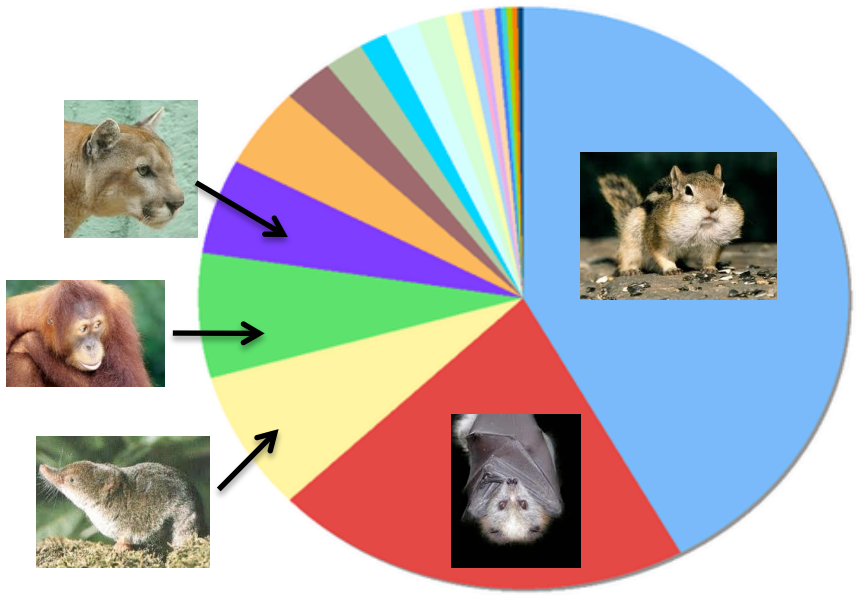
General biodiversity laws

The number of species is very heterogeneously distributed on the tree of life

« God has an inordinate fondness for beetles »

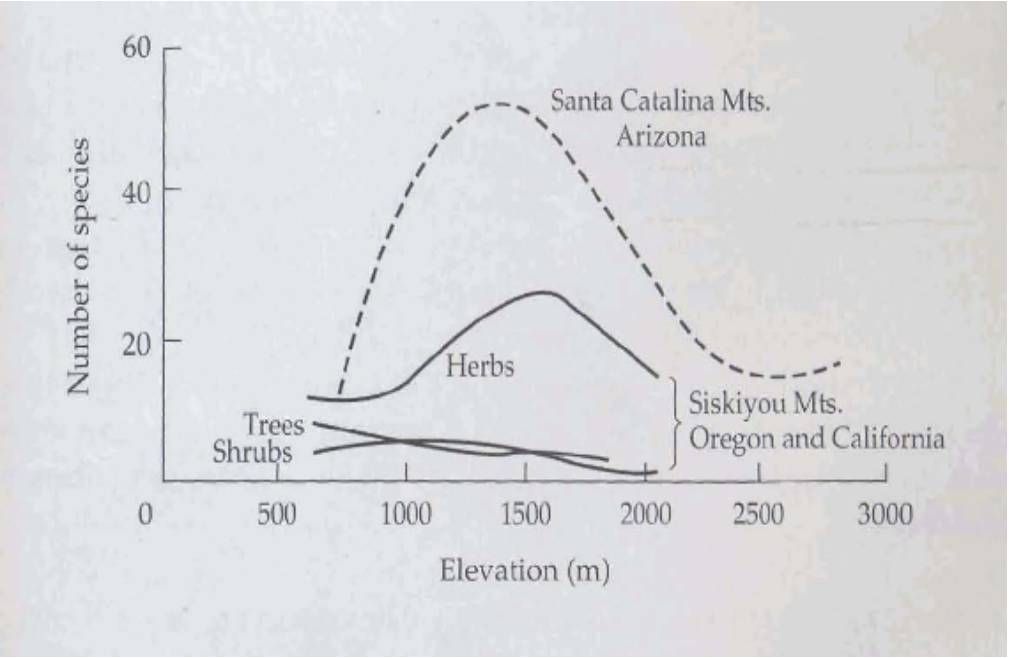
Haldane

… and rodents



General biodiversity laws

The number of species is highest at intermediate latitudes

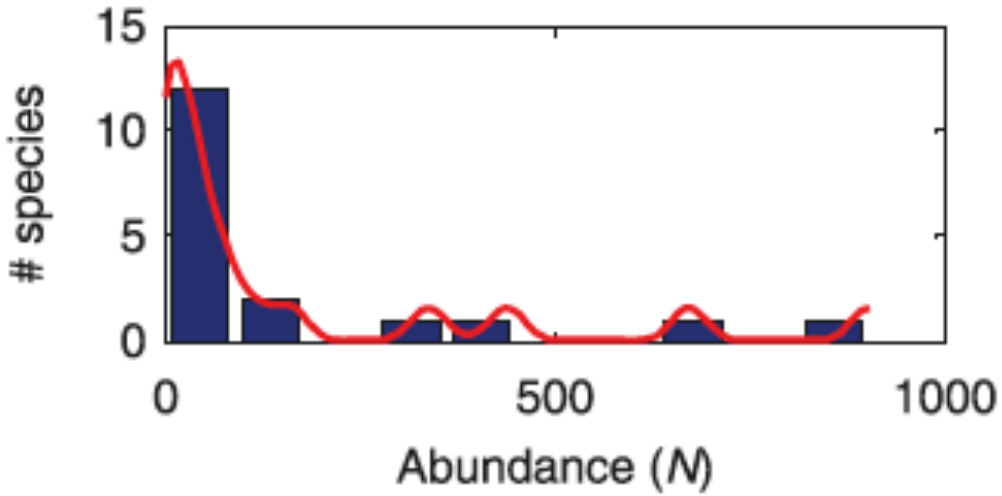


Flora in the Siskiyou mountains

Robert Whittaker, 1960

General biodiversity laws

Ecological communities are made of many rare and few abundant species

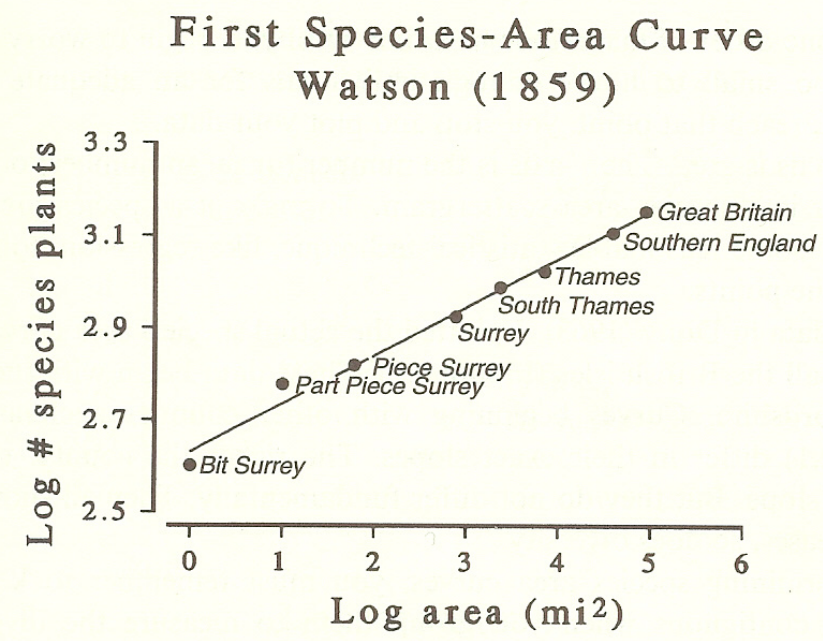


Flora in the Siskiyou mountains

Robert Whittaker, 1960

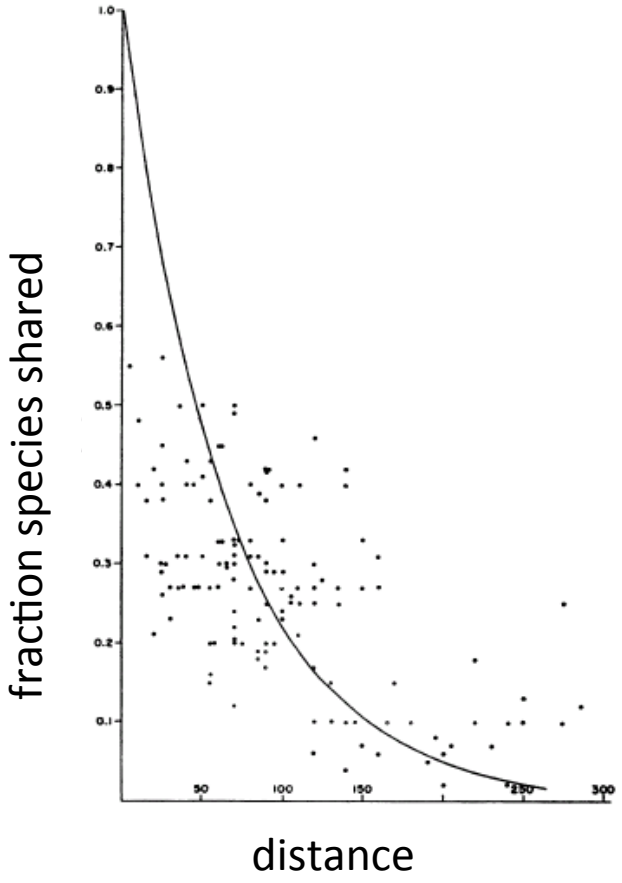
General biodiversity laws

The number of species increases with geographic area as a power-law



General biodiversity laws

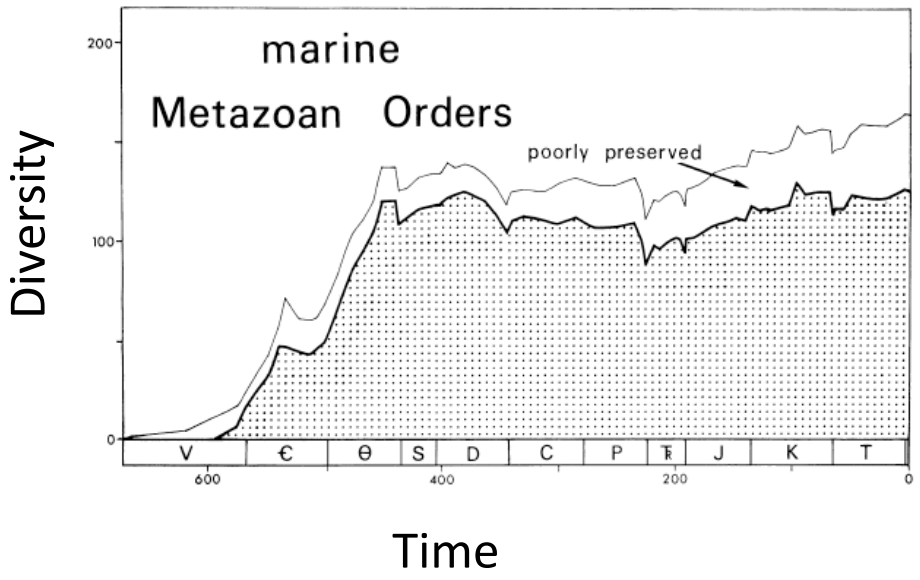
The similarity between ecological communities decreases with the geographic distance separating these communities



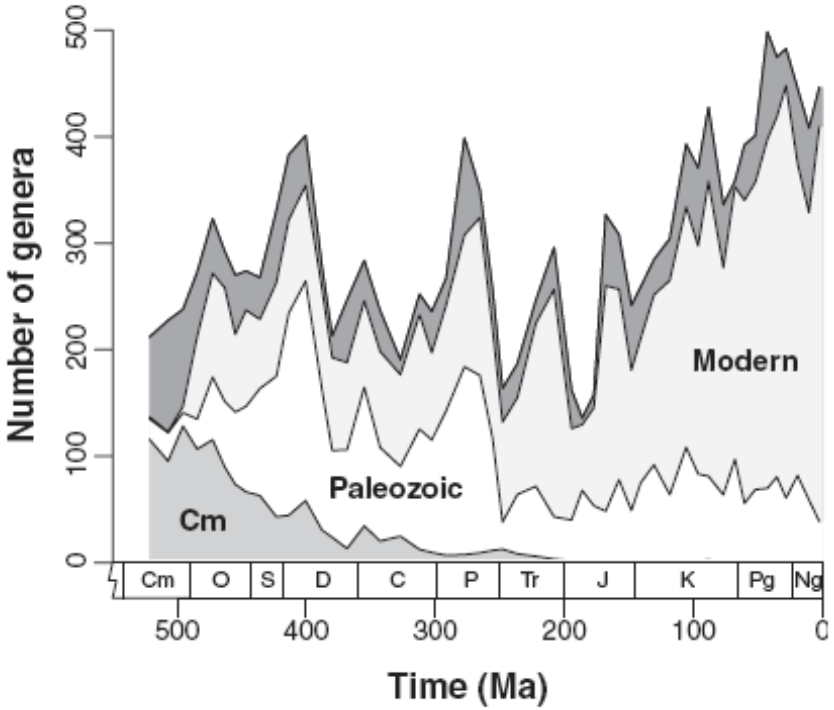
Preston 1960

Flora in the Galapagos islands

General biodiversity laws



Sepkoski *Paleobiology* 1978



Alroy *Science* 2010

Diversity reaches a plateau between mass extinction events …

… or not

How to explain general biodiversity laws?

spatial biodiversity laws

macroecological models

deep-time biodiversity laws

macroevolutionary models

How to explain general biodiversity laws?

spatial biodiversity laws

macroecological models

deep-time biodiversity laws

macroevolutionary models

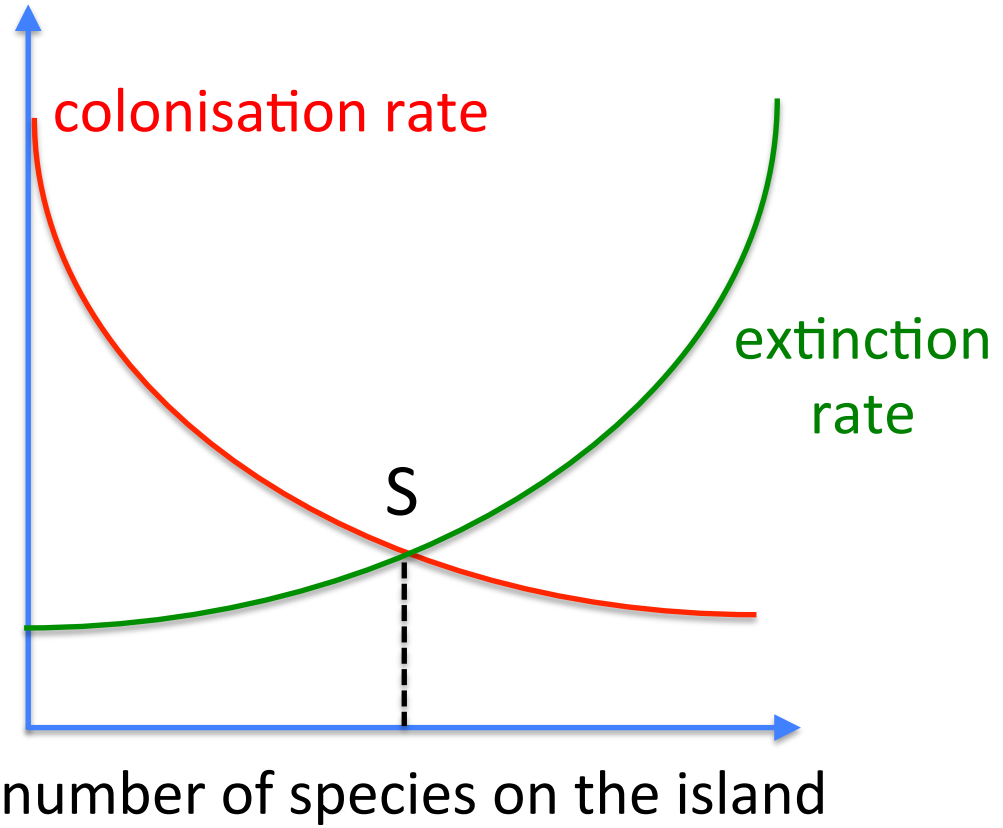
How to explain general biodiversity laws?

