Theory-Driven Analysis of Ecological Data

Day 3: Spatial data

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Outline of the day

Morning :

- **Introduction** : typical data? typical questions?
- **Part 1** : Descriptive approaches (aka statistical models)
- **Part 2** : Process-based approaches (aka mechanistic models)
- **Conclusion** : what's best, if anything?

Afternoon :

- **Practical:** simulating metacommunity data, fitting a patch occupancy model to infer competitive interactions

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Evening speaker : Davide Martinetti, INRAE, Avignon

"Predicting the risk of invasion of the Japanese beetle *Popillia japonica* in Europe".

What are ecological communities ?

A set of species occurring at the same place, at the same time

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Spatial boundaries can be arbitrary (study plots)

Plants on forest

Invertebrates in grassland

Corals on reefs

What are ecological communities ?

A set of species occurring at the same place, at the same time

Snails in ponds

Ants on islands

Flies on fruits

What are ecological communities ?

A set of species occurring at the same place, at the same time

Not restricted to one trophic level or resource use

Plants & herbivores on forest

Invertebrates & plants in grassland

Corals & fishes on reefs

The typical spatial dataset

The core thing

Species (S)

Sampling units

Community matrix

Presence/Absence
(Detection/Non Detection)

Abundance

Detection only

The typical spatial dataset

Additional data

The core thing

Species (S)

Sampling units (N)

Community matrix

Presence/Absence
(Detection/Non Detection)

Abundance

Detection only

Env. var. (P)

Sampling units (N)

Environmental variables

Coordinates

Sampling units (N)

Spatial positions

The typical spatial dataset

The core thing

Species (S)

Sampling units (N)

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Detection only

Env. var. (P)

Sampling units (N)

Environmental variables

Coordinates

Sampling units (N)

Spatial positions

Additional data

Species (S)

Species (S)

Phylogeny

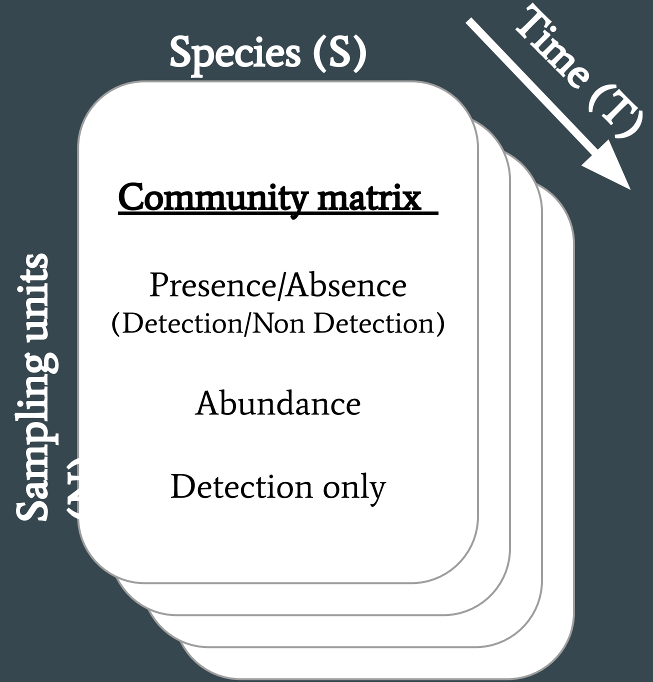
Traits (T)

Species (S)

Sp. traits

The typical spatial dataset

And observations can be repeated in time


Species (S)

Time (T)

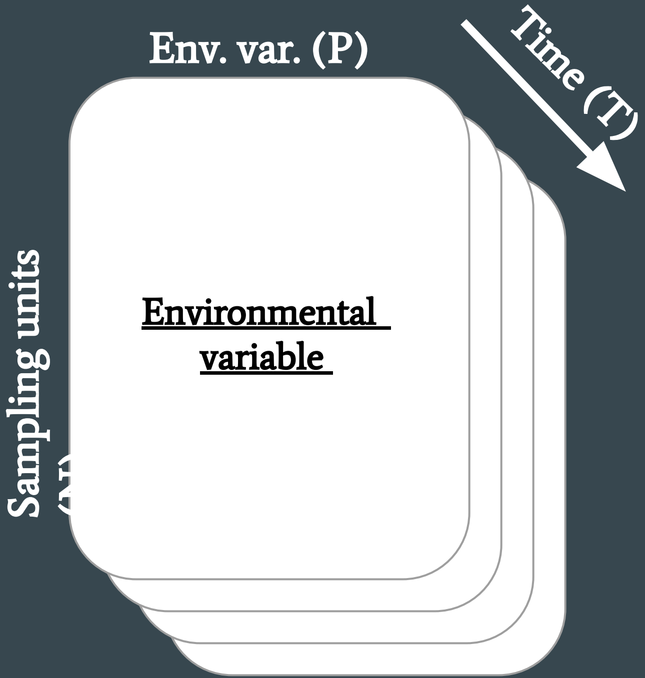
Sampling units

Community matrix

Presence/Absence
(Detection/Non Detection)

Abundance

Detection only


Env. var. (P)

Time (T)

Sampling units

Environmental variable

The typical spatial dataset

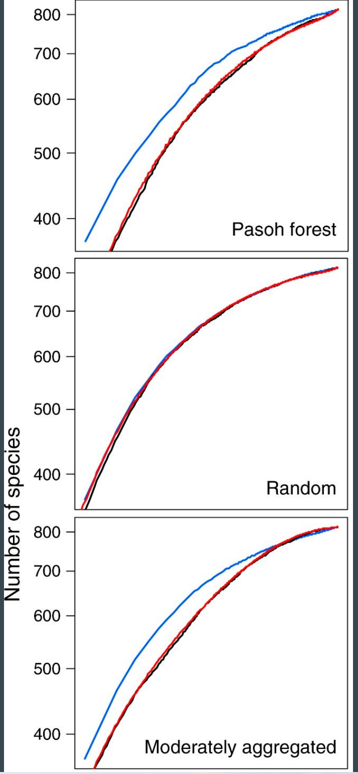
And observations can be repeated in time

Note: having temporally-repeated can greatly improve things

– we can avoid assumptions about system equilibrium (species dyn. and/or envt/species relationships)
– it can help identify interactions among species
– we can more properly account for species detection/non detection (short-term repeats)

The typical questions addressed

- Patterns of ecological diversity
  - Species-area relationships (SAR curves)
  - Distribution of species richnesses (α, γ)
  - How similar / dissimilar communities are? (β)



He & Hubbell. 2013


Pasoh Nature Reserve of Malaysia

The typical questions addressed

- Patterns of ecological diversity
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- Species distributions
    - Habitat preferences / specialization / generalism?
    - Are species interacting, and if so, how?
    - How important is dispersal versus habitat or competition?
    - How contingent is community assembly?
    - ... many more

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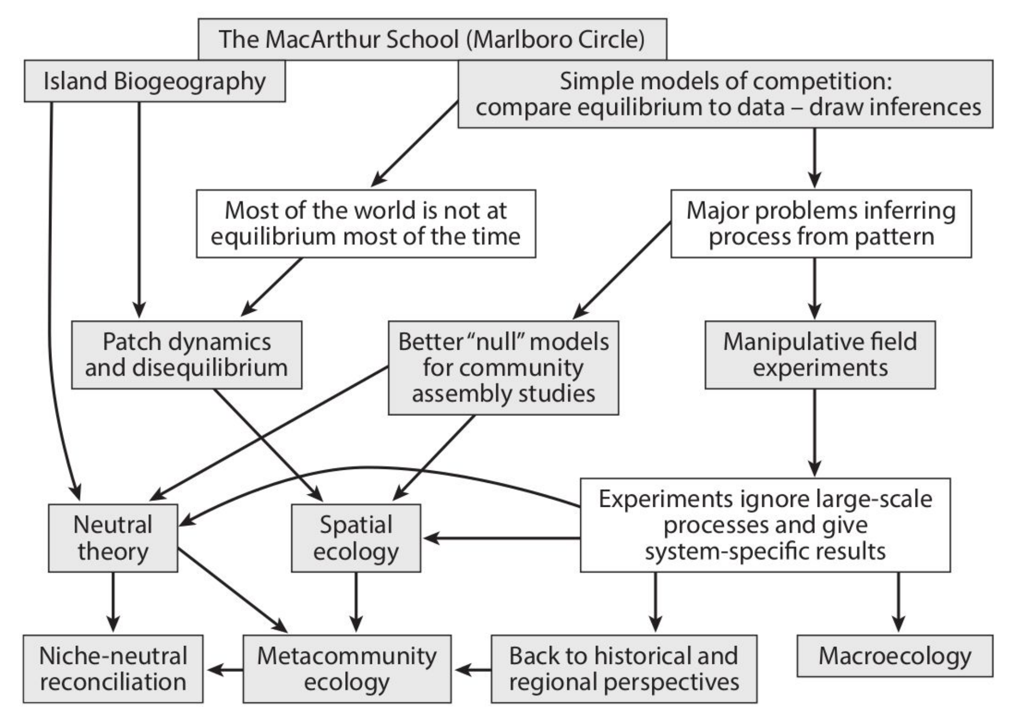
    - … many more

- **Theoretical frameworks to guide analyses?**

Theoretical frameworks

- We'll make a long story short...



Vellend 2016

Theoretical frameworks

A. The ‘assembly rules’ framework

Theoretical frameworks

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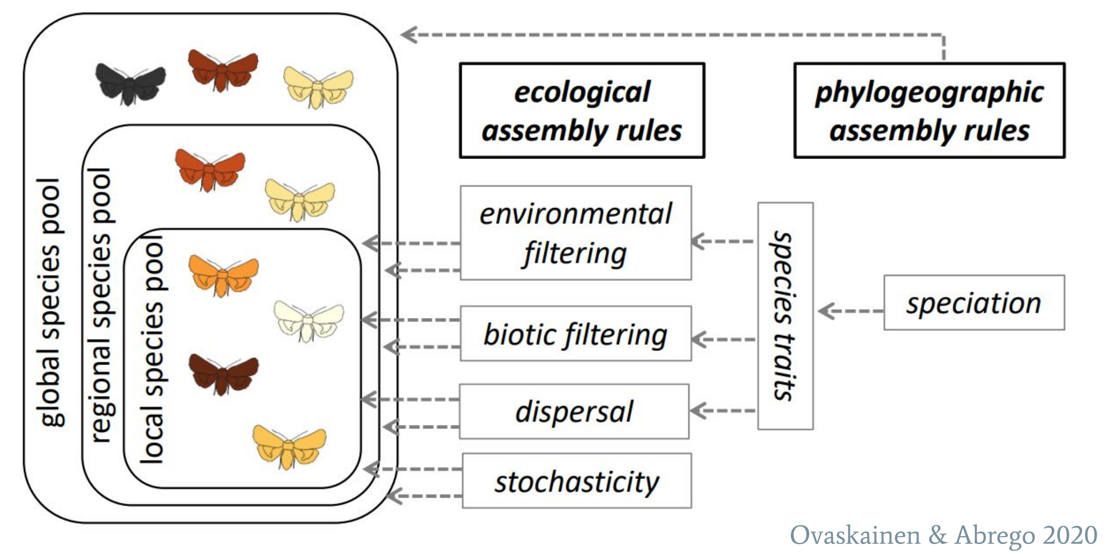
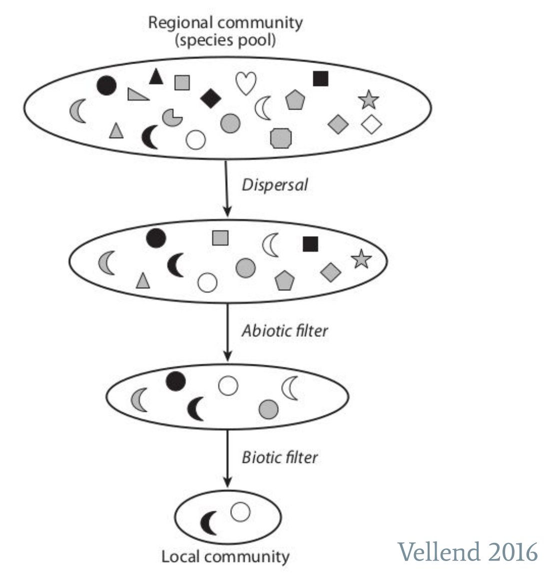


Ovaskainen & Abrego 2020



Vellend 2016

Theoretical frameworks

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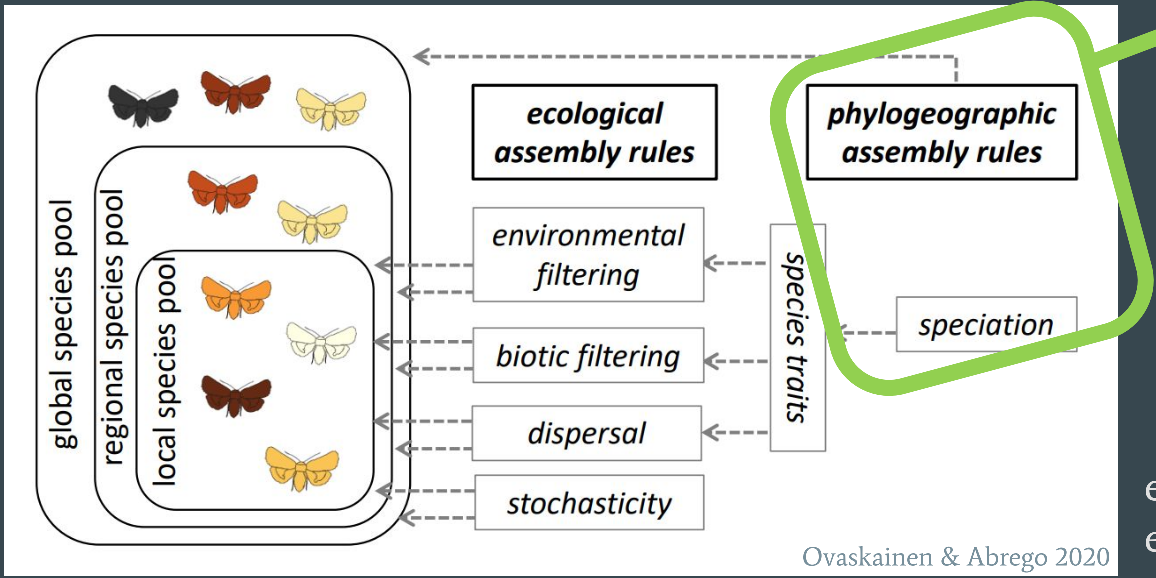


Ovaskainen & Abrego 2020

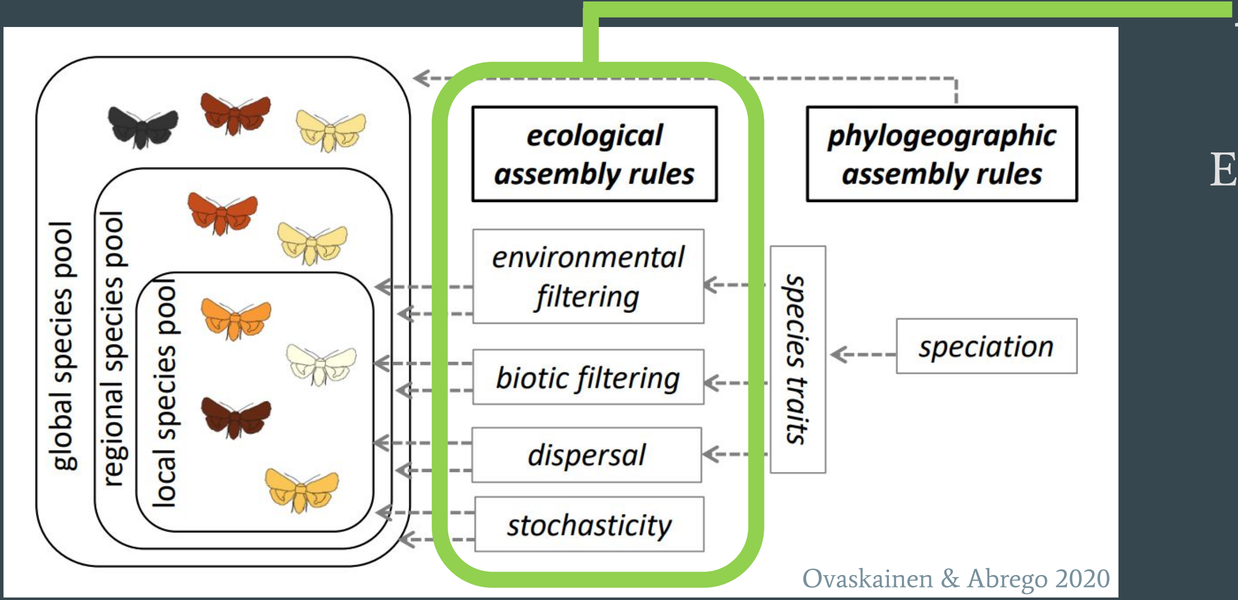
Historical contingencies
(large spatio-temporal scales)

