# Prospecting for unconventional hypotheses in macroevolution modeling Presentation for Tanja Stadler's group in Basel

Marc Manceau

October 15, 2018





Introduction	Diversification	Phenotypic evolution	Molecular clock	
Macroevolution Comparative approach				
Concrete questi	ons :			

- 1. What determines the color, size, shape of the gills ?
- 2. What did the ancestor of all nudibranchs look like ?
- 3. How to classify them in distinct species ?
- 4. What is the tempo of speciation and extinction events ?



- 1. Compare traits observed in the wild.
- 2. Propose scenarios of evolution:
  - probabilistic models
  - process-based models
- 3. Fit these models to observed data.

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Introduction ○●		Phenotypic evolution 0000000		
Stochastic model For three types of obs	ing servations			
Phylogen	ies	Phenotypes	Genetic sequences	
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A minimalist individual-based model with out-of-equilibirium metapopulation dynamics.

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Stochastic mode For three types of ob	ling		



Traits implicated in inter-specific interactions.

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Punctual evolution of some genetic sequences.

#### Introduction

Macroevolution Stochastic modeling

#### Diversification

State of the art The species definition in modeling work Application to diversification studies

#### Phenotypic evolution

State of the art Coevolution of traits from different species Proposed framework Examples of applications

### Molecular clock

State of the art A new relaxation Inference method

#### Conclusion







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- Empirical trees are unbalanced.
- They show nodes quite close to the root.
- Could we reproduce such observations with a minimalist individual-based model ?

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#### Each species :

- gives birth at rate b.
- is independent of all others.
- dies at rate d.

Produces trees :

- too balanced.
- too tippy.

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Each species : gives birtl is independent dies at rage	h at rate <i>b</i> . Ident of all others. te <i>d</i> .	<ul><li>Produces trees :</li><li>too balanced.</li><li>too tippy.</li></ul>		

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Population dyn	amics :	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
fixed size		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
discrete g	generations.	•																			
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►	discrete generations.		•													•						
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# State of the art Individual-based modeling

Population dynamics :

- fixed size.
- discrete generations.
- uniform choice of a parent in the previous generation.

Superimposition of a speciation model.


Diversification		
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	Diversification OO●○○○○○○	Phenotypic evolution	
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Diversification OO●○○○○○○	Phenotypic evolution	



Diversification		
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- Models produce species that are non-monophyletic groups of individuals.
- Leads to a difficulty to build the phylogeny from the genealogy.
- Simulated trees are enough unbalanced, but are way too tippy.

Jabot and Chave, 2009, *Ecol. Lett.* Davies and al., 2011, *Evolution*.



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	Diversification ○○○○●○○○○○	Phenotypic evolution	
The species defin	ition in modeling wo	rk	

Proposing two new definitions

- Loose The finest monophyletic partition such that any two individuals from distinct clusters are always phenotypically different.
- Lacy The coarsest monophyletic partition such that any two individuals from the same cluster are always phenotypically similar.



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	Diversification	Phenotypic evolution	
Application to div Two new hypotheses	versification studies		

Loose species definition.



Manceau, Lambert and Morlon, 2015, Ecol. lett.

	Diversification	Phenotypic evolution	
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	Diversification	Phenotypic evolution	
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	Diversification ○○○○●○○○○	Phenotypic evolution	
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Application to div Two new hypotheses	versification studies		



Manceau, Lambert and Morlon, 2015, Ecol. lett.

Diversification		
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# Application to diversification studies Comparison to empirical trees

The model generates trees with compatible

- branching times distribution.
- balance level.



Diversification		
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# Application to diversification studies Comparison to empirical trees

The model generates trees with compatible

- branching times distribution.
- balance level.



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A 12	10 10 11 1 11 11			

We numerically compute the likelihood of an observed tree.



We estimate parameters by numerically optimizing the likelihood

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Application t	o diversification studi	6C	

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But we have no signal for b.



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Application t	a diversification studie		

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Application t	o diversification studies		

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- But we have no signal for b.



An inference method

	Diversification			
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Application to diversification studies				

#### Application to diversification studies Project summary

An individual-based model of diversification proposing two unconventional hypotheses:

- 1. population dynamics given by a birth-death process,
- 2. the loose species definition.