One of the first quantitative biodiversity model in macroecology:
MacArthur & Wilson's theory of island biogeography (1967)

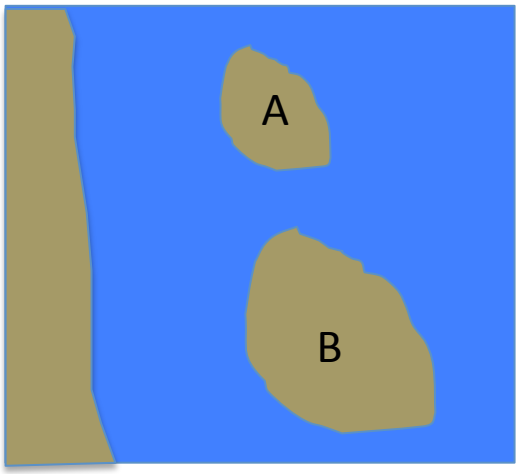
How many species to expect on a given island?

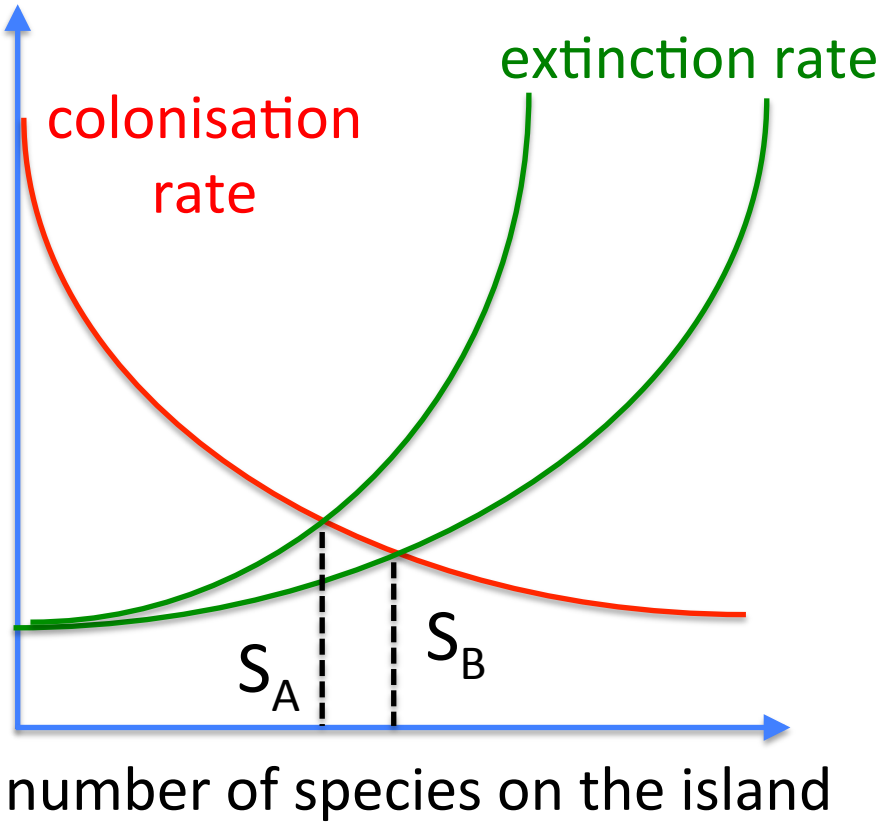
The number of species results from a dynamic equilibrium between colonisation and extinction :
species go extinct locally but they are replaced by colonists

MacArthur & Wilson (1967)



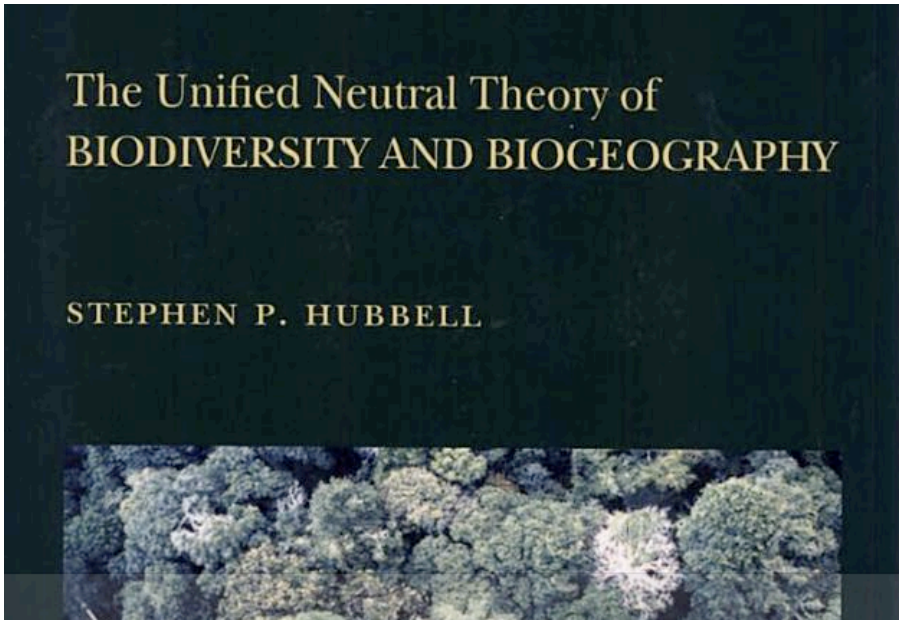
How many species to expect on a given island?





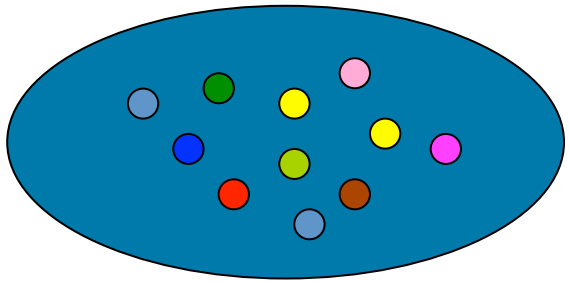
How to explain general biodiversity laws?

One of the model for which we have most quantitative predictions:
Hubbell's neutral model (2001)



Hubbell's neutral model at the metacommunity scale

Metacommunity: regional pool of individuals and species of similar trophic level

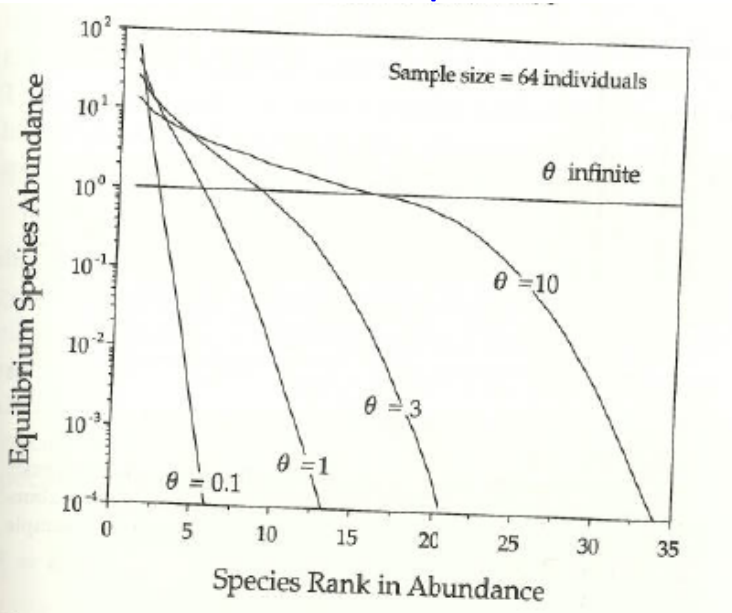


We consider a metacommunity of constant size J. The community is panmictic and there is no overlap between generations. Each individual from generation k+1 chooses a parent randomly and uniformly from the individuals of generation k. With probability (1-ν) the individual inherits it's parent type. With probability ν the individual is of an entirely new type (new species)

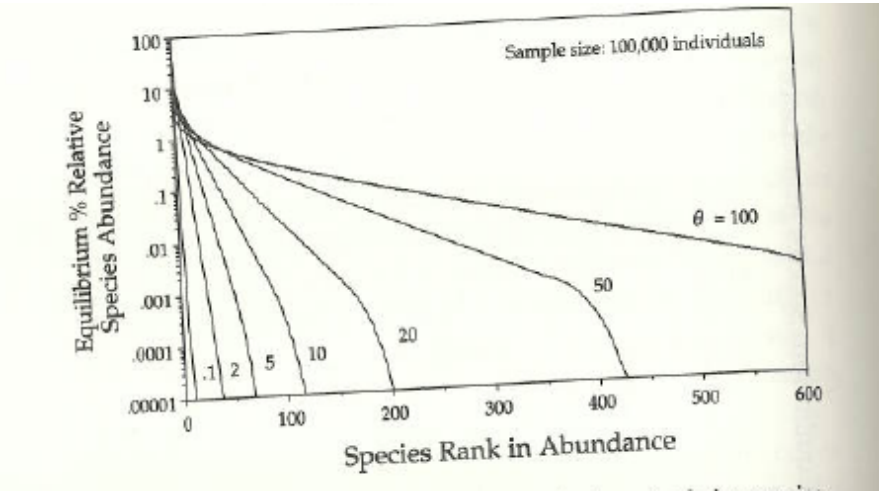
$\Theta = J\nu$ rate at which new species emerge

The neutral theory of biodiversity provides analytical predictions for the species abundance distribution

small sample

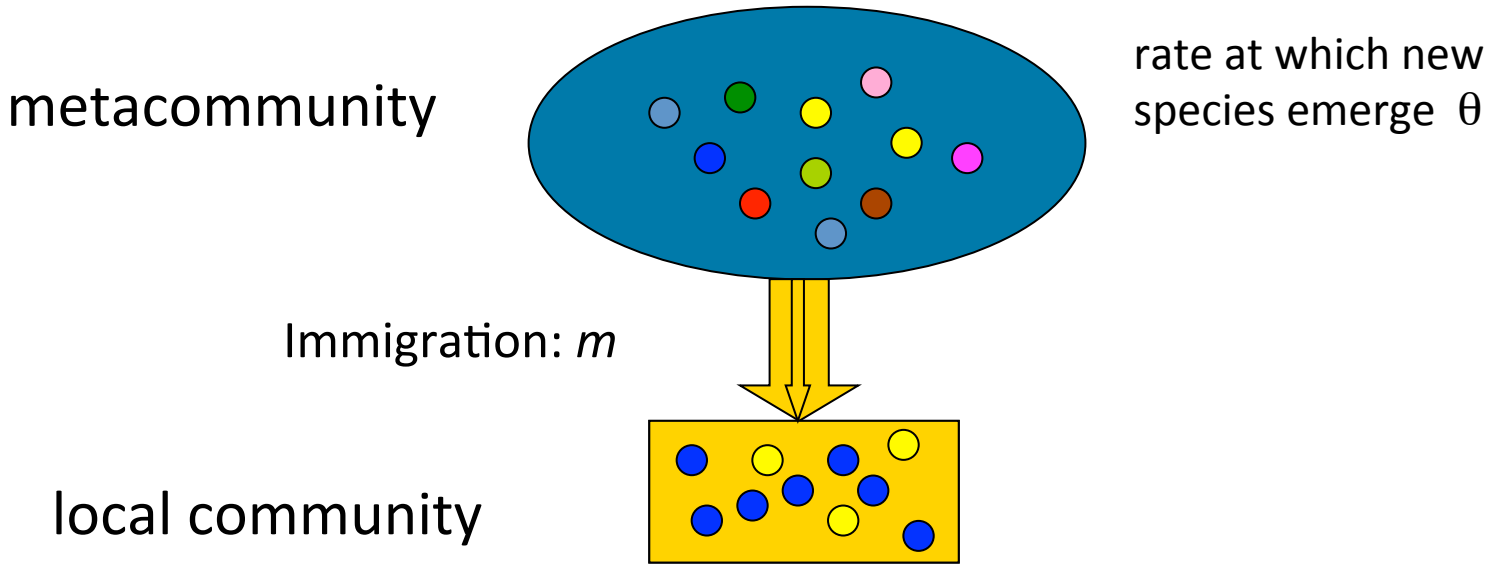


sample size tending to infinity



Hubbell's neutral model at the community scale

2 parameter model



The neutral theory of biodiversity provides analytical predictions for the species abundance distribution (with dispersal limitation)

