« Sélection naturelle multi-niveaux, des gènes aux écosystèmes »

Hommage à Sébastien Ibanez

"It's like what Lenin said... you look for the person who will benefit, and, uh, uh..."

Le personnage The Dude dans The Big Lebowski (1998), Joel et Ethan Coen. Cité par Lion, Jansen et Day (2011)

FIGURE 8.9. *Pleopsidium flavum* en jaune et *Xanthoria elegans* en orange. Photo S. Ibanez.

Biological levels of organization

Genes

…

Cells

…

Organisms

…

Populations

…

Species

…

Communities

…

Ecosystems

Biological levels of organization

Genes

…

Cells

…

Organisms

→ ‘Darwinian’ individuals, natural selection

Populations

…

Species

…

Communities

…

Ecosystems

OUTLINE OF THE PRESENTATION

Part I : WHAT ARE SPECIES ?

Part II : DISCOVERY OF NEW SPECIES

Part III : MULTILEVEL SELECTION

Part I : WHAT ARE SPECIES ?

50% teaching :

- Biology, Ecology, Evolution - Licence & Master
- Responsible for the whole Licence de Biologie

50% research :

- Ecology and evolution of high alpine cushion plants
- **Community assembly and ecosystem functioning : empirical, theoretical & philosophical aspects**

ENS Ulm → M2 Paris → Doctorat → Post-docs → Maître de conférences USMB

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- Plant Biology - Licence 1 & 2
- Evolutionary Biology – Licence 1 & 2, Master 1

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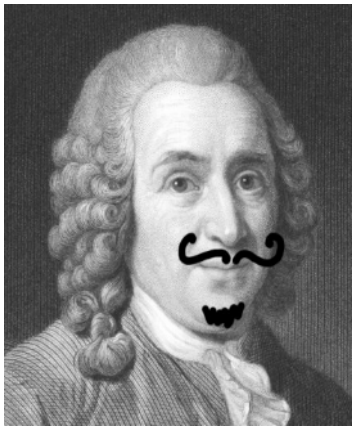
- Model development for trait evolution on phylogenies
- **Phylogenetics & systematics of Alpine plants**

SYSTEMATICS: AN OLD (-SCHOOL?) SCIENCE



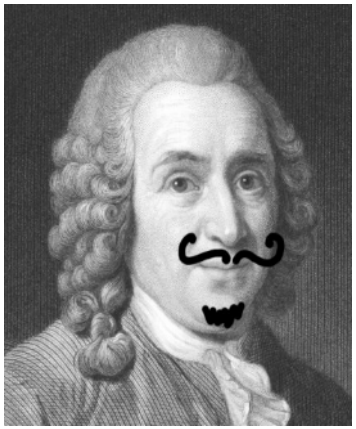
Systematics (and taxonomy) : describing taxa (species) and their relationships

Heritage from the pre-Darwinian era?

Purely descriptive?

Dealt-with already, at least in Europe and North America?

SYSTEMATICS IS NOT DEAD!



Systematics (and taxonomy) : describing taxa (species) and their relationships

Heritage from the pre-Darwinian era?

Purely descriptive?

Dealt-with already, at least in Europe and North America?

HUGE DEMAND FROM <u>FIELD</u> CONSERVATION BIOLOGY !

ONE RANK ABOVE ALL : SPECIES

Species are a fundamental unit in biology, especially important for **conservation**.

IN FOCUS NEWS

Habitats such as coral reefs have been hit hard by pollution and climate change.

BIODIVERSITY

One million species face extinction

Landmark United Nations report finds that human activities threaten ecosystems around the world.

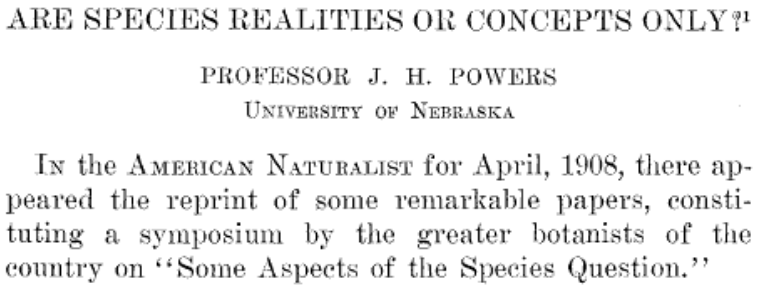
RED LIST

THE IUCN RED LIST OF THREATENED SPECIES™

BUT ARE SPECIES REAL ?

Taxonomic ranks (orders, family, genera, species, subspecies, etc.) have long been criticized for being arbitrary :

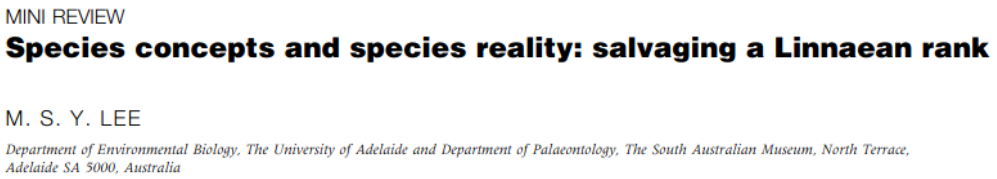
'so long as the [Linnean] hierarchic arrangement is maintained, ranks within it are assigned by art rather than by science.' GG Simpson, 1990



ARE SPECIES REALITIES OR CONCEPTS ONLY?[1]

PROFESSOR J. H. POWERS
UNIVERSITY OF NEBRASKA

IN the AMERICAN NATURALIST for April, 1908, there appeared the reprint of some remarkable papers, constituting a symposium by the greater botanists of the country on "Some Aspects of the Species Question."



MINI REVIEW

Species concepts and species reality: salvaging a Linnaean rank

M. S. Y. LEE

Department of Environmental Biology, The University of Adelaide and Department of Palaeontology, The South Australian Museum, North Terrace, Adelaide SA 5000, Australia

Many **problematic cases** with unclear/non-standardized species definitions (continuum ?)…

… but on the other hand **folk taxonomy usually aligns with scientific classification** (Coyne & Orr 2004, morphological discontinuities in nature ?)