- Compatible with empirical tree shapes.
- What is the relative importance of the two hypotheses ?

	Diversification ○○○○○○○○○●	Phenotypic evolution	
Application to Project summary	diversification studies		

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	Diversification	Phenotypic evolution	
Application to Project summary	diversification studies	5	

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|                                   | Diversification<br>○○○○○○○○○ | Phenotypic evolution |  |
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| Application to<br>Project summary | diversification studies      |                      |  |

An individual-based model of diversification proposing two unconventional hypotheses:

- 1. population dynamics given by a birth-death process,
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Conclusion and perspectives:

- Compatible with empirical tree shapes.
- What is the relative importance of the two hypotheses ?

#### Introduction

Macroevolution Stochastic modeling

## Diversification

State of the art The species definition in modeling work Application to diversification studies

## Phenotypic evolution

State of the art Coevolution of traits from different species Proposed framework Examples of applications

## Molecular clock

State of the art A new relaxation Inference method

## Conclusion







	Phenotypic evolution	
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# State of the art Central hypothesis: independent lineages

#### We compare:

## traits of different species.

which phylogenies is known (fixed).

#### Modeling framework:

- the trait at the root is drawn in a given law.
- along a branch it follows a given stochastic trajectory.
- it is copied in two independent processes at each branching event.



#### Felsenstein, 1973, Am. J. Hum. Genet.

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State of the art Stochastic process alo	ng a fixed tree		

## Overview of some stochastic trajectories:

Brownian motion  $dX_t = \sigma dB_t$ 

Ornstein-Uhlenbeck  $dX_t = \psi( heta - X_t)dt + \sigma dB_t$ 

Drifted Brownian motion  $dX_t = adt + \sigma dB_t$ 



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		Phenotypic evolution			
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Coevolution of traits from different species					

Attraction or repulsion in the trait space

## Some examples of non-independent traits:

Mimicry attraction toward the mean trait of a community. Mutualism coevolution of traits in two clades.

- We would like to study the traits in a similar framework.
- Without the independence hypothesis from traits evolving in distinct lineages.

	Phenotypic evolution	
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	Phenotypic evolution	
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The trait distribution at present is Gaussian.

• We show how to numerically compute its mean and variance.

Introduction Divers	sification	Phenotypic evolution	Molecular clock	Conclusion
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	Phenotypic evolution	

# Proposed framework Most models fit within this framework

 $dX_t = (a - AX_t)dt + \Gamma dW_t$ 



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	Phenotypic evolution	
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# Examples of applications Competition leading to trait displacement



Anolis lizards on Caribbean islands.

Traits under study:

- skull, jaws.
- femur, tibia, humerus, radius, …
- ▶ pelvis, tail.



Drury and al., 2016, Syst. Biol.

	Phenotypic evolution	
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Drury and al., 2016, Syst. Biol.

		Phenotypic evolution ○○○○○○●	
Examples of appl Coevolving traits in d	ications istinct clades		

- Coevolution of traits implicated in mutualistic interactions.
- Could be coupled with a model of interaction network evolution.



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## Conclusion







		Phenotypic evolution	Molecular clock ●000000000	
State of the art The strict clock, back	in the 60's, with Zucker	kandl and Pauling		

> Pairwise differences are compatible with branch lengths of an ultrametric tree.



We can imagine that mutation happen through a constant rate Poisson process.

#### Zuckerkandl and Pauling, 1962.

		Phenotypic evolution	Molecular clock ●000000000	
State of the art	in the 60's. with Zuckerk	andl and Pauling		

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Zuckerkandl and Pauling, 1962.

	Phenotypic evolution 0000000	Molecular clock O●OOOOOOOO	
State of the art			

- We are given a stationary Markov chain on  $\{A, T, G, C\}$ .
- Nucleotides at the root are iid according to the stationary law.
- Each nucleotide evolves independently of the others along a branch.
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		Molecular clock	Conclusion
		000000000	
State of the art The strict or fully rel	axed versions		



		Phenotypic evolution	Molecular clock OO●OOOOOOO	
State of the art	laxed versions			



	Phenotypic evolution	Molecular clock OO●OOOOOO	
State of the art			



The strict or fully relaxed versions

	Phenotypic evolution	Molecular clock OO●OOOOOO	
State of the art			

### State of the art The strict or fully relaxed versions



	Phenotypic evolution	Molecular clock 000●000000	
State of the art			

The many relaxations



#### Branch lengths follow a prior law.

- The substitution rate can vary amon branches, in an auto-correlated way...
- ... or in a non-auto-correlated way.

