



Isabelle Maréchaux

INRAE, UMR AMAP, Montpellier, FR

Principal investigator for INTRACO

Research fields: functional ecology and process-based modeling.
Main focus: tropical forests

- Using process-based models to understand tropical forest dynamics
- Focus on accounting for the wide specific and functional diversity in these models
- Functional and physiological plant trait measurements to inform models



Ghislain Vieilledent

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Principal investigator for INTRACO

Research fields: community ecology, conservation biology, and applied statistics.
Main focus : tropical forests

- Understanding the role of tropical forests in the global carbon cycle
- Studying the impact of climate change and land-use change on tropical forest biodiversity
- Developing theoretical models to test new hypothesis
- Field work in Madagascar, French Guiana and New Caledonia

REVISITING THE ROLE OF INTRASPECIFIC VARIABILITY ON SPECIES COEXISTENCE

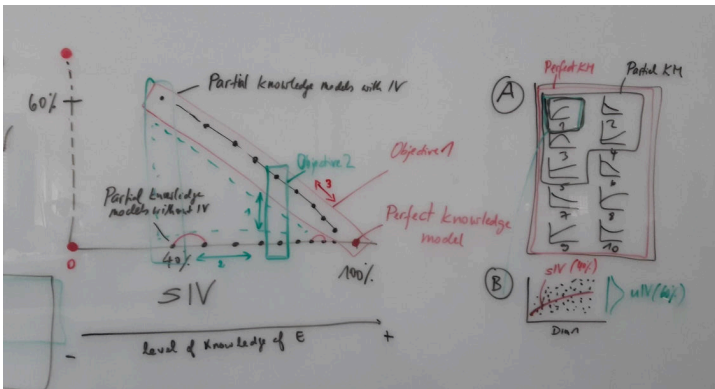
Insights from data and modelling approaches

INTRACO



CESAB
CENTRE FOR THE SYNTHESIS AND ANALYSIS
OF BIODIVERSITY





$$V = \text{cov}(X) \rightarrow M \times Q$$

$$C = \sum_{\text{all } l} \sum_{\text{all } m} \text{cov}(l, m) \rightarrow Q \times S$$

$$C_{i,j} = \sum_{l=1}^E \sum_{m=1}^E \text{cov}(l, m) \cdot (\beta_{im} \cdot \beta_{jm})$$

$$C_{i,i} = \sum_{l=1}^E \sum_{m=1}^E 2 \cdot \text{cov}(l, m) \cdot \beta_{ij} \cdot \beta_{ji}$$

disjoint
of day
= E x (E-2)

if E=2: $C_{i,j} = 2V_{12} \cdot \beta_{12} \beta_{21} + 2 \cdot V_{22}$

$C_{i,i} = 2V_{12} \cdot \beta_{12}^2 + 2V_{22} \beta_{12}^2 + 2V_{22}$

if E=3: $C_{i,j} = 2V_{12} \beta_{12} \beta_{32} + 2V_{22} \beta_{12} \beta_{32} + 2V_{32} \beta_{32}$



Adam T. Clark, James S. Clark, Benoît Courbaud, Claire Fortunel, Camille Girard-Tercieux, Joannès Guillemot, Georges Küntler, Gueric Le Maire, Isabelle Maréchaux, Raphaël Pélissier, Ghislain Vieilledent.

Communities in nature can shelter an amazing species diversity...




Communities in nature can shelter an amazing species diversity...

.. but, despite decades of research, how they can stably coexist remains unclear



Communities in nature can shelter an amazing species diversity...

.. but, despite decades of research, how they can stably coexist remains unclear

An aerial photograph of a dense forest. The majority of the trees are green, but there are several prominent trees with yellow, orange, and red foliage, indicating the start of autumn. The canopy is thick and textured, with some bare branches visible in the lower parts of the trees.

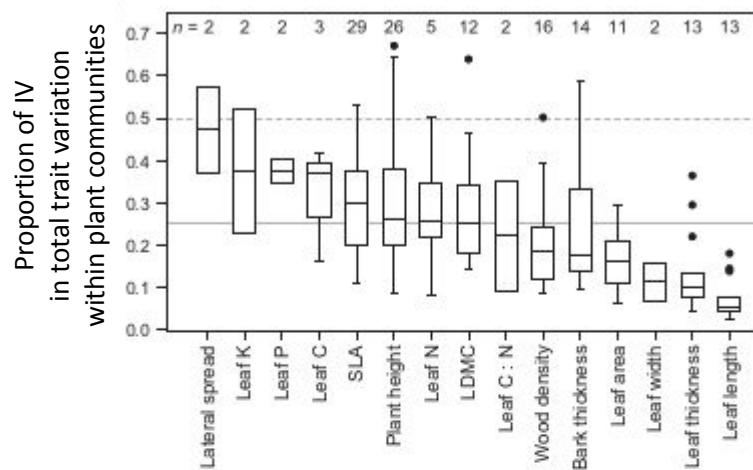
Models remain unable to simulate diversity without unrealistic assumptions, although this is critical to predict global change effect on ecosystem functions and diversity

THE COEXISTENCE PARADOX AND INTRASPECIFIC VARIABILITY

- Most hypotheses and tests to resolve the coexistence paradox have been developed under the **assumption that different individual within a species are fully identical** (i.e. using species mean attributes, such as performance, traits...).

THE COEXISTENCE PARADOX AND INTRASPECIFIC VARIABILITY

- Most hypotheses and tests to resolve the coexistence paradox have been developed under the **assumption that different individual within a species are fully identical** (i.e. using species mean attributes, such as performance, traits...).
- However, the variability among individuals within species (IV) can be surprisingly high.



WHAT IS THE ROLE OF IV IN SPECIES COEXISTENCE ?

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VOL. 170, NO. 6 THE AMERICAN NATURALIST DECEMBER 2007

Intraspecific Variation and Species Coexistence

Jeremy W. Lichstein,^{*} Jonathan Dushoff,[†] Simon A. Levin,[‡] and Stephen W. Pacala[§]

Ecology Letters, (2016) 19: 825–838

doi:10.1111/ele.12618

IDEA AND
PERSPECTIVE

How variation between individuals affects species coexistence

Simon P. Hart,^{*} Sebastian J. Schreiber[†] and Jonathan M. Levine[‡]

Abstract

Although the effects of variation between individuals within species are traditionally ignored in studies of species coexistence, the magnitude of intraspecific variation in nature is forcing ecologists to reconsider. Compelling intuitive arguments suggest that individual variation may provide a previously unrecognized route to diversity maintenance by blurring species-level competitive dif-

©

Theor Ecol (2012) 5:61–71
DOI 10.1007/s12080-010-0095-8

ORIGINAL PAPER

Intra-specific variability and the competition–colonisation trade-off: coexistence, abundance and stability patterns

Benoît Courbaud · Ghislain Vieilledent ·
Georges Kunstler

Ecology Letters, (2018) 21: 1496–1504

doi:10.1111/ele.13130

LETTER

Variation between individuals fosters regional species coexistence

María Uriarte^{*} and
Duncan Menge[†]

Abstract

Although individual-level variation (IV) is ubiquitous in nature, it is not clear how it influences species coexistence. Theory predicts that IV will hinder coexistence but empirical studies have shown that it can facilitate, inhibit or have a neutral effect. We use a theoretical model to explore

Ecological Monographs, 0(0), 2021, e01493

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Synthesizing the effects of individual-level variation on coexistence

SIMON MACCRACKEN STUMP¹, CHULIANG SONG², SERGUEI SAAVEDRA,²
JONATHAN M. LEVINE,³ AND DAVID A. VASSEUR^{1,4}

WHAT IS THE ROLE OF IV IN SPECIES COEXISTENCE ?

VOL. 170, NO. 6 THE AMERICAN NATURALIST DECEMBER 2007

Intraspecific Variation and Species Coexistence

Jeremy W. Lichstein,[†] Jonathan M. Levine,[†] Simon A. Levin,[‡] and Stephen W. Pacala[§]

It depends...

It prevents coexistence

IDEA AND PERSPECTIVE Ecology Letters, (2016) 19: 825–838 doi:10.1111/ele.12618

How variation within species affects species coexistence

Abstract
Although intraspecific variation between individuals within species are traditionally ignored in models of species coexistence, recent studies have shown that the magnitude of intraspecific variation in nature is forcing ecologists to re-evaluate their intuitive arguments suggest that individual variation may provide different routes to diversity maintenance by blurring species-level competitive differences.

Simon P. Hart,[†] Sebastian J. Schreiber[†] and Jonathan M. Levine[†]

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DOI 10.1007/s12080-010-0095-8

ORIGINAL PAPER

Intra-specific variability and the trade-off: coexistence, competitive exclusion and stability patterns

Benoit Courbaud · Ghislain Vieilledent · Georges Kunstler

It slows down competitive exclusion...

LETTER Ecology Letters, (2018) 21: 1496–1504 doi:10.1111/ele.13130

Variation between individuals within species affects species coexistence

Abstract
Although individual variability within species is ubiquitous in nature, it is not clear how it influences species coexistence. Theoretical studies suggest that IV will hinder coexistence but empirical studies have shown that it can have a neutral effect. We use a theoretical model to explore the role of IV in species coexistence.

María Uriarte^{*} and Duncan Menge[†]

It can foster coexistence

Ecological Monographs, 0(0), 2021, e01493
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Synthesizing the effect of individual-level variation on coexistence

SIMON MACCRACKEN¹, CHULIANG SONG², SERGUEI SAAVEDRA², JONATHAN M. LEVINE³ AND DAVID A. VASSEUR^{1,4}

Contrasting results across studies..

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ORIGINAL PAPER

down
ie

Our goal:
revisiting the role of IV in species coexistence

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Synthesizing the effect of individual-level variation on coexistence

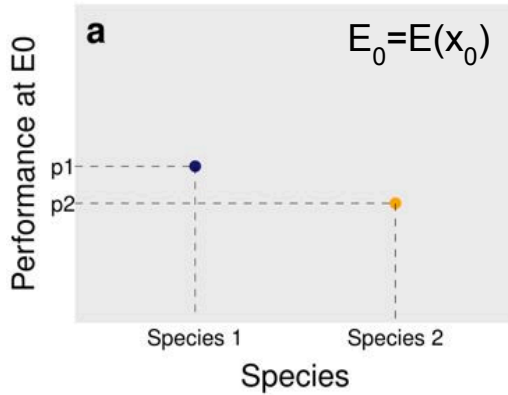
SIMON MACCRACKEN¹, CHULIANG SONG², SERGUEI SAAVEDRA²,
JONATHAN LEVINE³ AND DAVID A. VASSEUR^{1,4}

Contrasting results
across studies..

On the sources of IV and their consequences on conspecifics' similarity

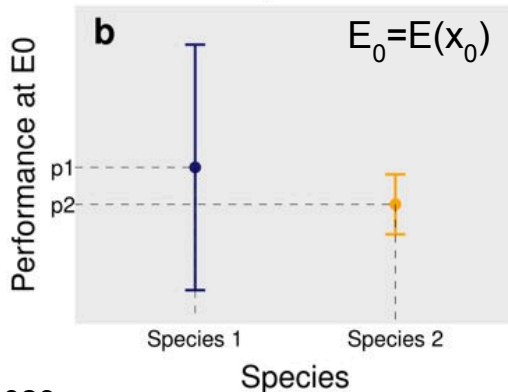
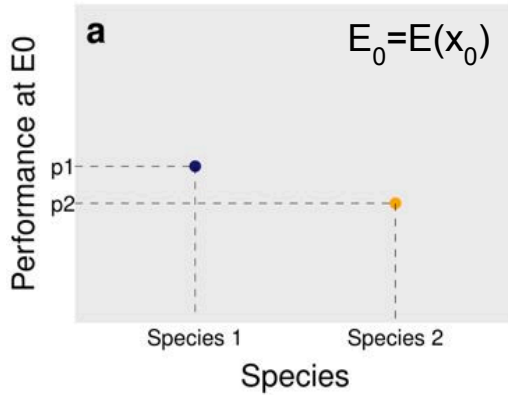


Where does *observed* IV come from ?