(TOO) MANY 'SPECIES CONCEPTS'

Species concept	Property(ies)	Advocates/references
Biological	Interbreeding (natural reproduction resulting in viable and fertile offspring)	Wright (1940); Mayr (1942); Dobzhansky (1950)
Isolation	*Intrinsic reproductive isolation (absence of interbreeding between heterospecific organisms based on intrinsic properties, as opposed to extrinsic [geographic] barriers)	Mayr (1942); Dobzhansky (1970)
Recognition	*Shared specific mate recognition or fertilization system (mechanisms by which conspecific organisms, or their gametes, recognize one another for mating and fertilization)	Paterson (1985); Masters et al. (1987); Lambert and Spencer (1995)
Ecological	*Same niche or adaptive zone (all components of the environment with which conspecific organisms interact)	Van Valen (1976); Andersson (1990)
Evolutionary	Unique evolutionary role, tendencies, and historical fate	Simpson (1951); Wiley (1978); Mayden (1997)
(some interpretations)	*Diagnosability (qualitative, fixed difference)	Grismer (1999, 2001)
Cohesion	Phenotypic cohesion (genetic or demographic exchangeability)	Templeton (1989, 1998a)
Phylogenetic	Heterogeneous (see next four entries)	(see next four entries)
Hennigian	Ancestor becomes extinct when lineage splits	Hennig (1966); Ridley (1989); Meier and Willmann (2000)
Monophyletic	*Monophyly (consisting of an ancestor and all of its descendants; commonly inferred from possession of shared derived character states)	Rosen (1979); Donoghue (1985); Mishler (1985)
Genealogical	*Exclusive coalescence of alleles (all alleles of a given gene are descended from a common ancestral allele not shared with those of other species)	Baum and Shaw (1995); see also Avise and Ball (1990)
Diagnosable	*Diagnosability (qualitative, fixed difference)	Nelson and Platnick (1981); Cracraft (1983); Nixon and Wheeler (1990)
Phenetic	*Form a phenetic cluster (quantitative difference)	Michener (1970); Sokal and Crovello (1970); Sneath and Sokal (1973)
Genotypic cluster (definition)	*Form a genotypic cluster (deficits of genetic intermediates; e.g., heterozygotes)	Mallet (1995)

from de Queiroz 2007 Syst. Bio.

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SHALL WE GIVE UP ?

from de Queiroz 2007 Syst. Bio.

TOWARDS A UNIFIED SPECIES CONCEPT

Michael Ghiselin's proposal (1970's) :

rather than being classes defined by some physical characteristics, species are **historical entities**, **individuals with a cohesion** given by sexual reproduction

Kevin de Queiroz's proposal (2000's) :

all proposed 'species concepts' share a key component,
species are **independent meta-population level lineages**

species are individuals formed by independent lineages (and this is all!)

CONSEQUENCES OF A UNIFIED SPECIES CONCEPT

No single diagnostic criterion is necessary to recognize species.

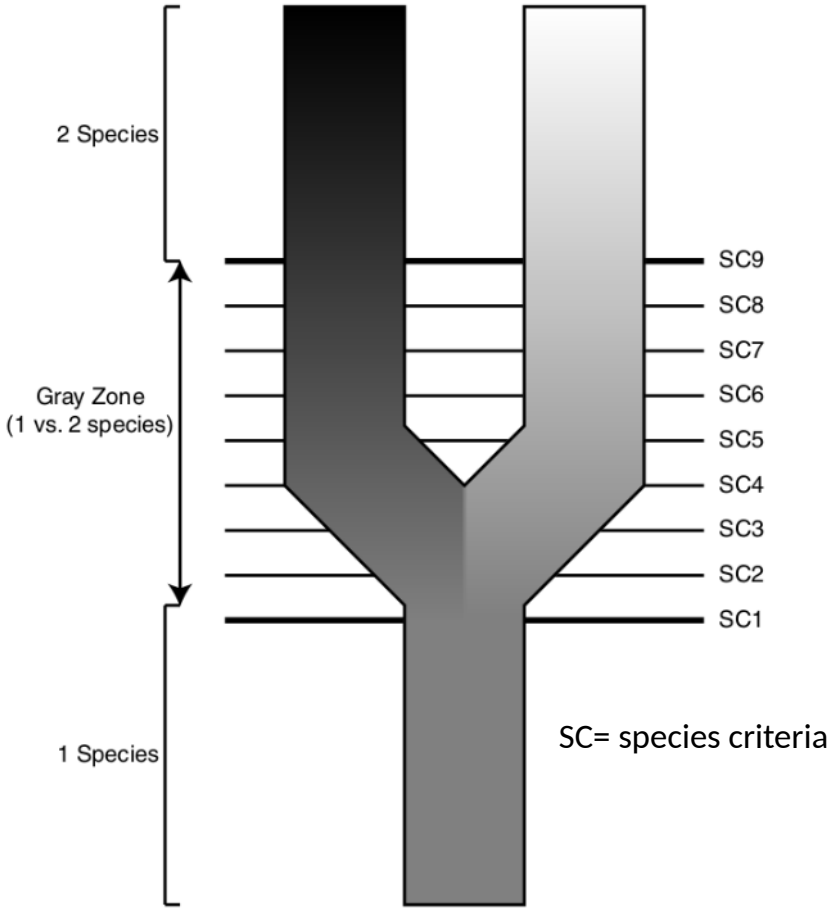
This leads to some difficult truths to admit:

- 2 species might be **exactly similar** (cryptic)
  → issue for field naturalists!

- 2 species might **have the same niche**
  → issue for community ecologists!

- 2 species might be extremely **difficult to distinguish using genomic data**
  → issue for phylogeneticists!

- 2 species might be perfectly able to reproduce and might **fuse into a single one** in the future
  → issue for high school biology teachers
  … and Ernst Mayr's ultras



NOT AN EASY PROBLEM

Systematists and philosophers of science are still working on it

Chapter

We Are Nearly Ready to Begin the Species Problem

By Matthew J. Barker

Book Species Problems and Beyond

Edition	1st Edition
First Published	2022

HOW TO APPLY THIS CONCEPT ?

Even if the species concept is clarified, **delimiting species in practice is difficult** and remains a challenge.

Need to do it objectively and consistently for different taxa.