Ecology Letters, (2005) **8**: 253–260 doi: 10.1111/j.1461-0248.2004.00717.x

LETTER

A new sampling formula for neutral biodiversity

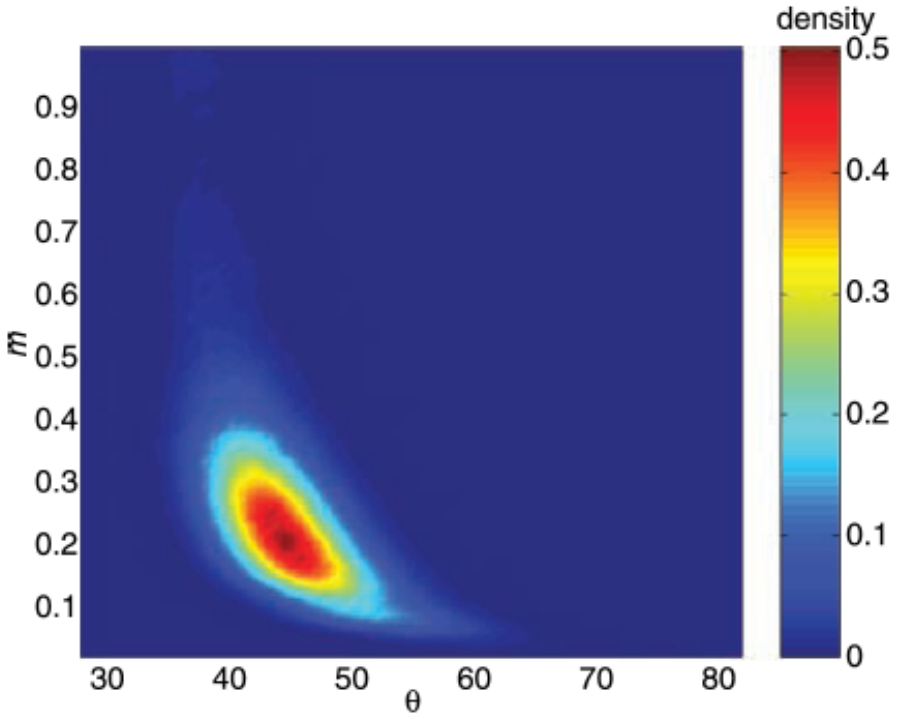
Rampal S. Etienne
Community and Conservation Ecology Group, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

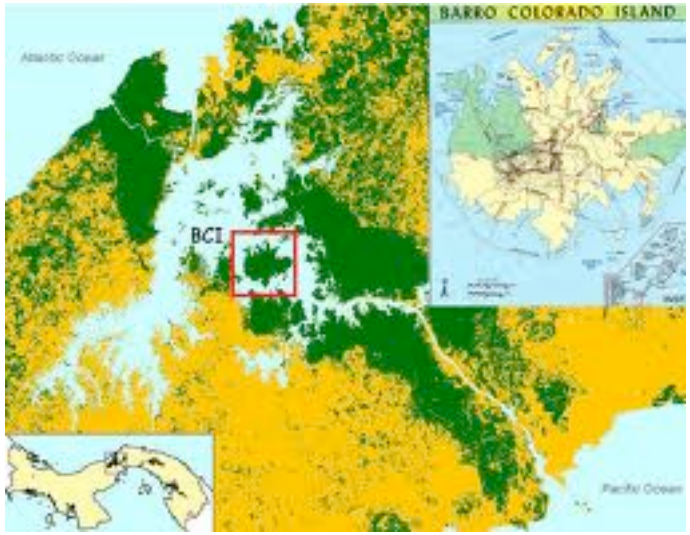
Abstract

The neutral model of biodiversity, proposed by Hubbell (*The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton University Press, Princeton, NJ, 2001) to explain the diversity of functionally equivalent species, has been subject of hot debate in community ecology. Whereas Hubbell studied the model mostly by simulations, recently analytical treatments have yielded expressions of the expected number of species of a

$$P[D|\theta, m, J] = \frac{J!}{\prod_{i=1}^{S} n_i \prod_{j=1}^{J} \Phi_j!} \frac{\theta^S}{(I)_J} \sum_{A=S}^{J} K(D, A) \frac{I^A}{(\theta)_A}$$

Application 1:
Estimating the parameters of the model by maximum likelihood





Neutral Ecological Theory Reveals Isolation and Rapid Speciation in a Biodiversity Hot Spot

Andrew M. Latimer,[1*] John A. Silander Jr.,[1] Richard M. Cowling[2]

Site	Θ				m			
	MLE	Post. mode	0.025 quantile	0.975 quantile	MLE	Post. Mode	0.025 quantile	0.975 quantile
Cederberg	394.6	370	198.9	2350.5	0.0055	0.0053	0.0032	0.0090
Hangklip	640.3	530	328.3	3033.7	0.0020	0.0018	0.0014	0.0029
Zuurberg	30.2	29	15.3	52.5	0.037	0.045	0.015	0.13
Manu	187.4	183	154.9	228.3	0.53	0.55	0.34	0.81
Yasuní	152.8	153	121.9	188.6	0.50	0.50	0.34	0.80
BCI	47.7	45	31.3	67.0	0.093	0.10	0.048	0.44

Science 2005

Application 2:
comparing the support of different models

Is the coexistence of trees in tropical forests explained by an advantage to rare species (Janzen-Connell hypothesis) or by neutral models?

density-dependent model
(individuals from rare species are favored)

neutral model with dispersal limitation

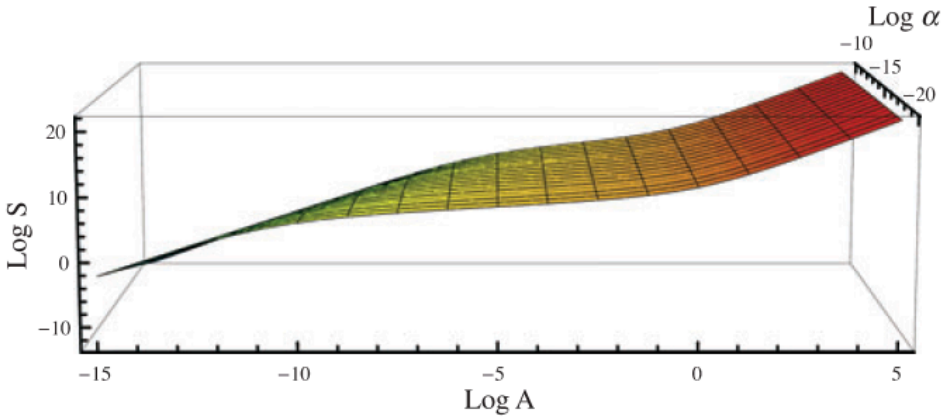
neutral model without dispersal limitation

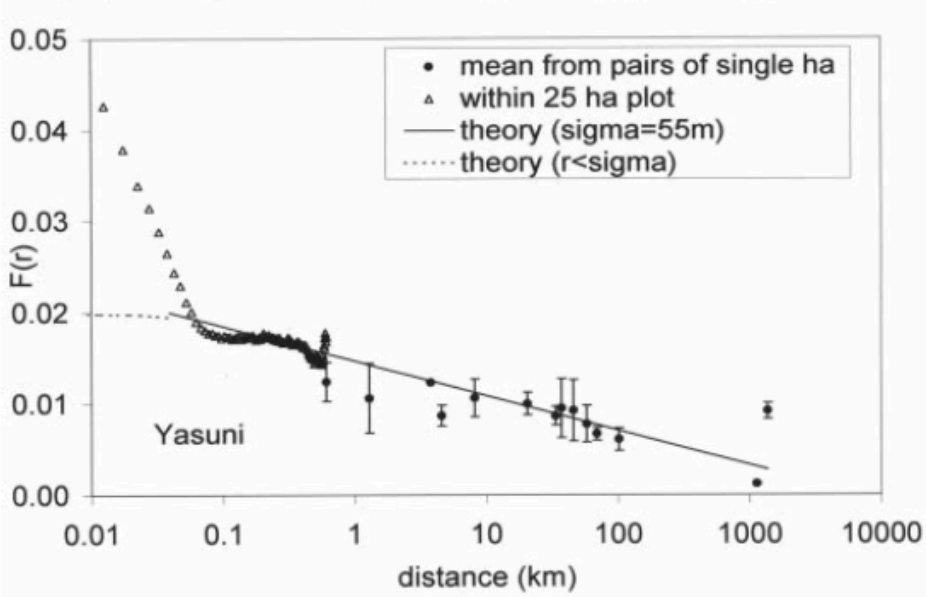
Table 1 | Comparison of species-abundance models

Site	S	J	Θ	m	L_1	L_2	L_3	Model ranking	w_2	w_3
BCI	225	21,457	47.7	0.093	−308.7	−315.0	−318.8	1>2>3	0.0018	0.0001
Yasuni	821	17,546	204.2	0.429	−297.2	−303.6	−307.6	1>2>3	0.0017	0.0001
Pasoh	678	26,554	190.9	0.093	−359.4	−365.3	−392.5	1>2>3	0.0027	0.0000
Korup	308	24,591	52.7	0.547	−317.0	−323.1	−318.7	1=3>2	0.0022	0.3318
Lambir	1,004	33,175	285.6	0.115	−386.4	−391.2	−437.9			
Sinharaja	167	16,936	436.8	0.0019	−252.9	−258.5	−253.8			

Chave et al. *Nature* 2004

The neutral theory of biodiversity also provides realistic quantitative predictions for the species-area and the distance-decay relationships





O'dwyer & Green *Eco. Lett.* 2010

Condit et al. *Science* 2002

How to explain general biodiversity laws?

spatial biodiversity laws

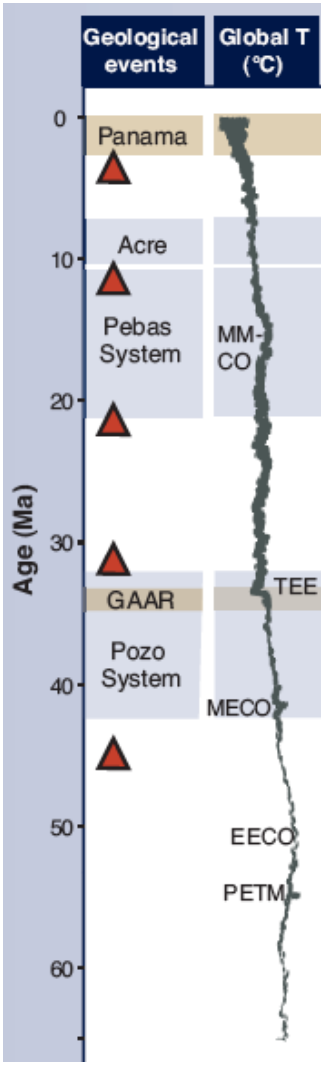
macroecological models

deep-time biodiversity laws

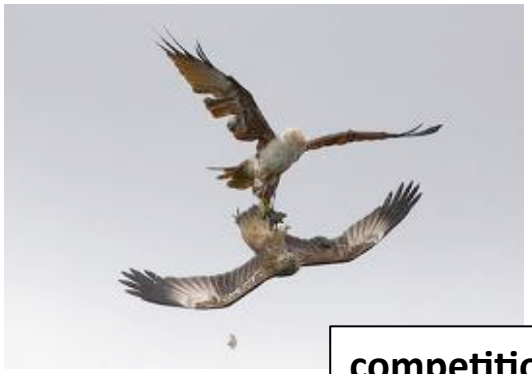
macroevolutionary models

Species richness results from speciation and extinction events, themselves influenced by various ecological and evolutionary processes

Abiotic factors



Biotic factors



competition

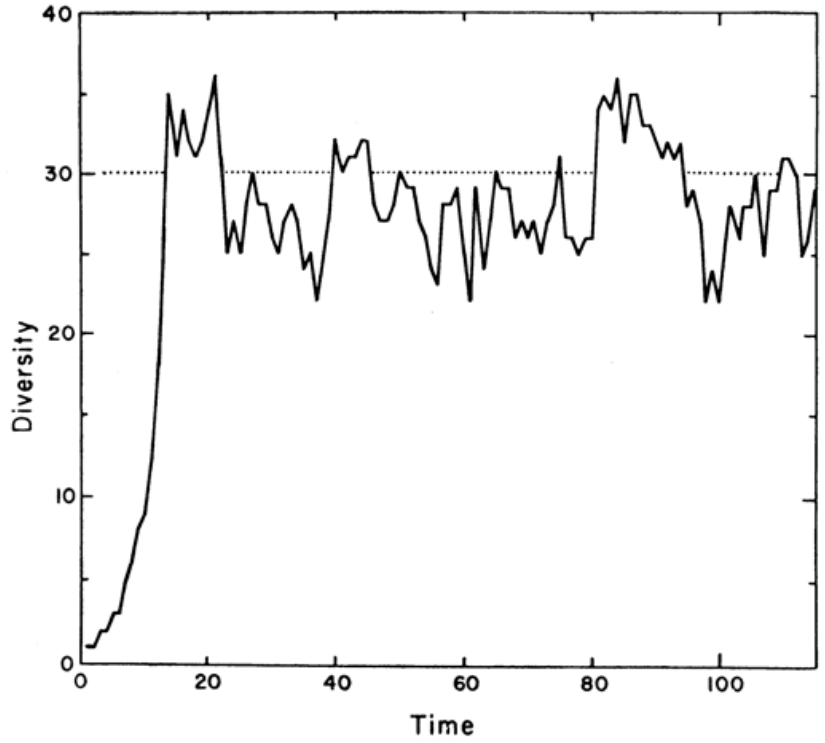
predation

parasitism

mutualism

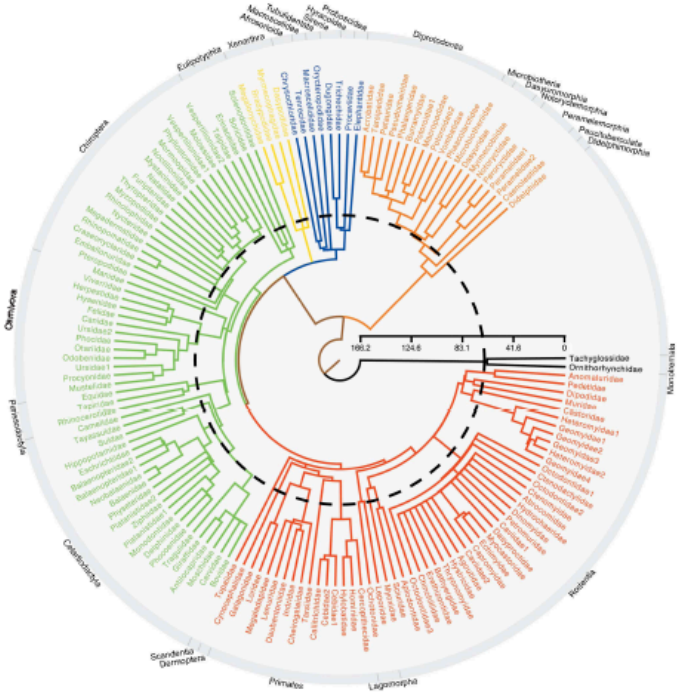
Birth-death models of cladogenesis

Birth-death models of cladogenesis were initially introduced by Raup (1973) to explain patterns in the fossil record



