Pourquoi certains groupes d'espèces diversifient-ils plus ou moins rapidement que d'autres?





Hélène Morlon

Ecole Normale Supérieure



Some species groups are much more species rich than others





Some species groups are much more species rich than others



Some regions of the planet are much more species rich than others



Davies et al. PNAS 2008

Current levels of species richness result from the balance of speciation and extinction events





Present-day species richness

Speciation rate average number of speciation events per Myr per lineage

Extinction rate

average number of extinction events per Myr per lineage

Net diversification rate speciation rate – extinction rate



Have species poor groups always been poor or are they the remnants of a diverse past?





Historically, processes of speciation and extinction have been studied through the fossil record



Studying deep time variations in biodiversity using the phylogenies of present-day species



6 000 mammal species Upham et al. PloSB 2019



> 7 000 amphibian species
Jetz & Pyron Nat Ecol Evol 2018



2.2 Million species on a single tree



10 000 bird species

Jetz et al. Nature 2012





Phylogenies represent the order and timing of divergences between ancestral species that led to present-day species

> Phylogenies are constructed from the genetic (and sometimes phenotypic) similarity between present-day species



The datation is performed with fossil calibrations and the molecular clock



By fitting birth-death models of cladogenesis to phylogenies, we can estimate speciation and extinction rates and how they vary through time and species groups



Under the homogeneous constant rate birth-death process with speciation rate λ and extinction rate μ , extinction leaves a distinctive signal in reconstructed phylogenies even though extinct taxa are not observed



Figure from Ricklefs TREE 2007

Nee et al. PTB 1994

Given an empirical phylogeny, we can compare the statistical support of different diversification models, and estimate parameters of these models, i.e. λ and μ , using likelihood-based statistical inference



From the 90's to today:

a battery of new models to quantify how diversification rates vary...

... across lineages



Stadler *et al.* PNAS 2011, Morlon *et al.* PNAS 2011, May *et al.* MEE 2016, etc...



Alfaro *et al.* PNAS 2009, Rabosky *et al.* PloS One 2014, Maliet *et al.* NEE 2019, Barido-Sottani *et al.* Syst Bio 2020, etc...

Speciation rates vary widely across lineages



Maliet et al. Nature Ecol Evol 2019

Extinction rates are harder to estimate, but evidence suggests they can vary widely across lineages



Morlon et al. PNAS 2011

Levels of species richness result from the balance of speciation and extinction events: reconstructing paleodiversity curves



speciation rate extinction rate
$$N(t) = N_0 e^{\int_0^{t} (-\lambda(s) + \bar{\mu}(s)) ds}$$

number of species today



Current levels of species richness result from the balance of speciation and extinction events





Current levels of species richness result from the balance of speciation and extinction events





Morlon et al. PNAS 2011

Levels of species richness result from the balance of speciation and extinction events: reconstructing paleodiversity curves while accounting for uncertainties





Olivier Billaud



Dan Moen



Todd Parsons

Billaud et al. Syst Bio 2019

Old and poor frog families are the remnant of a diverse past



Billaud et al. Syst Bio 2019

Other examples of old and poor groups that are the remnant of a diverse past

2500 20 --- Confidence interval at 95% Number of species (subclades) 2000 Number of Species 1000 1000 10 5 500 0 - 0 P Q Eoc. Oligocene Miocene -25 -20 -15 Time (Myrs) -5 -10 0 -35 -30 500 400 Number of specie 300 200 100 Mazet *et al.* in prep. 11111111 -250 -230 -210 -190 Time (Myrs)

100

60

40

20

Pierre-Henri Fabre

Nathan Mazet



Fabien Condamine



Current levels of species richness result from the balance of speciation and extinction events





Present-day species richness

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Extinction rate

average number of extinction events per Myr per lineage

Net diversification rate speciation rate – extinction rate



What are the factors that modulate speciation & extinction rates?



The Court Jester

EXTRINSIC



The Red Queen

Abiotic factors climatic variation geological context

Biotic factors competition mutualistic and antagonistic interactions

Species-specific traits reproduction mode life-history traits dispersal capacity

INTRINSIC

From the 90's to today: a battery of new models to quantify why diversification rates vary through time and across lineages



Condamine *et al.* Eco Lett 2013, Cantalapiedra *et al.* PRSB 2012, etc...