MOLECULAR ECOLOGY
Molecular Ecology (2013) 22, 4369–4383 doi: 10.1111/mec.12413

INVITED REVIEWS AND META-ANALYSES

How to fail at species delimitation

BRYAN C. CARSTENS,* TARA A. PELLETIER,* NOAH M. REID† and JORDAN D. SATLER*
Department of Evolution, Ecology and Organismal Biology, The Ohio State University, 318 W. 12th Avenue, Columbus, OH43210-1293, USA, †Department of Biological Sciences, Louisiana State University, Life Sciences Building, Baton Rouge, LA 70803, USA

Current Zoology 61 (5): 846–853, 2015

The art and science of species delimitation

Bruce RANNALA*
Department of Evolution and Ecology, University of California Davis Davis, CA 95616, USA

Received: 16 April 2018 | Accepted: 8 November 2018
DOI: 10.1111/eva.12748

REVIEWS AND SYNTHESES

WILEY Evolutionary Applications

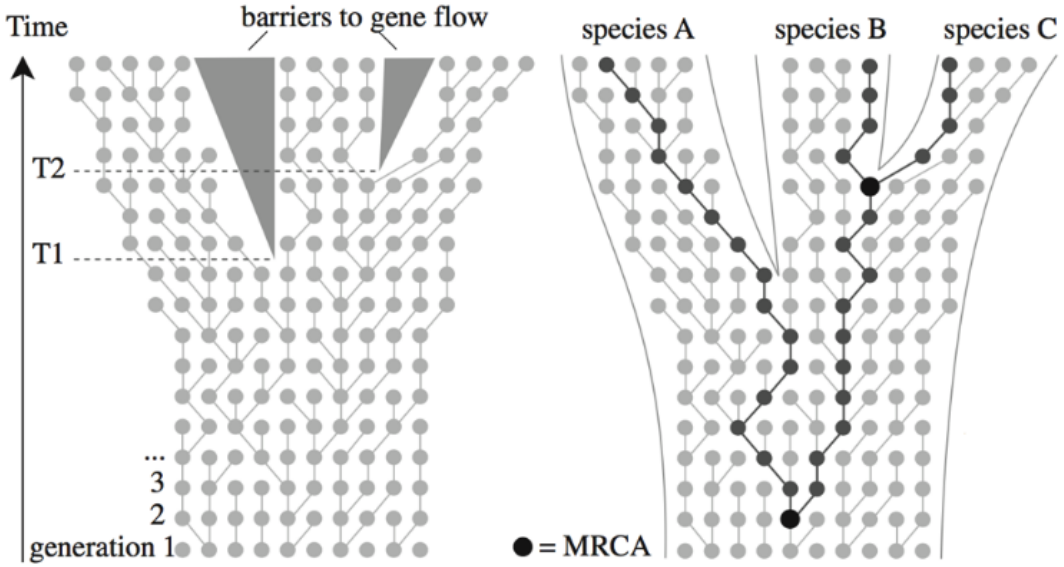
Delineating species in the speciation continuum: A proposal

Nicolas Galtier

MOLECULAR SPECIES DELIMITATION

Modern phylogenomics : distinction between gene trees and species trees

→ multi-species coalescent (MSC) model : **evolution of gene trees within species trees**



Bayes Estimation of Species Divergence Times and Ancestral Population Sizes Using DNA Sequences From Multiple Loci

Bruce Rannala* and Ziheng Yang†,1

The probability of the gene tree and coalescent times for the locus is the product of such probabilities across all the populations. Thus, for the gene genealogy of Figure 1, we have

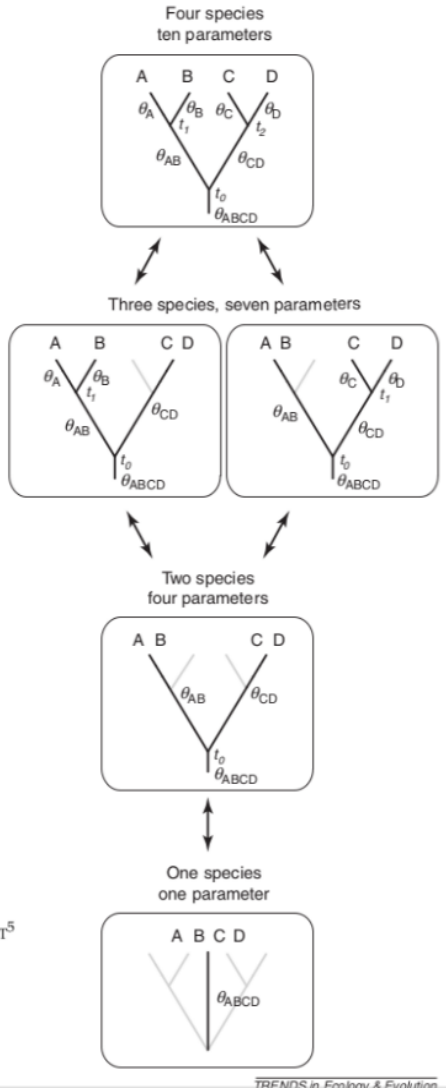
$$f(G_i|\Theta) = [2/\theta_H \exp[-6t_3^{(H)}/\theta_H] \exp[-2(\tau_{HC} - t_3^{(H)})/\theta_H]]$$
$$\times [2/\theta_C \exp[-2t_2^{(C)}/\theta_C]]$$
$$\times [2/\theta_{HC} \exp[-6t_3^{(HC)}/\theta_{HC}] \times 2/\theta_{HC} \exp[-2t_2^{(HC)}/\theta_{HC}]]$$
$$\times [\exp[-2(\tau_{HCG} - \tau_{HC} - (t_3^{(HC)} + t_2^{(HC)}))/\theta_{HCG}]]$$
$$\times [2/\theta_{HCGO} \exp[-6t_3^{(HCGO)}/\theta_{HCGO}] \times 2/\theta_{HCGO} \exp[-2t_2^{(HCGO)}/\theta_{HCGO}]]. \quad (9)$$

MOLECULAR SPECIES DELIMITATION

Molecular species delimitation : use DNA data from multiple *loci* to identify idependently evolving lineages (= species)

→ **testing** for independent lineages under the MSC

(mutation & drift dominate within species,
relatively little gene flow between species)



Unguided Species Delimitation Using DNA Sequence Data from Multiple Loci

Ziheng Yang[1,2] and Bruce Rannala*[1,3]

Syst. Biol. 63(4):534–542, 2014

DOI:10.1093/sysbio/syu018
Advance Access publication March 12, 2014

Species Delimitation using Genome-Wide SNP Data

ADAM D. LEACHÉ[1,2,*], MATTHEW K. FUJITA[3], VLADIMIR N. MININ[1,4], AND REMCO R. BOUCKAERT[5]

Part II : DISCOVERY OF NEW SPECIES

- Ecology and evolution of high alpine cushion plants

Doctorat

École Polytechnique **M2 Paris** **Doctorat**

- **Phylogenetics & systematics of Alpine plants**

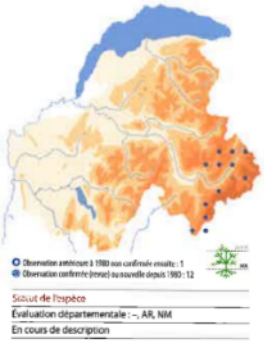
THE *ANDROSACE* GENUS

Androsace (Primulaceae) : c. 150 species from temperate and cold regions of the Northern Hemisphere

Some high-altitude species in the Alps (>3000m) that host entire ecosystems *(PhD thesis K. Dumas - sup. S. Ibanez)*

<u>Field</u> observations → their taxonomy deserves scrutiny !