- Conspecifics are identical
- Species 1 outcompetes Species 2 in E_0

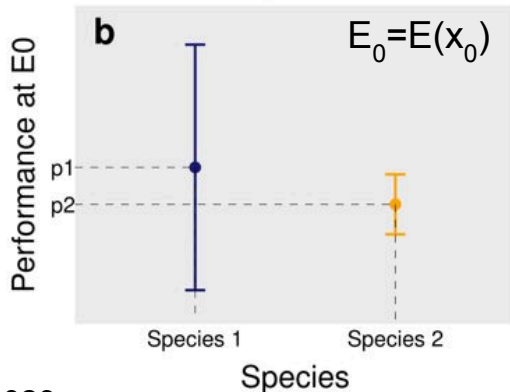
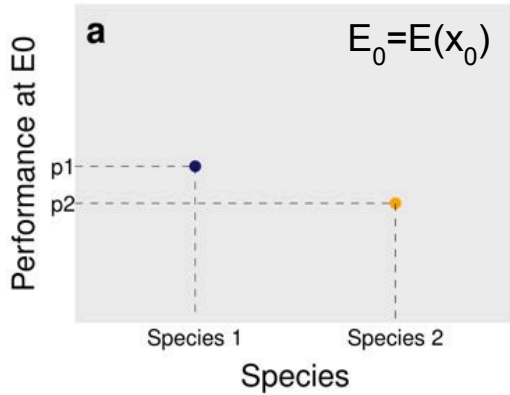
Where does *observed* IV come from ?



One observation

data actually shows a range of values for each species at E_0

Where does *observed* IV come from ?

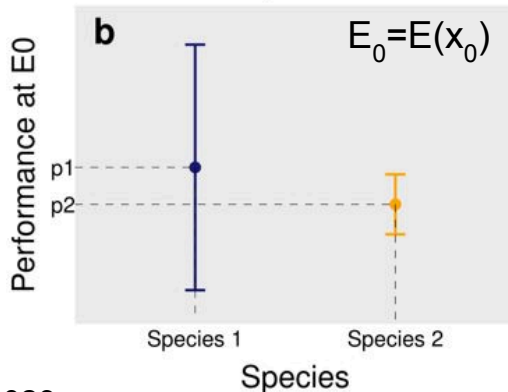
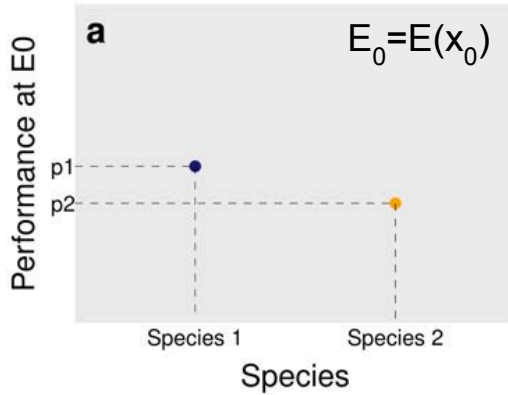


One observation

data actually shows a range of values for each species at E_0

Two interpretations

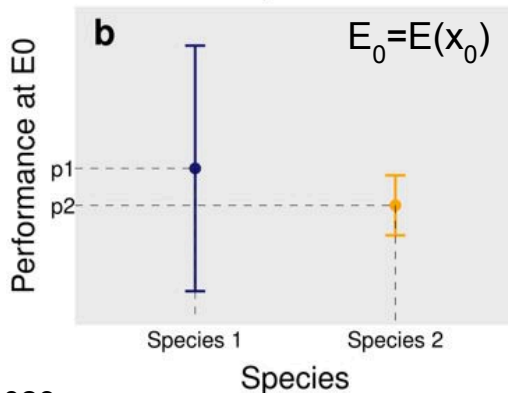
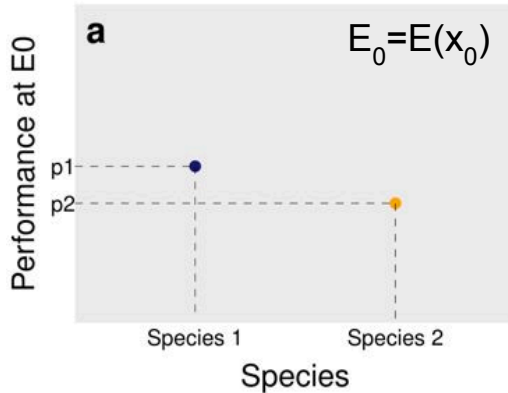
Where does *observed* IV come from ?



Interpretation 1

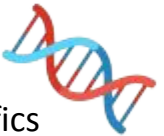
- Conspecifics are intrinsically different
- Some heterospecifics have more similar performance in comparison to some conspecifics

Where does *observed* IV come from ?

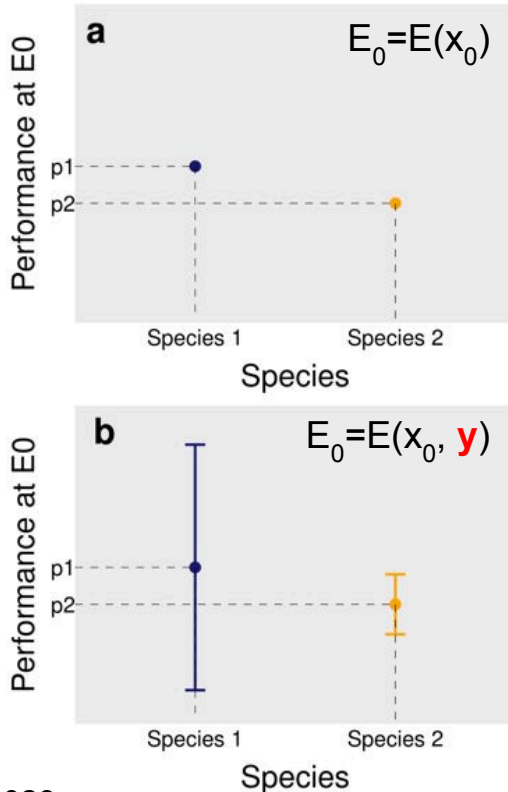


Interpretation 1

- Conspecifics are intrinsically different
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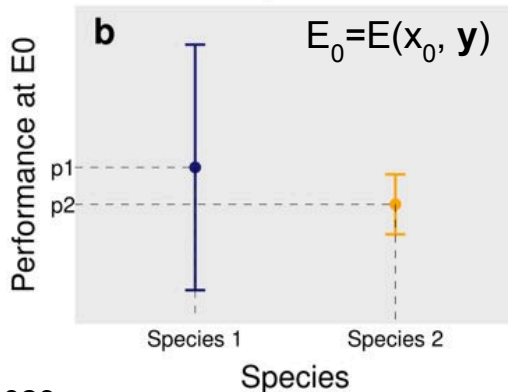
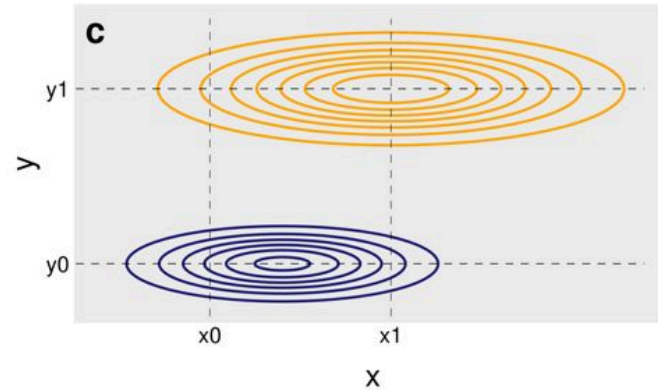
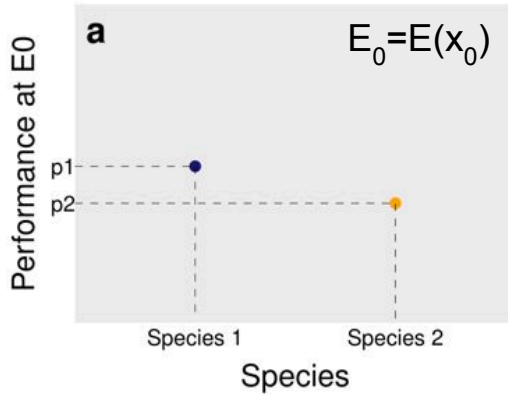
Where does *observed* IV come from ?



Interpretation 2:

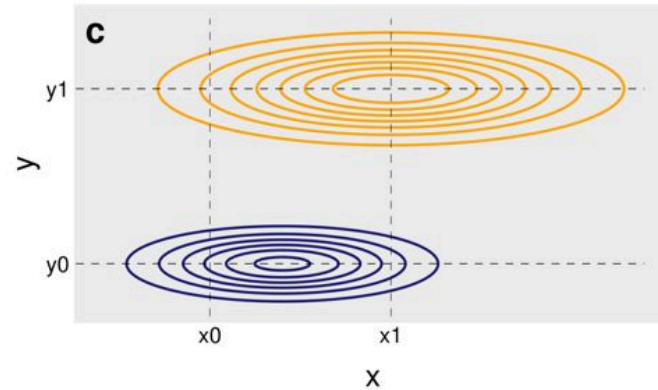
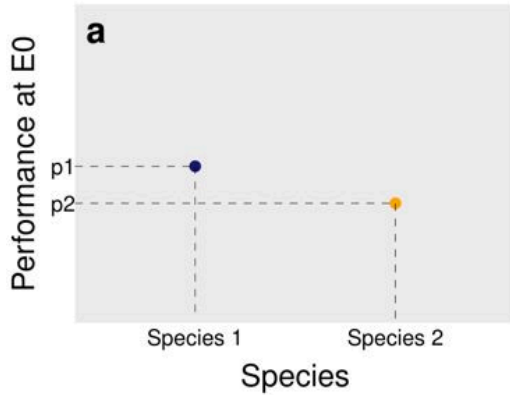
- what if some ***unobserved*** environmental dimensions actually influence individual performance at E_0 ?

Where does *observed* IV come from ?

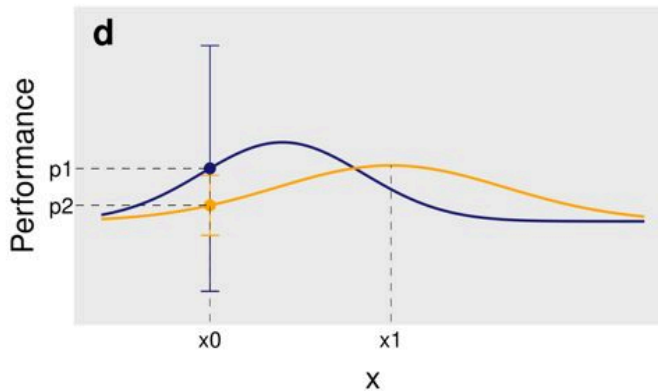
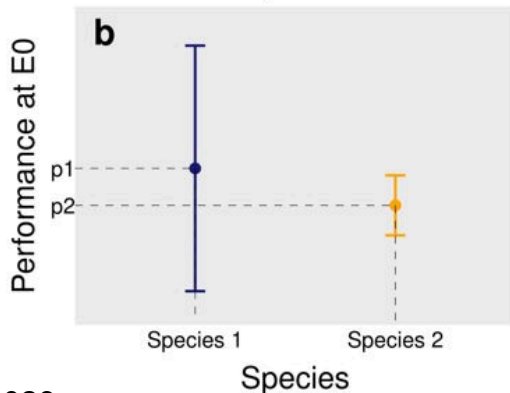


Contrasting performances among conspecific individuals in E_0 do not result from **intrinsic differences** among them but from **differences in the local environment they experience and that was poorly characterized.**

Where does *observed IV* come from ?