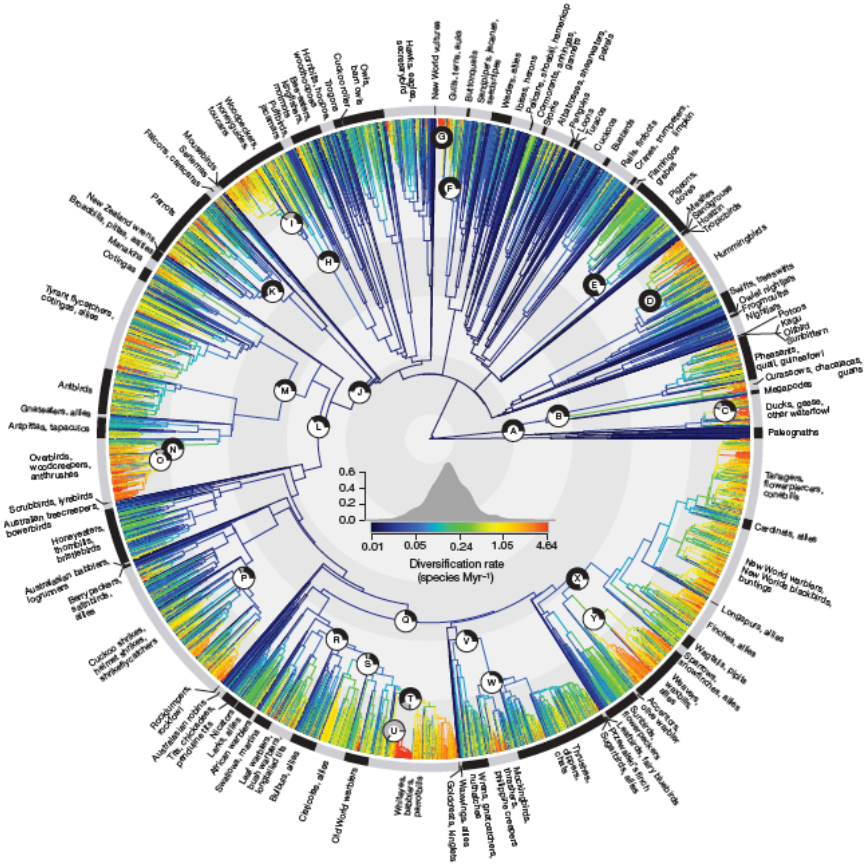
Many groups lack fossil data

Birth-death models are now heavily used to model phylogenies and infer rates of speciation and extinction



4 510 mammal species

Bininda-Edmond *et al. Nature* 2007



10 000 bird species

Jetz *et al. Nature* 2012

Phylogenetic approaches to diversification

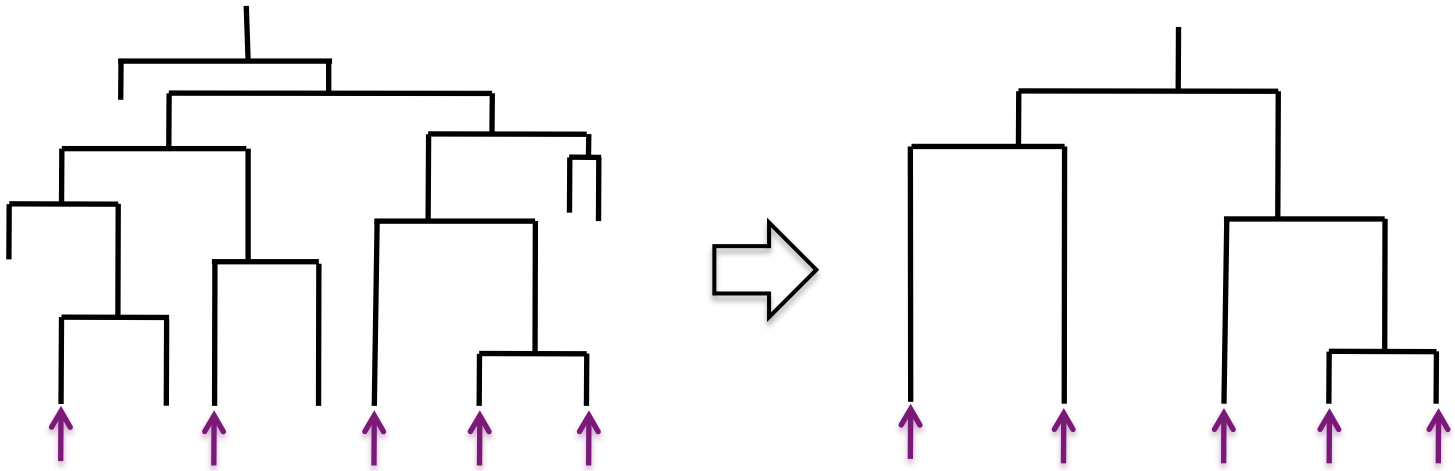
Stochastic birth-death process

Reconstucted phylogeny

The reconstructed evolutionary process

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

PTB 1994



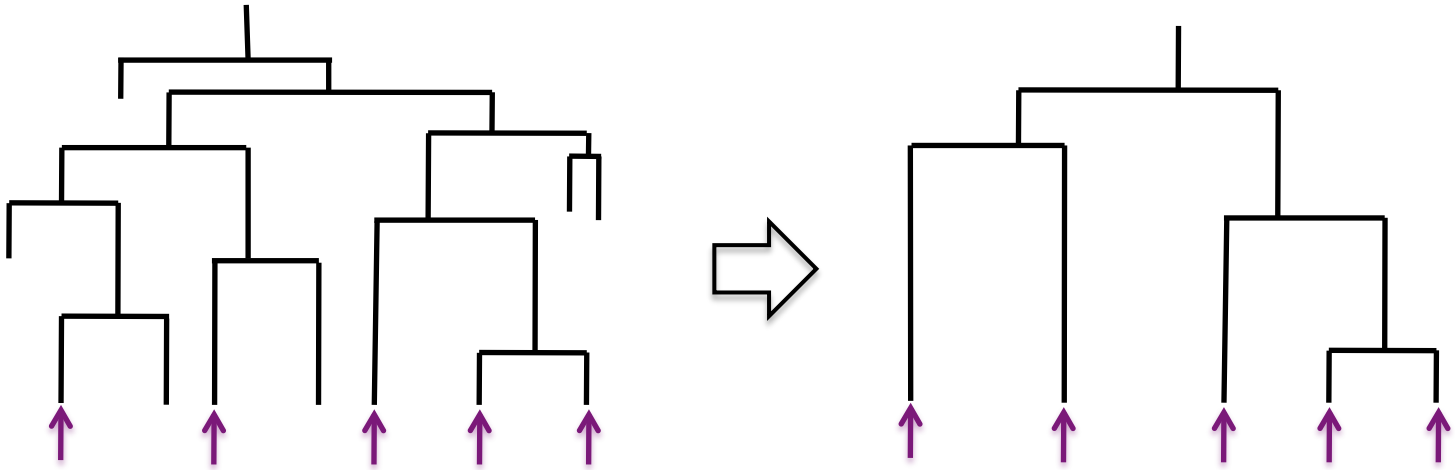
Phylogenetic approaches to diversification

Stochastic birth-death process

Reconstucted phylogeny

1. compute the likelihood of the reconstructed phylogeny

2. apply maximum likelihood or bayesian methods to fit the model to empirical data



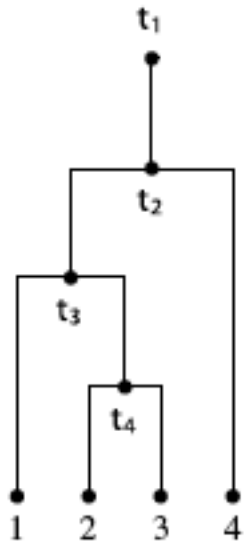
Calculating the likelihood of a reconstructed phylogeny

birth-death model

stem age t_1
speciation rate λ
extinction rate μ

+

λ and μ can vary over time
sampling fraction f



$$\mathcal{L}(t_1, \ldots, t_n) = \frac{f^n \Psi(t_2, t_1) \prod_{i=2}^{n} \lambda(t_i) \Psi(s_{i,1}, t_i) \Psi(s_{i,2}, t_i)}{1 - \Phi(t_1)},$$

Morlon *et al. PNAS* 2011

Calculating the likelihood of a reconstructed phylogeny

birth-death model

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speciation rate λ
extinction rate μ

+

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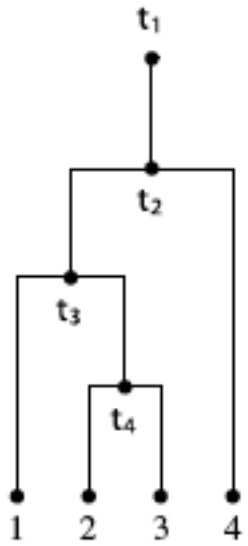

probability that n species are sampled today

$$\mathcal{L}(t_1, \ldots, t_n) = \frac{f^n \Psi(t_2, t_1) \prod_{i=2}^{n} \lambda(t_i) \Psi(s_{i,1}, t_i) \Psi(s_{i,2}, t_i)}{1 - \Phi(t_1)},$$

Morlon *et al. PNAS* 2011

Calculating the likelihood of a reconstructed phylogeny

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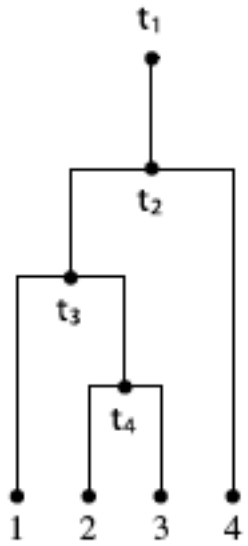


probability that a lineage survives from t_1 to t_2 and leaves no descendant in the sample

$$\mathcal{L}(t_1,\ldots,t_n) = \frac{f^n \Psi(t_2,t_1)\prod_{i=2}^{n}\lambda(t_i)\Psi(s_{i,1},t_i)\Psi(s_{i,2},t_i)}{1-\Phi(t_1)},$$

Morlon *et al. PNAS* 2011

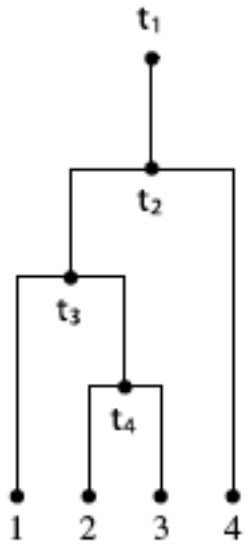
Calculating the likelihood of a reconstructed phylogeny

birth-death model

stem age t_1
speciation rate λ
extinction rate μ

+

λ and μ can vary over time
sampling fraction f



probability that a lineage survives from t_1 to t_2 and lives no descendant in the sample

$$\mathcal{L}(t_1,\ldots,t_n) = \frac{f^n \Psi(t_2,t_1)\prod_{i=2}^{n}\lambda(t_i)\Psi(s_{i,1},t_i)\Psi(s_{i,2},t_i)}{1-\Phi(t_1)},$$

probability of a speciation event at time t_i

Morlon *et al. PNAS* 2011

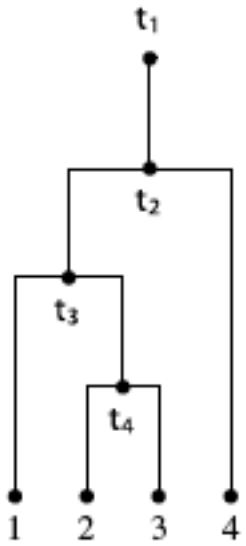
Calculating the likelihood of a reconstructed phylogeny

birth-death model

stem age t_1
speciation rate λ
extinction rate μ

+

λ and μ can vary over time
sampling fraction f



$$\mathcal{L}(t_1,\ldots,t_n) = \frac{f^n \Psi(t_2,t_1)\prod_{i=2}^{n}\lambda(t_i)\Psi(s_{i,1},t_i)\Psi(s_{i,2},t_i)}{1-\Phi(t_1)},$$

probability that a lineage alive at time t_1 has no descendant in the sample

Morlon *et al. PNAS* 2011

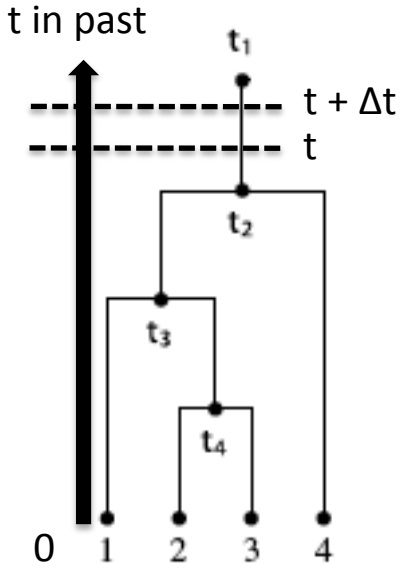
Calculating the likelihood of a reconstructed phylogeny

birth-death model

stem age t_1
speciation rate λ
extinction rate μ

+

λ and μ can vary over time
sampling fraction f



$\Phi(t) = \mathbb{P}\{\text{a lineage is } \textit{not} \text{ in the sample} | \text{it was alive at the time } t\}$

$$\begin{aligned}\Phi(t+\Delta t) = {} & \mu(t)\Delta t \\ & + (1-\mu(t)\Delta t)\lambda(t)\Phi^2(t) \\ & + (1-\mu(t)\Delta t)(1-\lambda(t)\Delta t)\Phi(t) \\ & + o(\Delta t)\end{aligned}$$