Large-scale migrations
Geological events
Speciation
...

e.g. Great American Biotic Interchange
e.g. endemic/invasive species

Theoretical frameworks

A. The 'assembly rules' framework



Ovaskainen & Abrego 2020

Ecological filters
(smaller scales)

Environmental filtering
Biotic filtering

Niche

Dispersal
Stochasticity

Theoretical frameworks

A. The ‘assembly rules’ framework

- Strengths
    - Very intuitive and broadly applicable

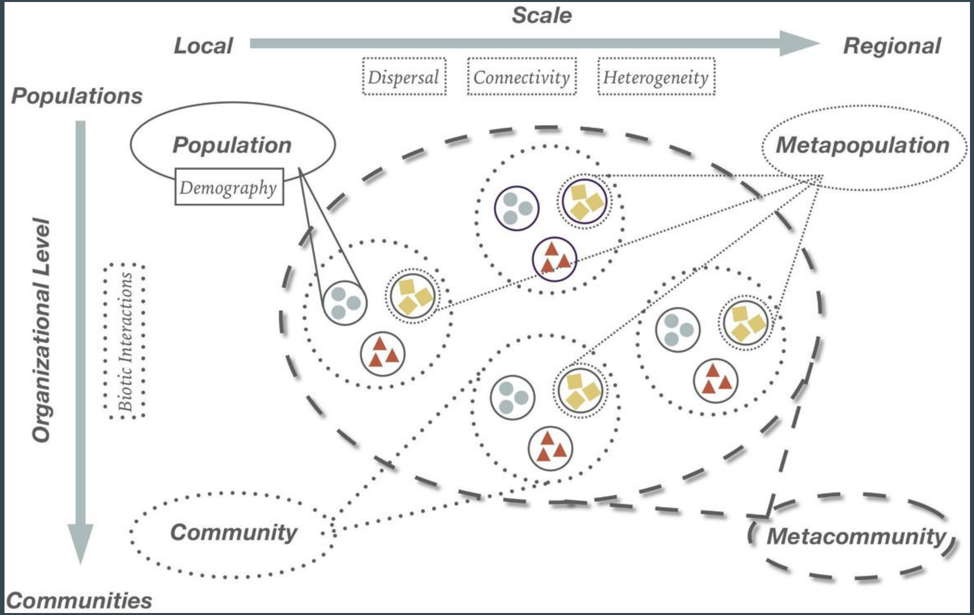
- Limitations
    - Mostly a static description, with a hierarchical set of filters
    - Focus on each individual site, not on the coupling between them

Theoretical frameworks

B. The metacommunity framework

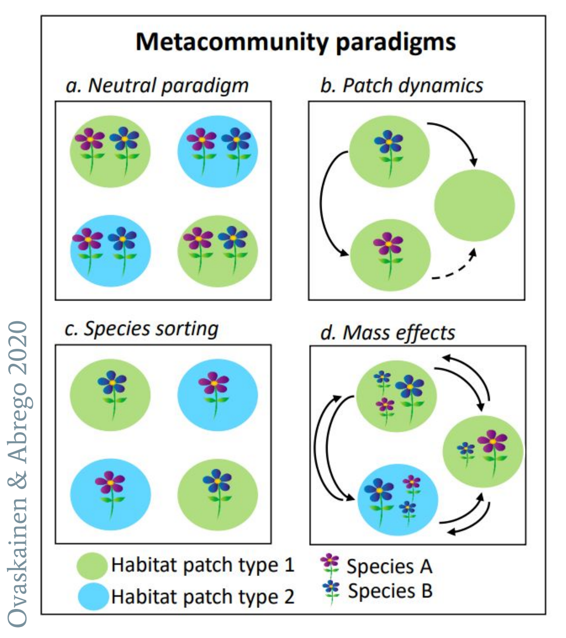
- A metacommunity is set of interconnected local communities
- Directly follows from the metapopulation paradigm

Chase et al 2020

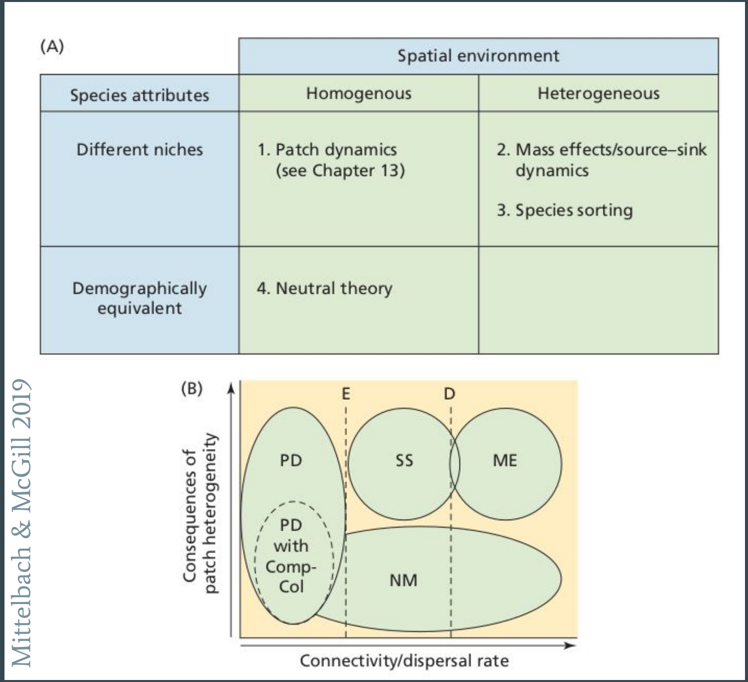


Theoretical frameworks

B. The metacommunity framework



Ovaskainen & Abrego 2020


(A)

	Spatial environment	
Species attributes	Homogenous	Heterogeneous
Different niches	1. Patch dynamics (see Chapter 13)	2. Mass effects/source–sink dynamics 3. Species sorting
Demographically equivalent	4. Neutral theory	

Mittelbach & McGill 2019

Theoretical frameworks

B. The metacommunity framework

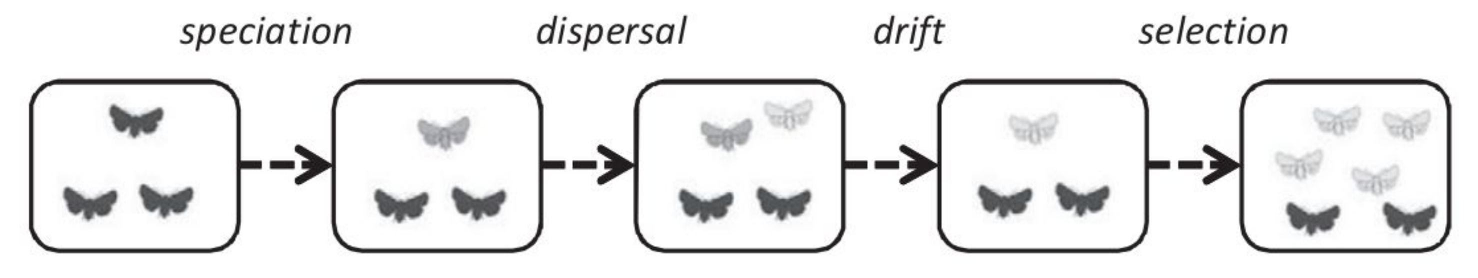
- Strengths
    - Emphasizes dynamical processes and the coupling of communities at different scales
    - Reunified niche, spatial and neutral perspectives

- Limitations
    - A collection of models that differ along many axes
    - The four paradigms are not mutually exclusive, and do not map to different processes. They are hard to disentangle

Theoretical frameworks

C. Vellends' theory of ecological communities

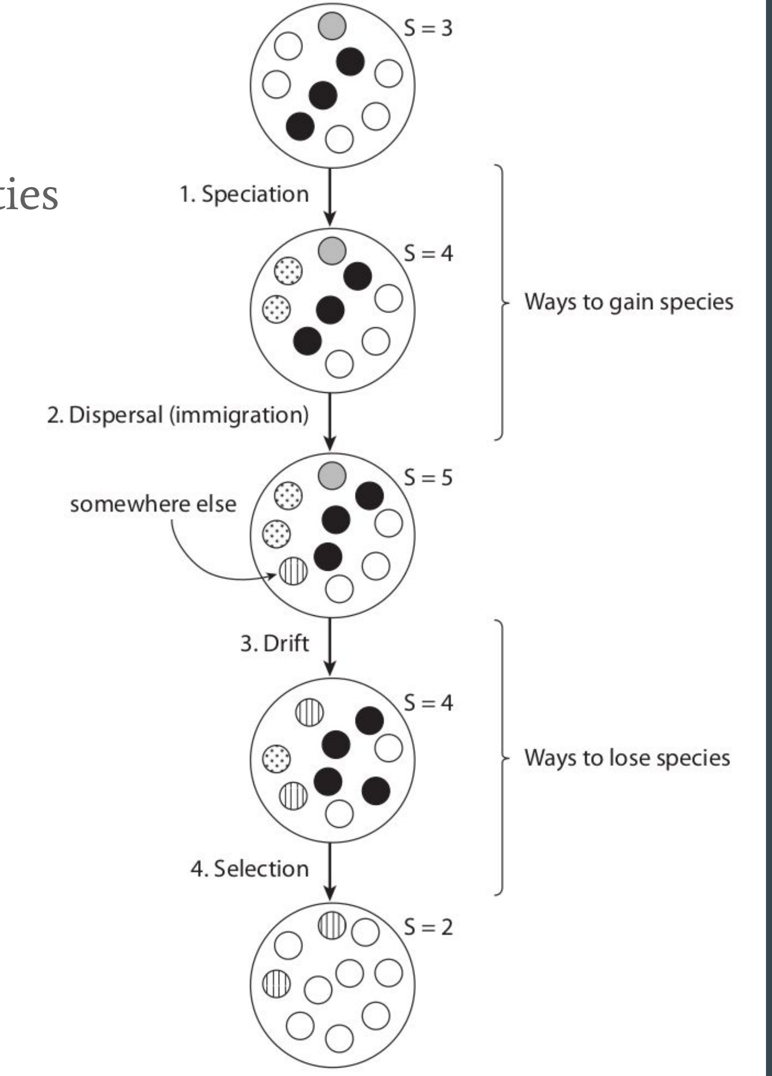
- Vellend's theory recycles the framework of population genetics (and its four evolutionary 'forces'):



Ovaskainen & Abrego 2020

Theoretical frameworks

C. Vellends' theory of ecological communities



Vellend 2016

Theoretical frameworks

C. Vellends’ theory of ecological communities

- Strengths
  - Emphasizes true and distinct dynamical processes
  - Proximity with population genetics and evolutionary theory
- Limitations
  - Order of the processes is arbitrary.
  - Speciation probably acts on a different timescale (same issue with Neutr
  - The theory is probably too abstract/generic to be very operational.

Go see
ttps://reflectionsonpaperspast.wordpress.c
m/2020/03/15/revisiting-vellend-2010/

Theory-driven data analysis

So, in practice: what analyses?

- Part 1: descriptive approaches (more related to assembly rules and metacommunity frameworks)

- Part 2: process-based approaches (more related to metacommunity and Vellend’s frameworks)

Bridge intro / part 1

- questions on Intro

Part 1. Descriptive approaches

- Statistical approaches (community level) - multivariate analyses (think PCA)

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    - (Unconstrained) ordination methods (CA, PCoA, MDMS)
      - multivariate similarity among species / patches,
      - main axis can be (linearly or not) linked to environmental gradients or traits *a posteriori*
    - (Constrained) ordination methods (CCA, RDA, dbRDA, ...)
      - environmental data / spatial positions are incorporated to constrained the ordination
      - variance can be partitioned among multiple explicative tables (e.g. envt vs. space)

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Based on the notion of a distances among sampling units / species.

Numerous (dis)similarity measures: Euclidean, Bray-Curtis, Chi Square or Euclidean dist. on transformed data (Profiles, Hellinger, ...)
Numerous ways of representing space: spatial neighborhood, spat. weighting matrices (SWM), spatial predictors (orth. polynomials of coordinates, PCNMs, MEMs, etc.)

Part 1. Descriptive approaches

e.g. Guadeloupe Mollusks

D. surinamense

P. columella (1997)

M. cornuarietis (1973)

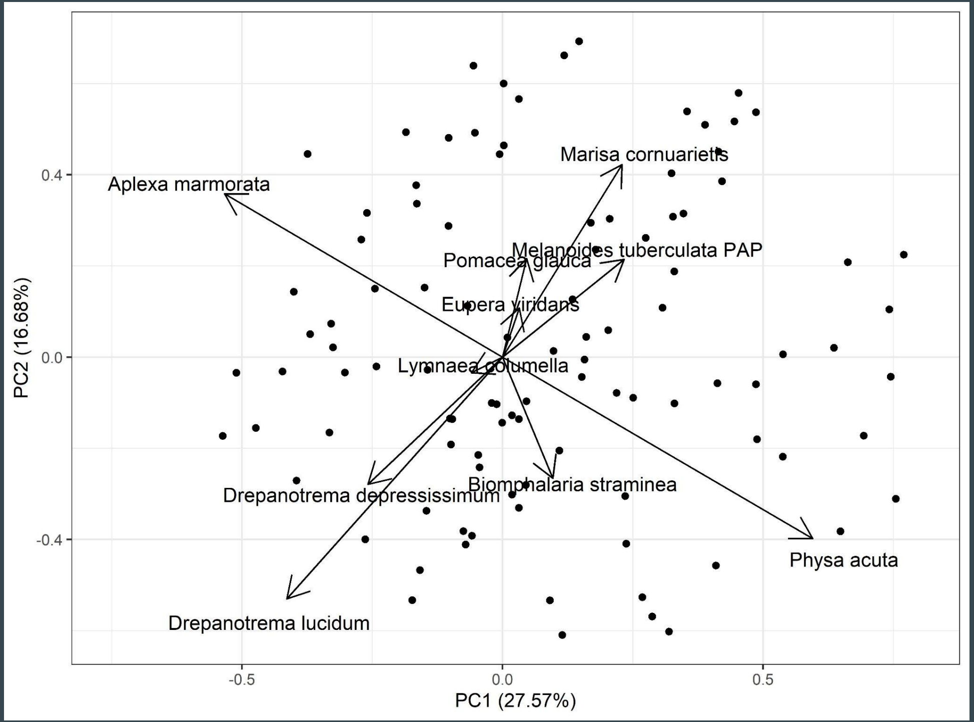
M. tuberculata (1979)

P. glauca

P. acuta (1972)

Part 1. Descriptive approaches

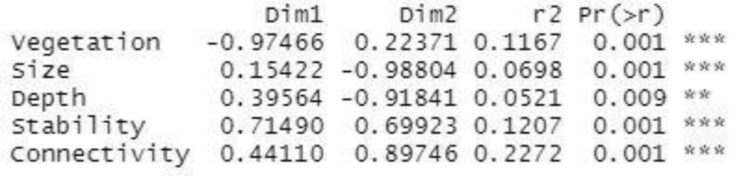
e.g. Guadeloupe Mollusks: unconstrained (PCoA)



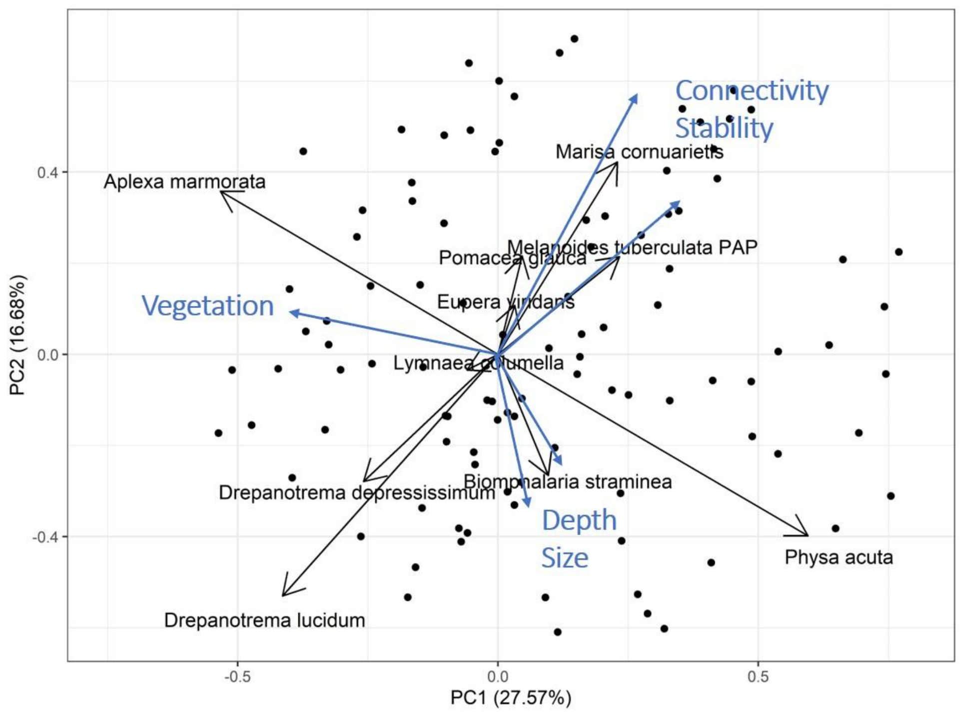
Part 1. Descriptive approaches

e.g. Guadeloupe Mollusks: unconstrained (PCoA)