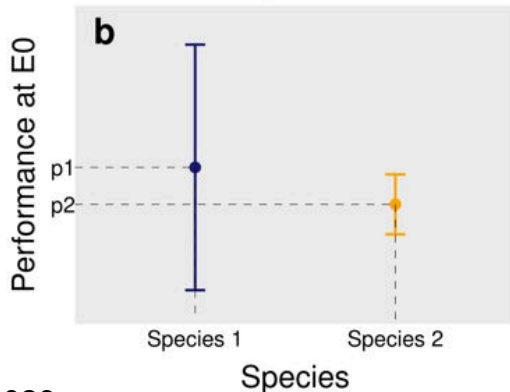
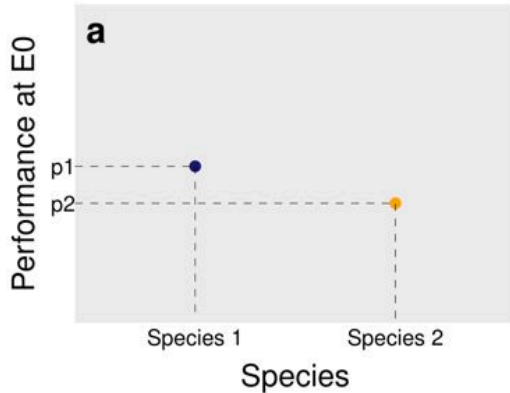


No niche overlap in two dimensions



Apparent niche overlap in one dimension

Where does *observed IV* come from ?



Two (not mutually exclusive) interpretations

Different signatures of IV: **unstructured vs. structured in space and time**

Very different consequences for **conspecifics' similarity and coexistence**

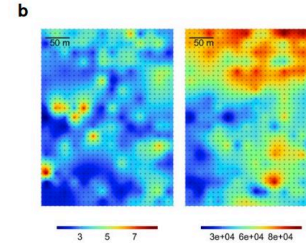
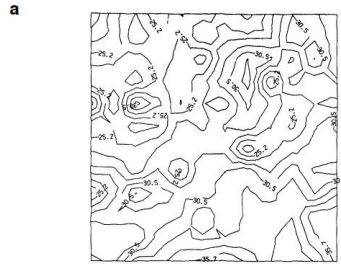
Where does *observed* IV come from ?
In search of evidence in data

LITERATURE
Micro-environment, species
differences

Where does *observed* IV come from ?

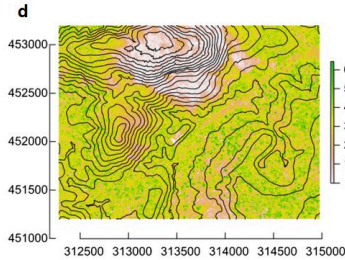
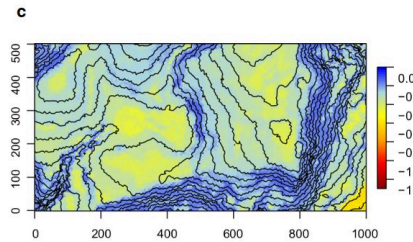
In search of evidence in data

Soil nitrogen content
12×12 m
USA
Tilman 1982



% C and Al in soil 250×500 m
French Guiana
Zinger et al. 2019

Soil water content
1000×500 m
Panama
Kupers et al. 2019



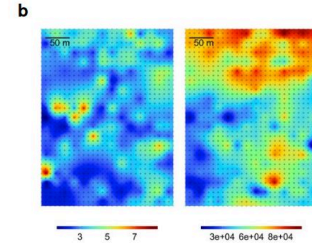
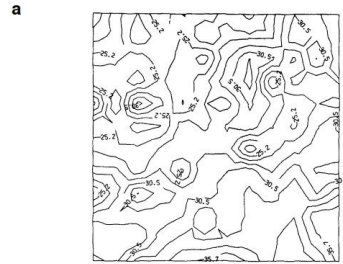
Topography
2500×2000 m French
Guiana
Tymen et al. 2017

LITERATURE
Micro-environment, species
differences

Where does *observed* IV come from ?

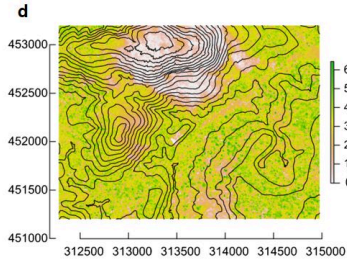
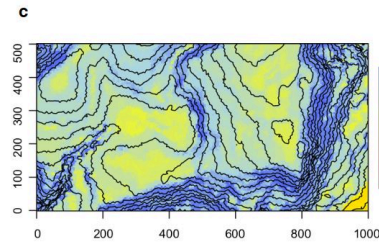
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LITERATURE
Micro-environment, species
differences

Environmental variation is
high dimensional and multiscale

Where does *observed* IV come from ?

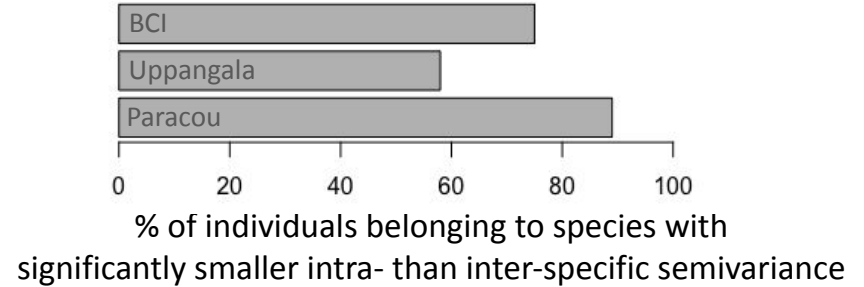
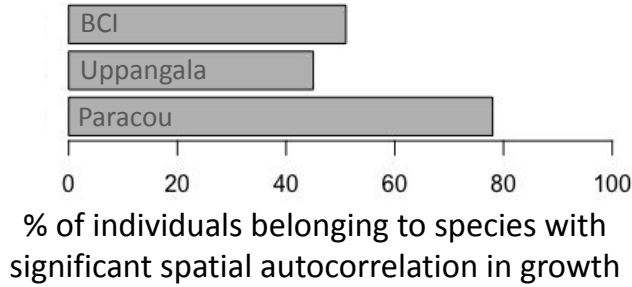
In search of evidence in data

EMPIRICAL
Tree inventories in three
natural tropical forests

LITERATURE
Micro-environment, species
differences

Where does *observed* IV come from ?

In search of evidence in data



EMPIRICAL
Tree inventories in three
natural tropical forests

Individual growth is largely spatially
autocorrelated across three tropical forest sites

LITERATURE
Micro-environment, species
differences

Where does *observed* IV come from ?

In search of evidence in data

EXPERIMENTAL
Clonal *Eucalyptus* plantations

EMPIRICAL
Tree inventories in three
natural tropical forests

LITERATURE
Micro-environment, species
differences

Where does *observed* IV come from ?

In search of evidence in data

Clonal *Eucalyptus* plantations

an extreme case of controlled genetic variation
and minimized environmental variation

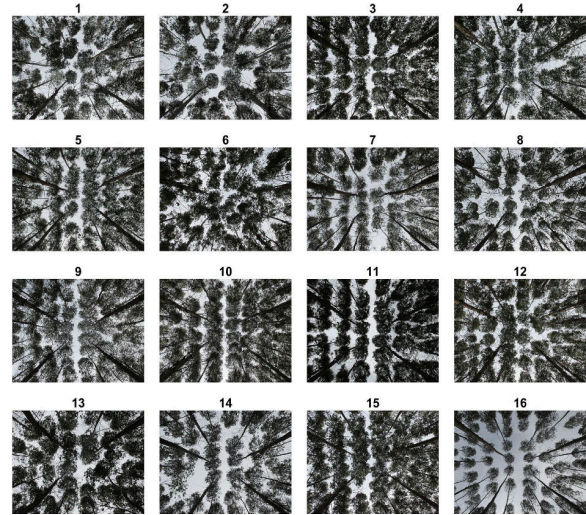
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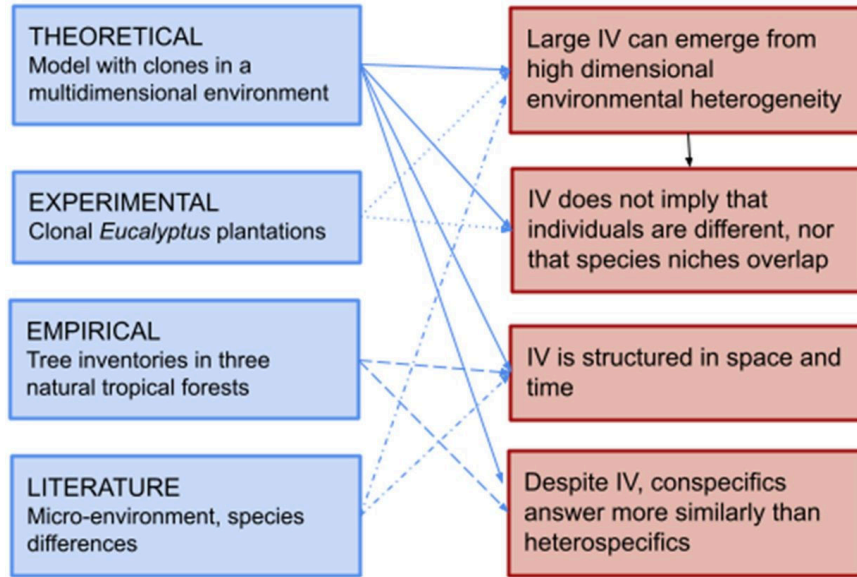
The variability between
individuals was almost
twice as high as the
variability between
genotypes