Lepage et al., 2007, Mol. Biol. Evol.

	Diversification	Phenotypic evolution	Molecular clock	Conclusion
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OO		OOOOOOO		Conclusion
State of the art The datation principle				
рата	shark         A         T         C         G         A         A           tuna         -         -         G         -         C         T           whale         -         A         G         -         -         -           dugong         -         A         G         -         -         -           turtle         -         -         G         G         -         -           penguin         -         -         G         G         -         -	G C	orgeong turte Peqeum	
MODEL				
RESULT	<sup>th</sup> at t <sup>trins</sup>	<sup>briade</sup> digong turne Borg an	0 time ¥ 1	

	O000000000	Phenotypic evolution	Molecular clock	Conclusion
State of the art The datation principle				
DATA	shark         A         T         C         G         A         A           tuna         -         -         G         -         C         T           whale         -         A         G         -         -         -           dugong         -         A         G         -         -         -           turtle         -         -         G         G         -         -           penguin         -         -         G         G         -         -	G C	olikong turtio Panguri	
MODEL			$\mathcal{T}$ = Tree	
			$\mathbb{P}(\mathcal{T})$	
RESULT	lite, Interior	tates	0 time	

Presentation in Basel

OO		OOOOOOO		Conclusion
State of the art The datation principle				
рата	shark         A         T         C         G         A         A           tuna         -         -         G         -         C         T           whale         -         A         G         -         -         -           dugong         -         A         G         -         -         -           turtle         -         -         G         G         -         -           penguin         -         -         G         G         -         -	G C	<sup>-14c</sup> <sup>-14c</sup> <sup>14th</sup> <sup>14th</sup>	
MODEL		$\mathcal{R} = \text{Substitution rate}$ $\mathbb{P}(\mathcal{R} \mid \mathcal{T})$	$\mathcal{T} = \operatorname{Tree}_{\mathbb{P}(\mathcal{T})}$	
RESULT	li ar	<sup>by</sup> Aa <sub>le</sub> dogong turthe Pangaug	0 time ¥ 1	

	O000000000	Phenotypic evolution	Molecular clock	Conclusion
State of the art The datation principle				
рата	shark         A         T         C         G         A         A           tuna         -         -         G         -         C         T           whale         -         A         G         -         -         -           dugong         -         A         G         -         -         -           turtle         -         -         G         G         -         -           penguin         -         -         G         G         -         -	G C	di@cyage turrie Pacration	
MODEL	$ \begin{array}{c} \land & & \uparrow \\ c & c \\ \end{array} $ $ \begin{array}{c} \mathcal{A} = \text{Alignment} \\ \mathbb{P}(\mathcal{A} \mid \mathcal{T}, \mathcal{R}) \end{array} $	$\mathcal{R} = \text{Substitution rate}$ $\mathbb{P}(\mathcal{R} \mid \mathcal{T})$	$\mathcal{T} = \operatorname{Tree}_{\mathbb{P}(\mathcal{T})}$	
RESULT	the second s	<sup>14</sup> NM <sub>6</sub> <sup>10</sup> NM <sub>6</sub>	0 time ¥ 1	



Presentation in Basel

		Phenotypic evolution	Molecular clock ○○○○●●○○○○	
A new relaxation Biological motivation:	genomics of speciation			

# Strong divergent selection at speciation :

- use of distinct resources,
- adaptation to distinct habitats,
- recognition of sexual partners.

- genomic islands of speciation,
- short rise of the substitution rate.

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		Phenotypic evolution	Molecular clock	
A new re Introduction	laxation n of spikes of mutations			
From	the whole process	to the red	constructed tree:.	
►	Birth-death process,	probab	pility $ u$ of having a <i>spike</i> at a	
►	probability $\nu$ of having a <i>spike</i> a	t birth. branching time,		
	01.1	an inhorithe branch		

2223



• On a spike, each nucleotide of the sequence mutates with probability  $\kappa$ .