A posteriori environmental fit

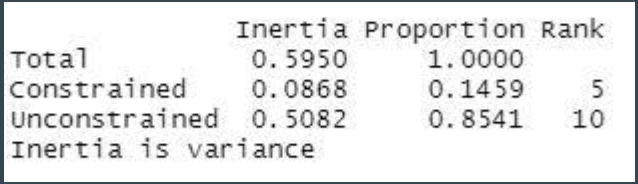


```
                  Dim1      Dim2     r2 Pr(>r)    
Vegetation    -0.97466   0.22371 0.1167  0.001 ***
Size           0.15422  -0.98804 0.0698  0.001 ***
Depth          0.39564  -0.91841 0.0521  0.009 ** 
Stability      0.71490   0.69923 0.1207  0.001 ***
Connectivity   0.44110   0.89746 0.2272  0.001 ***
```

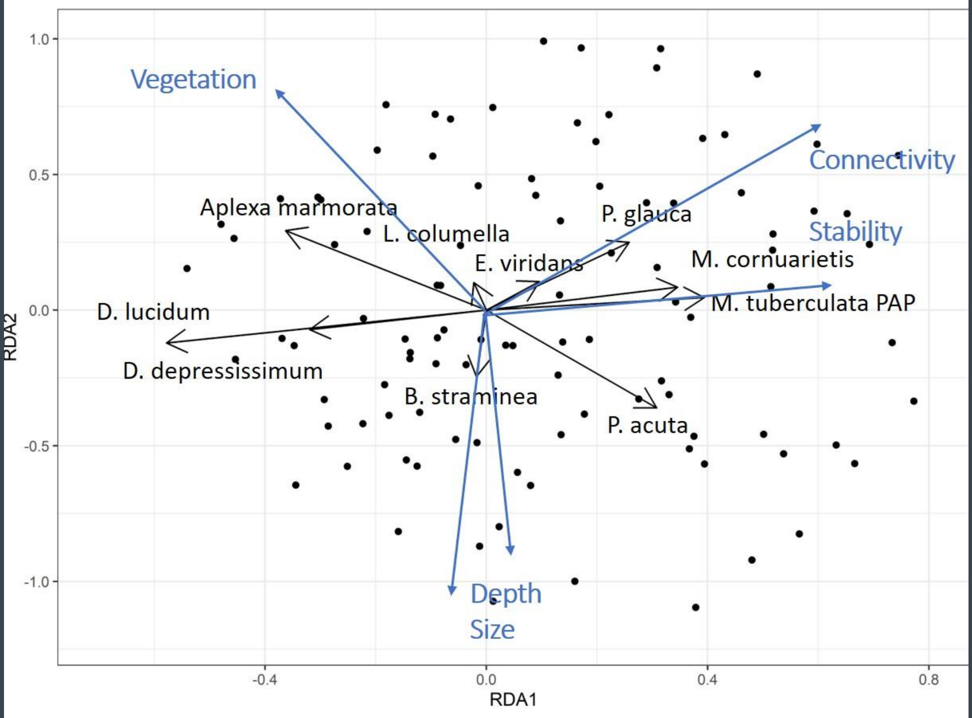


Part 1. Descriptive approaches

e.g. Guadeloupe Mollusks: RDA (constrained)



```
               Inertia Proportion Rank
Total           0.5950     1.0000
Constrained     0.0868     0.1459    5
Unconstrained   0.5082     0.8541   10
Inertia is variance
```



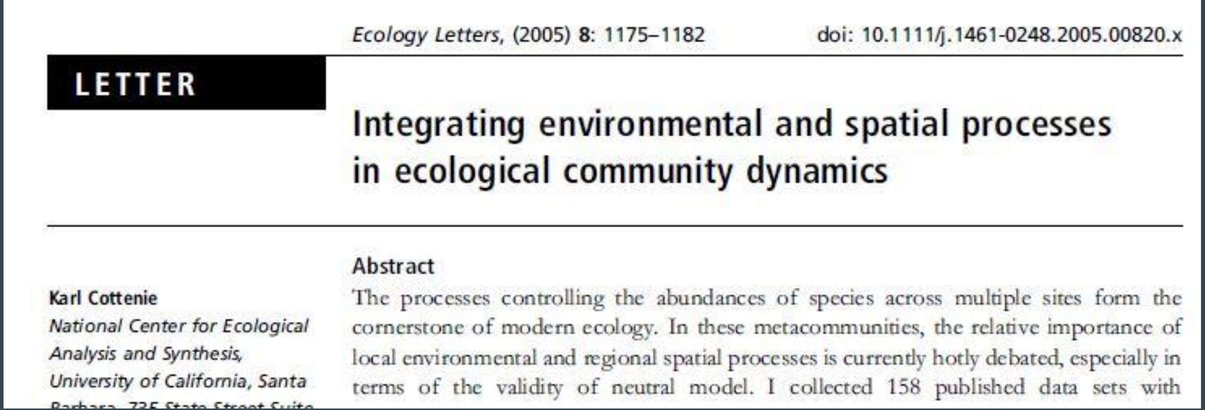
Part 1. Descriptive approaches

e.g. Guadeloupe Mollusks: partial-RDA & **variance partitioning** with PCNMs

Widely used after Cottenie (2005) publication

the idea, partitioning variance between environmental and spatial predictors

as a way to distinguish whether communities result from niche-based or neutral-based processes...



Ecology Letters, (2005) **8**: 1175–1182 doi: 10.1111/j.1461-0248.2005.00820.x

LETTER

Integrating environmental and spatial processes in ecological community dynamics

Karl Cottenie
National Center for Ecological Analysis and Synthesis, University of California, Santa

Abstract

The processes controlling the abundances of species across multiple sites form the cornerstone of modern ecology. In these metacommunities, the relative importance of local environmental and regional spatial processes is currently hotly debated, especially in terms of the validity of neutral model. I collected 158 published data sets with

Part 1. Descriptive approaches

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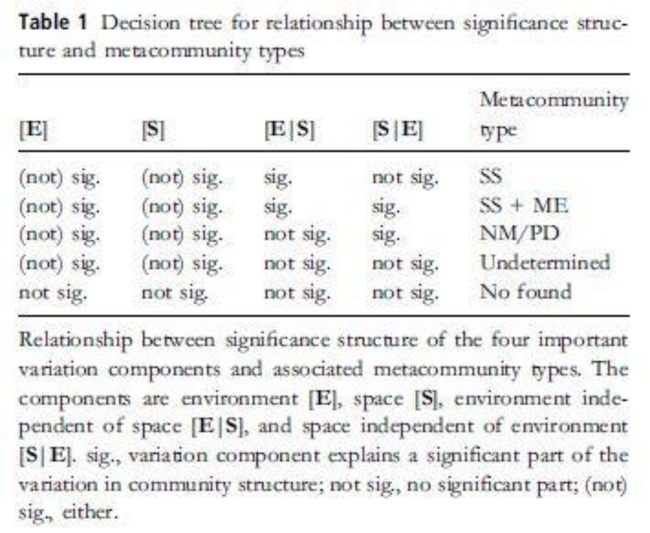


Table 1 Decision tree for relationship between significance structure and metacommunity types

[E]	[S]	[E|S]	[S|E]	Metacommunity type
(not) sig.	(not) sig.	sig.	not sig.	SS
(not) sig.	(not) sig.	sig.	sig.	SS + ME
(not) sig.	(not) sig.	not sig.	sig.	NM/PD
(not) sig.	(not) sig.	not sig.	not sig.	Undetermined
not sig.	not sig.	not sig.	not sig.	No found

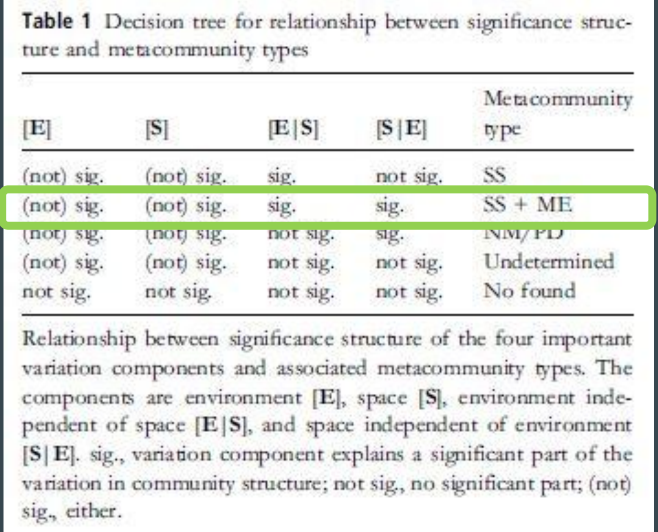
Relationship between significance structure of the four important variation components and associated metacommunity types. The components are environment [E], space [S], environment independent of space [E|S], and space independent of environment [S|E]. sig., variation component explains a significant part of the variation in community structure; not sig., no significant part; (not) sig., either.

Deeply rooted in the metacommunity framework

Part 1. Descriptive approaches

e.g. Guadeloupe Mollusks, partial-RDA & **variance partitioning** with PCNMs

Using Principal Coordinates of Neighbourhood Matrix (PCNM, Borcard & Legendre, 2002) as spatial descriptors



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[E]	[S]	[E|S]	[S|E]	Metacommunity type
(not) sig.	(not) sig.	sig.	not sig.	SS
(not) sig.	(not) sig.	sig.	sig.	SS + ME
(not) sig.	(not) sig.	not sig.	sig.	NM/PD
(not) sig.	(not) sig.	not sig.	not sig.	Undetermined
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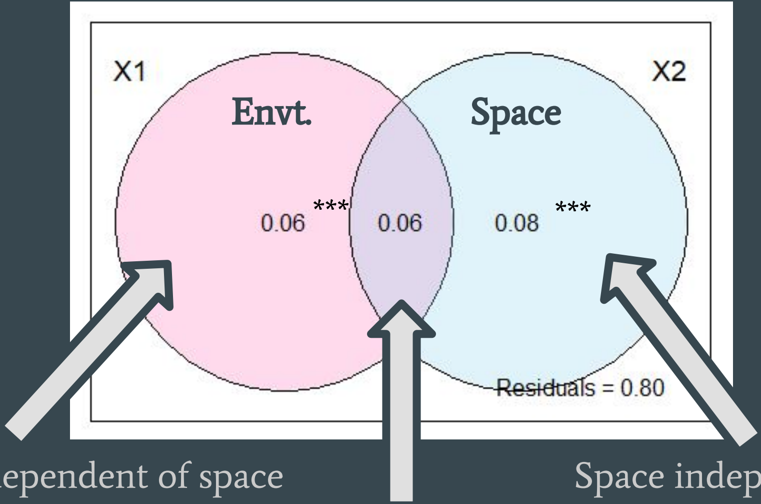

Envt. independent of space

Space independent of envt.

Spatially autocorrelated envt. gradient

Part 1. Descriptive approaches

- Statistical approaches (community level) - multivariate analyses
  - Among distance matrices regressions
    - Mantel and partial Mantel tests
    - MRM (Lichstein, 2007)

Might be better suited for testing some theories (e.g. Neutral Theory),
See Tuomisto & Ruokolainen, 2006.

But ... see also Tuomisto, Ruokolainen & Ruokolainen, 2012.

Part 1. Descriptive approaches

- Statistical approaches (species level)

Rationale : species that do not interact and have the same habitat affiliations should be distributed **independently** over sites*.

*Think it through

Part 1. Descriptive approaches

- Statistical approaches (species level)
    - Fitting null distributions, pairwise tests of species independence (Forbes 1907, Veech et al . 2013)

	species 1 present	species 1 absent
species 2 present	a	c
species 2 absent	b	d

Number of sites

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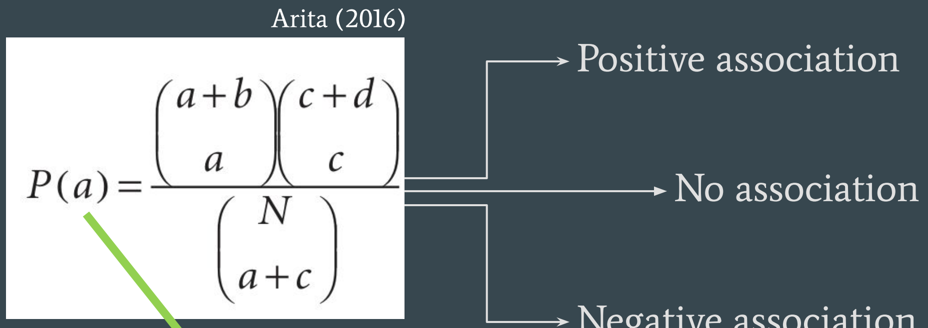

Arita (2016)

$$P(a) = \frac{\binom{a+b}{a}\binom{c+d}{c}}{\binom{N}{a+c}}$$

Expected number of co-occurrences (if independent)

Part 1. Descriptive approaches

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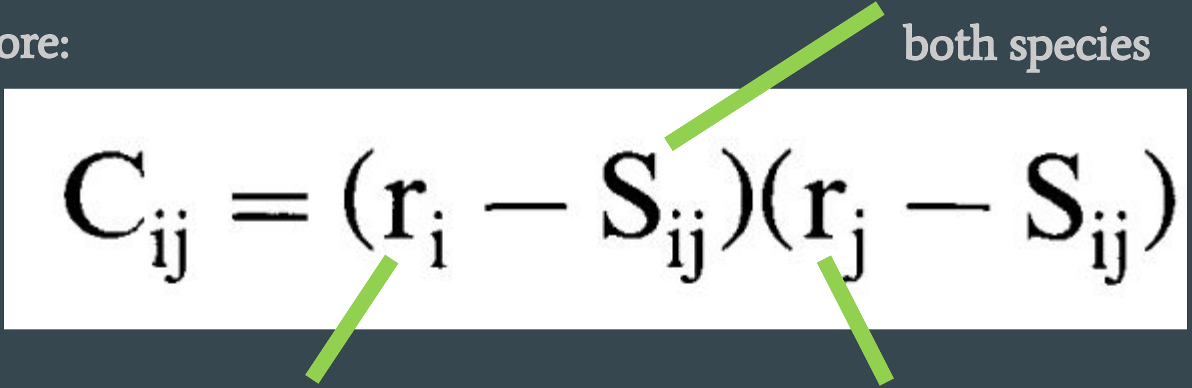
The C-score:



$$C_{ij} = (r_i - S_{ij})(r_j - S_{ij})$$

Number of sites with both species

Number of sites with species i

Number of sites with species j

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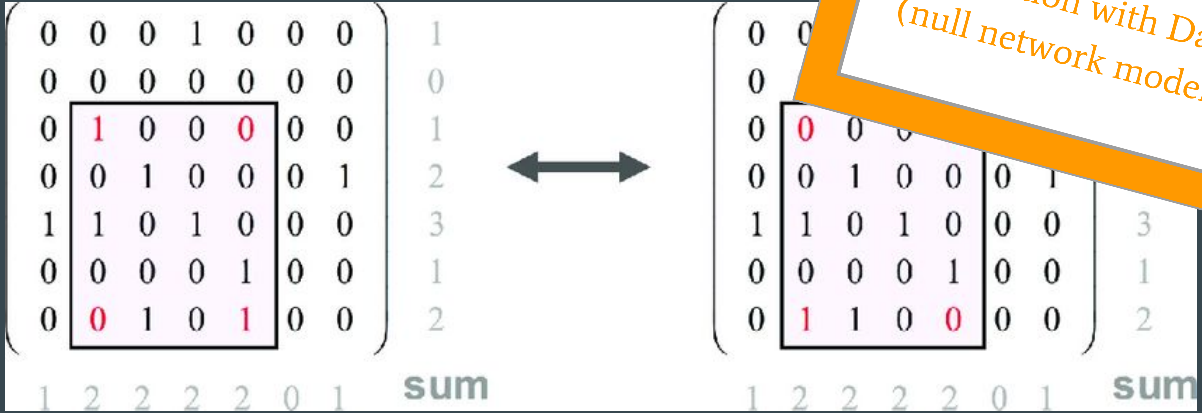
Reshuffle the matrix many times (fixed-fixed swap algorithm):