Le Maire *et al.* 2019



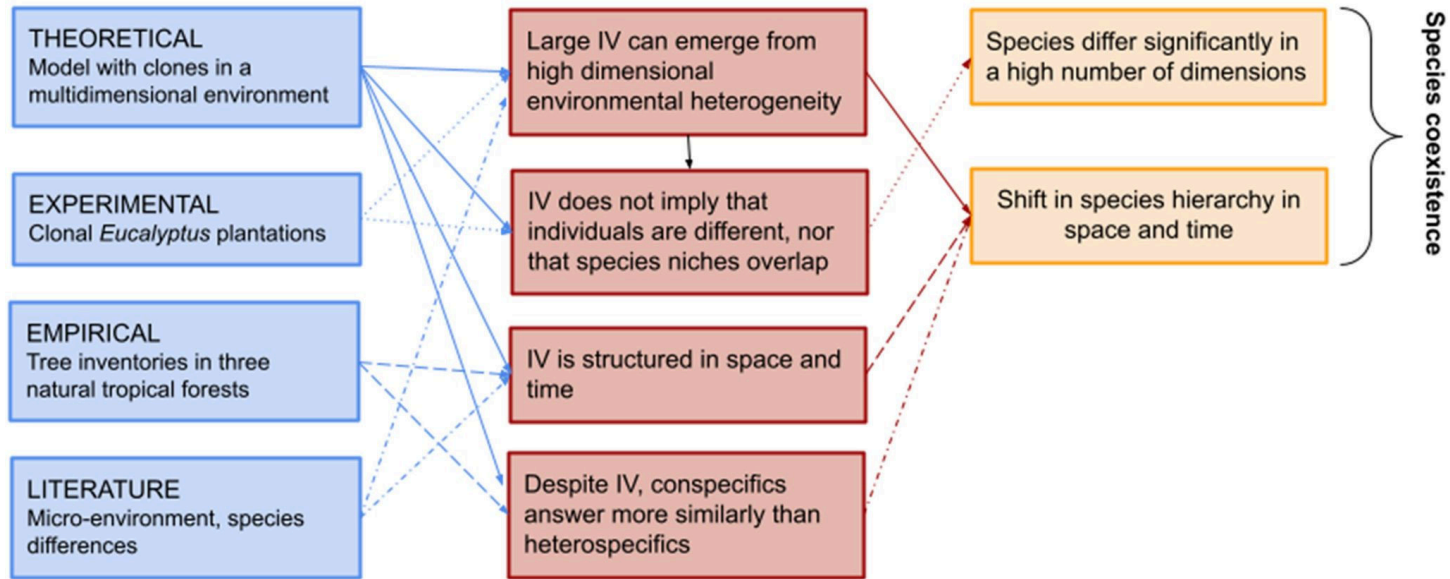
Where does *observed* IV come from ?

Insights on intraspecific variability



Where does *observed* IV come from ?

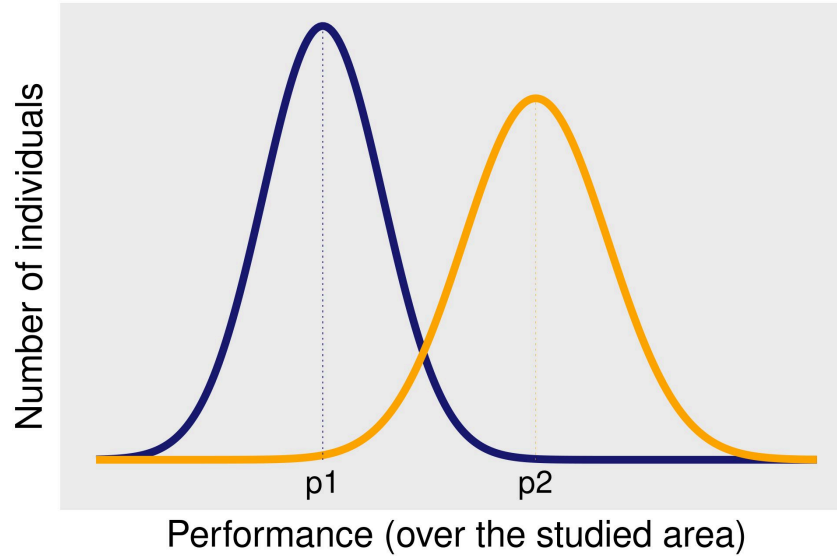
Consequences on species coexistence



On the representation of IV in models of community dynamics



How is *observed* IV included in models ?



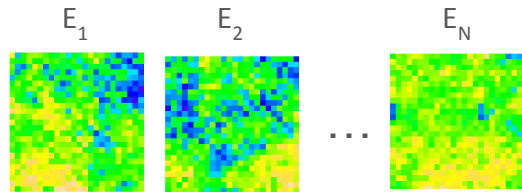
A random noise around species means

A virtual experiment

To explore the effect of using **random, unstructured IV** as a substitute for **environmentally-driven, structured IV**, in a coexistence model.

A virtual experiment

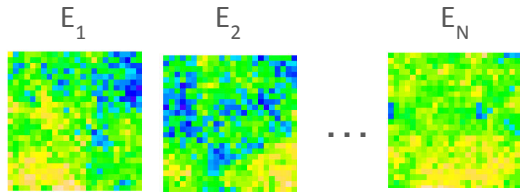
A virtual world



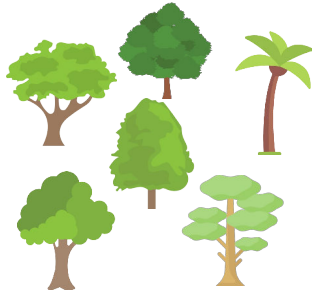
N independent, spatially-autocorrelated variables, in a $D \times D$ cell grids

A virtual experiment

A virtual world



N independent, spatially-autocorrelated
variables, in a $D \times D$ cell grids



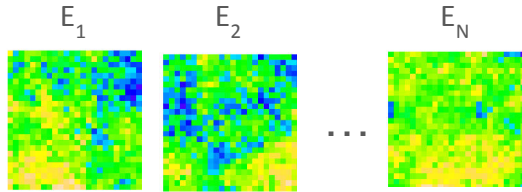
S species

whose performance is fully described by
N independent optima

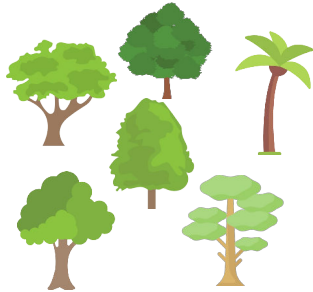
$$\mathbf{TrueP} = f(E_1, E_2, \dots, E_N)$$

A virtual experiment

A virtual world



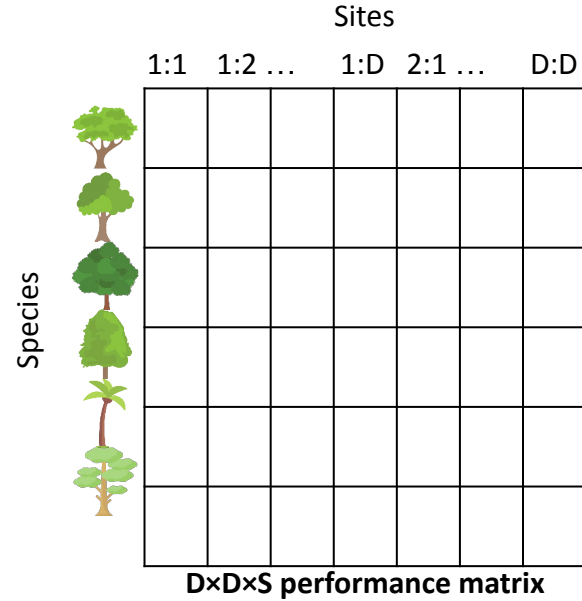
N independent, spatially-autocorrelated variables, in a $D \times D$ cell grids



S species

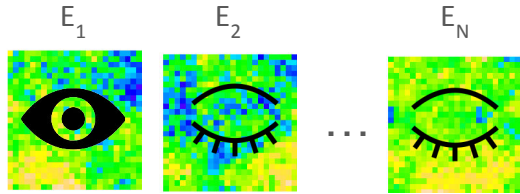
whose performance is fully described by N independent optima

$$\mathbf{TrueP} = f(E_1, E_2, \dots, E_N)$$

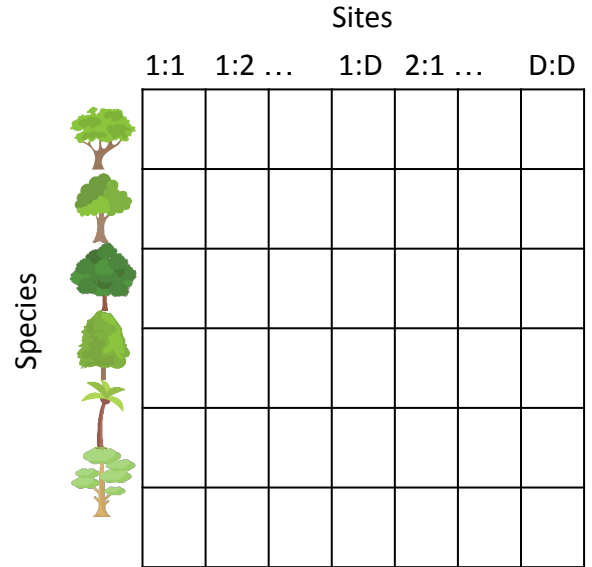


A virtual experiment

Our imperfect characterization of this world



Only a few environmental variables are actually observed and quantified at the relevant scales

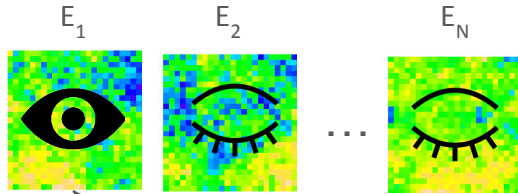


$D \times D \times S$ performance matrix

observed from, e.g., forest inventories

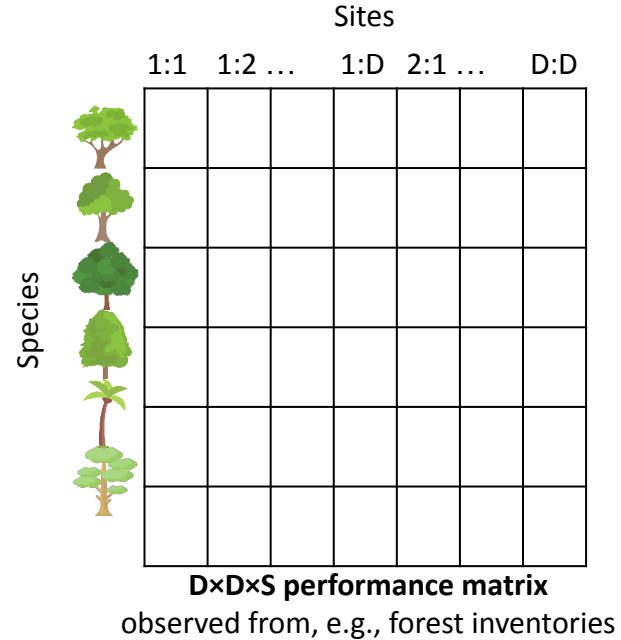
A virtual experiment

Our imperfect characterization of this world



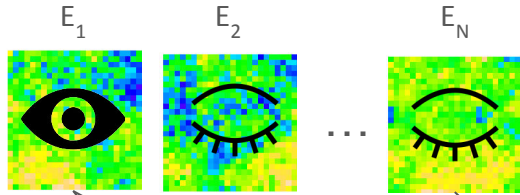
Statistical inference:

$$TrueP_{sp, site} = \beta_{0,sp} + \beta_{1,sp} \times Env I_{site} + \beta_{2,sp} \times Env I_{site}^2 + \epsilon_{sp, site}$$