Maddison *et al.* Syst Bio 2004, Fitzjohn *et al.* Syst Bio 2010, Goldberg *et al.* Syst Bio 2011, etc...

Species-specific traits can influence speciation and extinction rates

Transitions to clonality happen frequently, but clonal species have higher extinction rates



de Vienne et al. 2013 PLoS One Gouyon & Giraud 2009 Aux origines de la sexualité. Fayard



MedievalRich

Species-specific traits can influence speciation and extinction rates

Transitions to asexuality happen frequently, but sexual species have higher net diversification rates



Goldberg et al. Science 2010

Species-specific traits can influence speciation and extinction rates



rspb.royalsocietypublishing.org

Settling down of seasonal migrants promotes bird diversification

Jonathan Rolland^{1,2,3}, Frédéric Jiguet², Knud Andreas Jønsson^{4,5}, Fabien L. Condamine¹ and Hélène Morlon^{1,3}

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The Court Jester

Abiotic factors, such as climatic changes, can influence speciation and extinction rates



Condamine et al. Eco Lett 2013

Temperature affects major aspects of biology through its effect on metabolic rates, body-size, and productivity



Based on the metabolic, body-size and productivity hypotheses, temperature should (positively) affect speciation rates



Based on the metabolic, body-size and productivity hypotheses, temperature should (negatively) affect extinction rates



Models of diversification with rates that depend on measured (a)biotic variables



 $\widetilde{\lambda}(t) = \lambda(t, E_1(t), E_2(t), \dots, E_k(t))$ $\widetilde{\mu}(t) = \mu(t, E_1(t), E_2(t), \dots, E_k(t))$





Condamine et al. Eco Lett 2013 Lewitus et al. Syst Bio 2017

A meta-analysis of the effect of environmental changes on diversification



Comparison of 21 models including constant rate diversification models, models with time-varying rates, diversity-dependent models, and temperature-dependent models

Temperature-dependent models:

exponential dependence:
$$\tilde{\lambda}(t) = \lambda_0 \times e^{\alpha T(t)}$$
linear dependence: $\tilde{\lambda}(t) = \lambda_0 + \alpha T_{(t)}$ metabolic predictions : $\tilde{\lambda}(t) = \lambda_0 \times e^{\frac{\alpha}{T(t)}}$









Condamine et al. Eco Lett 2019
Climate cooling during the Cenozoic results in a slowdown in diversification



P

66

56

0

23.03

33.9

M

5.33 0

Late K

1.0 0.5 0.0

What are the environmental factors that shaped the diversification of diatoms?

« Thoroughly » sampled phylogeny of diatoms (~20,000 OTUs) obtained by grafting metabarcoding data from the *Tara* oceans expedition onto a robust phylogeny of reference sequences





Lewitus et al. Nature Ecol Evol 2018

Raphid pennate

How did past environmental conditions shape the diversification of diatoms?



5 abiotic and 4 biotic variables

Lewitus et al. Nature Ecol Evol 2018



Lewitus et al. Nature Ecol Evol 2018

Post-LE, distinct diatom clades are influenced by different environmental factors, and not necessarily in the same way





The Red Queen

Biotic factors, such as competition and mutualistic or antagonistic interactions, can influence speciation and extinction rates











In verbal evolutionary theories, such as the theory of adaptive radiations, interspecific competition is thought to induce fast speciation followed by a diversification slowdown as species fill ecological niche space

> Simpson 1953 Harmon et al. Science 2003





The effect of competition has been tested by testing the support for models with declining speciation rates ("early burst" models)



Rabosky & Lovette Evolution 2008



The effect of competition has also been tested by testing the support for models with diversity-dependent diversification

PROCEEDIN	IGS
THE ROYAL	B

Proc. R. Soc. B (2012) 279, 1300–1309 doi:10.1098/rspb.2011.1439 Published online 12 October 2011

Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record

Rampal S. Etienne^{1,*}, Bart Haegeman², Tanja Stadler³, Tracy Aze⁴, Paul N. Pearson⁴, Andy Purvis⁵ and Albert B. Phillimore⁵