$\Delta t \to 0$

$$\frac{d\Phi}{dt} = \mu(t) - (\lambda(t) + \mu(t))\Phi(t) + \lambda(t)\Phi^2(t)$$

$$\Phi(t) = 1 - \frac{e^{\int_0^t \lambda(u) - \mu(u)du}}{\frac{1}{f} + \int_0^t e^{\int_0^s \lambda(u) - \mu(u)du}\lambda(s)ds}$$

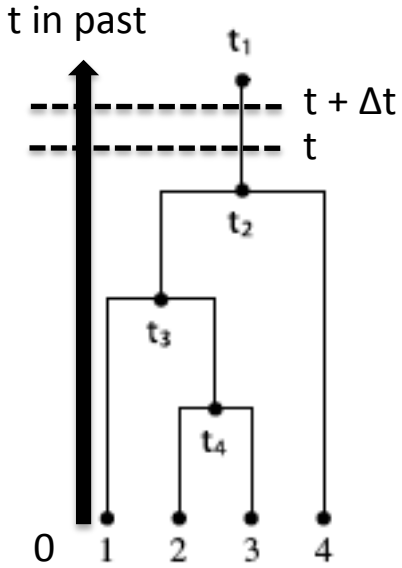
Calculating the likelihood of a reconstructed phylogeny

birth-death model

stem age t_1
speciation rate λ
extinction rate μ

+

λ and μ can vary over time
sampling fraction f



$\Psi(s, t)$ **probability that a lineage survives from t to s and lives no descendant in the sample**

$$\Psi(s,t) = e^{\int_s^t \lambda(u)-\mu(u)du}\left[1+\frac{\int_s^t e^{\int_0^\tau \lambda(\sigma)-\mu(\sigma)d\sigma}\lambda(\tau)d\tau}{\frac{1}{f}+\int_0^s e^{\int_0^\tau \lambda(\sigma)-\mu(\sigma)d\sigma}\lambda(\tau)d\tau}\right]^{-2}$$

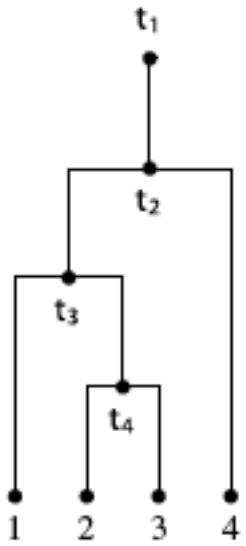
Calculating the likelihood of a reconstructed phylogeny

birth-death model

stem age t_1
speciation rate λ
extinction rate μ

+

λ and μ can vary over time
sampling fraction f



$$\mathcal{L}(t_1, \ldots, t_n) = \frac{f^n \Psi(t_2, t_1) \prod_{i=2}^{n} \lambda(t_i) \Psi(s_{i,1}, t_i) \Psi(s_{i,2}, t_i)}{1 - \Phi(t_1)},$$

Morlon *et al. PNAS* 2011

Support for a 4-shift rate model in the cetacean phylogeny

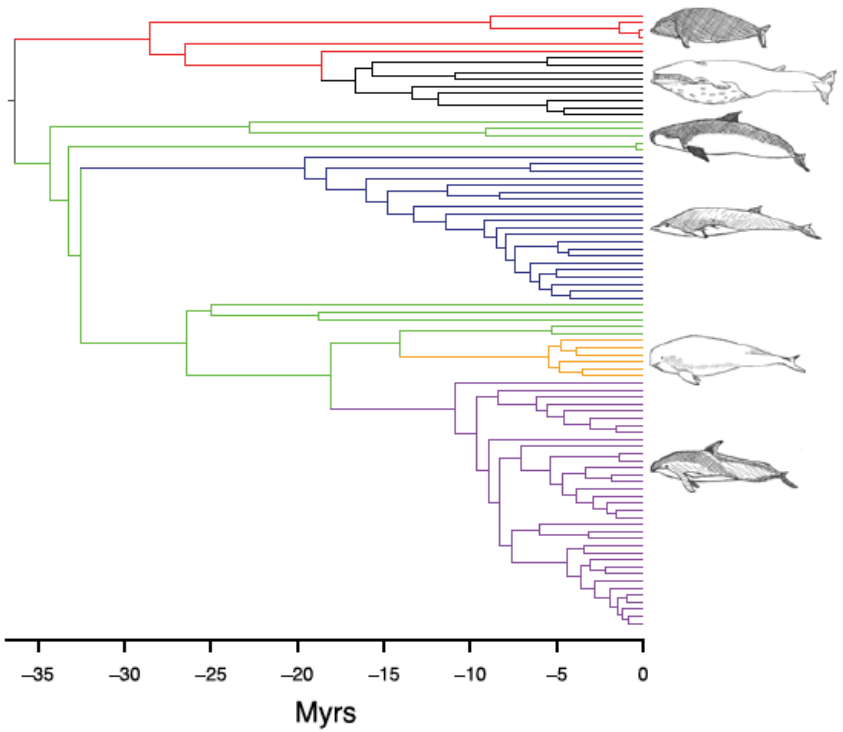
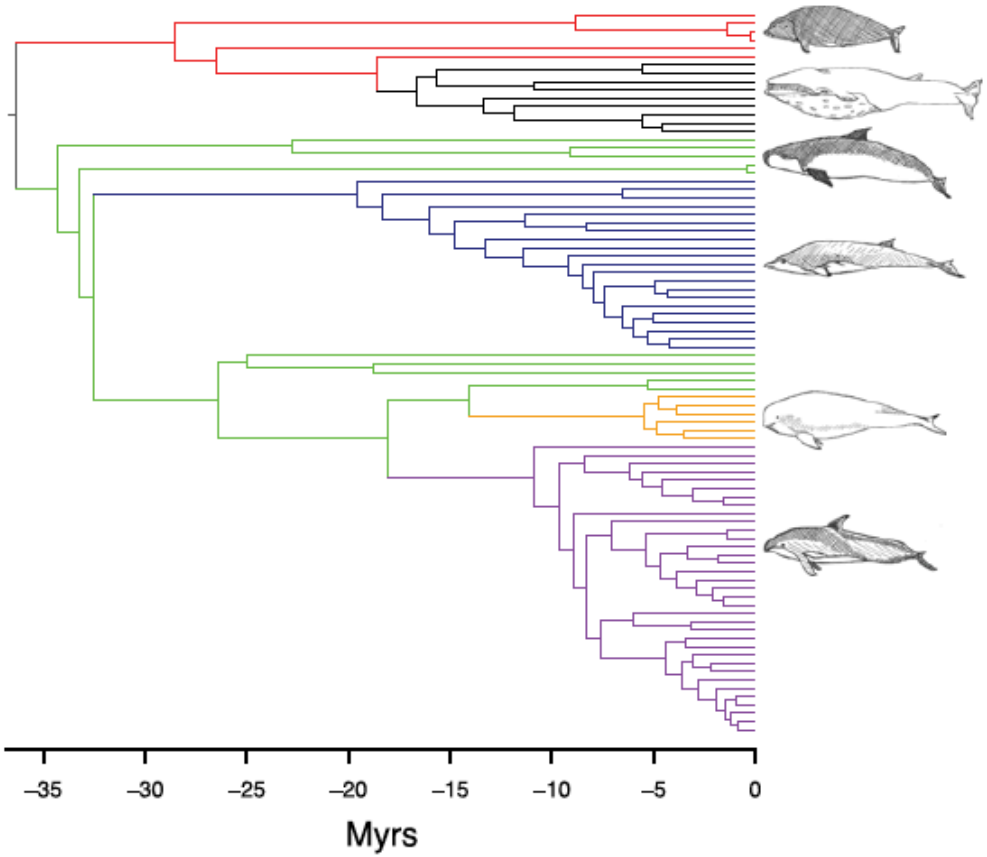
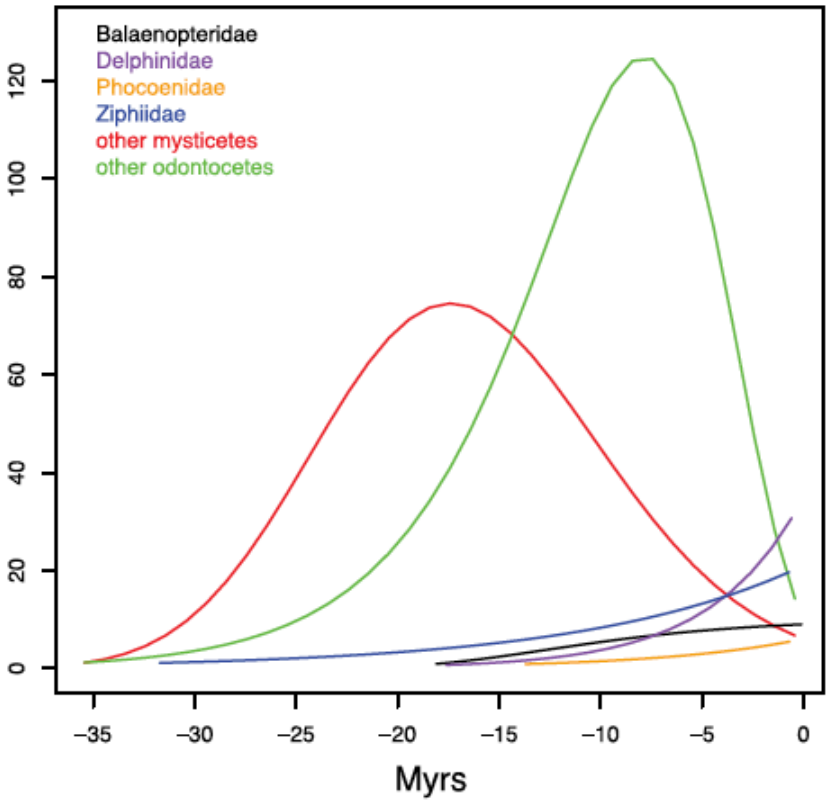


Table S2. Statistical support for rate shifts in the cetacean phylogeny

Model	nb	Description	LogL	AIC_c
No shift	1	Best fit model	–279.03	560.08
One shift	5	Best fit model: shift in the Delphinidae	–262.93*	536.22
Two shifts	6	Best fit model: shifts in the Delphinidae and Phocoenidae	–260.17†	532.85
Three shifts	7	Best fit model: shifts in the Delphinidae, Phocoenidae and Ziphiidae	–256.13‡	526.94
Four shifts	**8**	**Best fit model: shifts in the Delphinidae, Phocoenidae, Ziphiidae, and Balaenopteridae**	**–250.13**	**517.14**

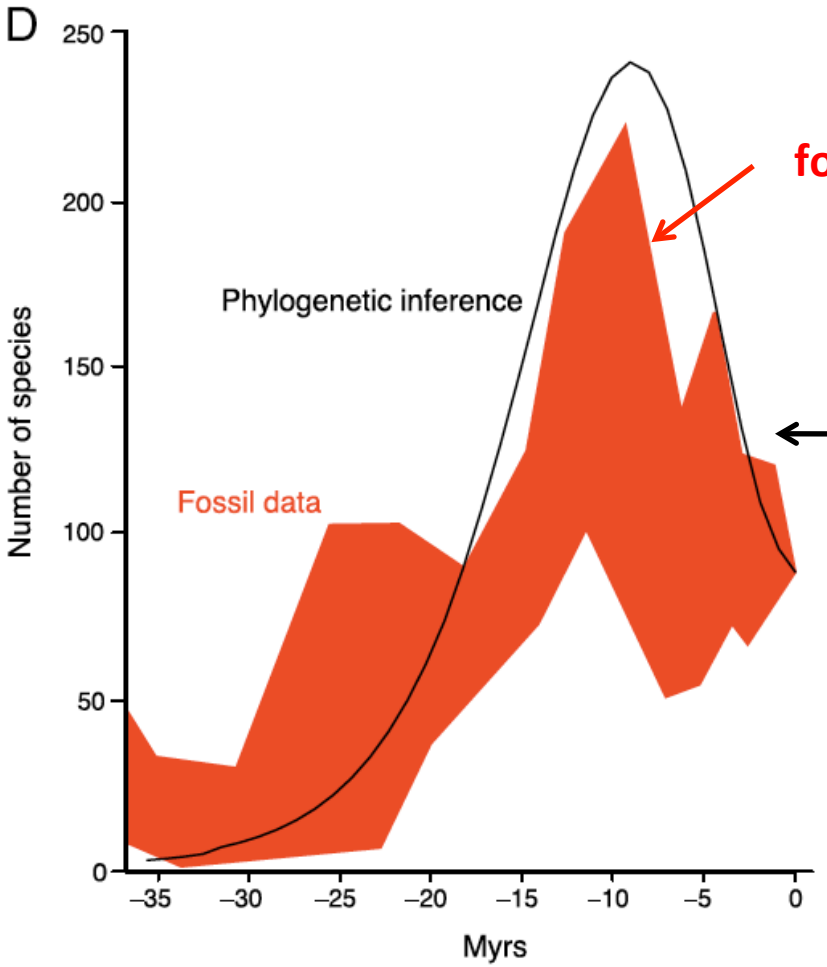
The resulting diversity curves show boom-then-bust diversity dynamics





Morlon *et al. PNAS* 2011

The resulting diversity curve is consistent with the fossil record



fossil record

phylogenetic inference, obtained by summing individual diversity curves

Morlon *et al. PNAS* 2011

Phylogenetic models of diversification have developed rapidly in the last decade

Ecology Letters, (2014) doi: 10.1111/ele.12251

REVIEW AND SYNTHESIS

Phylogenetic approaches for studying diversification

Hélène Morlon*

Center for Applied Mathematics, Ecole Polytechnique, Palaiseau, Essonne, France

**Correspondence: E-mail: helene.morlon@cmap.polytechnique.fr*

Abstract

Estimating rates of speciation and extinction, and understanding how and why they vary over evolutionary time, geographical space and species groups, is a key to understanding how ecological and evolutionary processes generate biological diversity. Such inferences will increasingly benefit from phylogenetic approaches given the ever-accelerating rates of genetic sequencing. In the last few years, models designed to understand diversification from phylogenetic data have advanced significantly. Here, I review these approaches and what they have revealed about diversification in the natural world. I focus on key distinctions between different models, and I clarify the conclusions that can be drawn from each model. I identify promising areas for future research. A major challenge ahead is to develop models that more explicitly take into account ecology, in particular the interaction of species with each other and with their environment. This will not only improve our understanding of diversification; it will also present a new perspective to the use of phylogenies in community ecology, the science of interaction networks and conservation biology, and might shift the current focus in ecology on equilibrium biodiversity theories to non-equilibrium theories recognising the crucial role of history.