A virtual experiment

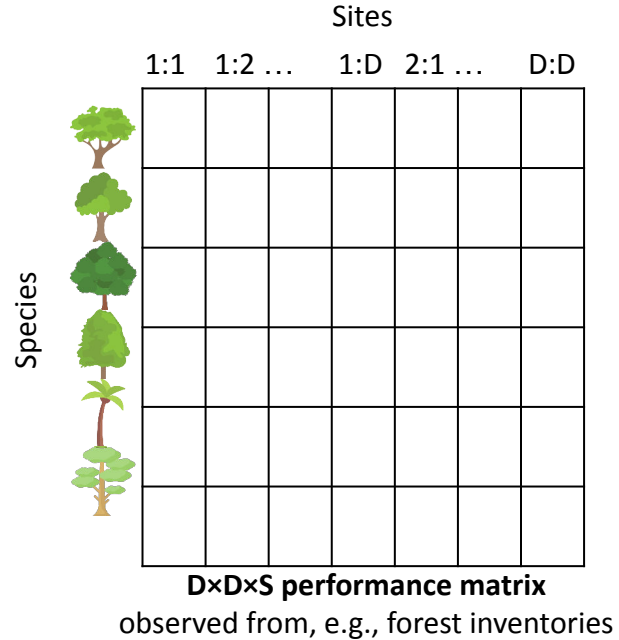
Our imperfect characterization of this world



Statistical inference:

$$TrueP_{sp, site} = \beta_{0,sp} + \beta_{1,sp} \times Env I_{site} + \beta_{2,sp} \times Env I_{site}^2 + \epsilon_{sp, site}$$

$$\epsilon_{sp, site} \sim N(0, V), V_{sp} = var(\epsilon_{sp})$$



A virtual experiment

Our imperfect characterization of this world

Two ways to predict performance:

$$\widehat{P}_{p, site} = \beta_{0,sp} + \beta_{1,sp} \times Env I_{site} + \beta_{2,sp} \times Env I_{site}^2$$

Partial knowledge without IV

A virtual experiment

Our imperfect characterization of this world

Two ways to predict performance:

$$\widehat{P}_{p, site} = \beta_{0,sp} + \beta_{1,sp} \times Env I_{site} + \beta_{2,sp} \times Env I_{site}^2$$

Partial knowledge without IV

$$\widehat{PuIV}_{p, site} = \beta_{0,sp} + \beta_{1,sp} \times Env I_{site} + \beta_{2,sp} \times Env I_{site}^2 + \widehat{\varepsilon}_{sp, site}$$

Partial knowledge with unstructured IV (uIV)

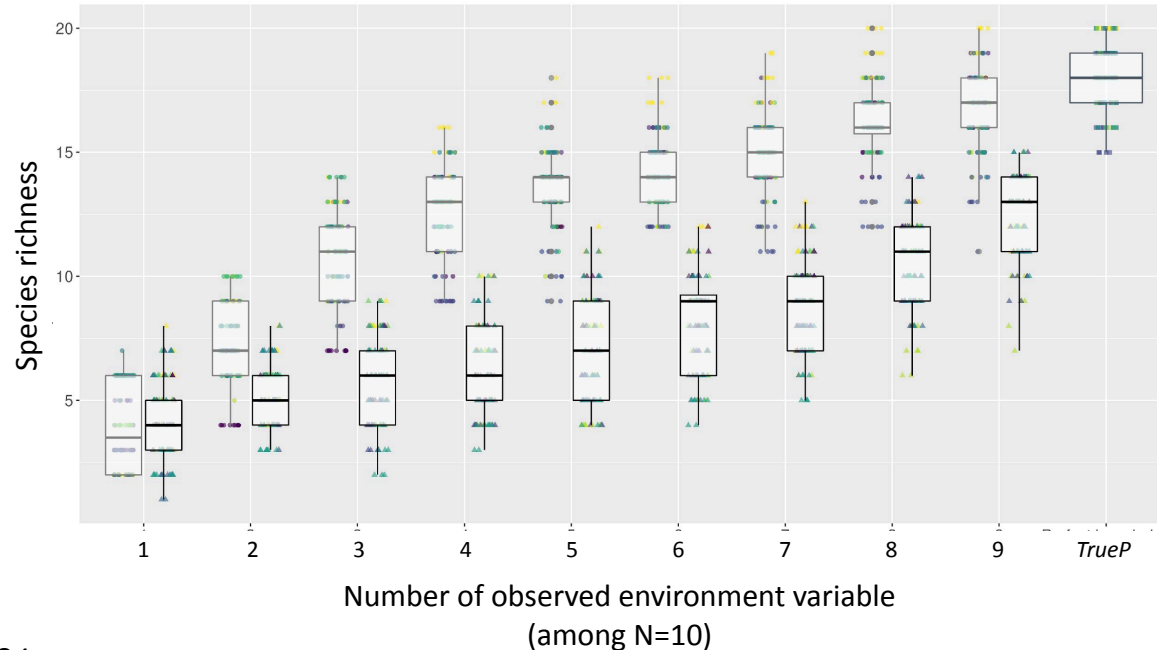
$$\widehat{\varepsilon}_{sp, site} \sim N(0, V_{sp})$$

A virtual experiment

Comparison of the communities simulated with the same simulator of community dynamics, but using TrueP, or one of the two predicted P

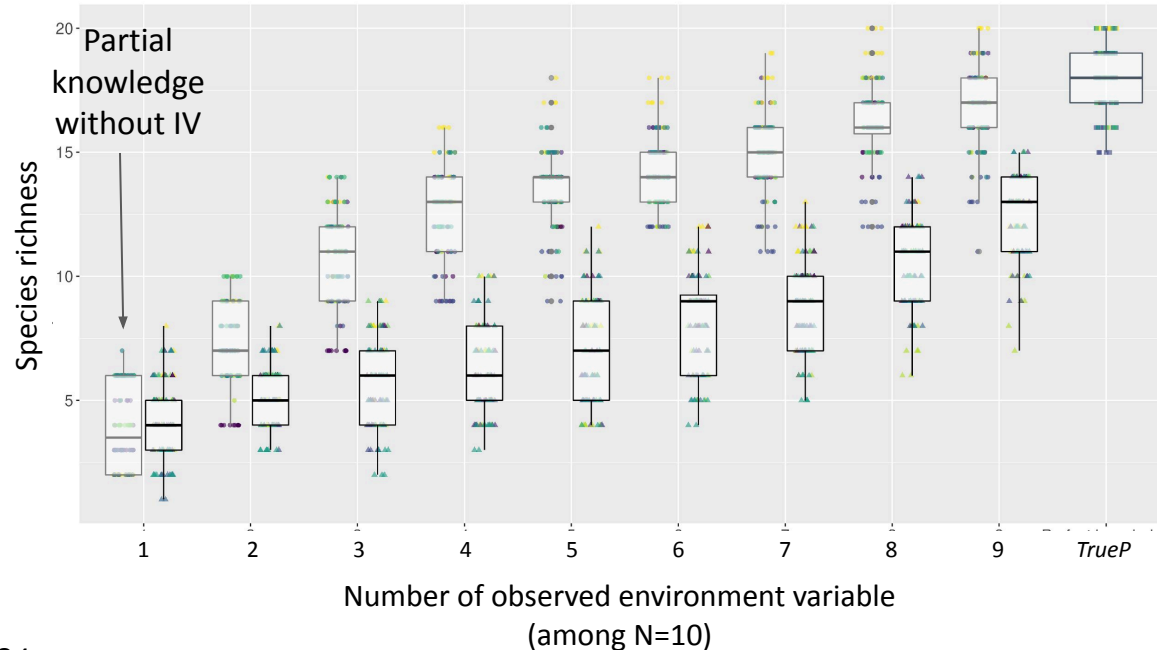
A virtual experiment

Comparison of the communities simulated with the same simulator of community dynamics, but using TrueP, or one of the two predicted P



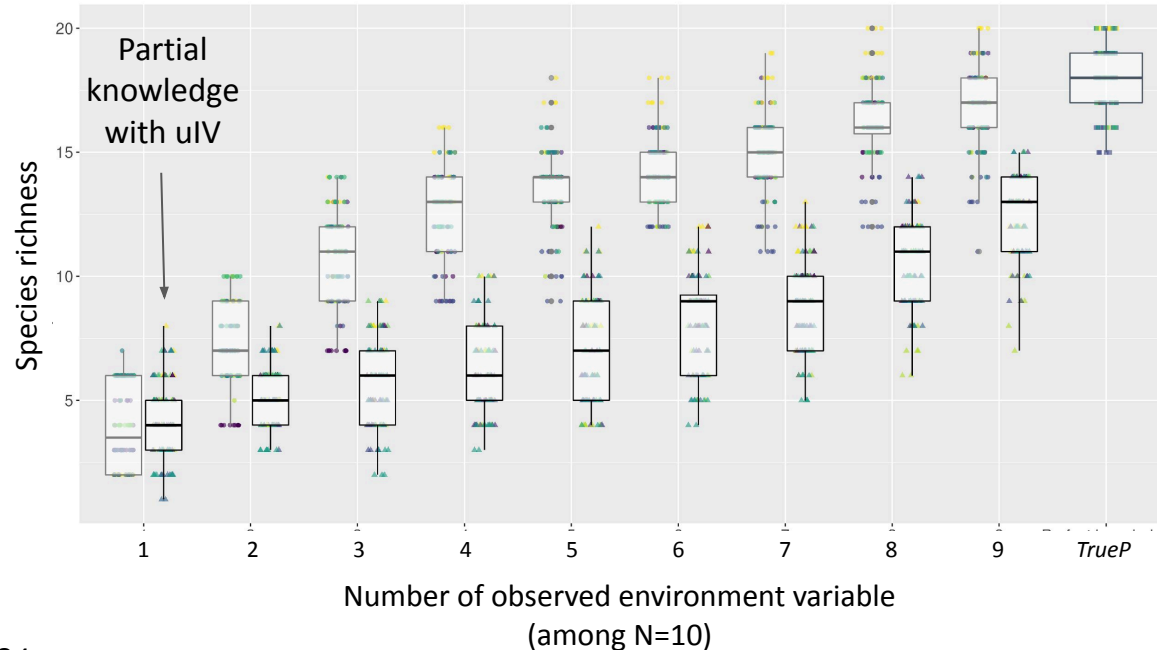
A virtual experiment

Comparison of the communities simulated with the same simulator of community dynamics, but using TrueP, or one of the two predicted P



A virtual experiment

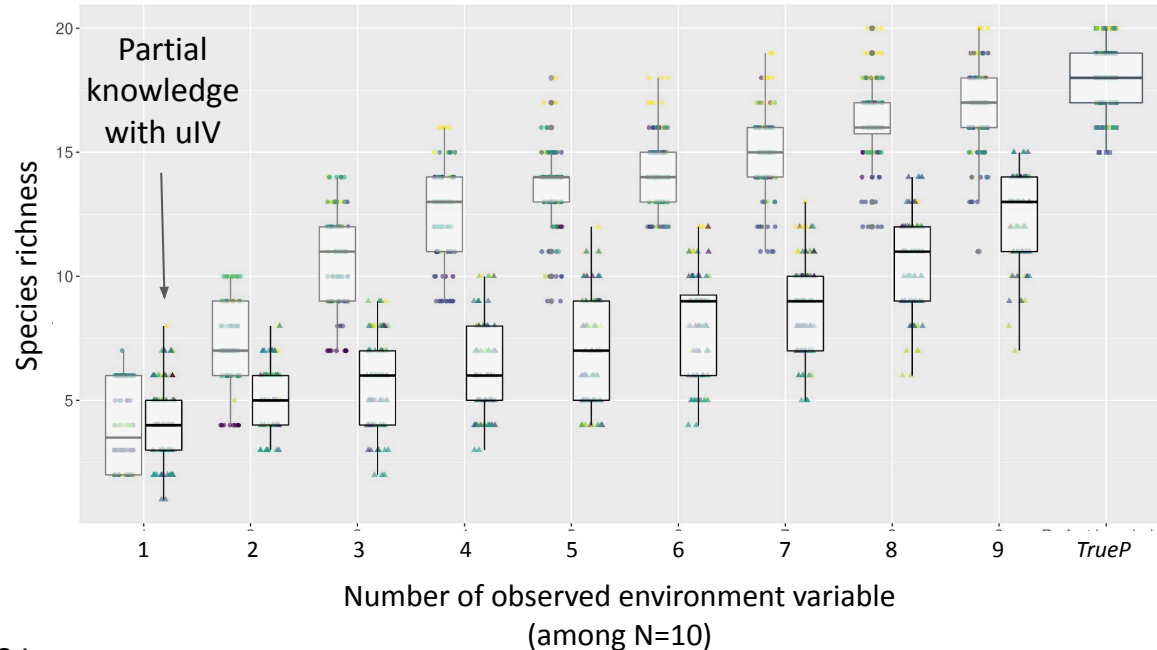
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A virtual experiment