Sébastien Ibanez started investigating them from 2010.



Androsace sp.

Androsace sans nom

(en cours de description par D. Jordan et F. Jacquemoud)

Famille des Primulacées

DESCRIPTION

Cette androsace partage des critères d'*Androsace alpina* et d'*A. pubescens*. Elle diffère d'*A. alpina* par les poils qui revêtent feuilles, calices et pédicelles. Ces derniers sont pour certains (la majorité) simples et longs, d'autres plus courts, en forme de bois de cerf, sont 1 à 3 fois bifurqués alors que les poils d'*A. alpina* sont très courts et tous 2 à 3 fois bifurqués. Elle diffère d'*A. pubescens* par les fleurs roses et les poils, dont certains en forme de bois de cerf sont 1 à 3 fois bifurqués, tandis que chez *A. pubescens* les poils sont longs et tous simples et les fleurs sont blanches. Floraison juillet–août.

Statut de l'espèce

Évaluation départementale : –, AR, NM

En cours de description

All photos : Sébastien Ibanez

THREE NEW *ANDROSACE* SPECIES

Species delimitations in a group of three high-altitude *Androsace* species *(Boucher et al. 2021 Scientific Reports)*

Statistical comparison between alternative species delimitation scenarios **: strong support for 6 species**

Plants that were formerly known as *A. pubescens* split into 4 species:

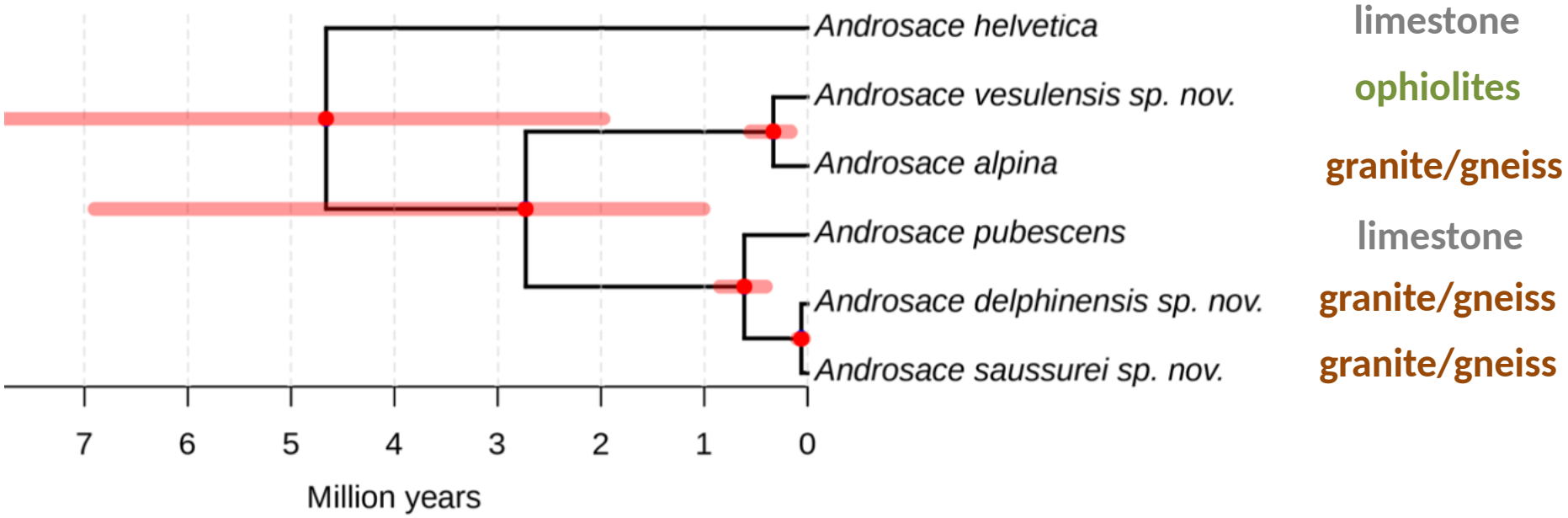
- *A. pubescens s. s.* → limestone

+ 3 new (cryptic) species described:

- ***A. delphinensis sp. nov.*** → acidic rocks / Dauphiné
- ***A. saussurei sp. nov.*** → acidic rocks / Savoie
- ***A. vesulensis sp. nov.*** → ophiolites / Mont Viso

INSIGHTS INTO SPECIATION

Dated species tree of the six species



- New species have allopatric distributions and grow on <u>distinct substrates</u>

  → **geographic isolation** (glaciers/valleys) + **divergent adaptation to substrate** drove speciation?

- Dating suggests **Pleistocene speciation**

SPECIES LEVEL SELECTION ?

Natural selection (differential production of offspring) at the species level ≠ natural selection on organisms that has consequences for species

Causes of high speciation rates in high-altitude *Androsace* species

- **divergent adaptation to substrate**

→ natural selection on organisms (strictly Darwinian), with consequences at the species level

- **geographic isolation** (glaciers/valleys)

→ natural selection directly on species characteristics/traits : fragmented geographic distribution in Alpine landscapes, prone to speciation

UNFORESEEN CONSEQUENCES

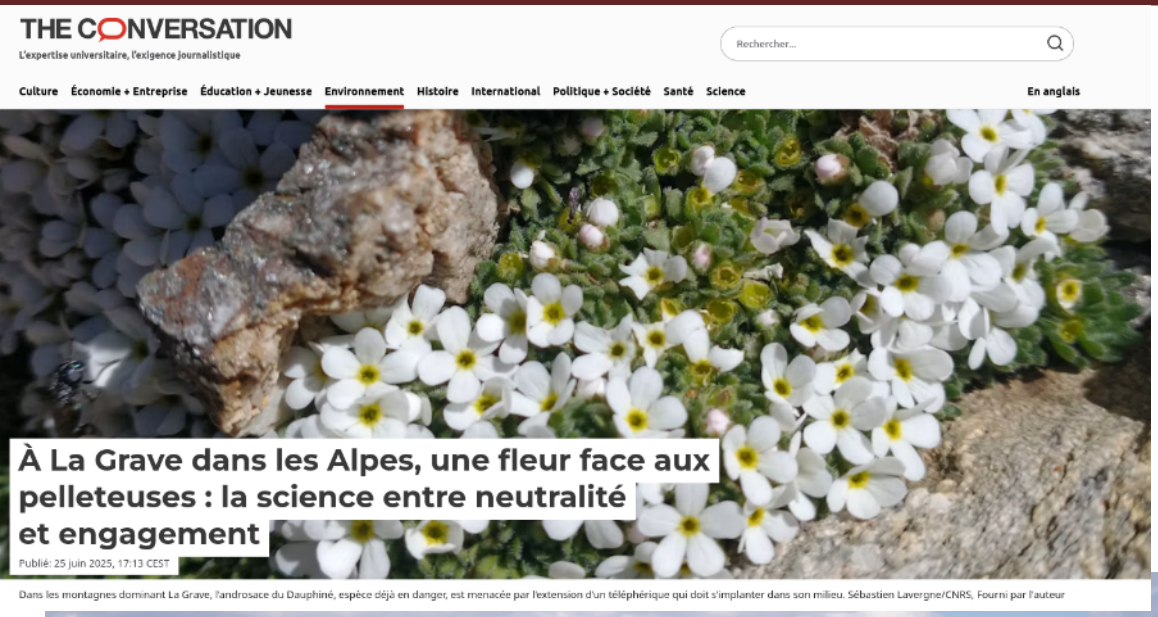
All three new species directly enter the French red list of protection

Used as a reglementary argument for protecting an environment… and a flagship for a social movement!