Connection with Day 4 (null network models)

Part 1. Descriptive approaches

- Statistical approaches (species level)
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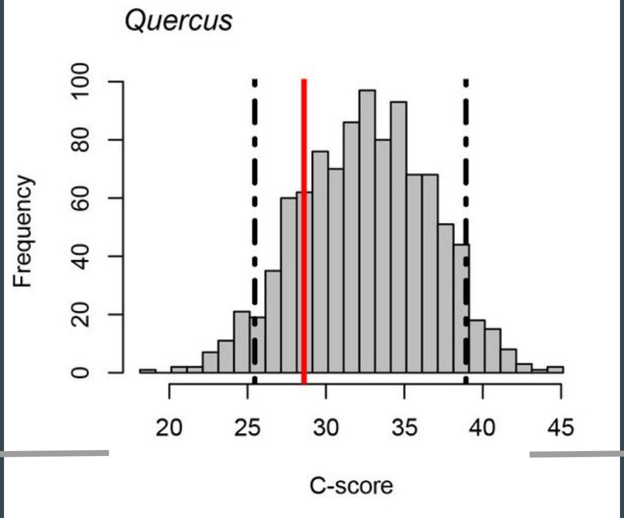
Generate null distribution for C_{ij} and decide significance and standardized effect size:



Positive association

Negative association

Part 1. Descriptive approaches

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    - Extension to constrained null models by Peres Neto et al (2001)

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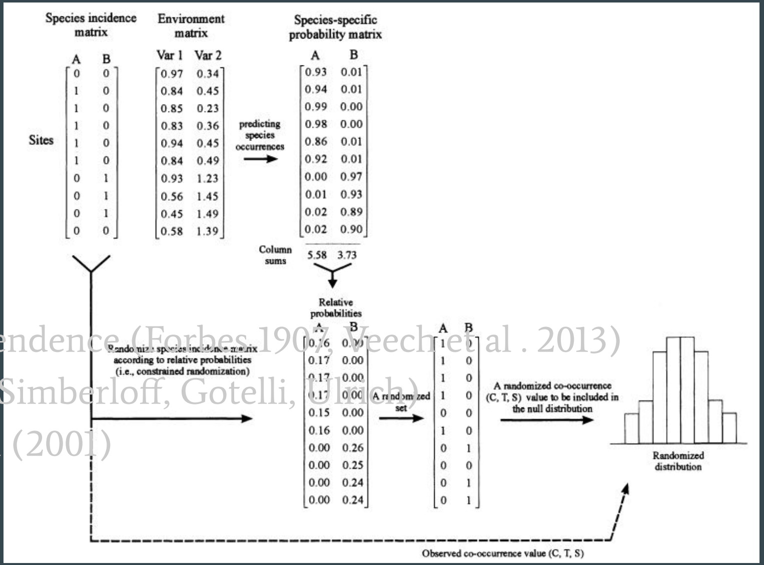

Species incidence matrix

A	B
0	0
1	0
1	0
1	0
1	0
1	0
0	1
0	1
0	1
0	0

Environment matrix

Var 1	Var 2
0.97	0.34
0.84	0.45
0.85	0.23
0.83	0.36
0.94	0.45
0.84	0.49
0.93	1.23
0.56	1.45
0.45	1.49
0.58	1.39

Species-specific probability matrix

A	B
0.93	0.01
0.94	0.01
0.99	0.00
0.98	0.00
0.86	0.01
0.92	0.01
0.00	0.97
0.01	0.93
0.02	0.89
0.02	0.90
5.58	3.73

Relative probabilities

A	B
0.16	0.00
0.17	0.00
0.17	0.00
0.17	0.00
0.15	0.00
0.16	0.00
0.00	0.26
0.00	0.25
0.00	0.24
0.00	0.24

A randomized set

A	B
1	0
1	0
1	0
1	0
0	0
1	0
0	1
0	0
0	1
0	1

Peres Neto et aL. 2001

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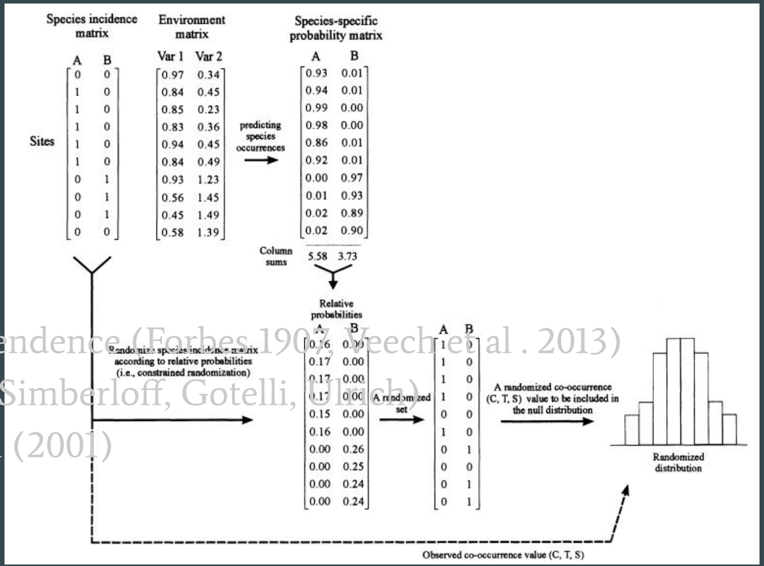
  - Extension to constrained null models by Peres Neto et al (2001)

Peres Neto et aL. 2001



$$\begin{array}{cc} A & B \\ 0 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 1 \\ 0 & 1 \\ 0 & 0 \end{array} \quad \begin{array}{cc} \text{Var 1} & \text{Var 2} \\ 0.97 & 0.34 \\ 0.84 & 0.45 \\ 0.85 & 0.23 \\ 0.83 & 0.36 \\ 0.94 & 0.45 \\ 0.84 & 0.49 \\ 0.93 & 1.23 \\ 0.56 & 1.45 \\ 0.45 & 1.49 \\ 0.58 & 1.39 \end{array} \quad \begin{array}{cc} A & B \\ 0.93 & 0.01 \\ 0.94 & 0.01 \\ 0.99 & 0.00 \\ 0.98 & 0.00 \\ 0.86 & 0.01 \\ 0.92 & 0.01 \\ 0.00 & 0.97 \\ 0.01 & 0.93 \\ 0.02 & 0.89 \\ 0.02 & 0.90 \\ \hline 5.58 & 3.73 \end{array}$$

$$\begin{array}{cc} A & B \\ 0.16 & 0.00 \\ 0.17 & 0.00 \\ 0.17 & 0.00 \\ 0.17 & 0.00 \\ 0.15 & 0.00 \\ 0.16 & 0.00 \\ 0.00 & 0.26 \\ 0.00 & 0.25 \\ 0.00 & 0.24 \\ 0.00 & 0.24 \end{array} \quad \begin{array}{cc} A & B \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 1 & 0 \\ 0 & 0 \\ 1 & 0 \\ 0 & 1 \\ 0 & 0 \\ 0 & 1 \\ 0 & 1 \end{array}$$

Salticus scenicus @wikipedia

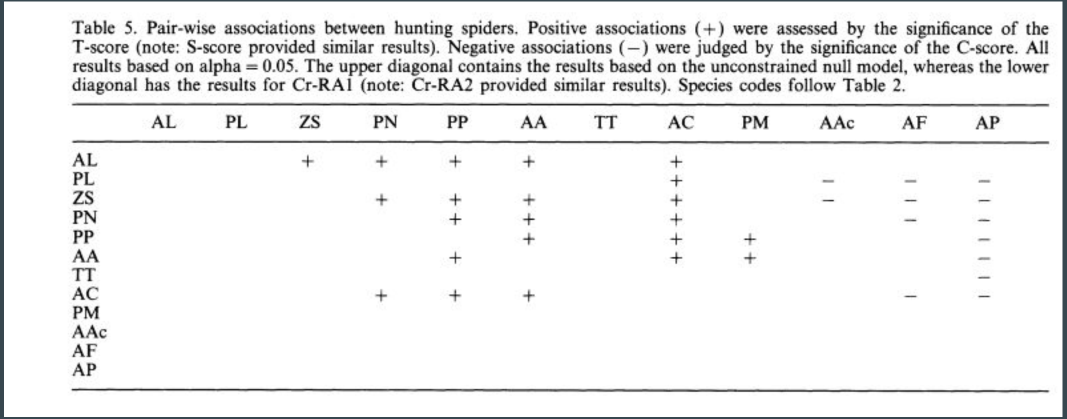


Table 5. Pair-wise associations between hunting spiders. Positive associations (+) were assessed by the significance of the T-score (note: S-score provided similar results). Negative associations (−) were judged by the significance of the C-score. All results based on alpha = 0.05. The upper diagonal contains the results based on the unconstrained null model, whereas the lower diagonal has the results for Cr-RA1 (note: Cr-RA2 provided similar results). Species codes follow Table 2.

	AL	PL	ZS	PN	PP	AA	TT	AC	PM	AAc	AF	AP
AL			+	+	+	+		+				
PL								+		−	−	−
ZS				+	+	+		+		−	−	−
PN					+	+		+			−	−
PP						+		+	+			−
AA					+			+	+			−
TT												−
AC				+	+	+					−	−
PM												
AAc												
AF												
AP												

Part 1. Descriptive approaches

- Statistical approaches (species level)
    - (Joint) Species Distribution Modelling
    - Occupancy models (emphasis on detection process)

Part 1. Descriptive approaches

- Statistical approaches (species level): Species Distribution Models (SDM)
  - From a theoretical viewpoint : they catch the ‘realized niche’ of one species through regression or a broad range of statistical/classification methods
  - **Main aim : making predictions - on past, contemporary, and future sp. distributions**
  - Have been criticized regarding the lack of consideration for :
    - equilibrium assumption (species are wherever they can) (Araújo & Pearson, 2005)
    - dispersal, dispersal limitation in particular
    - species interactions (but see Anderson, 2017, JoB)
    - but also sampling, methods, model transferability…

Part 1. Descriptive approaches

- Statistical approaches (species level): Species Distribution Models (SDM)

A **lot** of methods...

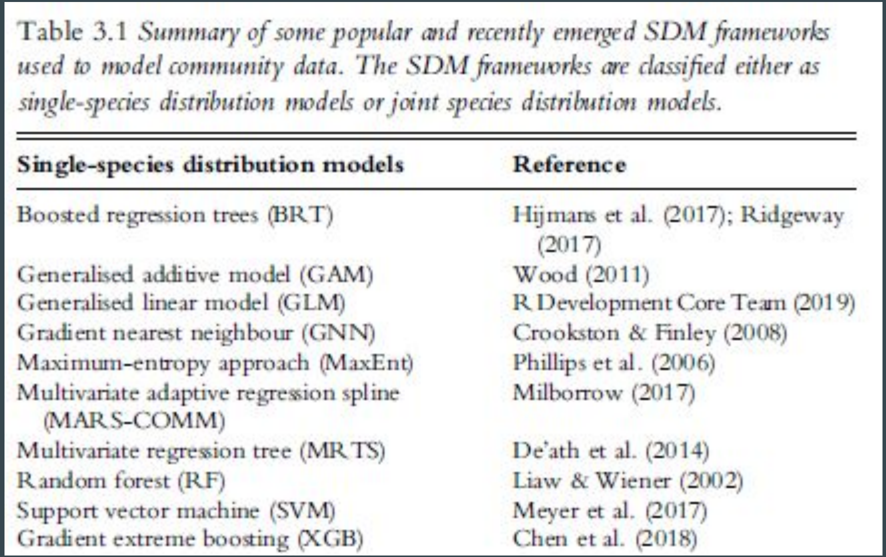


Table 3.1 *Summary of some popular and recently emerged SDM frameworks used to model community data. The SDM frameworks are classified either as single-species distribution models or joint species distribution models.*

Single-species distribution models	**Reference**
Boosted regression trees (BRT)	Hijmans et al. (2017); Ridgeway (2017)
Generalised additive model (GAM)	Wood (2011)
Generalised linear model (GLM)	R Development Core Team (2019)
Gradient nearest neighbour (GNN)	Crookston & Finley (2008)
Maximum-entropy approach (MaxEnt)	Phillips et al. (2006)
Multivariate adaptive regression spline (MARS-COMM)	Milborrow (2017)
Multivariate regression tree (MRTS)	De'ath et al. (2014)
Random forest (RF)	Liaw & Wiener (2002)
Support vector machine (SVM)	Meyer et al. (2017)
Gradient extreme boosting (XGB)	Chen et al. (2018)

From Ovaskainen & Abrego, 2020

Part 1. Descriptive approaches

- Statistical approaches (species level): Species Distribution Models (SDM)

With several species:

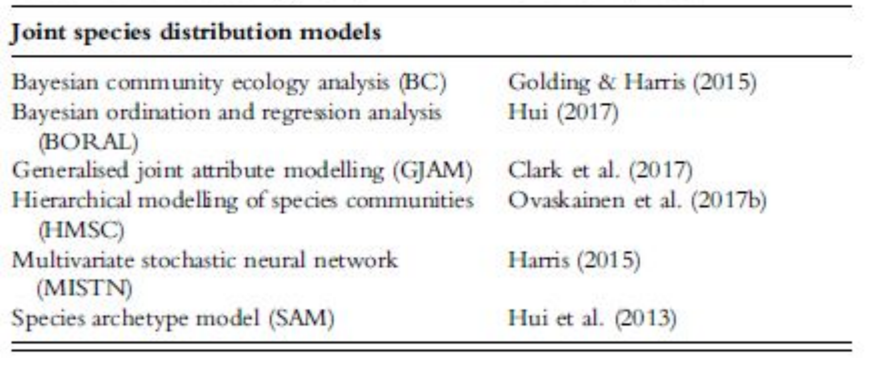
- One SDM per species, then combine —> **Stacked** SDMs
- SDM for all species at the same time —> **Joint** SDMs (JSDMs)

Think: several point estimates of means *versus* one ANOVA

Part 1. Descriptive approaches

- Statistical approaches (species level): Species Distribution Models (SDM)

Even more methods...



Joint species distribution models	
Bayesian community ecology analysis (BC)	Golding & Harris (2015)
Bayesian ordination and regression analysis (BORAL)	Hui (2017)
Generalised joint attribute modelling (GJAM)	Clark et al. (2017)
Hierarchical modelling of species communities (HMSC)	Ovaskainen et al. (2017b)
Multivariate stochastic neural network (MISTN)	Harris (2015)
Species archetype model (SAM)	Hui et al. (2013)

From Ovaskainen & Abrego, 2020

Part 1. Descriptive approaches

- JSDMs: one relatively simple and flexible approach
  - **Hierarchical Models of Species Composition** (HMSC) - Ovaskainen et al. (2017)

  - Bayesian framework
  - Several latent factors (random effects)
  - Species occupancies + habitat variables + species traits + Phylogeny + ….

Part 1. Descriptive approaches

- JSDMs: one relatively simple and flexible approach
  - **Hierarchical Models of Species Composition** (HMSC) - Ovaskainen et al. (2017)

New Results

🔔 Follow this preprint

Accelerating joint species distribution modeling with Hmsc-HPC: A 1000x faster GPU deployment

Anis Ur Rahman, Gleb Tikhonov, Jari Oksanen, Tuomas Rossi, Otso Ovaskainen

doi: https://doi.org/10.1101/2024.02.13.580046

This article is a preprint and has not been certified by peer review [what does this mean?].