Comparison of the communities simulated with the same simulator of community dynamics, but using TrueP, or one of the two predicted P

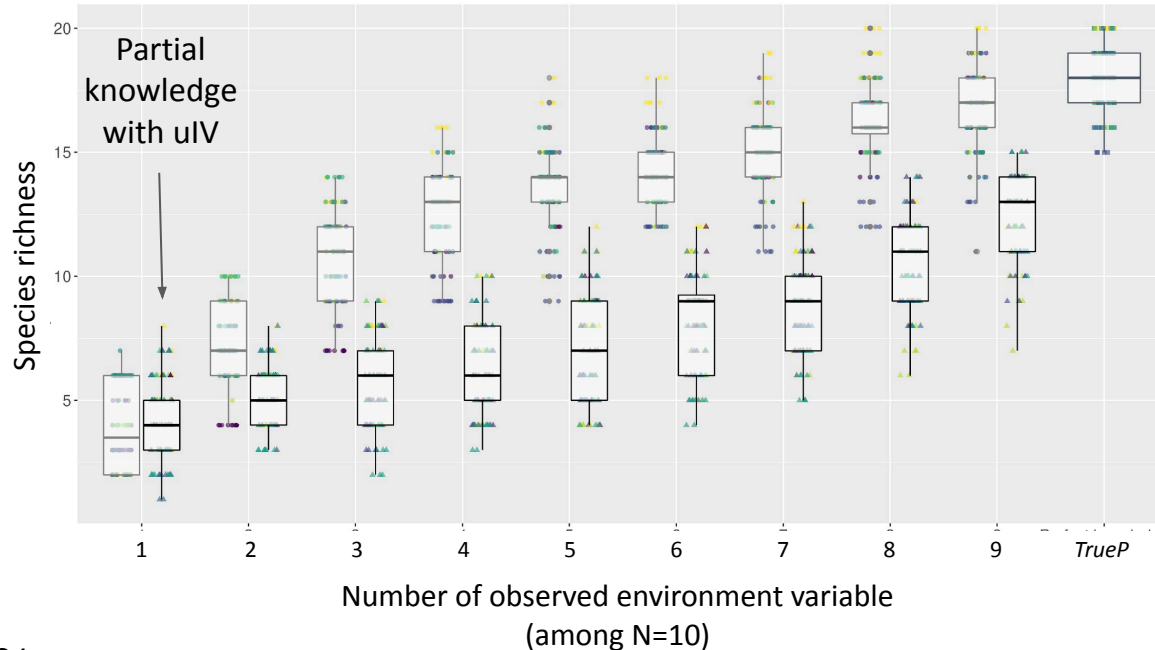
Partial
knowledge
models never
reach level of
TrueP model



A virtual experiment

Comparison of the communities simulated with the same simulator of community dynamics, but using TrueP, or one of the two predicted P

Starting from 2
observed axes,
adding uIV
lowers species
richness

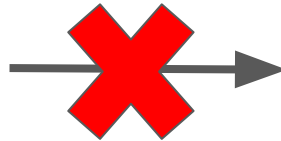
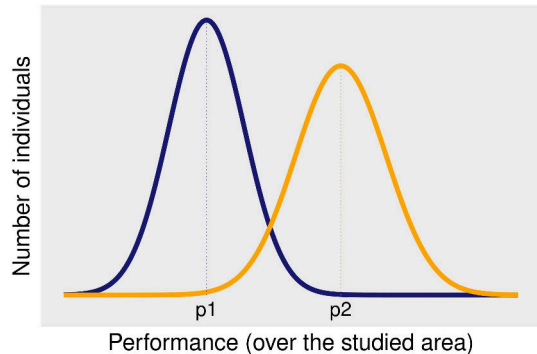


A virtual experiment

Take home messages:

Adding randomness does not compensate lack of knowledge

Unstructured IV is a bad surrogate for unobserved environmental variation



A simple mechanism to explain the stable coexistence of a high number of species



Context

- IV is not a direct cause of species coexistence.
- Can we provide a simple theoretical mechanism explaining species coexistence ?
- How IV is related to this mechanism ?
- How to integrate this mechanism in empirical community models ?

??

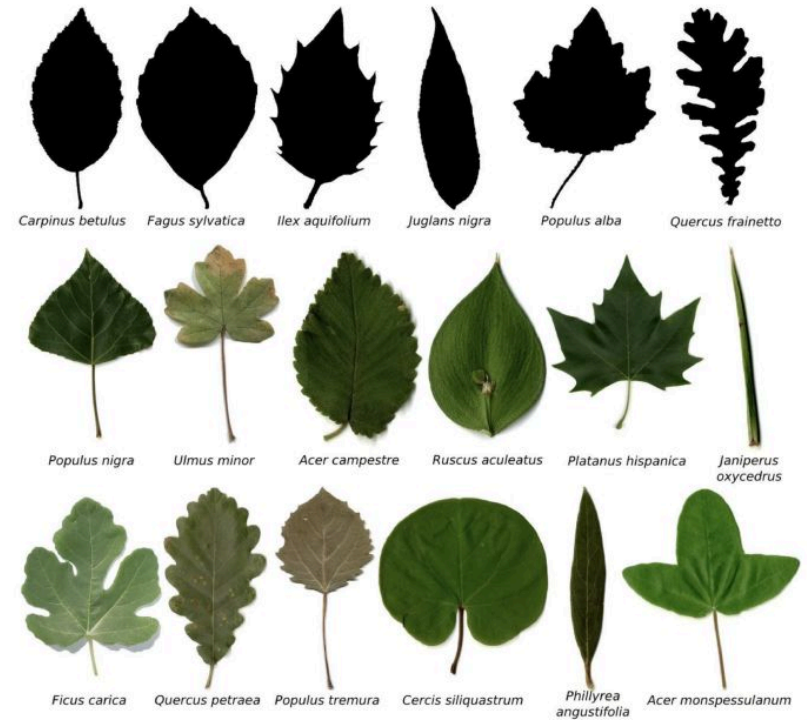


Context

Objectives

Using a theoretical model, we aim at showing that:

- Coexistence emerges from high-dimensional interactions between species and the environment ($E \times S$). Niche theory (Hutchinson).
- $E \times S$ can be modelled using a species **covariance** matrix.



Methods

Theoretical model

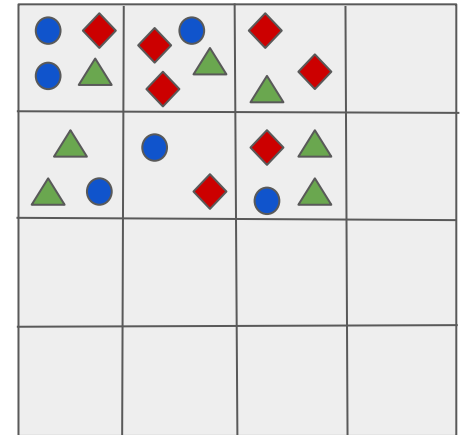
COMMUNITY

- Community: individuals of S species that interact locally over K sites.
- Each site have a particular environment defined by E dimensions x_1, \dots, x_E .

DEMOGRAPHY

- **Dispersal** \times **Performance** (\sim growth) \times **Survival**
- **Dispersal** is a fixed fraction of performance and uniform on all sites (same for all species).
- **Survival** is density dependent (same for all species).
- **Performance**: three different models (SK, SU, UU).

S species on K sites
(several individuals from different species compete in each site)



Methods

Theoretical model

Three models for performance $\mathbf{g}_{i(s,k)t}$ (individual i , species s , site k , time t)

1. **SK** model (structured, known): Performance is a function of species parameters and environment ($E \times S$).

$$\mathbf{g} = f(E \times S)$$

2. **SU** model (structured, unknown): Performance depends on species covariance matrix (Σ) derived from E and S .

$$\mathbf{g} = f(\Sigma)$$

3. **UU** model (unstructured, unknown): Performance is random.

$$\mathbf{g} = f(\sigma^2 I)$$

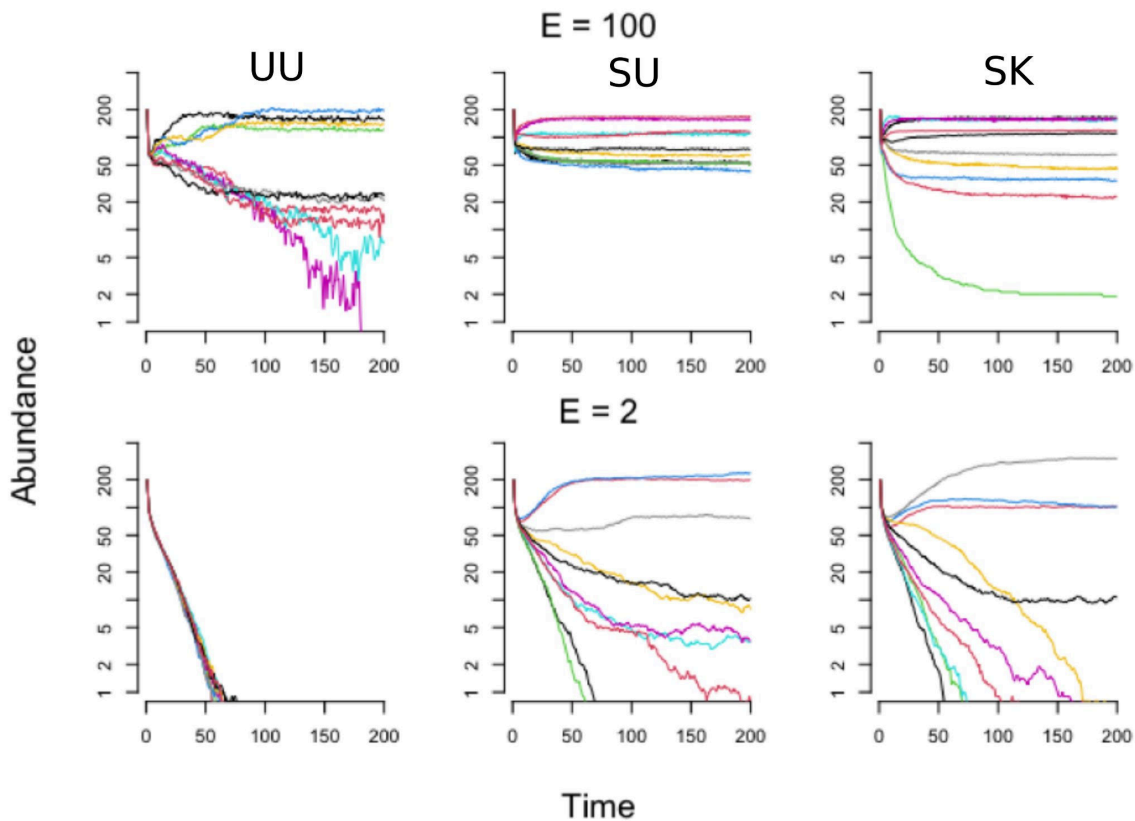
Preliminary results

Simulation outputs

If E is large ($E \gg 1$):

SK ($E \times S$) and **SU** (Σ): stable coexistence.