Image credit:

Alessandro Pignocchi, *Girose : Défendre le glacier de La Grave*

SCIENTISTS IN ACTION



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- Model development for trait evolution on phylogenies
- **Phylogenetics & systematics of Alpine plants**

SELECTION BEYOND ORGANISMS ?

Genes

→ ‘selfish’ genes ?

Cells

→ selection for co-operation of organelles ?

Organisms

→ ‘Darwinian’ individuals, natural selection

Populations

→ group selection ?

Species

→ species selection ?

Communities

→ community-level selection ?

Ecosystems

→ ecosystem-wide selection ?

SELECTION BEYOND ORGANISMS ?

Difficult to explain some empirical observations based on selection at the level of organisms only :

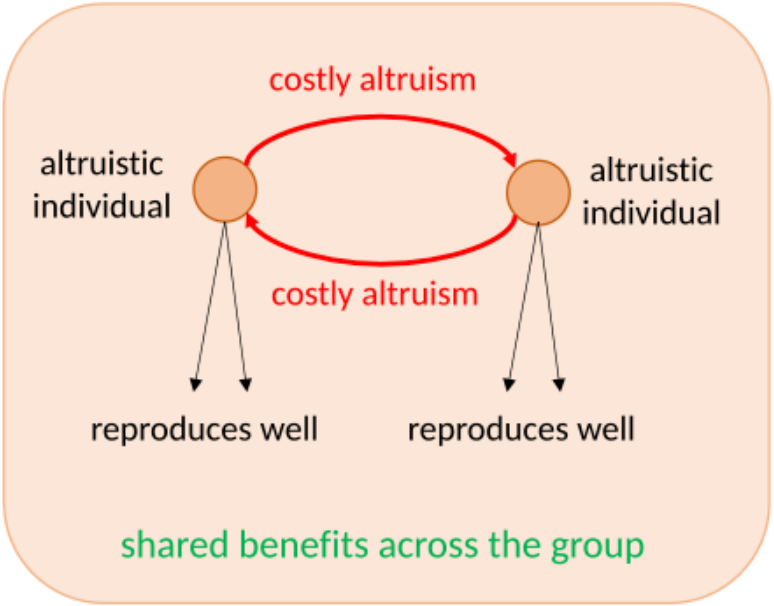
- cooperation of organelles within cells
- multi-cellularity
- altruism in groups
- diversity of some groups of organisms and not others
- mutualisms between species

Can natural selection **operate on other organizational levels** ?

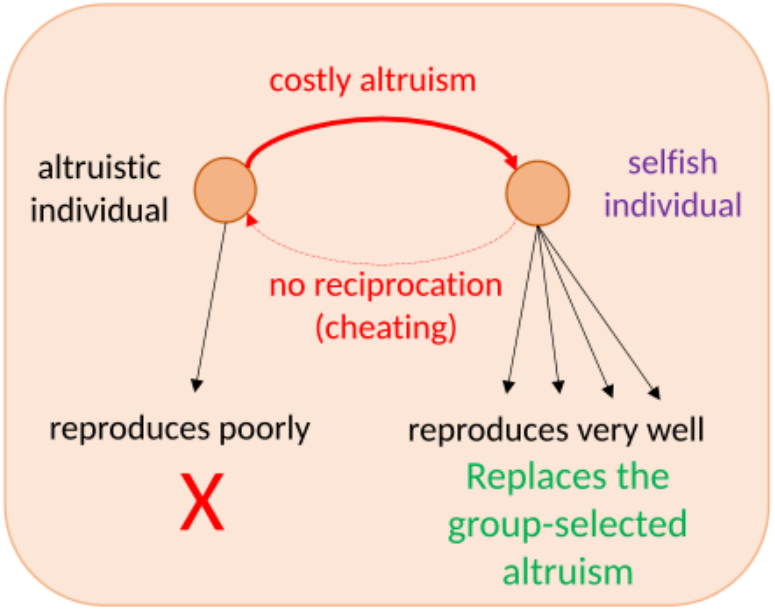
Can selection **act simultaneously on different organizational levels** ?

THE EXAMPLE OF ALTRUISM

How can altruism/cooperation evolve when they are costly for individuals ?



Group Selection



Individual Selection

Model proposed by Wilson (1975) : if groups formed by a majority of altruists survive better, then the altruistic behaviour will increase in frequency

Balance between organismal selection and group selection.

ALTERNATIVE MULTILEVEL SELECTION SCENARIOS

MLS1 : organisms leave groups for reproduction

→ fitness measured at the individual level, weak integration

MLS2 : groups re-produce as such

→ fitness measured at the group level, strong integration

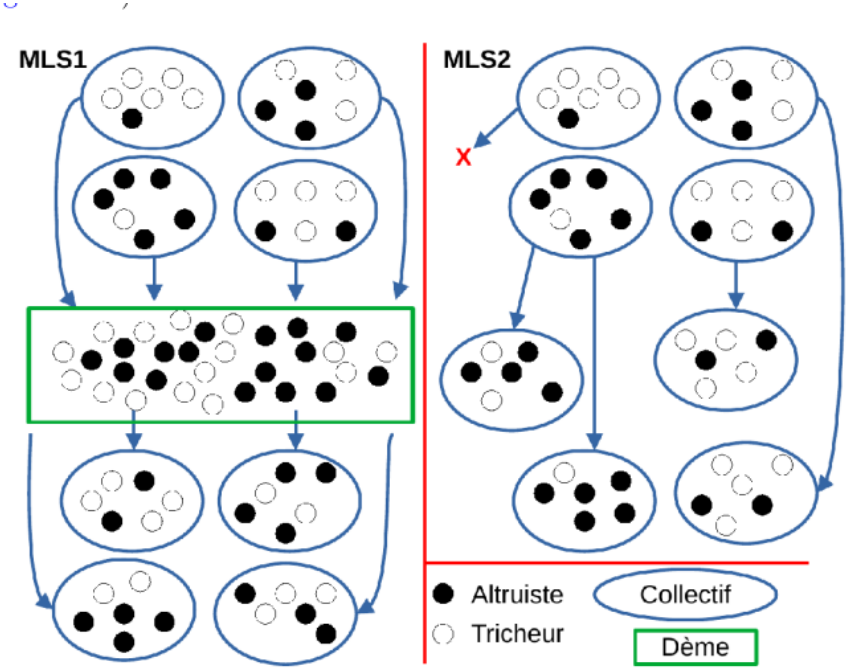


FIGURE 10.1. Les deux scénarios de la MLS.