Keywords

Birth–death models, cladogenesis, diversity dynamics, extinction, speciation, stochastic biodiversity models.

Testing the hypothesis of equilibrium dynamics

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Inferring the Dynamics of Diversification: A Coalescent Approach

Hélène Morlon[1]*, Matthew D. Potts[2], Joshua B. Plotkin[1]*

Testing the hypothesis of equilibrium dynamics

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PLoS BIOLOGY

Inferring the Dynamics of Diversification: A Coalescent Approach

Hélène Morlon[1]*, Matthew D. Potts[2], Joshua B. Plotkin[1]*

Inferring periods of diversity decline

Reconciling molecular phylogenies with the fossil record

Hélène Morlon[a,b,1], Todd L. Parsons[b], and Joshua B. Plotkin[b]

[a]Center for Applied Mathematics, Ecole Polytechnique, 91128 Palaiseau, France; and [b]Biology Department, University of Pennsylvania, Philadelphia, PA 19104

Testing the hypothesis of equilibrium dynamics

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Inferring the Dynamics of Diversification: A Coalescent Approach

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Inferring periods of diversity decline

PNAS

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[a]Center for Applied Mathematics, Ecole Polytechnique, 91128 Palaiseau, France; and [b]Biology Department, University of Pennsylvania, Philadelphia, PA 19104

Testing the effect of abiotic factors on diversification

Ecology Letters, (2013) doi: 10.1111/ele.12062

IDEA AND PERSPECTIVE

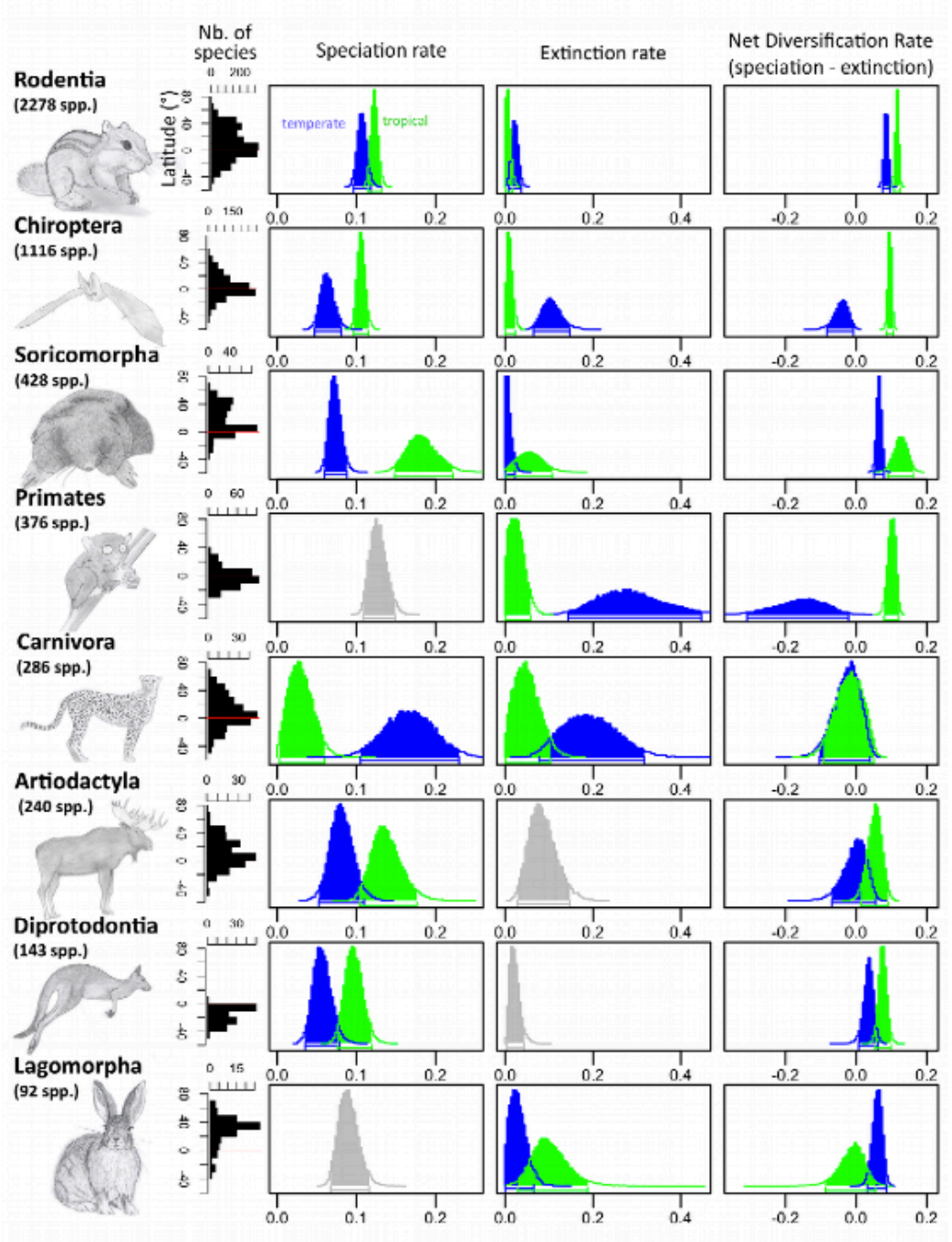
Macroevolutionary perspectives to environmental change

Fabien L. Condamine[1]* Jonathan Rolland[1] and Hélène Morlon[1]*

Abstract

Predicting how biodiversity will be affected and will respond to human-induced environmental changes is one of the most critical challenges facing ecologists today. Here, we put current environmental changes and their effects on biodiversity in a macroevolutionary perspective. We build on research in palaeontology

Application:
Why are there more species in the tropics?



Rolland, Condamine, Jiguet & Morlon *PloS B* (2014)

On-going developments

Towards merging
macroecological and macroevolutionary models

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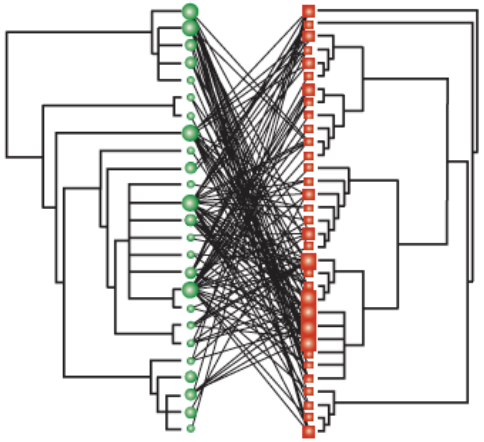
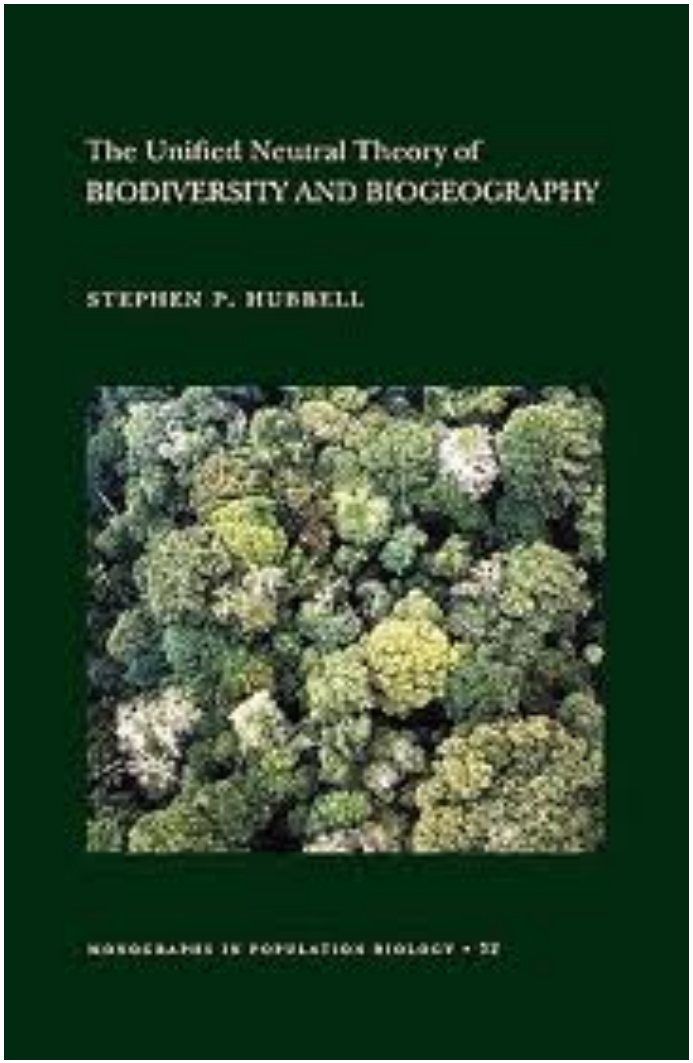
MARIE CURIE ACTIONS

Testing the effect of biotic interactions on diversification

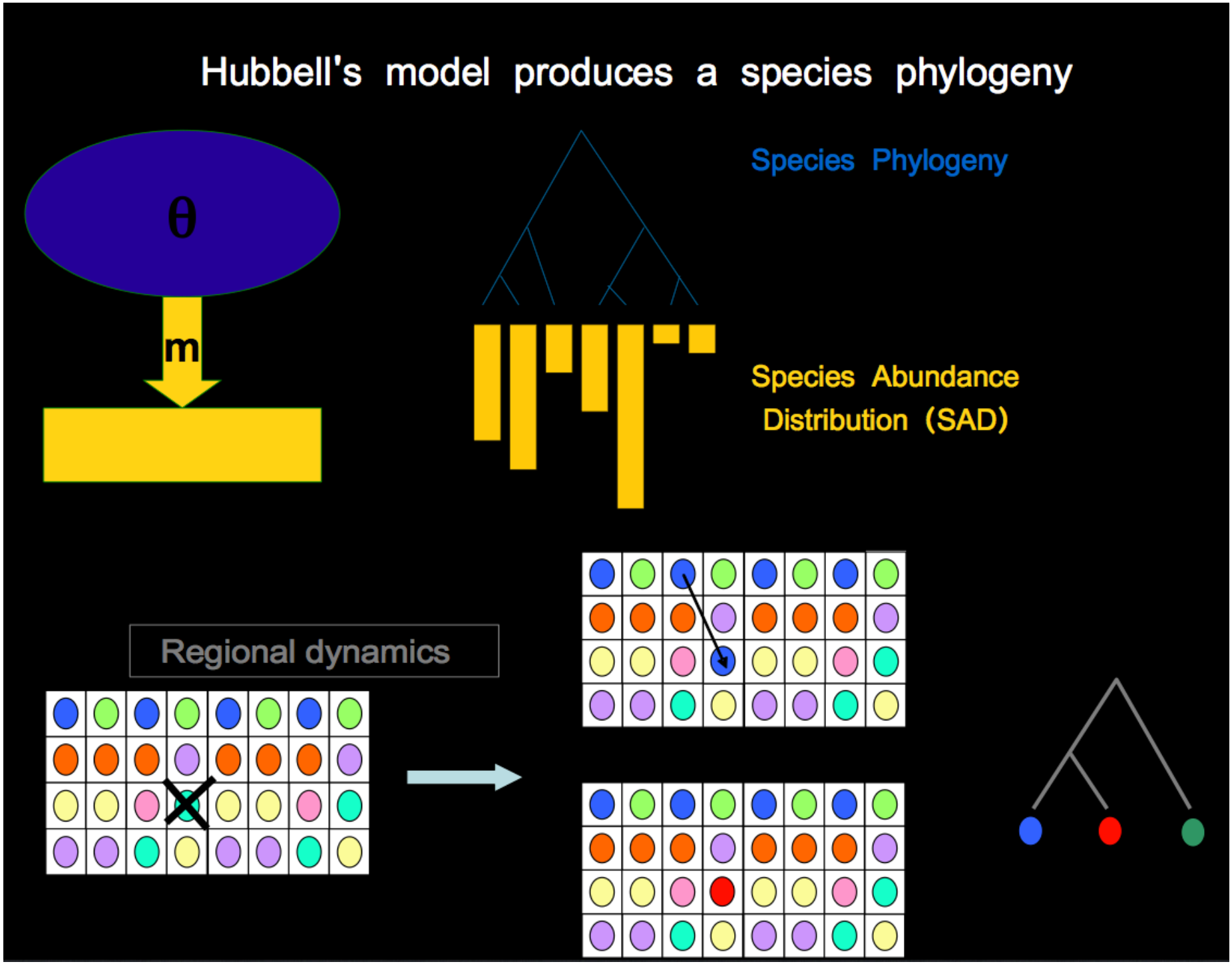
erc



Phylogenies arising from the Neutral Theory of Biodiversity (NTB)



Hubbell 2001


Hubbell's model produces a species phylogeny
θ
m
Species Phylogeny
Species Abundance Distribution (SAD)
Regional dynamics