¹Community and Conservation Ecology, Centre for Ecological and Evolutionary Studies,



Etienne et al. PRSB 2012

Beyond verbal expectations: a simulation model to assess under which conditions we can actually expect competition to generate a slowdown in diversification rates





Aristide & Morlon Eco Lett 2019

The matching competition birth-death model (MCBD)

1. Competition drives character displacement

$$x_{i}(t + dt) = x_{i}(t) + m\alpha \left[\sum_{j \neq i}^{n} sign\left(x_{i}(t) - x_{j}(t)\right) \times e^{-\alpha \left(x_{i}(t) - x_{j}(t)\right)^{2}} \right] dt + \delta$$

$$\uparrow$$
value lineage i
stochastic displacement

α

trait value lineage i



Aristide & Morlon Eco Lett 2019

The matching competition birth-death model (MCBD)

2. Character displacement speeds up speciation

Protracted speciation model Etienne & Rosindell Syst Bio 2012

Speciation initiation: rate λ_1 Speciation completion: rate λ_2

$$\lambda_{2i}(t) = \tau_0 e^{\beta \left(x_j(t) - x_k(t)\right)^2}$$

Aristide & Morlon Eco Lett 2019

The matching competition birth-death model (MCBD)

3. Phenotypically similar species experience competitive exclusion

$$\mu_{i} = \alpha \mu_{0} e^{-\alpha (\sum_{j \neq i} (x_{i}(t) - x_{j}(t))^{2})} + \mu_{bg}$$



Aristide & Morlon Eco Lett 2019

Competition produces declines in diversification rates, even if trait space is unbounded



Aristide & Morlon Eco Lett 2019

Declines in diversification rates do not leave a clear signal in reconstructed phylogenetic trees, at least not as detected by currently available models



Aristide & Morlon Eco Lett 2019

Opinion

CellPress

Why does diversification slow down?

Daniel Moen and Hélène Morlon





Trends Ecol Evol 2014



Verbal evolutionary theories on the effect of mutualistic and antagonistic interactions on diversification rates remain poorly tested



Robustly testing such theories would require modeling the ecoevolutionary emergence of interaction networks and building associated inference tools to fit them to empirical data

REVIEW

wind Biology

Detecting the macroevolutionary signal of species interactions

Luke J. Harmon^{1,2} | Cecilia S. Andreazzi³ | Florence Débarre⁴ | Jonathan Drury⁵ | Emma E. Goldberg⁶ | Ayana B. Martins^{1,7} | Carlos J. Melián¹ | Anita Narwani⁸ | Scott L. Nuismer² | Matthew W. Pennell⁹ | Seth M. Rudman¹⁰ | Ole Seehausen^{1,11} | Daniele Silvestro¹² | Marjorie Weber¹³ | Blake Matthews^{1,14}

JEB 2018

Annual Review of Ecology, Evolution, and Systematics

Ecological Interactions and Macroevolution: A New Field with Old Roots

David H. Hembry^{1,2} and Marjorie G. Weber³

Review

TREE 2017

Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution

Marjorie G. Weber,^{1,*} Catherine E. Wagner,² Rebecca J. Best,^{3,4} Luke J. Harmon,^{3,5} and Blake Matthews³







BipartiteEvol: An individual based model for the ecoevolutionary emergence of bipartite interaction networks

Individuals from 2 guilds A and B and characterized by a 3-dimensional trait evolve on a fixed grid







Maliet et al. Ecology Letters 2020

An individual based model for the eco-evolutionary emergence of bipartite interaction networks



the replacing individual is the child from a parent drawn in A according to its fitness, which depends on its trait value and that of the interacting individual from B (trait matching)



the child can experience a mutation that generates a gaussian trait

REPEAT WITH GUILD B, AND REPEAT FOR MANY GENERATIONS

An individual based model for the eco-evolutionary emergence of bipartite interaction networks

We define species as "the smallest monophyletic group of individuals such that two individuals from different species are separated by at least s mutations"



Genealogy of individuals

Species phylogeny

Manceau et al. Eco Lett 2015 Rosindell et al. Eco Lett 2015

An individual based model for the eco-evolutionary emergence of bipartite interaction networks

Two individuals interact if they are on the same grid cell Two species interact if at least one individual from each species interact



Maliet et al. Ecology Letters 2020

Mutualist and antagonist interactions lead to very different eco-evolutionary dynamics



Maliet et al. Ecology Letters 2020

Antagonism fosters, while mutualism impedes, trait and species diversity



Co-evolution occurs in antagonistic, but not mutualistic networks



Mutualistic networks are nested, while antagonistic networks are modular, as observed in empirical communities



What are the factors that modulate speciation & extinction rates?