EVOLUTIONARY TRANSITIONS TOWARDS INDIVIDUALITY

Theoretical propositions to explain the ontogeny of individuals:

- multicellular organisms (Buss 1987)
- any kind of individual subject to selection (Maynard Smith & Szathmary 1995)

1) Initial phase = formation of collectives of particles, MLS1

2) Increased integration with re-production of the collective as a whole, MLS2

3) Full integration so that the collective is an individual by itself, former particles are its components

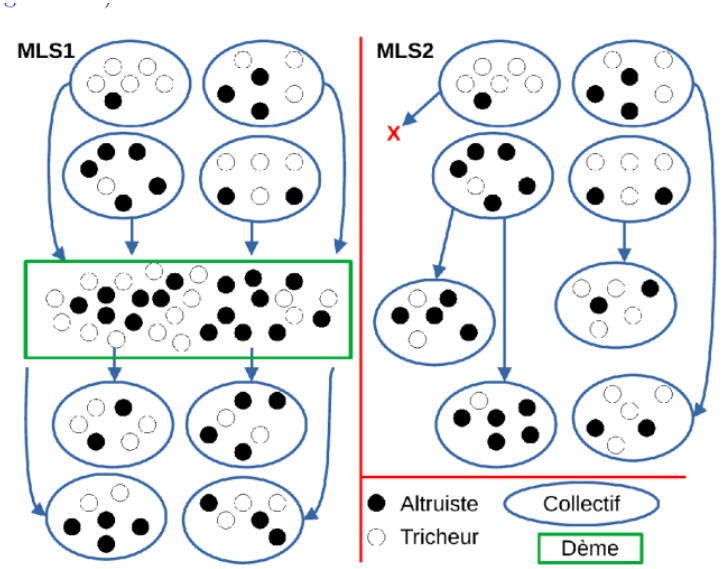
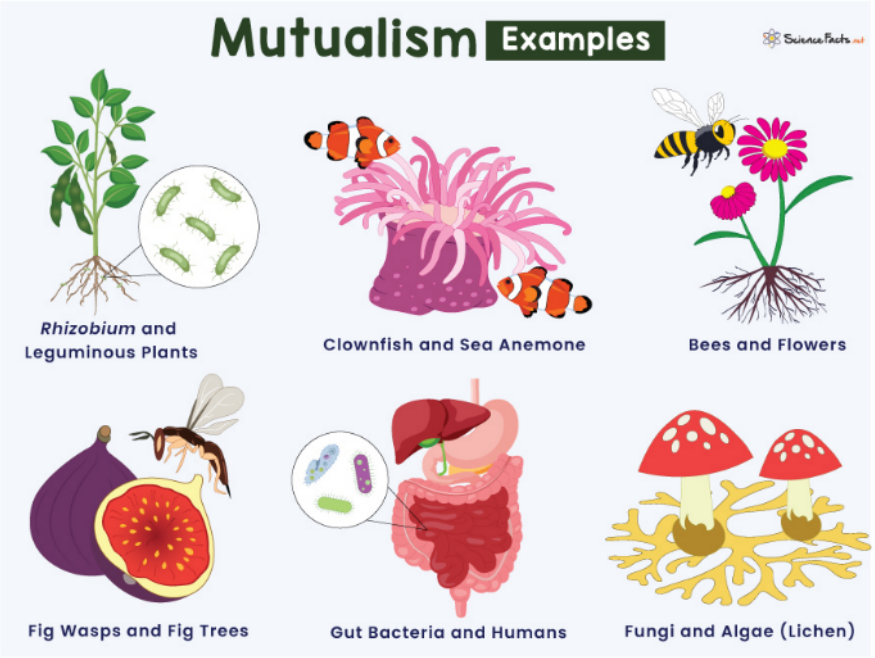


FIGURE 10.1. Les deux scénarios de la MLS.

EXTENSION TO SYSTEMS WITH MULTIPLE SPECIES

How do **mutualisms** originate ?



1) <u>Classic/mainstream explanation</u>

- partners in the interaction coevolve
- selection at the organismal level only
- requires specific mechanisms for partner choice and punishment/avoidance of cheaters

→ issue : these recognition mechanisms are complex and need to appear !

2) <u>Alternative explanation</u> (Sébastien's work)

- mutualistic behaviour might be costly for individuals
- but selection at the collective level might favour mutualism

→ issue : collectives of different species do not reproduce vertically (as collectives)

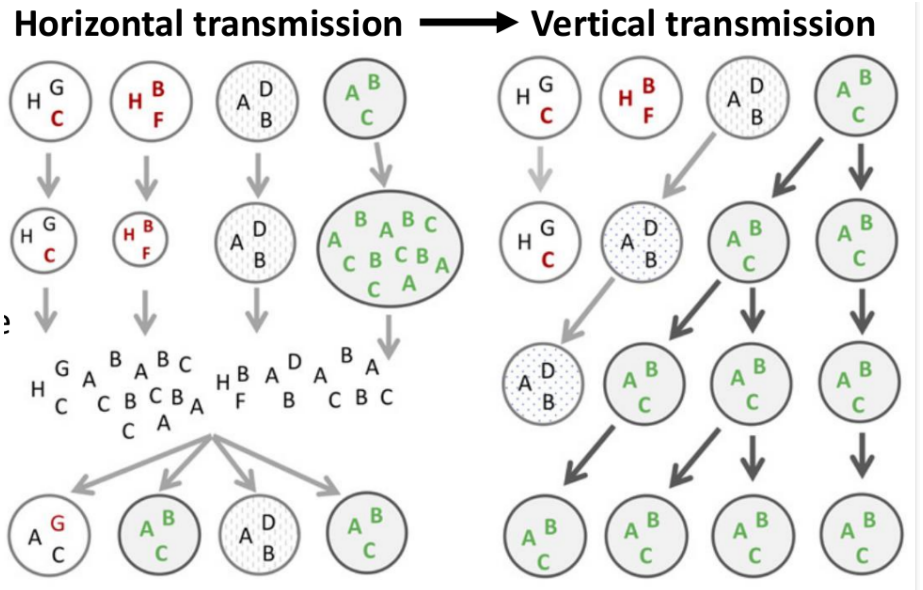
ISSUE WITH HORIZONTAL TRANSMISSION

In most mutualistic systems, interactors are not transmitted together :