Nice R package, nice book,

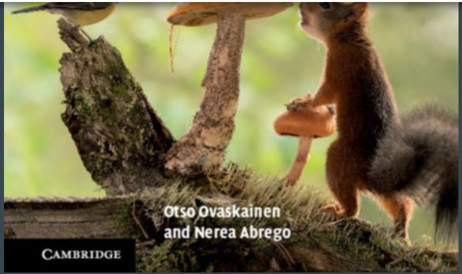
Methods in Ecology and E

APPLICATION | Open Access

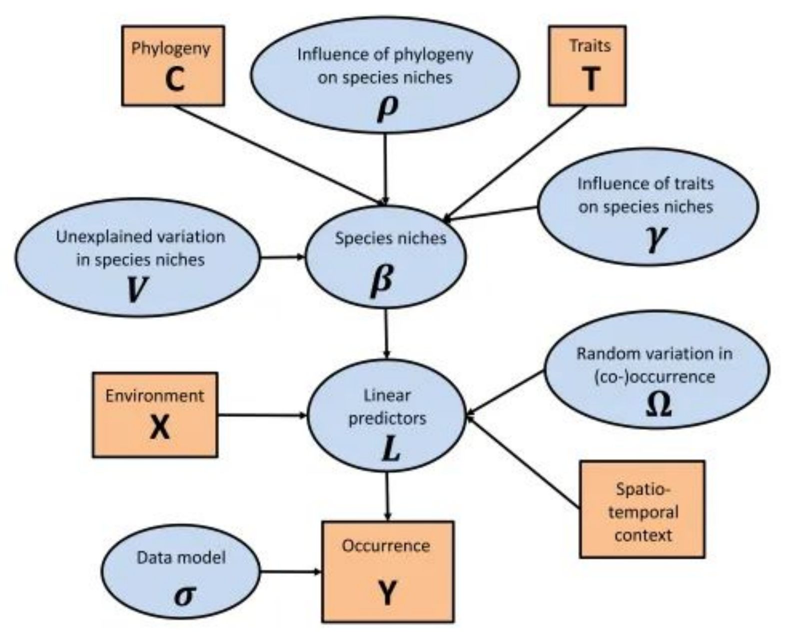
Joint species distribution modelling with the R-package HMSC

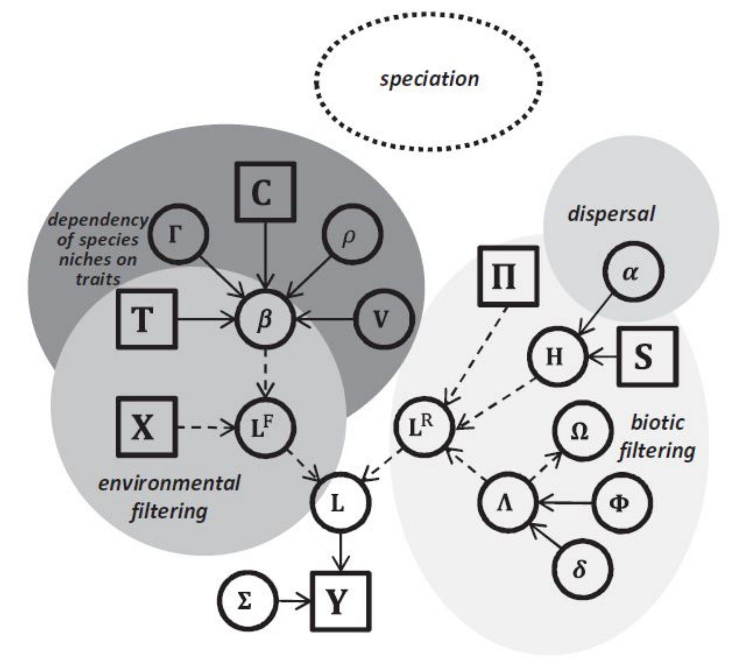
Gleb Tikhonov, Øystein H. Opedal, Nerea Abrego, Aleksi Lehikoinen, Melinda M. J. de Jonge, Jari Oksanen, Otso Ovaskainen

First published: 25 December 2019 | https://doi.org/10.1111/2041-210X.13345 | Citations: 5

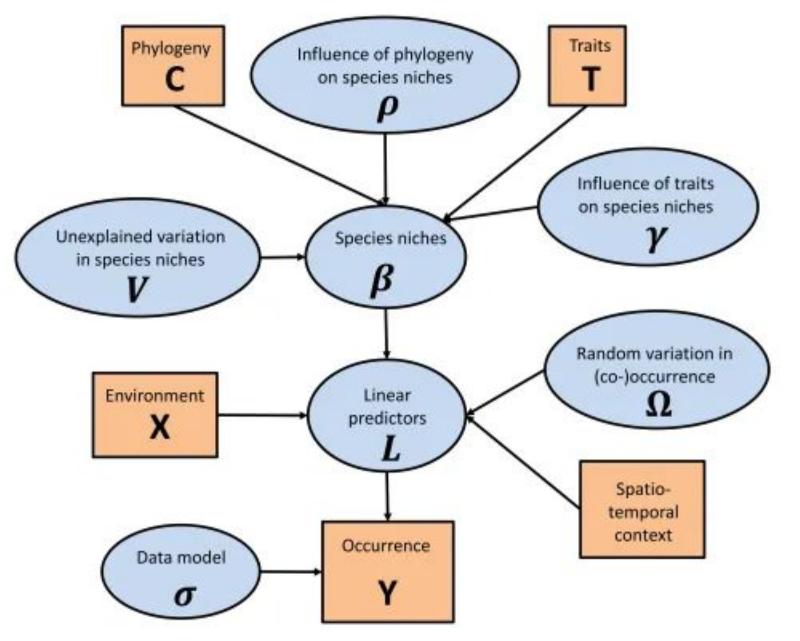


Part 1. Descriptive approaches

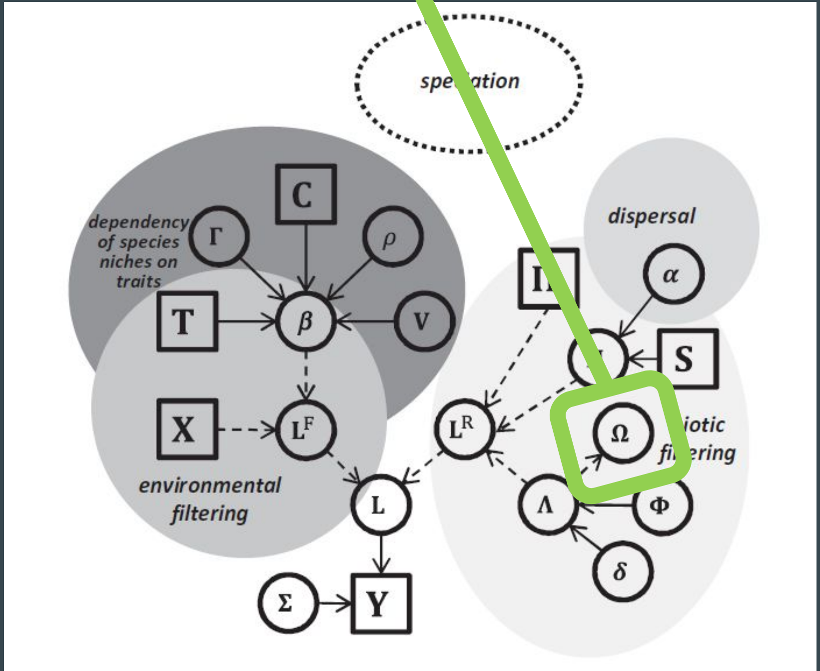




Part 1. Descriptive approaches



Species interactions must be deduced from **residual covariances***



*Same rationale as for null-model approach earlier

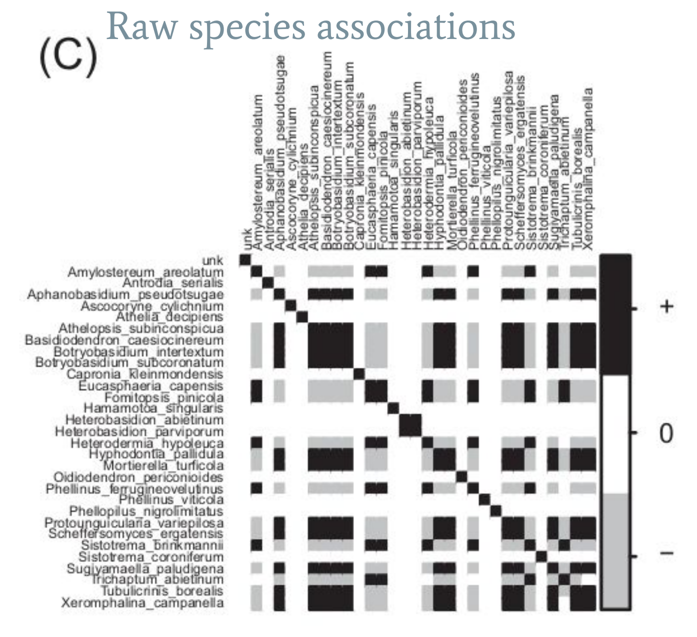
Part 1. Descriptive approaches

- An example of HMSC application: fungal communities of decaying trees

Botryobasidium subcoronatum (@Wikipedia)

Part 1. Descriptive approaches

- An example of HMSC application: fungal communities of decaying trees

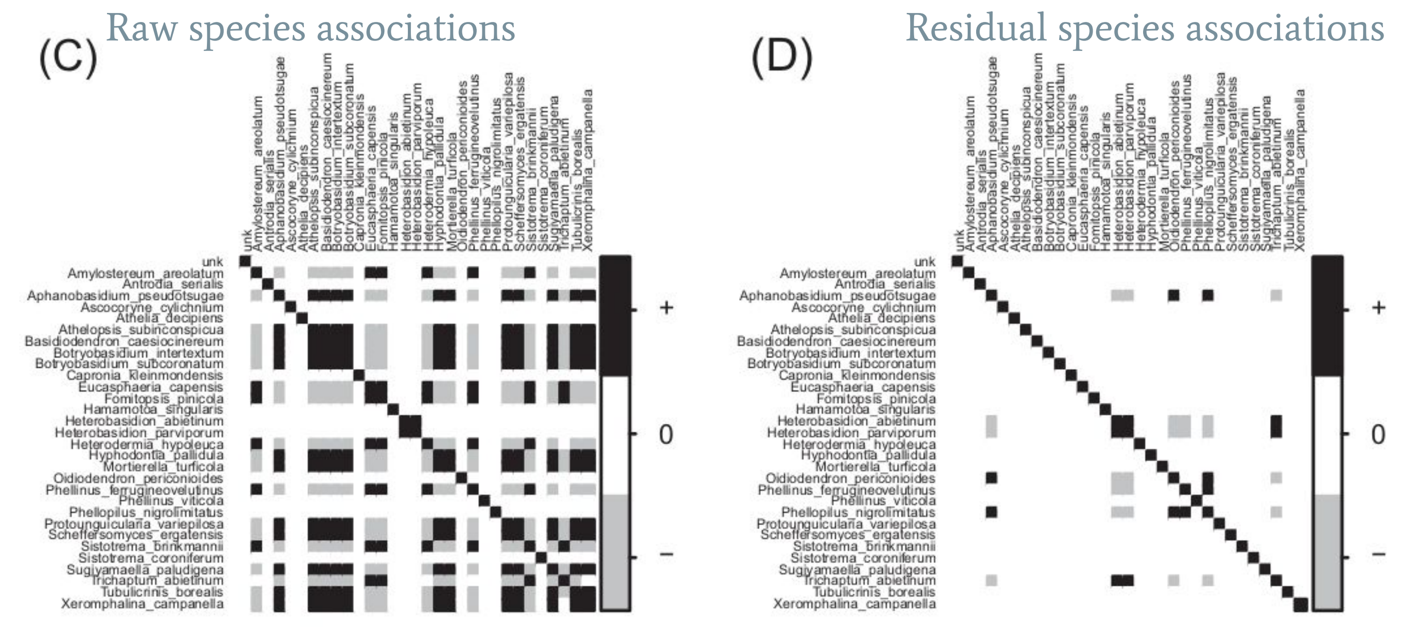

Raw species associations

From Ovaskainen & Abrego, 2020


Botryobasidium subcoronatum (@Wikipedia)

Part 1. Descriptive approaches

- An example of HMSC application: fungal communities of decaying trees

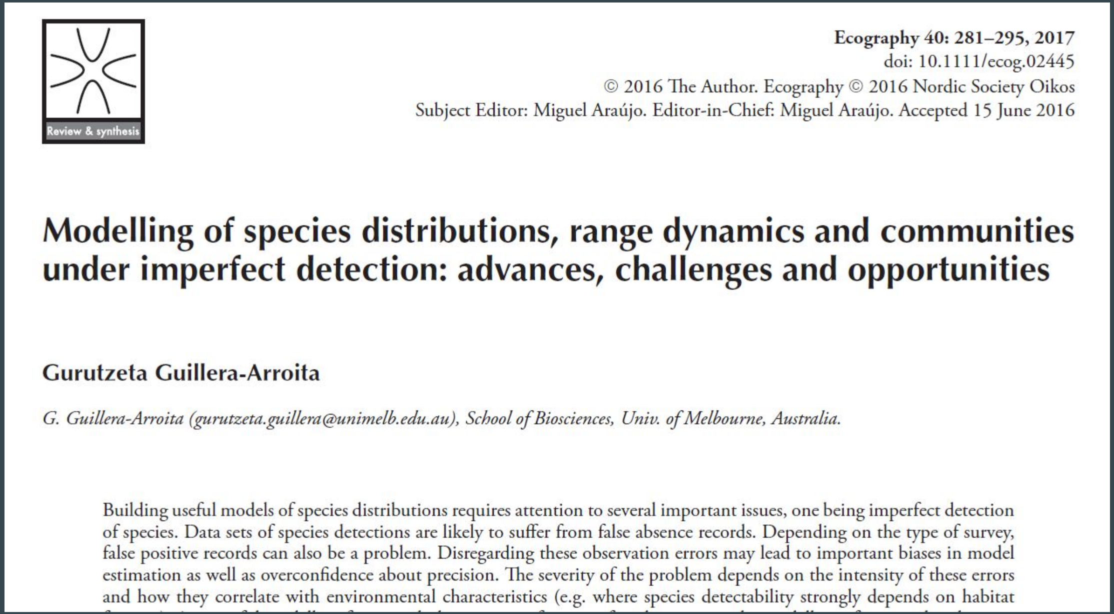

Raw species associations

Residual species associations

From Ovaskainen & Abrego, 2020

Part 1. Descriptive approaches

- Statistical approaches (species level): Occupancy models



Review & synthesis

Ecography 40: 281–295, 2017
doi: 10.1111/ecog.02445

Subject Editor: Miguel Araújo. Editor-in-Chief: Miguel Araújo. Accepted 15 June 2016

Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities

Gurutzeta Guillera-Arroita

G. Guillera-Arroita (gurutzeta.guillera@unimelb.edu.au), School of Biosciences, Univ. of Melbourne, Australia.

Building useful models of species distributions requires attention to several important issues, one being imperfect detection of species. Data sets of species detections are likely to suffer from false absence records. Depending on the type of survey, false positive records can also be a problem. Disregarding these observation errors may lead to important biases in model estimation as well as overconfidence about precision. The severity of the problem depends on the intensity of these errors and how they correlate with environmental characteristics (e.g. where species detectability strongly depends on habitat

Part 1. Descriptive approaches

- Statistical approaches (species level): Occupancy models

  Close to SDMs, but account for imperfect species detection (non-detection ≠ absence)

  The idea: distinguish *true* occupancy states from *observed* occupancy states,
  and estimate a **detection probability** which allows to account for false negatives

  Use short-term survey repeats (short enough to assume no change in occupancy state)

Part 1. Descriptive approaches

- Statistical approaches (species level): Occupancy models

Close to SDMs, but account for imperfect species detection (non-detection ≠ absence)

The idea: distinguish *true* occupancy states from *observed* occupancy states,

and estimate a **detection probability** which allows to account for false negatives

Bufo americanus

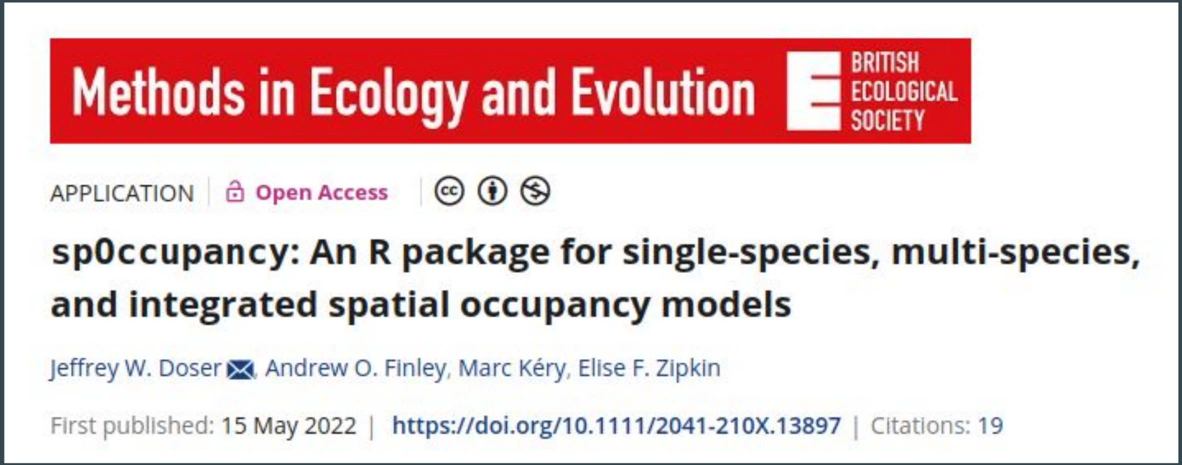
Initial survey: detected in *ca.* 30% of sites