Ecology Letters, (2008) 12: xxx–xxx doi: 10.1111/j.1461-0248.2008.01285.x

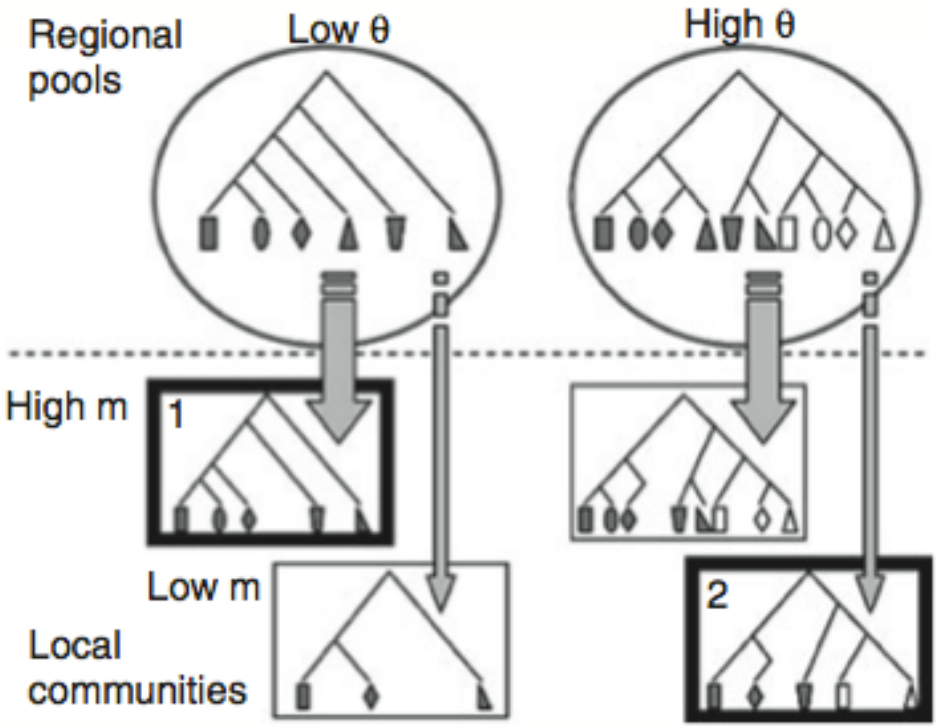
LETTER

Inferring the parameters of the neutral theory of biodiversity using phylogenetic information and implications for tropical forests

Franck Jabot* and Jérôme Chave

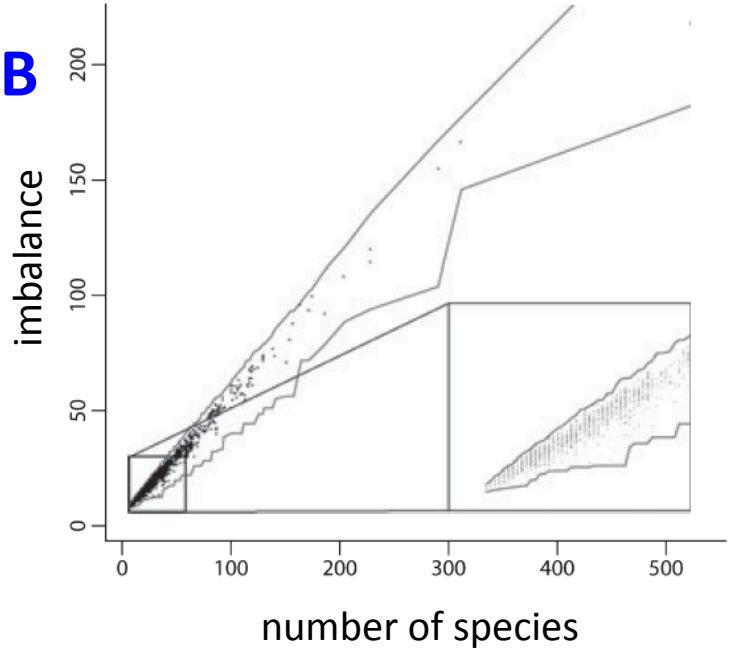
Abstract

We develop a statistical method to infer the parameters of Hubbell's neutral model of



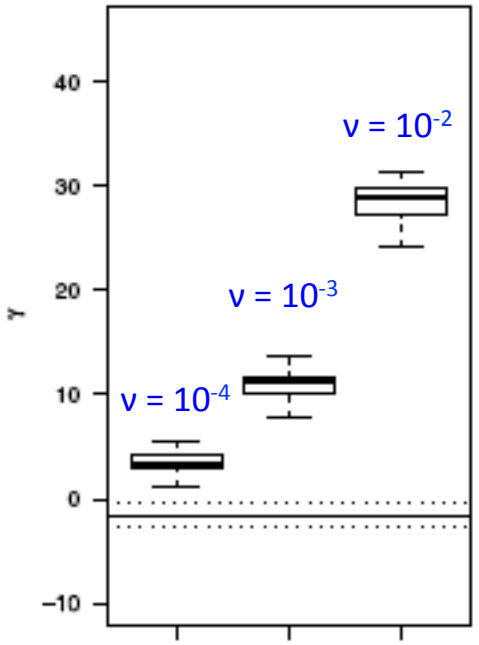
Method: Approximate Bayesian Computation

Phylogenies predicted by NTB have realistic imbalance…



Jabot & Chave
Eco. Lett. 2008

… but unrealistic branch-length patterns



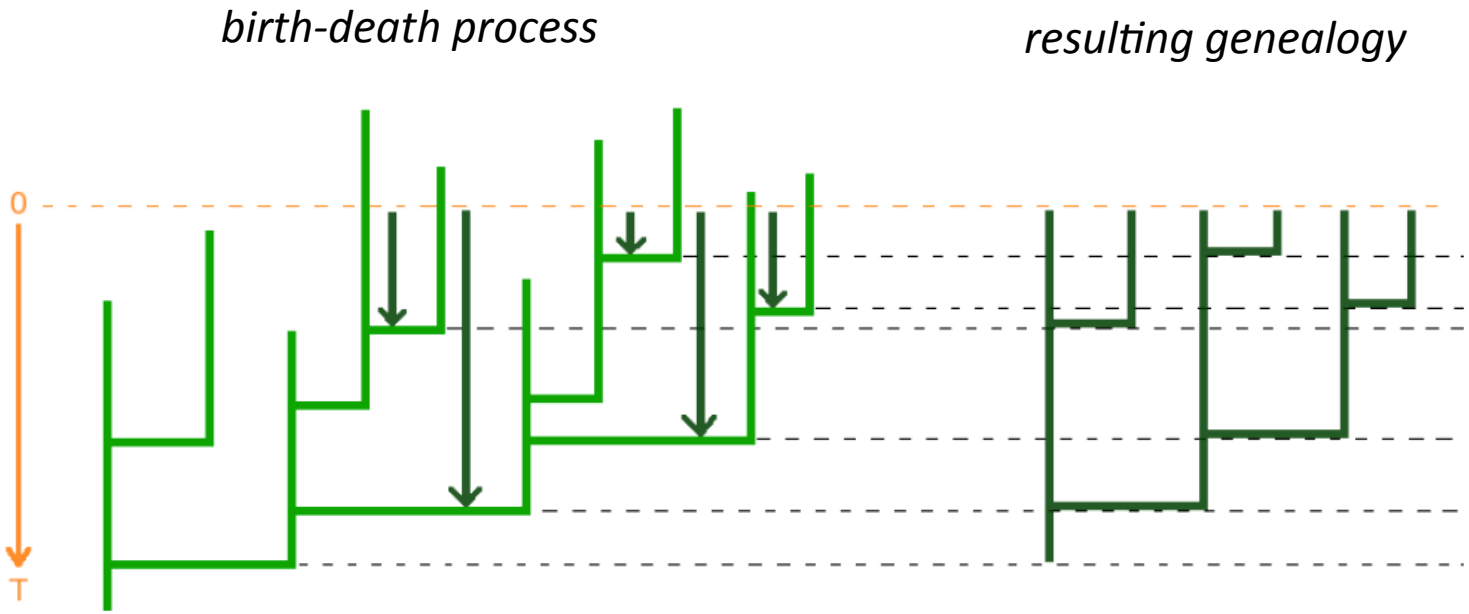
Davies et al.
Evolution 2011

The model of speciation by genetic differentiation

We relax a first limitation of NTB: constant total population size

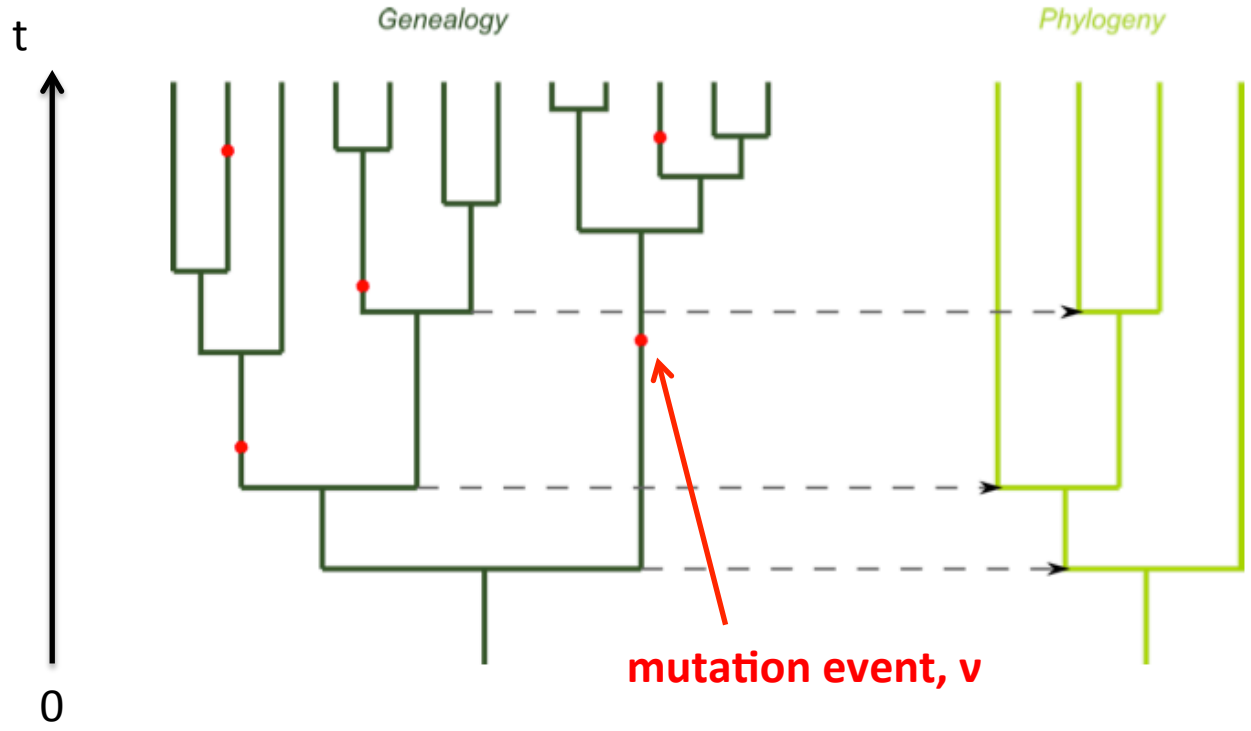
We assume individuals give birth with rate b and die with rate d