UU (random): no stable coexistence.



Preliminary results

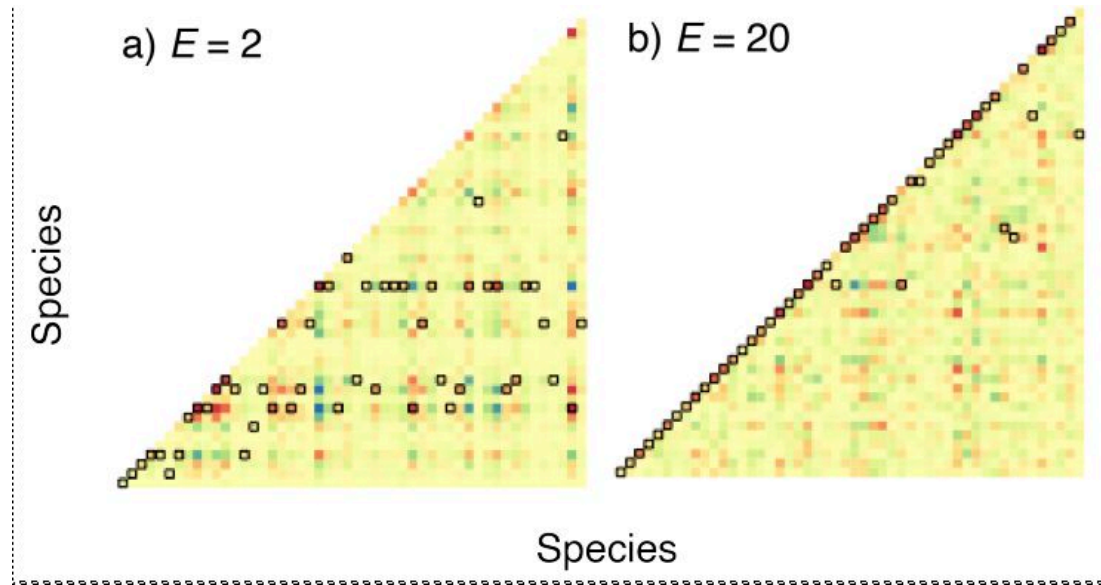
Covariance matrix and competition

If E is large ($E \gg 1$):

SK ($E \times S$) and **SU** (Σ): Strong diagonal dominance in the species covariance matrix.

Intra. correlations $>$ inter. correlations.

Competition concentrates within the species (a necessary condition for species coexistence).



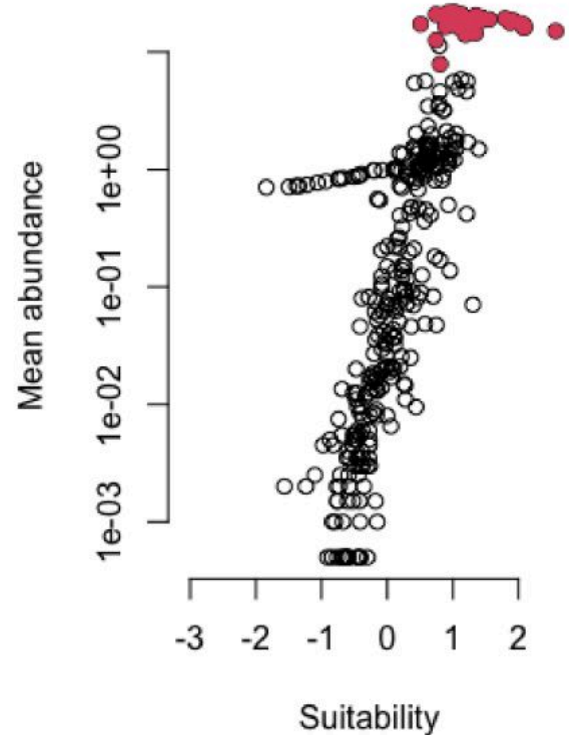
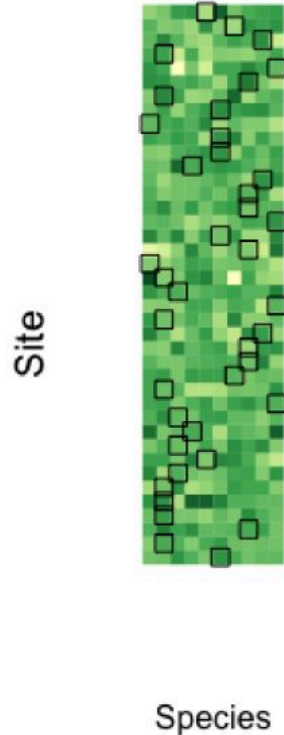
Results

Sorting

SK ($E \times S$)

Species sort according to where they can dominate.

Each species outperforms the others on particular sites.



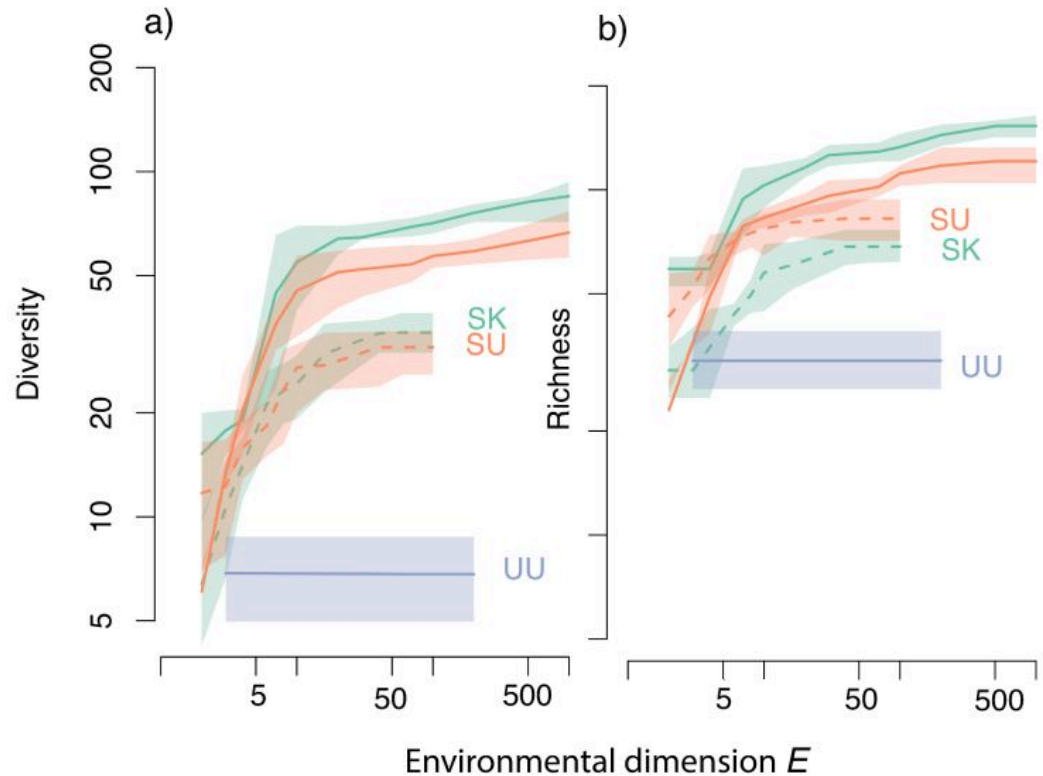
Results

Effect of dimensionality

SK and **SU** generate coexistence

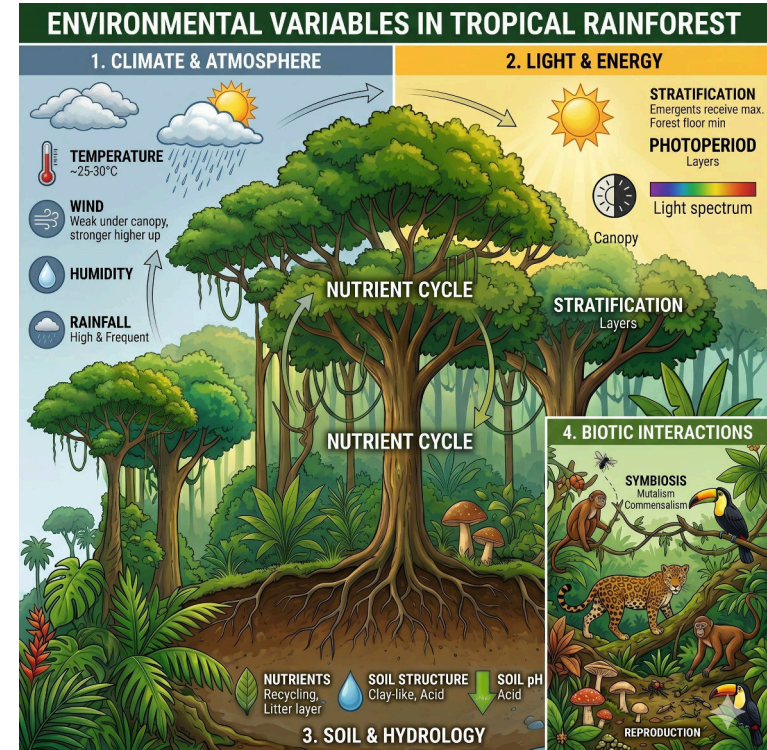
The number of coexisting species in **SK** and **SU** increases quickly with E

Number of coexisting species $\gg E$ (eg. >50 for $E=10$).



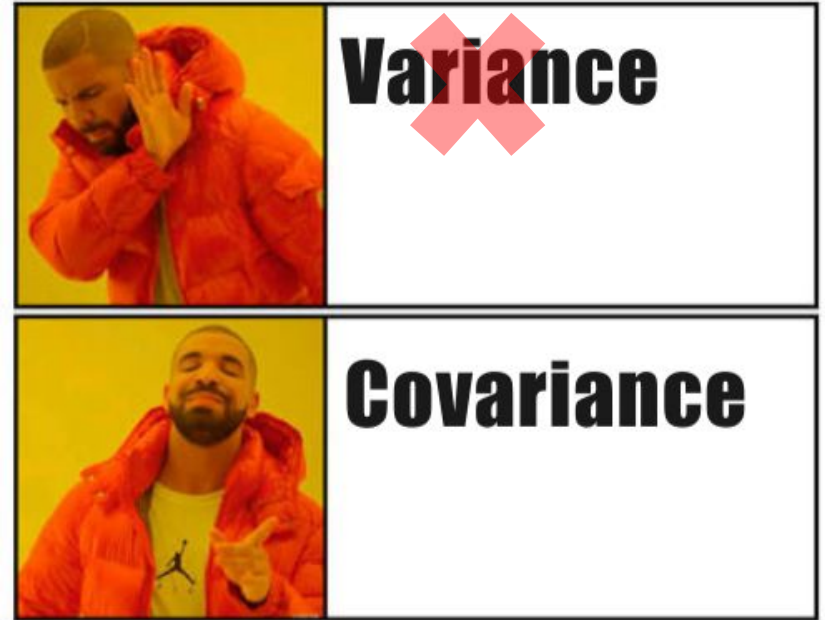
Conclusions

- Coexistence emerges from high-dimensional $E \times S$ interactions.
- Coexistence is obtained **without considering tight trade-offs**.
- High dimensional E does not mean a high number of resources (eg. light, water, nutrients).
- **E is high by nature:** [topography, soil, climate, resources] + [resources can be divided in bins (e.g. high/low light levels)].