Т

time

		Phenotypic evolution	Molecular clock	
A new relax	xation of spikes of mutations			
From tl	he whole process	to the recons	tructed tree:.	
► B	irth-death process, robability ν of having a <i>spike</i>	probability branching	u  u of having a <i>spike</i> at a time,	
-		an inhomo		



Presentation in Basel

	Phenotypic evolution	Molecular clock ○○○○○○●○○○	
A new relaxation			

# A new relaxation Introduction of spikes of mutations

From the whole process ...

- Birth-death process,
- probability  $\nu$  of having a *spike* at birth.
- ... to the reconstructed tree:.
  - probability v of having a spike at a branching time,
  - an inhomogeneous Poisson process along branches.



- Markovian evolution along branches,
- On a spike, each nucleotide of the sequence mutates with probability  $\kappa$ .

		Phenotypic evolution	Molecular clock ○○○○○○●○○○○	
A new relaxa	ition spikes of mutations			
From the	whole process	to the recons	tructed tree:.	
Birt	th-death process,	probability	$\nu$ of having a <i>spike</i> at a	
pro	• probability $\nu$ of having a <i>spike</i> at birth		time,	



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		Phenotypic evolution 0000000	Molecular clock ○○○○○○○○○○	
A new relaxat Introduction of sp	ion pikes of mutations			
From the v	vhole process	to the recons	structed tree:.	
Birth	-death process,	probability	/ $ u$ of having a <i>spike</i> at a	
proba	probability v of having a spike at birth	th. branching	time,	
C	]	an inhomo branches.	ogeneous Poisson process al	long



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		Phenotypic evolution	Molecular clock ○○○○○○○○○○	
A new relaxation Introduction of spi	D <b>n</b> kes of mutations			
From the wh	nole process	to the recons	structed tree:.	
Birth-	death process,	probability	u of having a <i>spike</i> at a	
probability v of having a spike at birth.		rth. branching	time,	
ol	1	an inhomo branches.	ogeneous Poisson process al	ong



Markovian evolution along branches,

On a spike, each nucleotide of the sequence mutates with probability κ.

		Phenotypic evolution 0000000	Molecular clock ○○○○○○●○○○	
A new relaxation Introduction of spike	ı s of mutations			
From the who Birth-de	le process ath process, ity w of having a sp <i>ike</i> at hir	to the reconstruc ▶ probability ν o branching time	ted tree:. of having a <i>spike</i> at a e,	
		<ul> <li>an inhomogen branches.</li> </ul>	eous Poisson process alc	ong



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Inference method Spikes on the reconst	ructed tree			
DATA	shark         A         T         C         G         A         A           tuna         -         -         G         -         C         T           whale         -         A         G         -         -         -           dugong         -         A         G         -         -         -           turtle         -         -         G         -         -         -           penguin         -         -         G         -         -         -	G C   A A E <sup>r</sup> E <sup>r</sup>	dugang turne Peurgauin	
MODEL		S := Spikes $\mathbb{P}(S \mid \mathcal{T})$	$\mathcal{T} := \operatorname{Tree}_{\mathbb{P}(\mathcal{T})}$	
RESULT	$\mathbb{P}\left(\mathcal{S}\mid\mathcal{A},\mathcal{T}\right)$	$\propto \mathbb{P}(\mathcal{A} \mid S, \mathcal{T}) \mathbb{P}(S \mid \mathcal{T})$		

			0000000000	
Inference method Spikes on the reconst	ructed tree			
DATA	shark         A         T         C         G         A         A           tuna         -         -         G         -         C         T           whale         -         A         G         -         -         -           dugong         -         A         G         -         -         -           turtle         -         -         G         -         -         -           penguin         -         -         G         -         -         -	G C  A transformed and transformed an	<sup>th</sup> gong	
MODEL		$\mathcal{S} := \text{Spikes}$ $\mathbb{P}(\mathcal{S} \mid \mathcal{T})$	$\mathcal{T} := \operatorname{Tree}_{\mathbb{P}(\mathcal{T})}$	
RESULT	$\mathbb{P}\left(\mathcal{S}\mid\mathcal{A},\mathcal{T}\right)$	$\propto \mathbb{P}(\mathcal{A} \mid \mathcal{S}, \mathcal{T}) \mathbb{P}(\mathcal{S} \mid \mathcal{T}) \mathbb{I}$		