The Court Jester

EXTRINSIC



The Red Queen

Abiotic factors climatic variation geological context

Biotic factors competition mutualistic and antagonistic interactions

Species-specific traits reproduction mode life-history traits dispersal capacity

INTRINSIC

By which processes do various factors modulate speciation and extinction rates?

Abiotic and biotic factors, in combination with speciesspecific traits, influence extinction rates by their effects on demography

By which processes do various factors modulate speciation and extinction rates?

Abiotic and biotic factors, in combination with species-specific traits, must influence speciation rates by somehow influencing the speciation process



Mixed support for an association between reproductive isolation and speciation rates

Macroevolutionary speciation rates are decoupled from the evolution of intrinsic reproductive isolation in *Drosophila* and birds

Daniel L. Rabosky^{a,1} and Daniel R. Matute^b



Michael G. Harvey^{a,b,c,d,1}, Glenn F. Seeholzer^{a,b}, Brian Tilston Smith^{a,b,e}, Daniel L. Rabosky^{c,d}, Andrés M. Cuervo^{a,b,f}, and Robb T. Brumfield^{a,b}

No link between population isolation and speciation rate in squamate reptiles

Sonal Singhal^{a,1}, Guarino R. Colli^b, Maggie R. Grundler^{c,d}, Gabriel C. Costa^e, Ivan Prates^{f,g}, and Daniel L. Rabosky^{f,g,1}

Are genetic diversity and speciation rates coupled in mammals? Genetic diversity > 0.017 0.011 - 0.017 0.008 - 0.011 0.006 - 0.008 0.005 - 0.006 0.003 - 0.005 0.002 - 0.003 < 0.002 53.58 Mbp

Are genetic diversity and diversification rates coupled?



Under geographic and ecological models of speciation, we expect a positive association between genetic diversity and speciation rate

Testing the impact of effective population size on speciation rates – a negative correlation or lack thereof in lichenized fungi

Jen-Pan Huang¹, Steven D. Leavitt² & H. Thorsten Lumbsch¹

Estimating intraspecific genetic diversity

GenBank "Mammalia"[Organism] AND CYTB NOT "Homo sapiens"[Organism] 124,289 sequences of mammals Cytochrome b

Split into 138 families for better alignments



Estimating branch-specific speciation rates

• ClaDS estimates on Upham's PLoS Biology 2019 mammals phylogeny



Negative correlation between genetic diversity and speciation rates



The negative correlation between genetic diversity and speciation rates is not linked to an indirect effect of life history traits

	θ_{π} ~ Traits				λ ~ Traits				$\theta_{\pi} \sim \lambda + \text{Traits}$			
···	PGLS		BLML		PGLS		BLML		PGLS		BLML	
Term	Estimate	SE	Estimate	95% CI	Estimate	SE	Estimate	95% CI	Estimate	SE	Estimate	95% Cl
λ									-0.264	0.077	-0.266	[-0.408; -0.107]
Body Mass	-0.145	0.026	-0.147	[-0.202; -0.095]	0.007	0.010	0.007	[-0.012; 0.025]	-0.139	0.025	-0.143	[-0.198; -0.09]
Range area	0.137	0.014	0.137	[0.109; 0.166]	-0.005	0.003	-0.005	[-0.011; 0]	0.131	0.015	0.131	[0.103; 0.159]
Range mean temperature	0.330	0.087	0.329	[0.167; 0.501]	-0.021	0.018	-0.021	[-0.057; 0.014]	0.307	0.087	0.307	[0.125; 0.475]
Litter size	-0.420	0.091	-0.420	[-0.609; -0.231]	0.051	0.028	0.050	[-0.004; 0.105]	-0.400	0.089	-0.406	[-0.581; -0.234]
Generation length	-0.074	0.105	-0.072	[-0.266; 0.139]	-0.008	0.030	-0.010	[-0.067; 0.049]	-0.084	0.102	-0.082	[-0.283; 0.129]
What might explain the negative association between genetic diversity speciation rate?