Considering detection probability:
probable presence in *ca.* 50% (+44%) of sites

MacKenzie et al. 2002

Part 1. Descriptive approaches

- Statistical approaches (species level): Occupancy models



Methods in Ecology and Evolution

BRITISH ECOLOGICAL SOCIETY

APPLICATION | Open Access |

spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models

Jeffrey W. Doser, Andrew O. Finley, Marc Kéry, Elise F. Zipkin

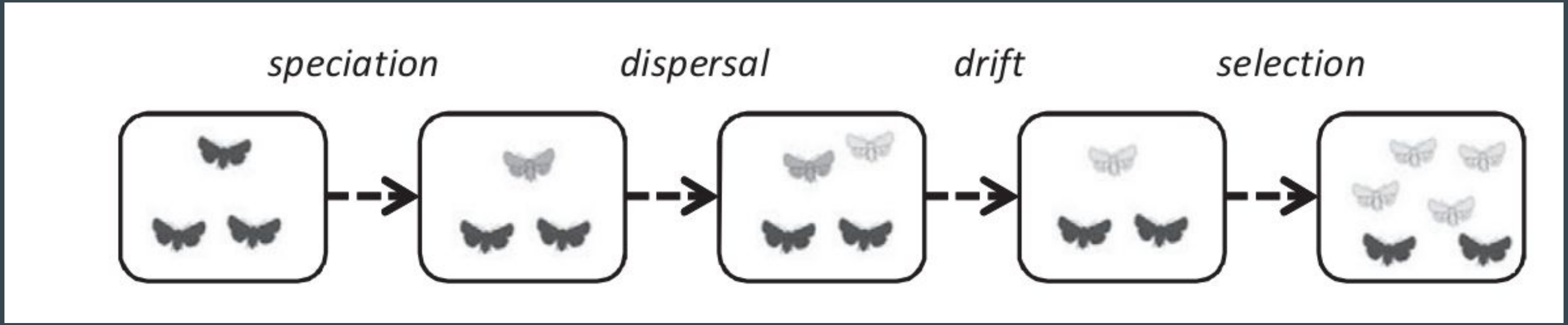
First published: 15 May 2022 | https://doi.org/10.1111/2041-210X.13897 | Citations: 19

Bridge part 1 / part 2

- Coffee break / questions on Part 1

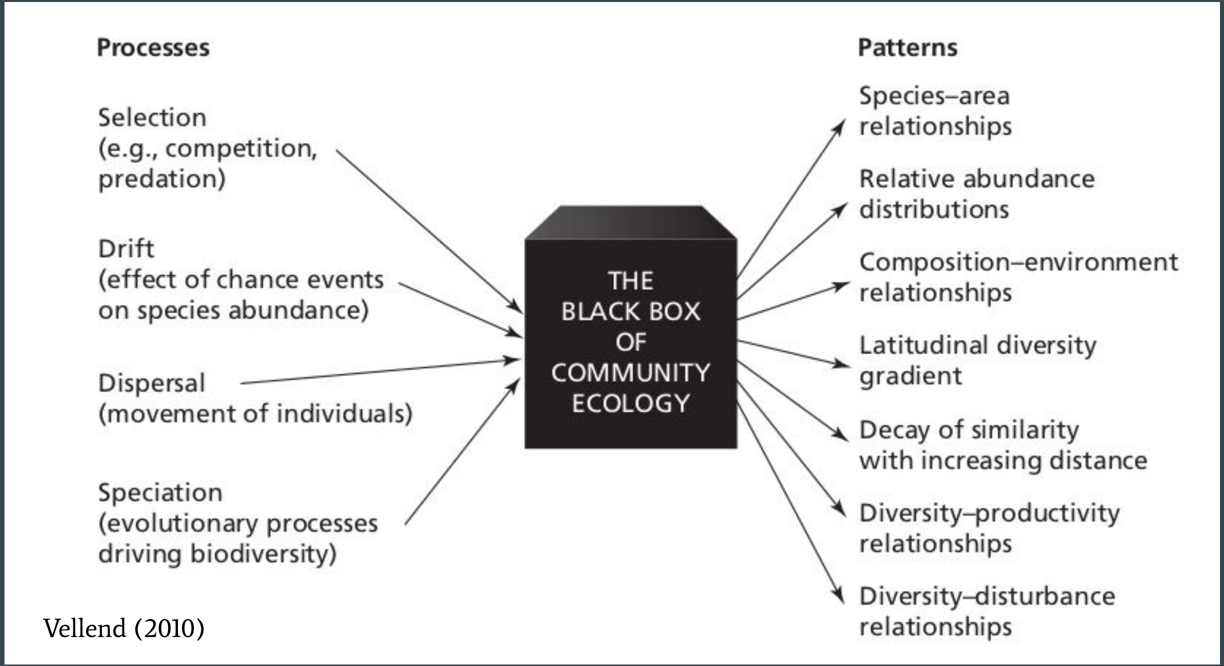
Part 2. Process-based approaches

- Describing the processes and how they operate in space and time



Part 2. Process-based approaches

- Describing the processes and how they operate in space and time



Processes

Selection
(e.g., competition,
predation)

Drift
(effect of chance events
on species abundance)

Dispersal
(movement of individuals)

Speciation
(evolutionary processes
driving biodiversity)

THE
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ECOLOGY

Patterns

Species–area
relationships

Relative abundance
distributions

Composition–environment
relationships

Latitudinal diversity
gradient

Decay of similarity
with increasing distance

Diversity–productivity
relationships

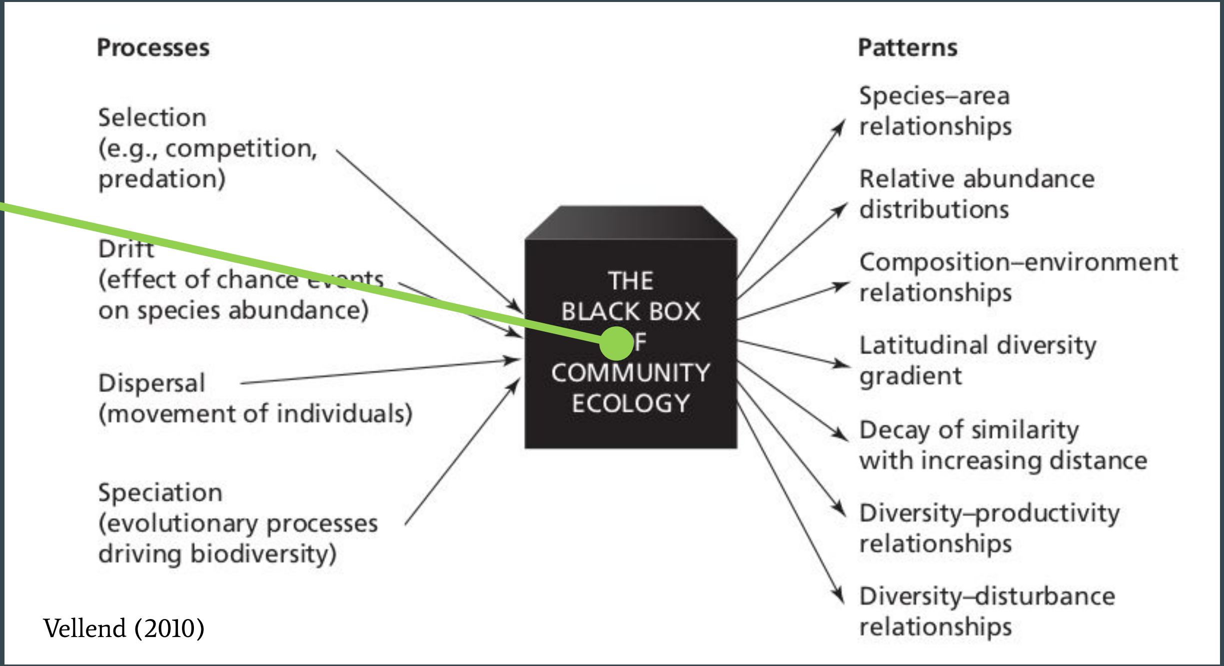
Diversity–disturbance
relationships

Vellend (2010)

Part 2. Process-based approaches

- Describing the processes and how they operate in space and time

Some mathematical (dynamical) model



Vellend (2010)

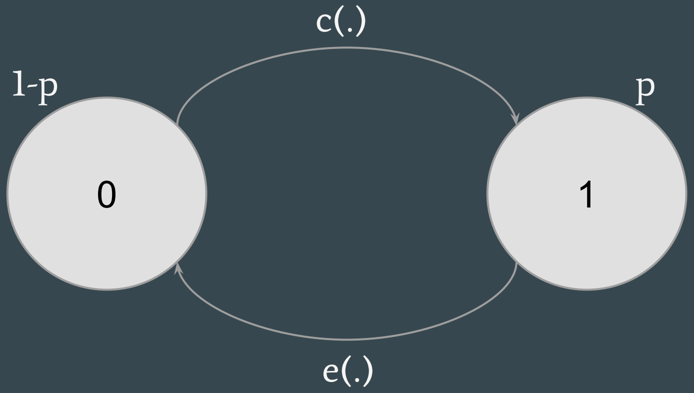
Part 2. Process-based approaches

- A. Patch occupancy models

In one site (patch), a species is either present (p) or absent (1-p)

Local dynamics can be neglected.

The probability of presence is a dynamic equilibrium between:
   - The rate of colonization (c)
   - The rate of extinction (e)



Part 2. Process-based approaches

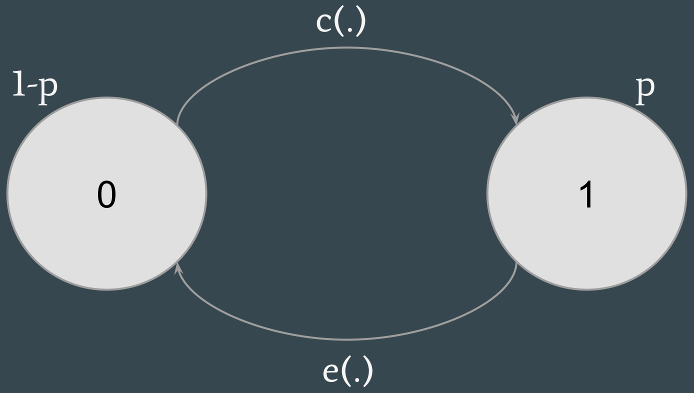
- A. Patch occupancy models

In one site (patch), a species is either present (p) or absent (1-p)

Local dynamics can be neglected.

The probability of presence is a dynamic equilibrium between:
- The rate of colonization (c)
- The rate of extinction (e)

$$\frac{dp}{dt} = c(.)(1-p) - e(.)p$$



Part 2. Process-based approaches

- A. Patch occupancy models

$$\frac{dp}{dt} = c(.)(1-p) - e(.)p$$

Now if you assume that:

- The extinction rate e(.) is just a constant: e(.) = e
- The colonization rate is proportional to the overall occupancy, which, if all patches are homogeneous, is just p: c(.) = c p

you get

$$\frac{dp}{dt} = cp(1-p) - ep$$

Levin's (1969) metapopulation model

$$p^* = 1 - \frac{e}{c}$$

Equilibrium metapopulation occupancy

Part 2. Process-based approaches

- A. Patch occupancy models

$$\frac{dp}{dt} = c(.)(1-p) - e(.)p$$

Now if you assume that:

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$$\frac{dp}{dt} = cp(1-p) - ep$$

Levin’s (1969) metapopulation model

$$p^* = 1 - \frac{e}{c}$$

Equilibrium metapopulation occupancy

*Note: you have seen this model yesterday. Noticed?

Part 2. Process-based approaches

- A. Patch occupancy models

$$\frac{dp}{dt} = c(.)(1-p) - e(.)p$$

Now if you assume that:
  - The extinction rate e(.) is just a constant: e(.) = e
  - The colonization rate is also just a constant: c(.) = c

you get

$$\frac{dp}{dt} = c(1-p) - ep$$

McArthur & Wilson’s (1967) continent-island model

$$p^* = \frac{c}{c+e}$$

Equilibrium island occupancy

Part 2. Process-based approaches

- A. Patch occupancy models

Levins' (1969) formed the basis of metapopulation theory
MW's (1967) model formed the basis of the theory of island biogeography (TIB)

In both cases:

Colonization should depend on isolation (**distance to mainland** or **patch isolation):**
nearer islands/more connected patches are more likely to received migrants

Extinction should depend on island or patch **size** (area):
larger islands/patches, having larger population sizes, have lower extinction risk

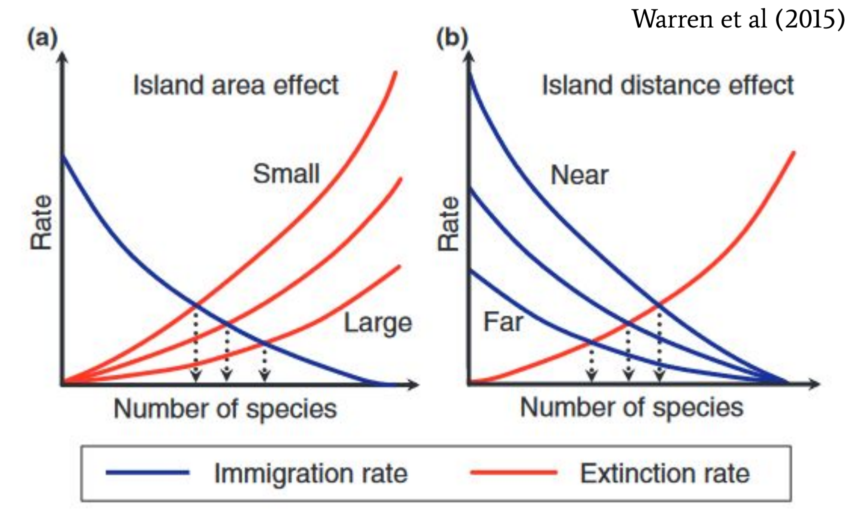
Part 2. Process-based approaches

- A. Patch occupancy models

With several species, we have one (independent) equation per species, and we must sum these equations to get the dynamics of the **number** of species.
Take the MW's model.

If all species were similar and non interacting, we'd get **linear** changes in the rates of extinction and colonizations with species richness

In practice , we rather expect* **convex** functions:
– colonization decreases slower than linearly
– extinction increases faster than linearly


Warren et al (2015)

*Why?

Part 2. Process-based approaches

- A. Patch occupancy models

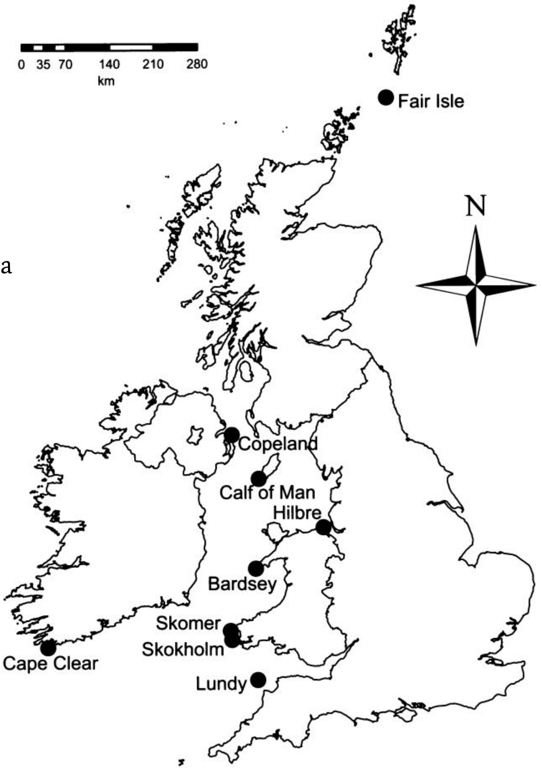
We can **adjust** the MW model to time series of colonizations and extinctions events on islands to test for this prediction: the example of Manne et al. (1998) JAE

The data: presence/absence of breeding birds on 13 British islands, followed over consecutive years (as many as 20 years)

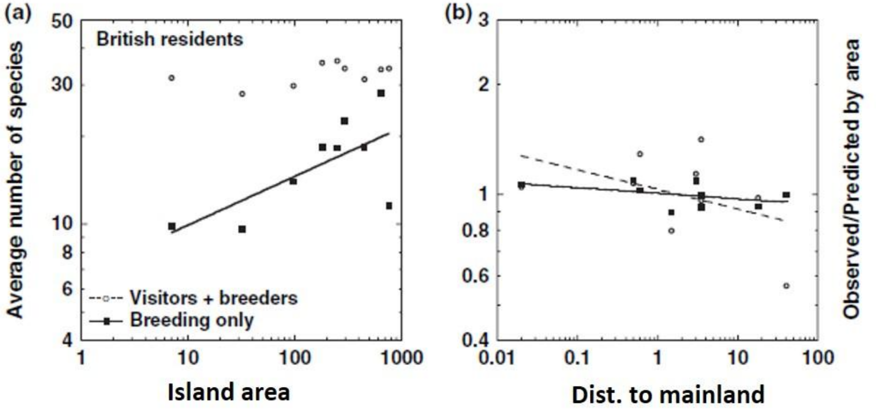
Manne et al. 1998

Oystercatcher pair @wikipedia

Bird immigration rates to small islands



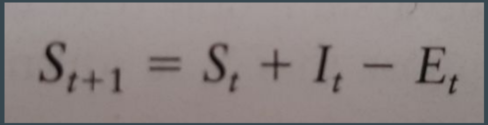
The location of the nine islands
 this study. Map modified from
l. (2006).