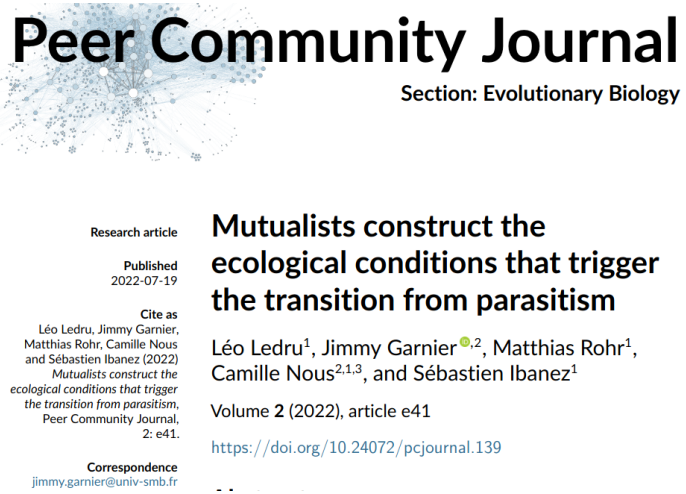
- plants and pollinators reproduce independently
- seeds do not disperse with their associated mycorhiza
- newborns do not have bacteria in their guts
- …

But several models show that horizontal transmission does not lead to mutualism

Some degree of pseudo-vertical transmission is required !



A MODEL FOR THE EVOLUTION OF MUTUALISM



Peer Community Journal

Section: Evolutionary Biology

Research article

Published
2022-07-19

Cite as
Léo Ledru, Jimmy Garnier, Matthias Rohr, Camille Nous and Sébastien Ibanez (2022) *Mutualists construct the ecological conditions that trigger the transition from parasitism*, Peer Community Journal, 2: e41.

Correspondence
jimmy.garnier@univ-smb.fr

Mutualists construct the ecological conditions that trigger the transition from parasitism

Léo Ledru[1], Jimmy Garnier[1,2], Matthias Rohr[1], Camille Nous[2,1,3], and Sébastien Ibanez[1]

Volume **2** (2022), article e41

https://doi.org/10.24072/pcjournal.139

- spatially explicit landscape made of cellular automatons
- initial state = some cells occupied by an host (H), other by an host with symbionts (S) that are *parasitic*
- mutations favoring mutualism in both H and S can occur, but they have a cost
- mutualism leads to higher reproduction of both H and S
- H and S reproduce independently → horizontal transmission

A MODEL FOR THE EVOLUTION OF MUTUALISM

Peer Community Journal
Section: Evolutionary Biology

Research article

Published
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Mutualists construct the ecological conditions that trigger the transition from parasitism

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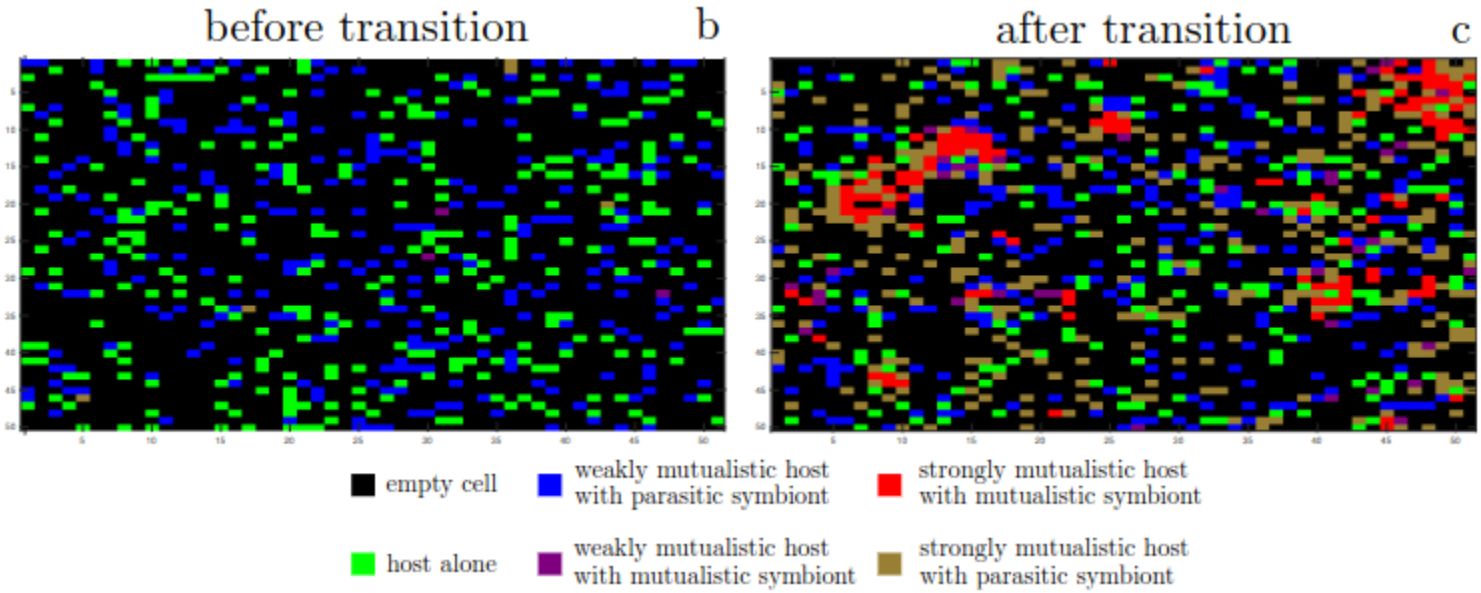
Key results from the model :

- if transmission is purely horizontal, stable mutualisms never establish !