Conclusions

- High dimensional $E \times S$ interactions can be modelled using a species covariance matrix.
- **To understand coexistence:** we should think in terms of **covariance** between individuals locally, not in terms of intraspecific variance (IV).



Conclusions

Preprint:

Clark J. S., A. T. Clark, B. Courbaud, C. Fortunel, C. Girard-Tercieux, G. Kunstler, I. Maréchaux, N. Rüger, and G. Vieilledent. A universal coexistence hypothesis resolves the biodiversity paradox: Species differences that generate diverse forests. *Authorea*: [au.166029509.96486640/v1](https://doi.org/10.21203/rs.3.rs-166029509.96486640/v1).

Testing the diagonal dominance in forests at the global scale



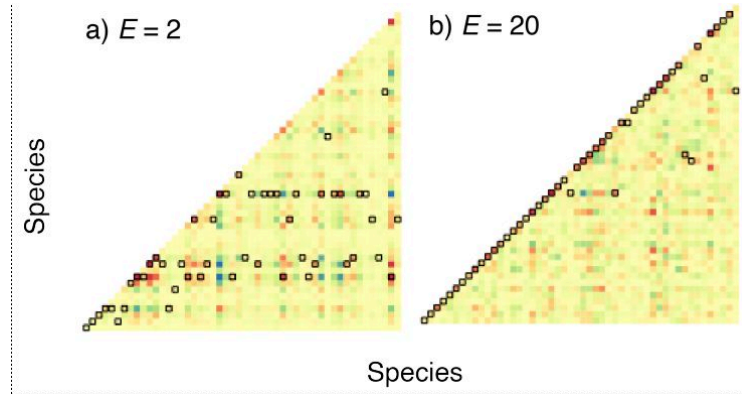
Objectives

Hypothesis

- Coexistence is obtained when there is diagonal dominance in the species covariance matrix, i.e. if intraspecific correlation $>$ interspecific correlation.

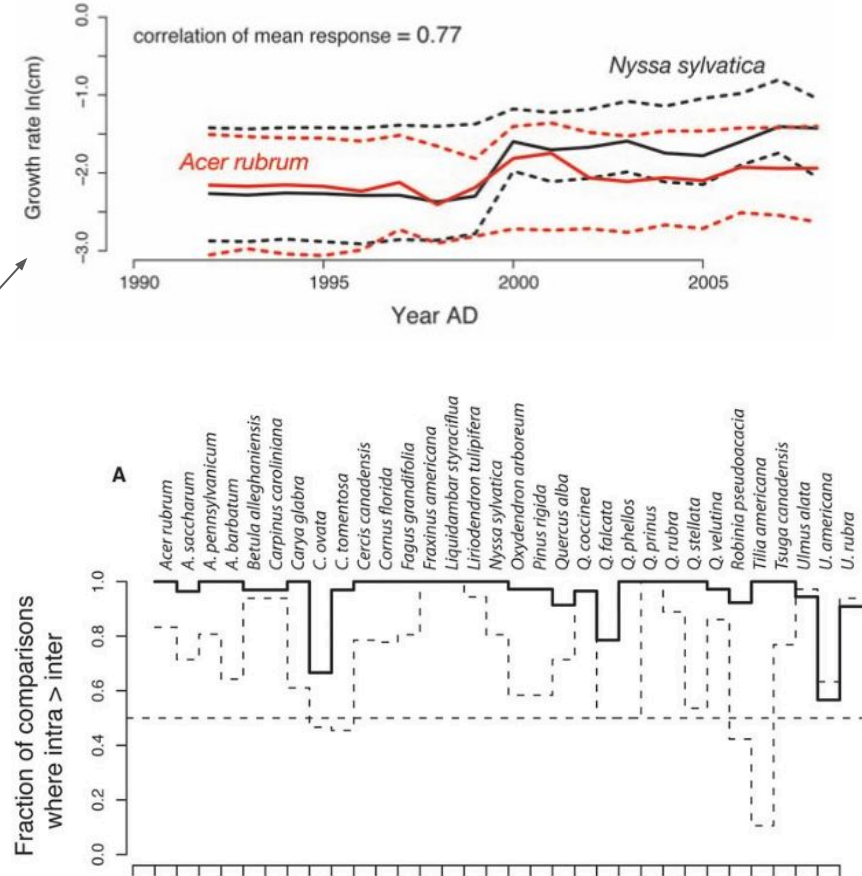
Question

- Is this true in forests at the global scale ?



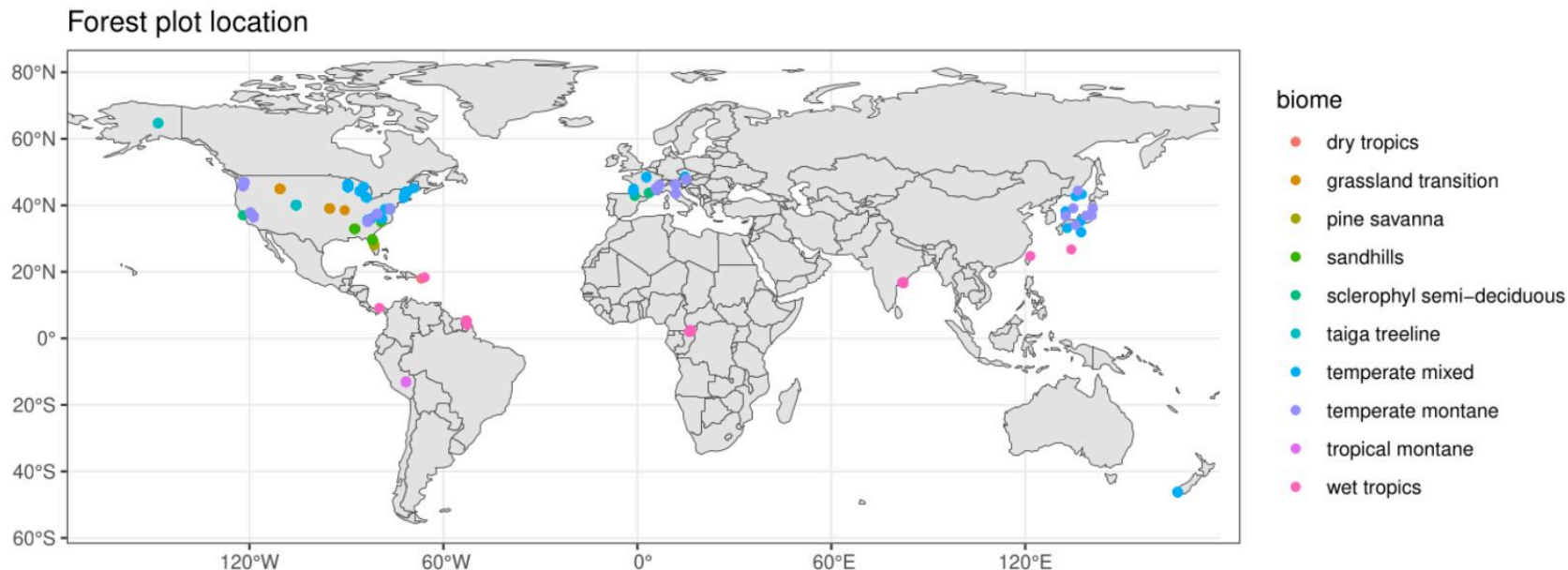
Objectives

- Partial answer for American temperate forests (Clark 2010, *Science*).
- Species tends to respond in the same direction to environmental change (eg. increase of growth with increase of light).
- **But** locally (on a same site) **intraspecific correlations** > **interspecific correlations**.



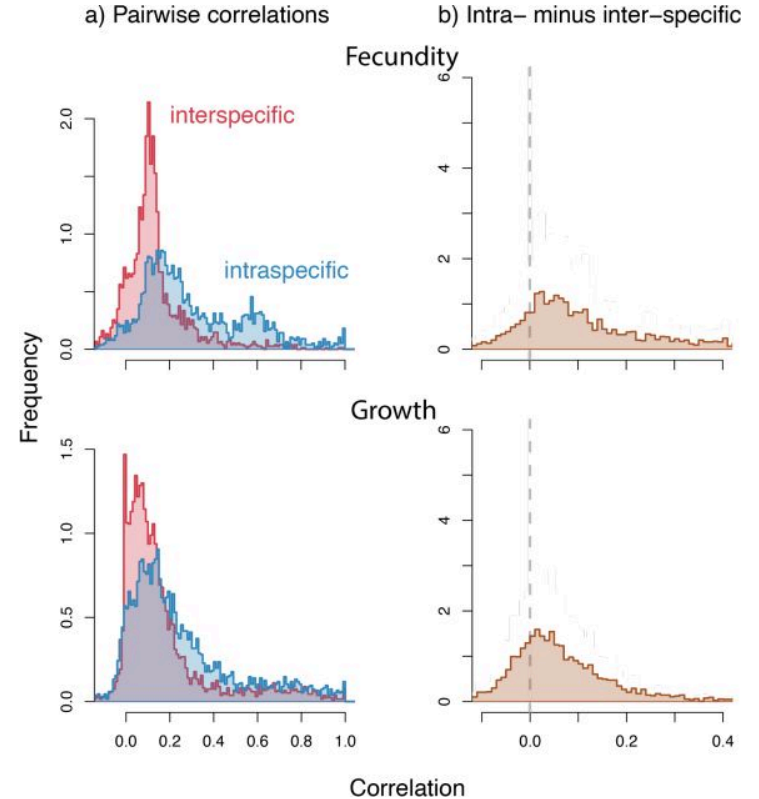
Methods

- Forest plot data with at least four consecutive inventories.
- In different forest biomes (**including tropical forests**) at the global scale.
- Comparing intra- vs inter-specific correlations for tree growth and fecundity.



Results

- All correlations were **positive**.
- For a high proportion of comparisons, **intraspecific correlations > interspecific correlations**.
- We observe in the data the diagonal dominance necessary for species coexistence.
- **Universal for all forest biomes** (although the magnitude of the difference differs between forests).



Towards realistic empirical community models generating diversity



Objectives

Context

- Empirical community models fitted on data (forest dynamics models, DGVMs) are not able to generate diversity without artefacts (seed rain, perfect trade-offs).
- Usually, diversity is not obtained because the number of environmental dimensions determining species demography is reduced.

Question

- **How to develop community models fitted on data that generate diversity while not having access to all environmental dimensions ?**

Methods

Inference

1. Fit a performance model at the individual level (eg. tree growth as a function of tree size and competition).
2. Compute a **residual species correlation matrix** from **residuals** of the demographic model.
3. Transform this species correlation matrix into a **species covariance matrix**.

Simulation

1. Transform the species covariance matrix into an **individual covariance matrix**.
2. Use this covariance matrix to **simulate individual performance** (eg.) tree growth = $f(\text{size, competition, species covariance})$.

Discussion

- **Work in progress.** We still need to implement such model.
- Such models would allow to test some hypothesis, scenarios (using the fixed part of the model), while **generating diversity** and **being realistic**.
- Simulations would account for both **species response to the environment** and **species correlations**, leading to more realistic and diverse communities.
- Off course, this approach do not prevent models to include **meaningful ecological processes in the fixed part**.






Thank you for your attention



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