Molecular clock

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Inference method Spikes on the reconst	ructed tree			
DATA	shark     A     T     C     G     A       tuna     -     -     G     -     C     T       whale     -     A     G     -     -     -       dugong     -     A     G     -     -     -       turtle     -     -     G     -     -     -       penguin     -     -     G     -     -     -	A G C  A A X <sup>e</sup> y y <sup>e</sup> y	<sup>cliceog</sup>	
MODEL		$S := Spikes$ $\mathbb{P}(S \mid \mathcal{T})$	$\mathcal{T}_{i=\text{Tree}} \\ \mathbb{P}(\mathcal{T})$	
RESULT	$\mathbb{P}\left(\mathcal{S}\mid\mathcal{A},\mathcal{T}\right)$	$\propto \mathbb{P}(\mathcal{A} \mid \mathcal{S}, \mathcal{T}) \mathbb{P}(\mathcal{S} \mid \mathcal{T})$		

Molecular clock



Presentation in Basel



	Molecular clock	
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# Inference method Posterior of spikes conditioned on branch-lengths and alignment



	Phenotypic evolution	Molecular clock ○○○○○○○○●○	

# Inference method Posterior of spikes conditioned on branch-lengths and alignment



	Phenotypic evolution	Molecular clock ○○○○○○○○●○	

# Inference method

Posterior of spikes conditioned on branch-lengths and alignment



	Phenotypic evolution 0000000	Molecular clock ○○○○○○○○○	
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# Inference method Summary

Model and methodological developments:

- A strong link between the speciation and substitution process.
- A preliminary inference procedure.

Perspectives :

- Test the relative support for gradual / punctuated relaxations of the molecular clock.
- Scan sequences to look for genes likely to evolve in a punctual way.



	Phenotypic evolution	Molecular clock ○○○○○○○○○	
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# Inference method Summary

Model and methodological developments:

- A strong link between the speciation and substitution process.
- A preliminary inference procedure.



- Test the relative support for gradual / punctuated relaxations of the molecular clock.
- Scan sequences to look for genes likely to evolve in a punctual way.


	Phenotypic evolution	Molecular clock ○○○○○○○○○	
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## Inference method Summary

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## Inference method Summary

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- A strong link between the speciation and substitution process.
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#### Introduction

Macroevolution Stochastic modeling

#### Diversification

State of the art The species definition in modeling work Application to diversification studies

#### Phenotypic evolution

State of the art Coevolution of traits from different species Proposed framework Examples of applications

#### Molecular clock

State of the art A new relaxation Inference method

### Conclusion







		Conclusion

# Inference method



Manceau and Lambert, 2018, Bull. Math. Biol. (under revisions) Manceau, Lambert and Morlon, 2015, Ecol. Lett.

		Conclusion

# Inference method



Manceau, Lambert and Morlon, 2016, Syst. Biol.

	Phenotypic evolution	Conclusion

## Inference method



Ongoing work with Hélène, Amaury and Julie Marin.

		Phenotypic evolution	Conclusion
Acknowledgment	5		



Thank you for your attention !

Intro	Chap 2	Chap 3	Chap 4	Chap 5	
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Evolution of tra	its along a tree				



Intro	Chap 2	Chap 3	Chap 4	Chap 5	Conclu
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Intro	Chap 2	Chap 3	Chap 4	Chap 5	
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Phylogenetic rec Maximum likelihood	onstruction				



Intro	Chap 2	Chap 3	Chap 4	Chap 5	
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Intro	Chap 2	Chap 3	Chap 4	Chap 5	
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	Chap 2 ●○○	Chap 000								Cha OC	ap 4							Ch OC	ap 5 D		
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	Chap 2 ●○○	Chap 00C								Cha OC	ap 4 00							C O				
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	Chap 2 ●○○	Chap 000								Cha OC	ap 4 00							CI O				
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	Chap 2 ●○○	Chap 3 000					Cha OC	ap 4 00							Chap ! DO			
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Intro 00000	Chap 2 ●○○	Chap 3 000							Chi OC	ap 4 00								hap 5 00			Conclu 0000
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	Chap 2 ●○○	Chap 3 000	Chap 4 000	Chap 5 Con 00 00	clu 00
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	Chap 2	Chap 3	Chap 4	Chap 5	
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The many m	odels of specia	tion			

Population dynamics :

- fixed size.
- discrete generations.
- uniform choice of the parent in the previous generation.