- if reproduction occurs locally this creates pseudo-vertical transmission and mutualistic clusters emerge



A MODEL FOR THE EVOLUTION OF MUTUALISM

When reproduction occurs locally and leads to pseudo-vertical transmission :

- the densities of H & S increase → selection !
- the transition is abrupt

Peer Community Journal
Section: Evolutionary Biology

Research article

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Mutualists construct the ecological conditions that trigger the transition from parasitism

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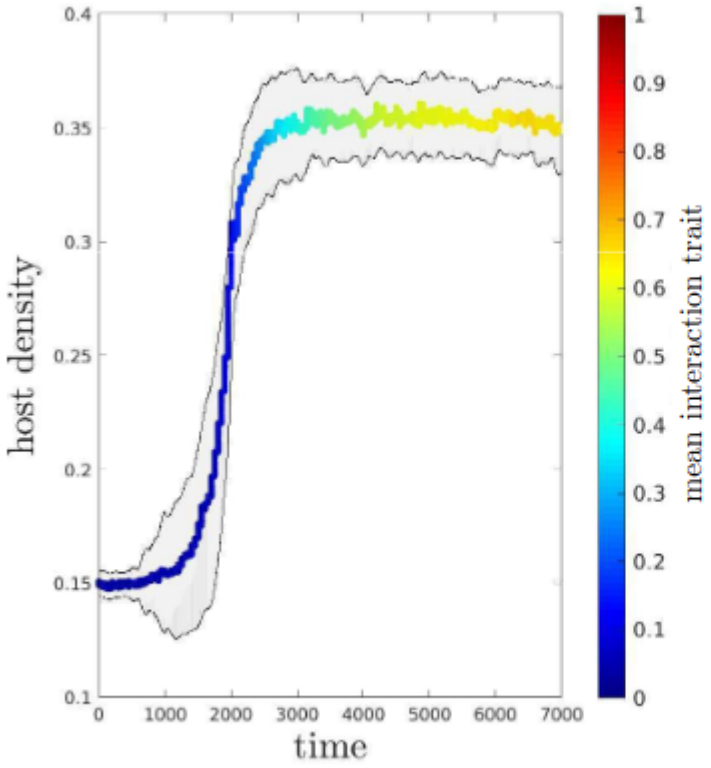
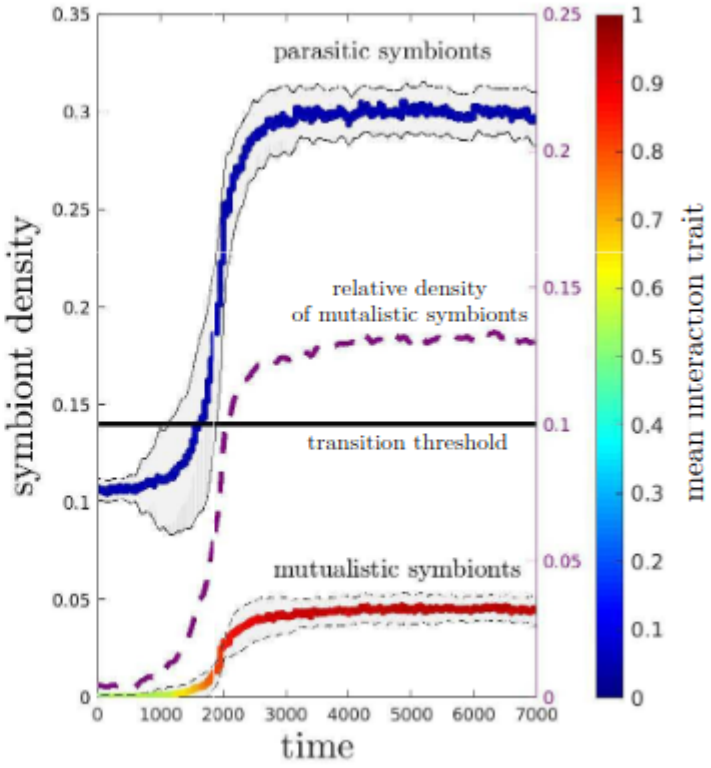
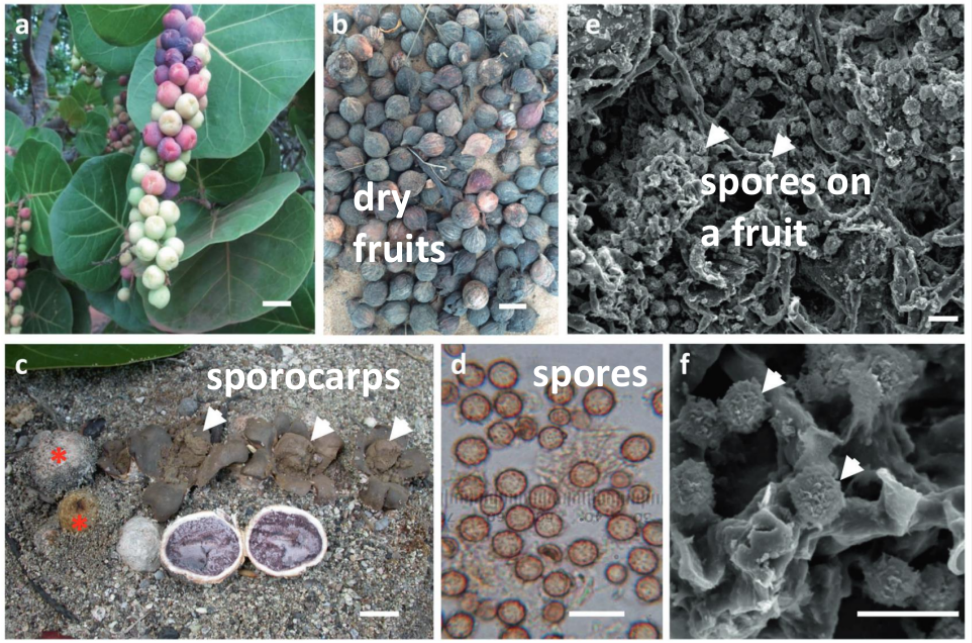




EMPIRICAL SUPPORT FOR PSEUDO-VERTICAL TRANSMISSION

- Some plant seeds (or fruits) do disperse with the spores of their mycorhiza !

The seagrappe *Coccoloba uvifera*



Co-dispersal of spores of the fungi *Scleroderma bermudense*
(Séne et al. 2018)

- Newborns in mammals might carry some bacteria from their mother's guts at birth

- Some plants and their specialized pollinators might disperse very locally

GOING BEYOND ?

Results obtained on relatively simple systems with only two species interacting, often for highly specialized interactions

… what about more real systems ?

Sébastien Ibanez's latest scientific interests *(Ibanez 2020, Arnoldi, … & Ibanez 2020)* **:**

- do higher-level 'collectives' like communities or ecosystems form individuals ?
- how do these collectives re-produce ?
- how does selection act directly at the level of these collectives ?
- examine how properties of the environment might be transmitted (!)

MERCI POUR VOTRE ATTENTION

Travail garanti 100% sans IA

'Ce qui est intéressant avec les philosophes des sciences, c'est qu'ils explorent les conséquences d'hypothèses auxquelles ils ne croient pas forcément'

Citation (approximative) de Sébastien Ibanez, 20/04/2026