Stracey & Pimm (2009) JoB

Manne et al. 1998

The number of species on a particular island at time t (S_t) is known exactly, and modelled as

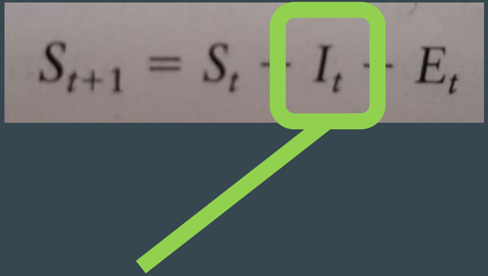


$$S_{t+1} = S_t + I_t - E_t$$

After Clark (2001)

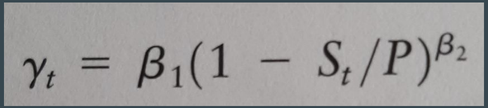
Manne et al. 1998

The number of species on a particular island at time t (S_t) is known exactly, and modelled as



$$S_{t+1} = S_t + I_t - E_t$$

Number of immigration events.
Probability:



$$\gamma_t = \beta_1(1 - S_t/P)^{\beta_2}$$

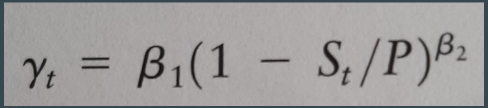
After Clark (2001)

Manne et al. 1998

The number of species on a particular island at time t (S_t) is known exactly, and modelled as

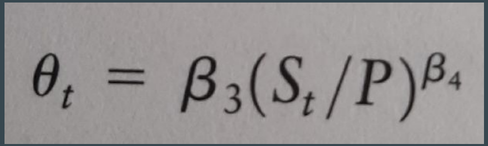
$$S_{t+1} = S_t + I_t - E_t$$

Number of immigration events.
Probability:



$$\gamma_t = \beta_1(1 - S_t/P)^{\beta_2}$$

Number of extinction events.
Probability:

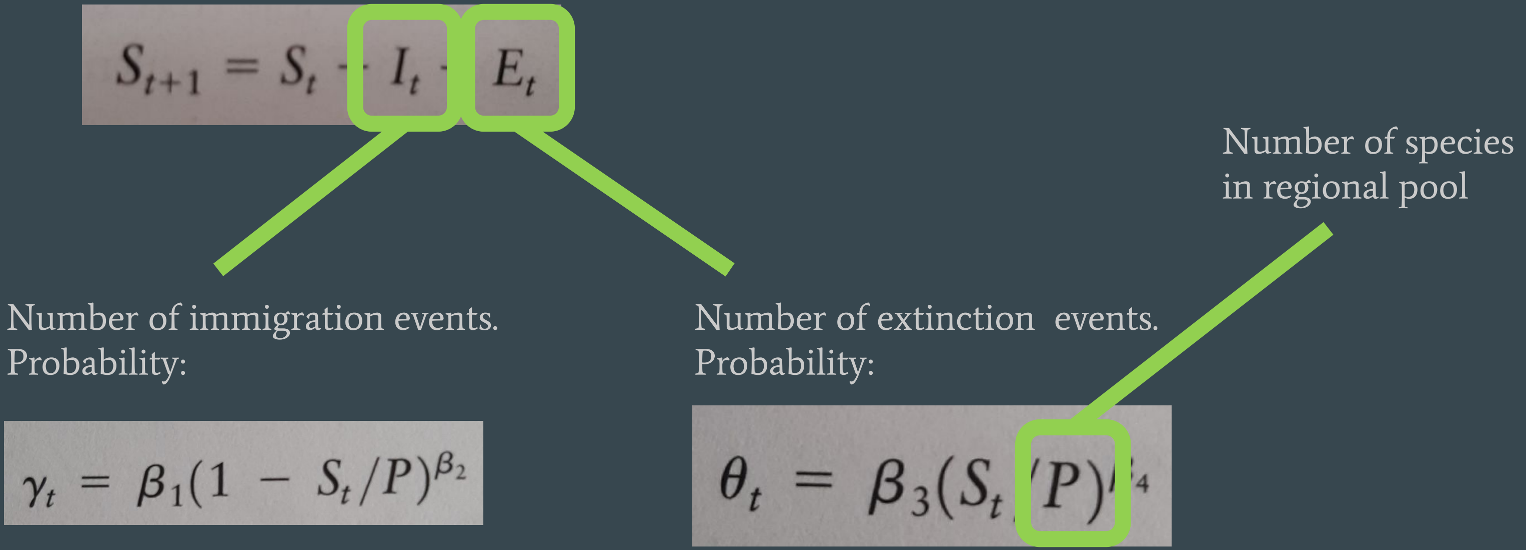


$$\theta_t = \beta_3(S_t/P)^{\beta_4}$$

After Clark (2001)

Manne et al. 1998

The number of species on a particular island at time t (S_t) is known exactly, and modelled as



$$S_{t+1} = S_t + I_t - E_t$$

Number of species in regional pool

Number of immigration events.
Probability:

$$\gamma_t = \beta_1(1 - S_t/P)^{\beta_2}$$

Number of extinction events.
Probability:

$$\theta_t = \beta_3(S_t/P)^{\beta_4}$$

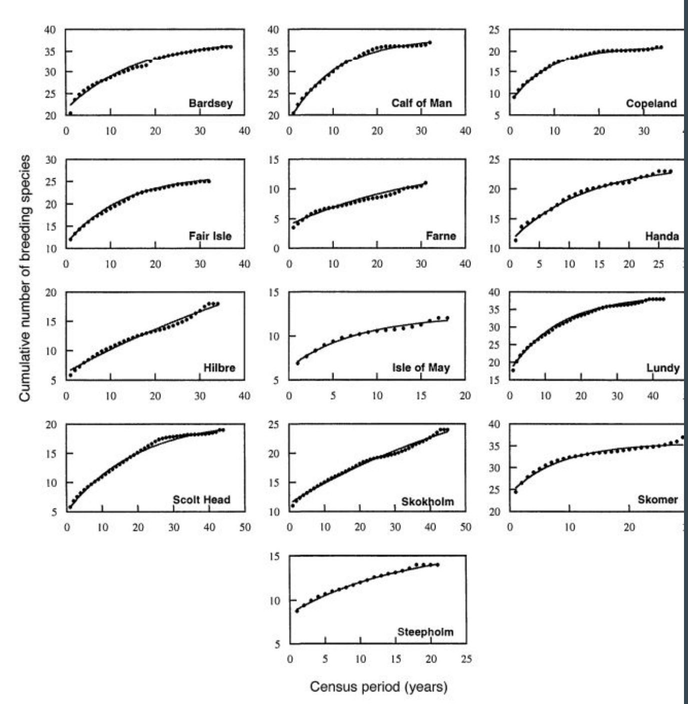
After Clark (2001)

Manne et al. 1998

Manne et al. 1998

From there, we need to:

1. Estimate the number of species in the regional pool(P)



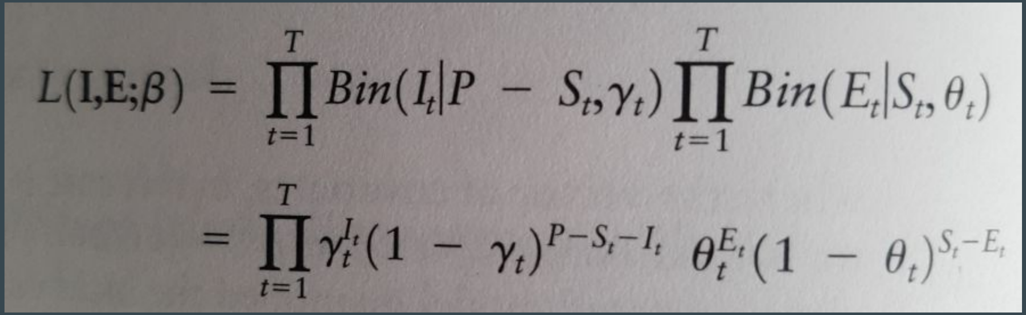
Manne et al. 1998

Manne et al. 1998

From there, we need to:

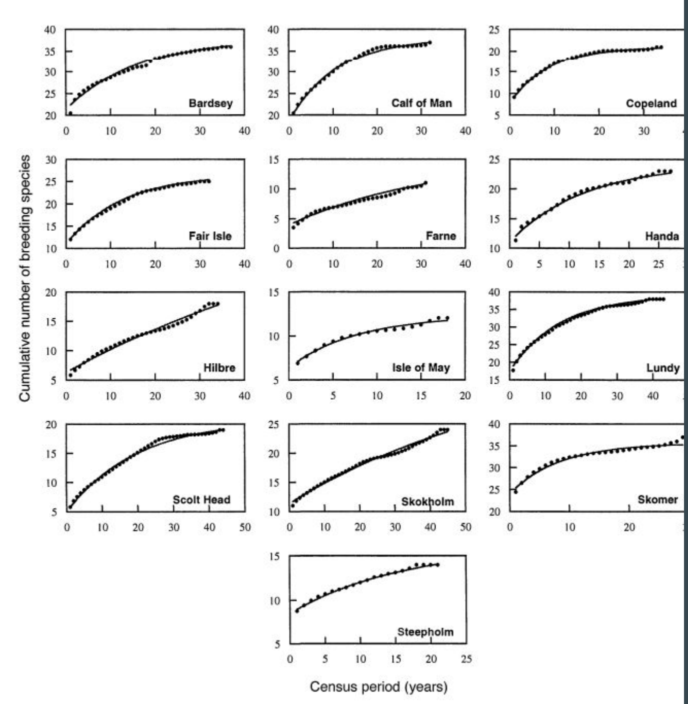
1. Estimate the number of species in the regional pool(P)

2. Express and maximize the likelihood



$$L(\mathbf{I},\mathbf{E};\beta) = \prod_{t=1}^{T} Bin(I_t|P - S_t,\gamma_t) \prod_{t=1}^{T} Bin(E_t|S_t,\theta_t)$$

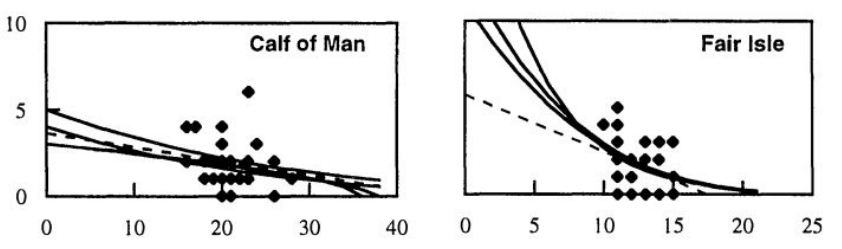
$$= \prod_{t=1}^{T} \gamma_t^{I_t}(1 - \gamma_t)^{P-S_t-I_t} \ \theta_t^{E_t}(1 - \theta_t)^{S_t-E_t}$$



After Clark (2001)

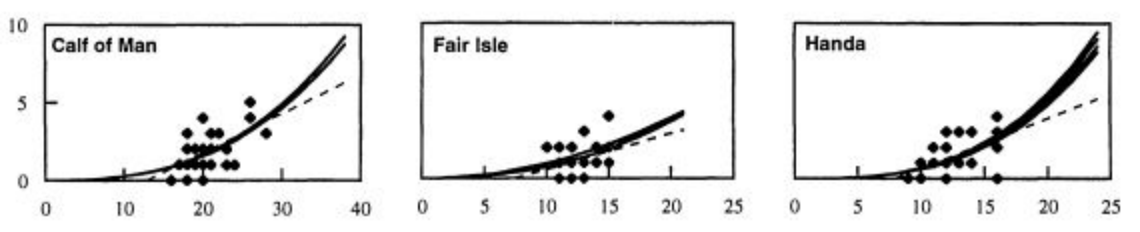
Manne et al. 1998

For a majority of islands, Manne et al. (1998) did find **non-linear curves** , as expected from theory*.



Immigration curves

Extinction curves



Manne et al. 1998

*What does it tell us already?

Part 2. Process-based approaches

- A. Patch occupancy models

The idea that colonization rate is a function of distance and patch extinction rate varies with patch size can also be incorporated in Levins' metapopulation model (**spatially realistic models**):
These are called **incidence function models** (IFM), starting from Hanski (1991)

Part 2. Process-based approaches

- A. Patch occupancy models

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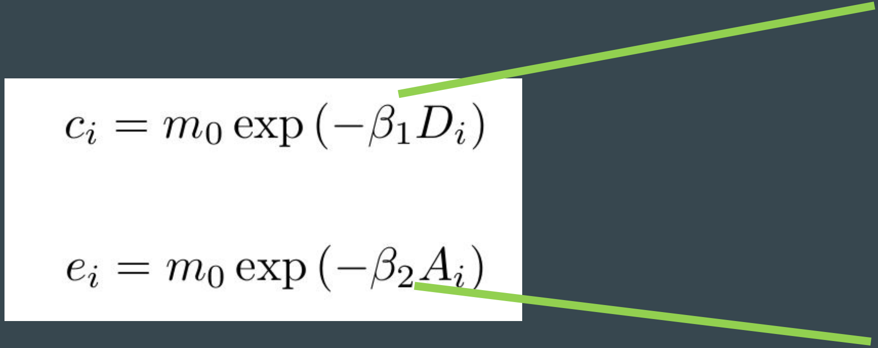


$$c_i = m_0 \exp\left(-\beta_1 D_i\right)$$

$$e_i = m_0 \exp\left(-\beta_2 A_i\right)$$

Decay rate of colonization with distance (Di)

Decay rate of extinction with patch area (Ai)

Part 2. Process-based approaches

- A. Patch occupancy models

  IFM models models can be fitted to (snapshot) occupancy data:
  - Some parameters have to be estimated separately from other data (e.g., decay rates)
  - We must assume dynamic equilibrium for fit, but can be used for projection

American Pika (Moilanen et al. 1998)

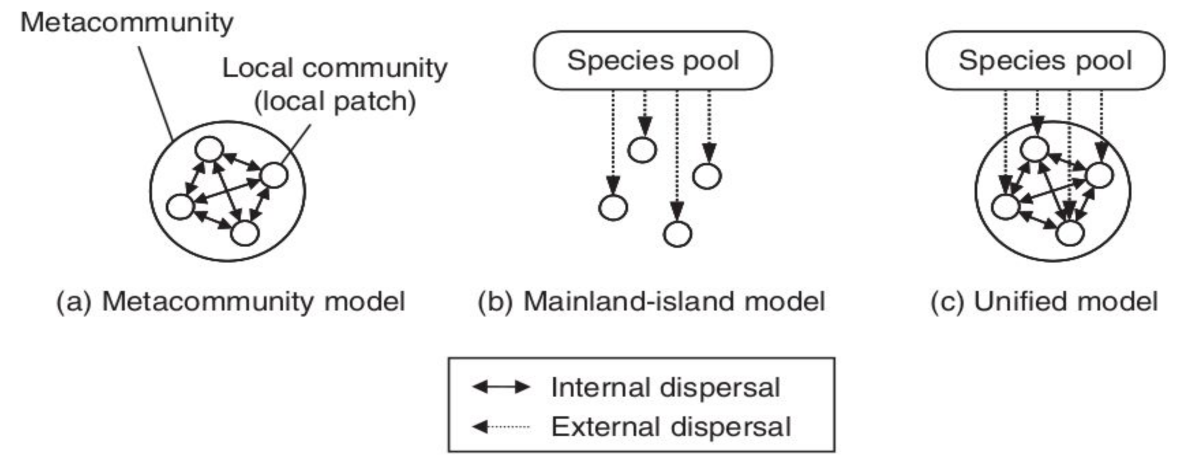
Melitaea cinxia (Wahlberg et al. 1996)

Hyla arborea (Vos et al. 2000)

Part 2. Process-based approaches

- A. Patch occupancy models

Of course, you can mix the two assumptions for colonization and obtain a “unified’ model*:



Modified from Fukami (2005)

*We let you do the maths as an exercise.