b and d can vary over time and we can have $b<d$

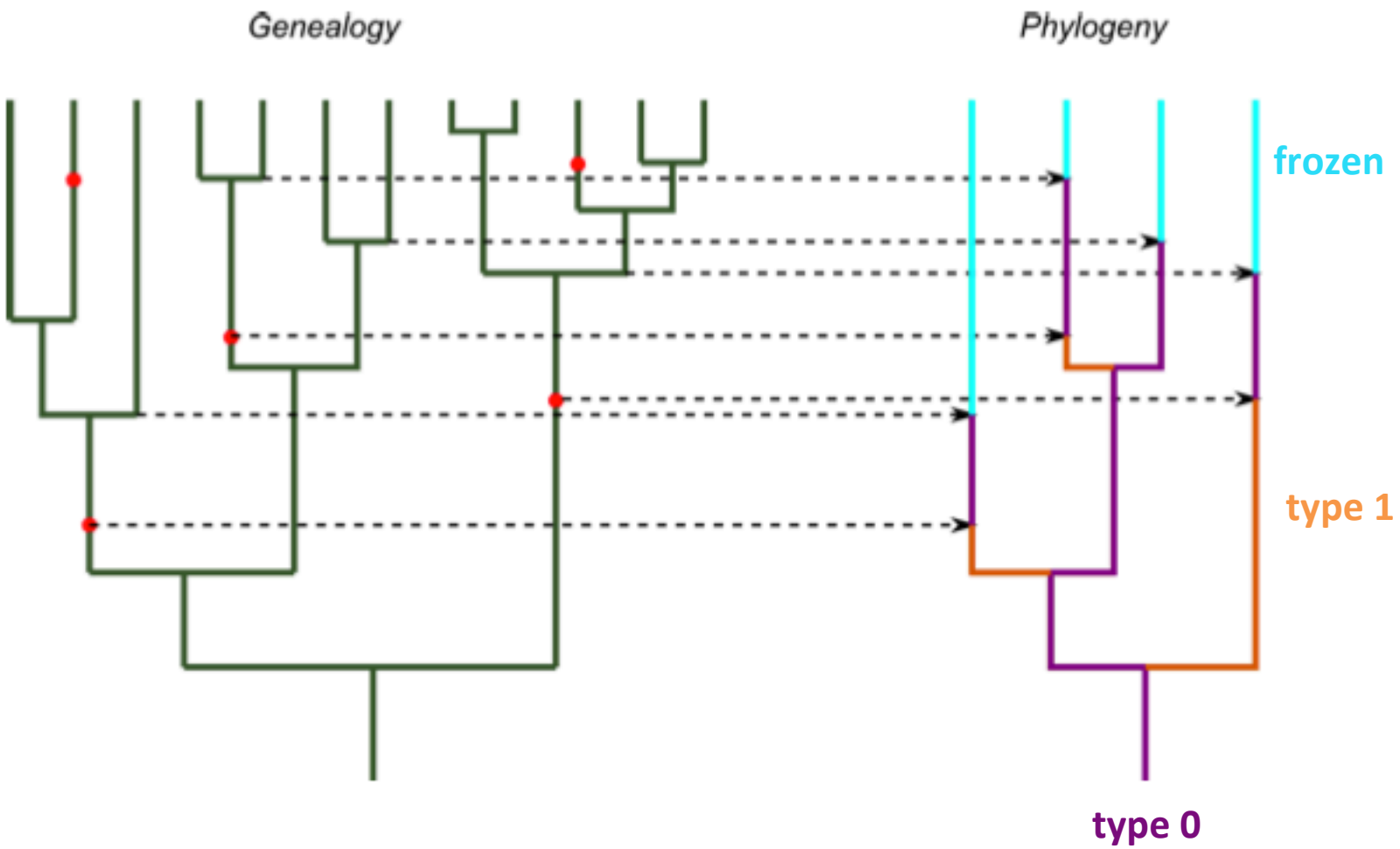


We relax a second limitation of NTB: the point mutation mode of speciation

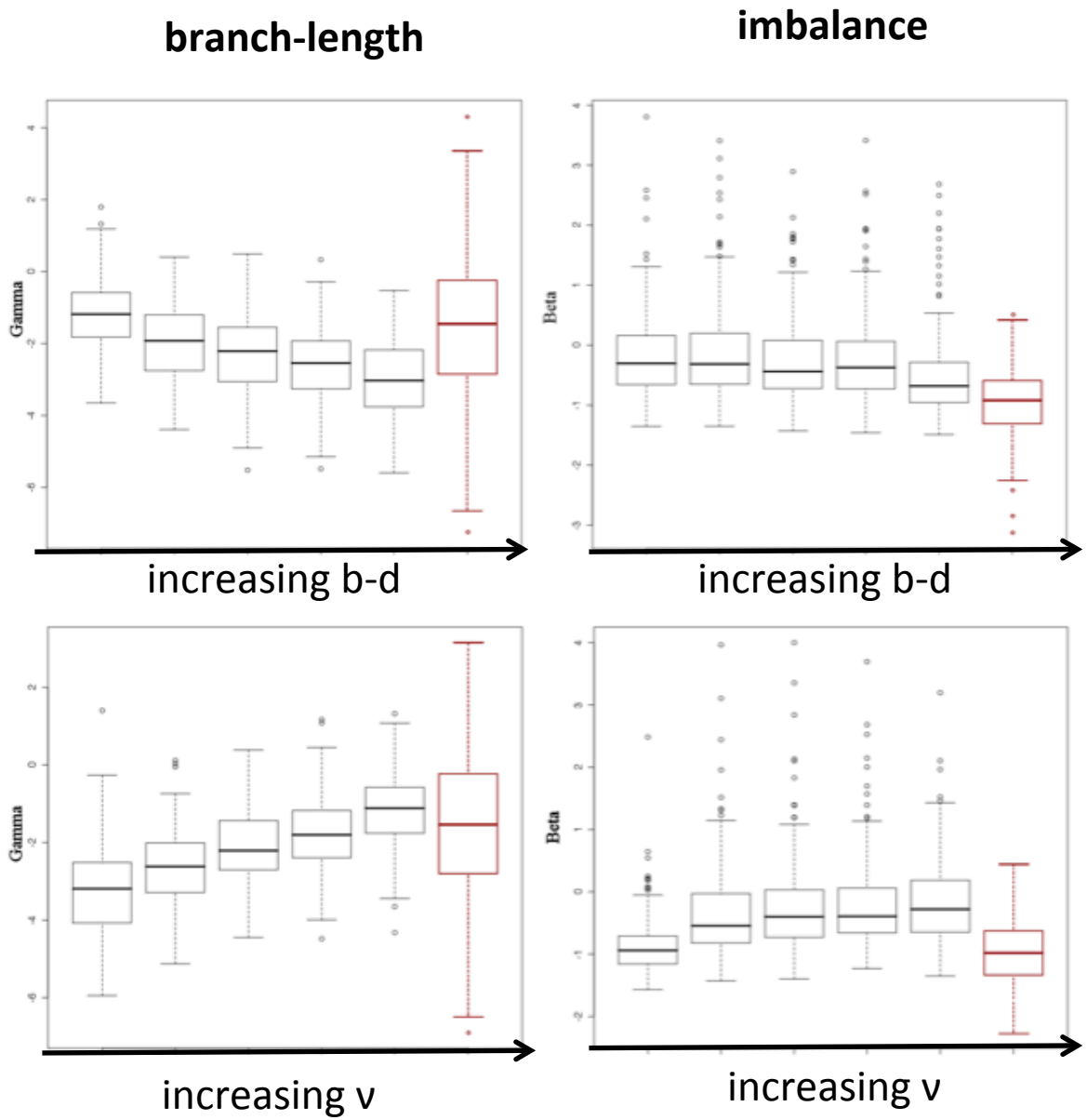
Speciation by genetic differentiation:
A node is a speciation event only if *all individuals*
of the two descendant populations are separated by *at least* one mutation



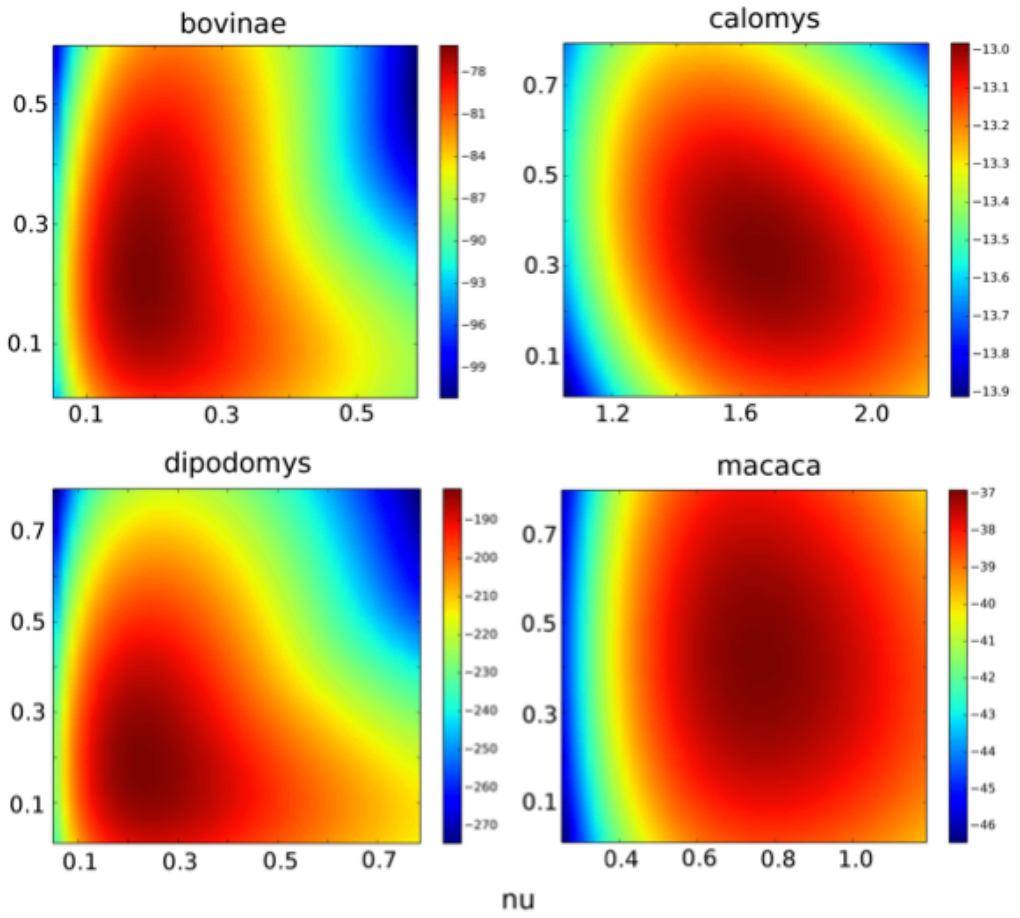
Phylogenies under SGD can be generated by a forward in time time-inhomogeneous branching process with three types



Phylogenies under SGD have realistic branch-lengths and imbalance



Likelihoods of trees under SGD can be computed efficiently



taxon	p	$\log(b)$	$b-d$	ν
bovinae	1	11.0	0.19	0.16
calomys	0.85	12.3	0.45	1.72
caprinae	0.89	10.7	0.40	0.39
dasyurid	0.92	10.8	0.20	0.23
dipodomys	0.95	11.2	0.05	0.30
duikers	0.83	11.2	0.38	0.30
genets	0.88	11.3	0.36	0.31
gibbon	1	8.8	0.53	0.32
howlerMonkey	0.91	11.5	0.20	0.39
macaca	0.95	6.4	0.42	0.76
microtus	0.69	6.9	1.84	1.05
mustelid	0.85	11.8	0.38	0.22
pikas	0.92	10.5	0.25	0.35
talpa	0.77	10.9	0.16	0.21

How to explain general biodiversity laws?

spatial biodiversity laws

macroecological models

deep-time biodiversity laws

macroevolutionary models

Ecologists and evolutionary biologists have favoured working with simple, tractable models

Are these models useful to make predictions in a changing world?

There is an increasing need for predictions, for scenarios of biodiversity and ecosystem services

Ecosystems: Time to model all life on Earth?

Drew Purves *et al. Nature 2013*

No report from the Intergovernmental Panel on Climate Change would fail to mention global climate models. Yet the international bodies that are charged with addressing global challenges in conservation, including the Intergovernmental Platform on Biodiversity and Ecosystem Services, cannot refer to analogous models of the world's ecosystems. Why? Because ecologists have not yet built them.

General ecosystem models (GEMs) could capture the broad-scale structure and function of any ecosystem in the world by simulating processes — including feeding, reproduction and death — that drive the distribution and abundance of organisms within that ecosystem. All of the organisms would be grouped not by species, but according to a few key traits such as whether they are plants, birds or mammals, cold blooded or warm blooded, diurnal or nocturnal. By encoding processes such as migration and predation into simple mathematical and computational forms, ecologists could model what happens to the various groups over time.

Metrics such as the diversity of animal types inhabiting the grasslands could be used to assess the savannas' health, stability and resilience, and to analyze the fate of particular groups of organisms such as top predators. Ecologists could explore how these attributes might change in response to, say, climate change, the introduction of invasive species or poaching. And, because the rules of play are likely to be broadly similar no matter what the ecosystem, the GEM could equally be applied to forests, lakes or the remotest parts of the ocean, providing a common framework for understanding and managing disparate ecosystems on local and global scales.

Modelling ecological phenomena at various scales is not new. Conservationists frequently use models to predict how much habitat fragmentation an endangered species can tolerate. But few ecologists have tried to build models of how general ecosystem properties emerge from the interactions of individuals. One attempt — known as Ecopath with Ecosim1 — is being developed at the University of British Columbia's Fisheries Centre to address management and ecological questions. This combines modelling at the phytoplankton scale with that at the level of fisheries and marine mammals. Another, called Atlantis2, developed by Australia's Commonwealth Scientific and Industrial Research Organisation, incorporates biophysical, economic and social factors to provide an integrated tool for modelling marine ecosystems. But these consider fewer processes and organisms than would a GEM.

The biggest stumbling block to constructing GEMs (after convincing ecologists that they can and should be built!) is obtaining the data to parameterize and validate them.

Constructing realistic GEMs is one thing. The real challenge is to produce models from which the predictions are trustworthy enough to guide the decisions of conservationists and policy-makers.

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PLOS | BIOLOGY

Emergent Global Patterns of Ecosystem Structure and Function from a Mechanistic General Ecosystem Model

Michael B. J. Harfoot[1,2,3]*, Tim Newbold[1,2,3], Derek P. Tittensor[1,2,3], Stephen Emmott[2], Jon Hutton[1], Vassily Lyutsarev[2], Matthew J. Smith[2], Jörn P. W. Scharlemann[1,4], Drew W. Purves[2]

1 United Nations Environment Programme World Conservation Monitoring Centre, Cambridge, United Kingdom, **2** Computational Science Laboratory, Microsoft Research, Cambridge, United Kingdom, **3** Dalhousie University, Halifax, Nova Scotia, Canada, **4** School of Life Sciences, University of Sussex, Falmer, Brighton, United Kingdom

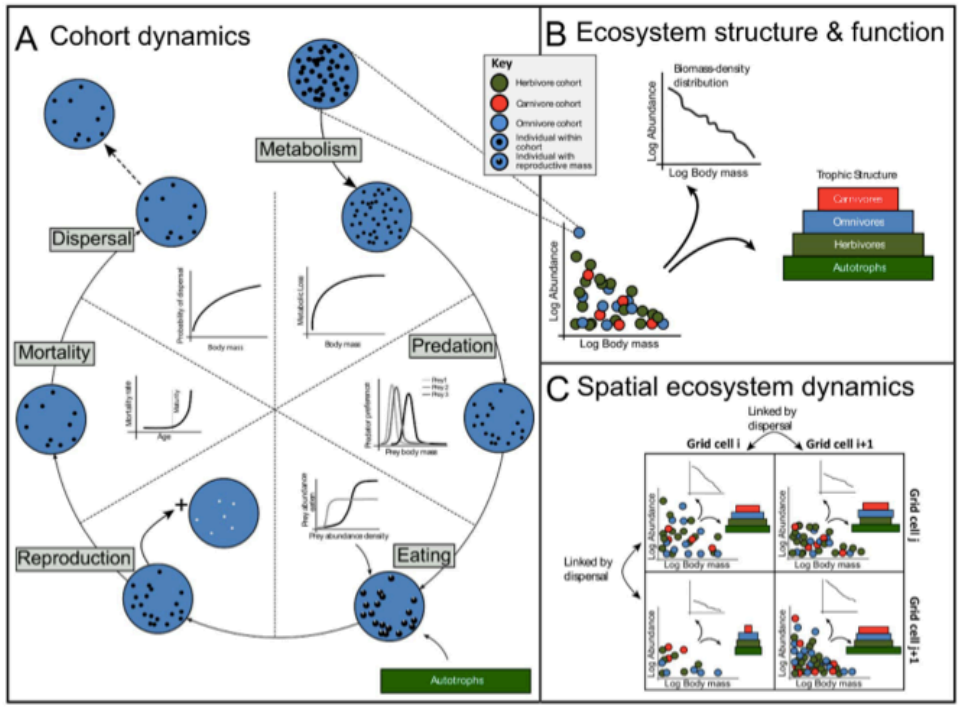

Figure 1. Schematic of the model. Ecosystem structure and function (B) emerges from a combination of processes operating on individual organisms within a grid cell (A), and exchange of individuals among grid cells via dispersal (C). Life histories (e.g., average lifespan, lifetime

We develop and use phylogenetic approaches to understand global biodiversity patterns, across the Tree of Life

Fabien Condamine

Dan Moen

Jonathan Rolland

Marc Manceau

Amaury Lambert

Frederic Jiguet

Joshua Plotkin

Todd Parsons

erc

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