Superimposition of a model of specia tion.



	Chap 2	Chap 3	Chap 4	Chap 5	
	000				
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	Chap 2	Chap 3	Chap 4	Chap 5	
	000				
The many mode	ls of speciation				
The many mode	is of speciation				
Individual-based mod	dels				



	Chap 2	Chap 3	Chap 4	Chap 5	
	000				
The many mode	els of speciation				
Individual-based mo	dels				



	Chap 2	Chap 3	Chap 4	Chap 5	
	000				
The many m	nodels of speciat	ion			
Individual-base	d models				



	Chap 2	Chap 3	Chap 4	Chap 5					
	000								
The many mode									
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Individual-based models									



	Chap 2	Chap 3	Chap 4	Chap 5	
	000				
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	Chap 2	Chap 3	Chap 4	Chap 5						
	000									
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Individual-base	ed models									



	Chap 2	Chap 3	Chap 4	Chap 5					
	000								
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	Chap 2	Chap 3	Chap 4	Chap 5					
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	Chap 2	Chap 3	Chap 4	Chap 5				
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	Chap 2	Chap 3	Chap 4	Chap 5					
	000								
The many mode									
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Individual-based models									



	Chap 2	Chap 3	Chap 4	Chap 5				
	000							
The many models of speciation								
Individual-based mo	dels							



	Chap 2	Chap 3	Chap 4	Chap 5				
	000							
<u>—</u> .								
The many models of speciation								
Individual-based	models							



	Chap 2	Chap 3	Chap 4	Chap 5							
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Where doe	Where does the paraphyly come from ?										



Intro	Chap 2	Chap 3	Chap 4	Chap 5	Conclu			
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From a general agusta a phylography								





	Chap 2	Chap 3	Chap 4	Chap 5			
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A three-types process							
Laws of reconstructed phylogenies							

The law of reconstructed phylogenies, under our model, is the same as:

a three-types branching process with types,

type 0 the clonal family survives until present. type 1 the clonal family does not survive until present. pe gelé two clonal families survive until present.

inhomogeneous in time, with known transition rates.


	Chap 2	Chap 3	Chap 4	Chap 5		
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Laws of reconstructed phylogenies						

a three-types branching process with types,

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	Chap 2	Chap 3	Chap 4	Chap 5	
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	Chap 2	Chap 3	Chap 4	Chap 5	
		000			
A three-tvp	oes process				



Chap 2	Chap 3	Chap 4	Chap 5	
	000			

# Influence of parameter values on the phylogenetic tree shape



	Chap 2 000	Chap 3 000	Chap 4 ●○○	Chap 5 OO	
Variance-covaria	nce matrix				



	Chap 2 000	Chap 3 000	Chap 4 ○●○	Chap 5 00	
Cartoon					



Chap 2	Chap 3	Chap 4	Chap 5	
		000		

## Generalist Matching Mutualism



	Chap 2 000	Chap 3 000	Chap 4 000	Chap 5 ●○	
Relaxed molecul Biological results	ar clock				



Chap 2	Chap 3	Chap 4	Chap 5	
			00	

### With a prior on our parameters

Posterior distribution of  $\alpha, \kappa, \nu$  conditioned on branch-lengths and alignment



Chap 2	Chap 3	Chap 4	Chap 5	
			00	

### With a prior on our parameters

Posterior distribution of  $\alpha, \kappa, \nu$  conditioned on branch-lengths and alignment



Chap 2	Chap 3	Chap 4	Chap 5	
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### With a prior on our parameters

Posterior distribution of  $\alpha, \kappa, \nu$  conditioned on branch-lengths and alignment



	Chap 2	Chap 3	Chap 4	Chap 5	Conclu
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Perspectives SG	D				

What if b, d and  $\nu$  change through time ?



	Chap 2	Chap 3	Chap 4	Chap 5	Conclu
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	Chap 2	Chap 3	Chap 4	Chap 5	Conclu
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	Chap 2	Chap 3	Chap 4	Chap 5	Conclu
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Other ways to model species and individuals in the literature

GMYC or multisecies coalescent