Hypothesis 1: Speciation exerts a limit on species genetic diversity rather than the other way round

Rapid speciation limits the accumulation of genetic diversity

What might explain the negative association between genetic diversity and speciation rate?



Hypothesis 2: Species that are highly geographically structured and with reproductively isolated populations indeed experience more frequent speciation events, but genetic diversity is inversely rather than positively correlated to geographic structure (Withlock 2004)

What might explain the negative association between genetic diversity and speciation rate?



Hypothesis 3: Under the demographic model of speciation, species with small rather than large effective population sizes accumulate reproductive incompatibilities faster because of a reduced efficiency of purifying selection (Maya-Lastra & Eaton 2021)





What might explain the negative association between genetic diversity and speciation rate?

Hypothesis 1: Speciation exerts a limit on species genetic diversity rather than the other way round

Hypothesis 2: Genetic diversity is inversely rather than positively correlated to population isolation

Hypothesis 3: Species with small rather than large effective population sizes accumulate reproductive incompatibilities faster

At which stage of the speciation cycle are we measuring genetic diversity (or genetic differentiation, or population isolation)?



At which stage of the speciation cycle are we measuring genetic diversity (or genetic differentiation, or population isolation)?



At which stage of the speciation cycle are we measuring genetic diversity (or genetic differentiation, or population isolation)?



Low genetic diversity in newly formed species

The reciprocal effect of speciation on microevolutionary (intraspecific) measures of differentiation complicates the interpretation of correlations



What are we actually measuring when we measure speciation rate using comparative methods?

Stochastic birth-death process

speciation rate λ extinction rate μ



Speciation is considered to be an instantaneous event by which two populations of the same ancestral species give rise to two distinct descendant species

What are we actually measuring when we measure speciation rate using comparative methods?





Cetartiodest

The protracted speciation model as a way to bridge micro and macroevolutionary speciation research?



Could we estimate the speciation initiation and extinction rates with intraspecific genetic data?

Could we estimate species-specific rates?

Etienne & Rosindell Syst Bio 2012

Etienne et al. Evolution 2014

The protracted speciation model as a way to bridge micro and macroevolutionary speciation research?



Etienne & Rosindell Syst Bio 2012

The protracted speciation model remains phenomenological, with no account of the interplay between speciation and demography / intraspecific genetic differentiation

Towards macroevolutionary models accounting for the interplay between speciation and demography / intraspecific

genetic differentiation



 σ^2 stochastic variation

Demographic process





each species follows density-dependent population dynamics

Overcast et al. in prep.

growth rate evolves as a Brownian

random split of individuals at speciation

Extinction naturally proceeds from the death of all individuals in a given species

+ Population genetics

demography controls Ne



The model predicts either a positive or negative association between speciation rate and genetic diversity depending of the relative pace of speciation and accumulation of genetic diversity



The model can be fitted to data using machine learning techniques

Overcast et al. in prep.

Towards macroevolutionary models accounting for the interplay between speciation and demography / intraspecific genetic differentiation



Conclusions

Speciation and extinction rates vary widely across lineages, explaining why some species groups are much more species rich than others

Differences in speciation and extinction rates can be linked to species specific traits as well as abiotic and biotic factors

We have well developed models to assess the effect of species-specific traits and abiotic factors on speciation and extinction rates; testing the effect of interspecific interactions remains challenging

Understanding which microevolutionary processes act a rate-limiting step in speciation (and therefore drive present day species richness patterns) also remains a major research frontier





Isaac Overcast



Odile Maliet



Olivier Billaud



Dan Moen





Leandro Aristide



Nathan Mazet

Fabien Condamine













What is the role of key innovations in the diversification of life?



Ronquist et al. Comm Biol 2021

Both mutation rates and Ne are negatively correlated to speciation rates



Silva et al. in prep.