Part 2. Process-based approaches

- A. Patch occupancy models

Patch occupancy models can be extended in many directions:

- multiple species with interactions (e.g. competition colonization trade-offs)
- different classes of patches (different habitats)
- food webs (trophic chains or networks)
- ...

Of course, the more you complicate them, the more difficult analysis is, and also, the more difficult it is to parametrize them and fit them to data.

Part 2. Process-based approaches

- A. Patch occupancy models

Even complex patch occupancy models can be fitted to temporal data (time series) - using the temporal turnover (i.e. apparent colonization and extinctions)

This is often called **dynamic occupancy modelling** (MacKenzie, 2003; Bailey et al. 2014)

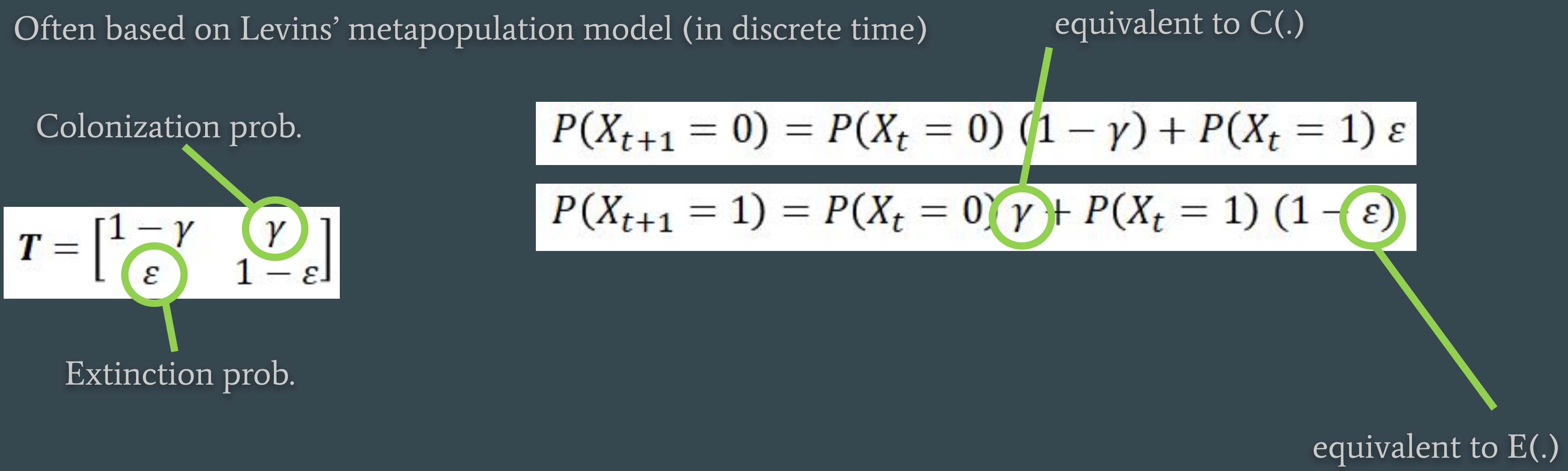
They usually include a detection layer (i.e. a statistical modelling of the observation process)

Part 2. Process-based approaches

- A. Patch occupancy models

The idea: modelling patch states (e.g., **X** = {0, 1}) and transition probabilities (matrix **T**) among states, such that $\mathbf{X}_{i,t+1} = \mathbf{X}_{i,t}\mathbf{T}$

Often based on Levins' metapopulation model (in discrete time)



equivalent to C(.)

Colonization prob.

$$\boldsymbol{T} = \begin{bmatrix} 1-\gamma & \gamma \\ \varepsilon & 1-\varepsilon \end{bmatrix}$$

Extinction prob.

$$P(X_{t+1} = 0) = P(X_t = 0)\,(1-\gamma) + P(X_t = 1)\,\varepsilon$$

$$P(X_{t+1} = 1) = P(X_t = 0)\,\gamma + P(X_t = 1)\,(1-\varepsilon)$$

equivalent to E(.)

Part 2. Process-based approaches

- A. Patch occupancy models

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Colonization and extinction can be patch and/or time specific, and then can include patch environmental characteristics, other species effects as well as distance-based dispersal

equivalent to E(.)

Part 2. Process-based approaches

One example: metapopulation dynamics of *D. depressissimum* in Guadeloupe (Lamy et al. 2013)

Transition matrix

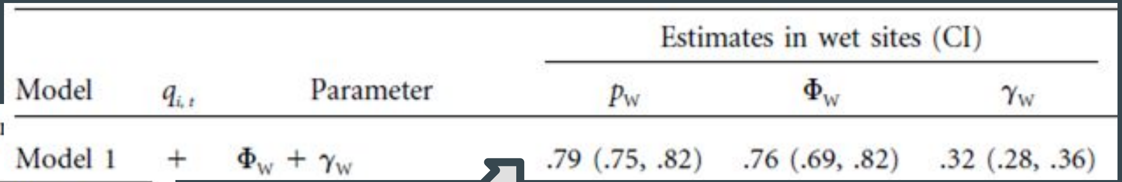
$$P_{WW} = \begin{array}{c|cc|} & 0 & 1 \\ 0 & 1-\gamma_W & \gamma_W \\ 1 & (1-\Phi_W)*(1-\gamma_W) & \Phi_W+(1-\Phi_W)*\gamma_W \end{array}$$

With $\mathbf{\Phi} = 1 - \varepsilon$; i.e. the persistence probability

© Jean-Pierre POINTIER/EPHE/USR 3278/CNRS Photothèque

Part 2. Process-based approaches

One example: metapopulation dynamics of *D. depressissimum* in Guadeloupe (Lamy et al. 2013)



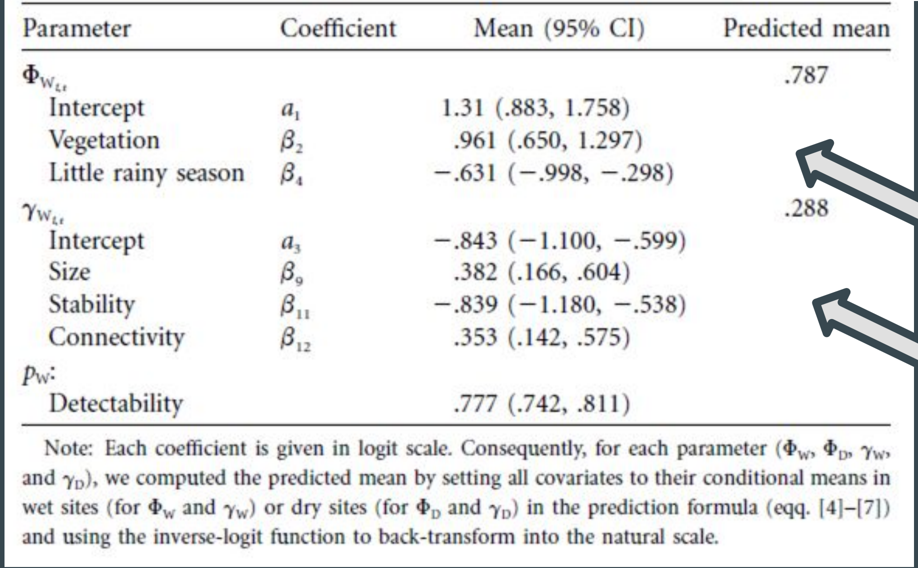
Model	$q_{i,t}$	Parameter	Estimates in wet sites (CI)		
			p_W	Φ_W	γ_W
Model 1	+	$\Phi_W + \gamma_W$	.79 (.75, .82)	.76 (.69, .82)	.32 (.28, .36)

Detection prob.

Mean persistence prob

Mean colonization prob.

Table 4: Posterior means of intercept and covariate effects in the fi
their 95% credible intervals (CIs)



Parameter	Coefficient	Mean (95% CI)	Predicted mean
$\Phi_{W_{i,t}}$			.787
Intercept	a_1	1.31 (.883, 1.758)	
Vegetation	β_2	.961 (.650, 1.297)	
Little rainy season	β_4	−.631 (−.998, −.298)	
$\gamma_{W_{i,t}}$			.288
Intercept	a_3	−.843 (−1.100, −.599)	
Size	β_9	.382 (.166, .604)	
Stability	β_{11}	−.839 (−1.180, −.538)	
Connectivity	β_{12}	.353 (.142, .575)	
p_W:			
Detectability		.777 (.742, .811)	

Note: Each coefficient is given in logit scale. Consequently, for each parameter (Φ_W, Φ_D, γ_W, and γ_D), we computed the predicted mean by setting all covariates to their conditional means in wet sites (for Φ_W and γ_W) or dry sites (for Φ_D and γ_D) in the prediction formula (eqq. [4]–[7]) and using the inverse-logit function to back-transform into the natural scale.

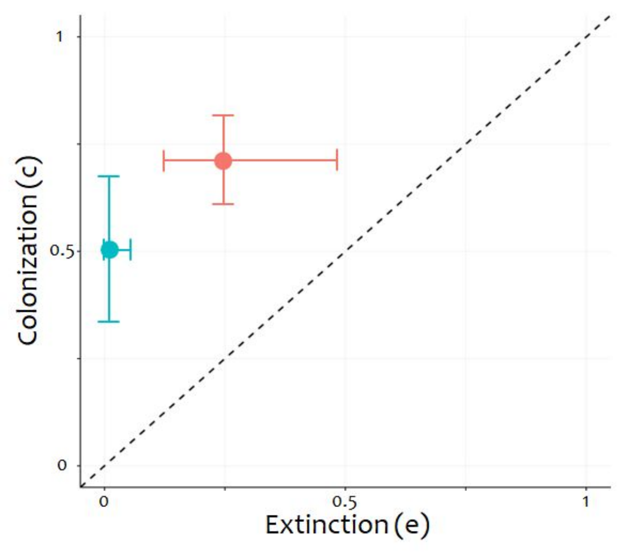
Envt. effects on persistence

Envt. effects on colonization

Part 2. Process-based approaches

With multiple species: *P. acuta & A. marmorata* - Guadeloupe

Rates in **absence** of the other species



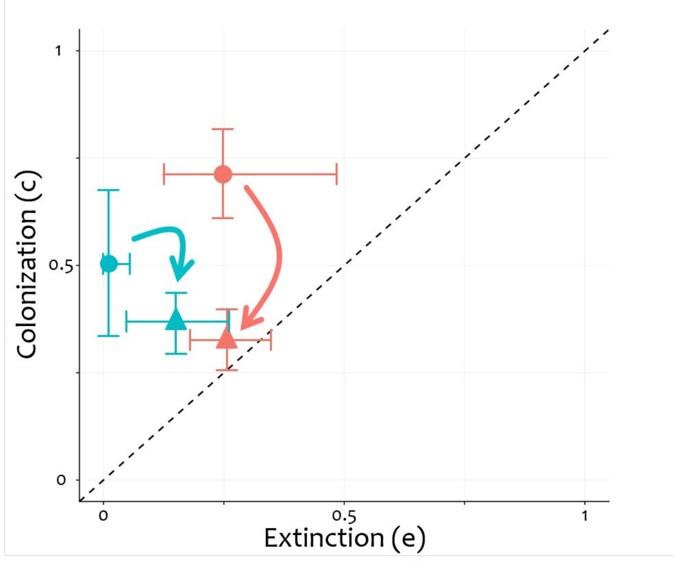
Aplexa marmorata

Physa acuta

Part 2. Process-based approaches

With multiple species: *P. acuta & A. marmorata* - Guadeloupe

Rates in **presence** of the other species



Aplexa marmorata

Physa acuta

A. marmorata increases *P. acuta* extinction rate

P. acuta reduces *A. marmorata* colonization rate

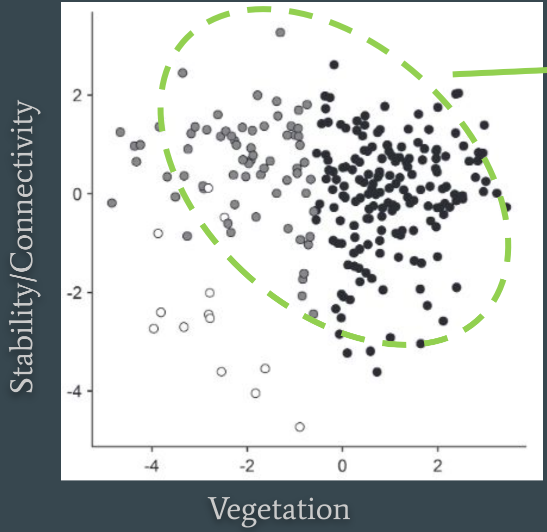
Part 2. Process-based approaches

With multiple species: *P. acuta & A. marmorata* - Guadeloupe

These interaction effects depends on environmental conditions

Aplexa marmorata

Physa acuta



A. marmorata fundamental niche

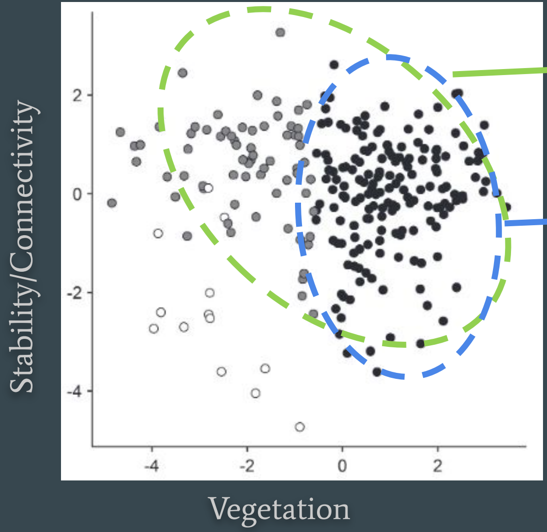
Part 2. Process-based approaches

With multiple species: *P. acuta & A. marmorata* - Guadeloupe

These interaction effects depends on environmental conditions

Aplexa marmorata

Physa acuta

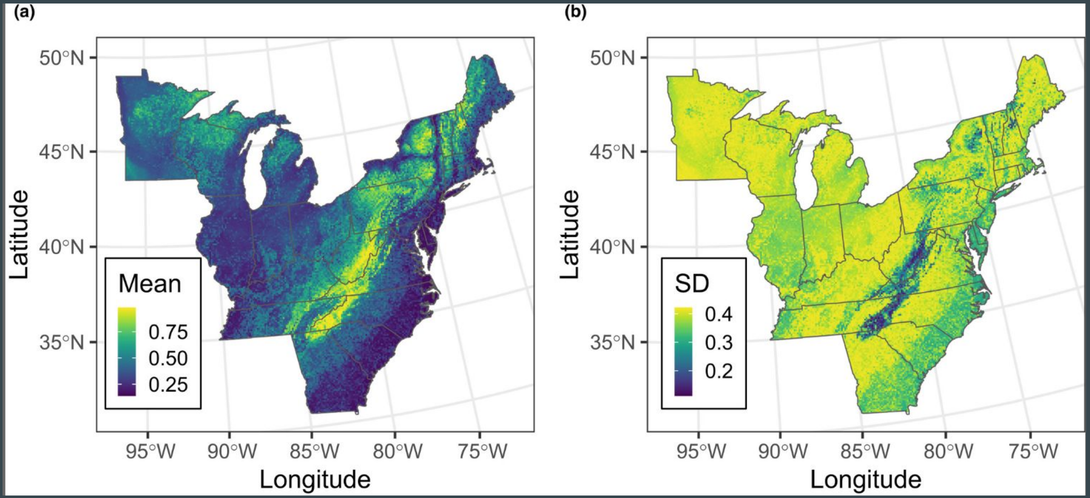


A. marmorata fundamental niche

A. marmorata realized niche

Part 2. Process-based approaches

There are increasingly flexible and easy-to-use solutions to implement occupancy models



Part 2. Process-based approaches

- B. Introducing local population dynamics

All previous mechanistic models describe presence/absence only (i.e. neglected local dynamics)

It may be more realistic to describe within patch population dynamics, and more data could be used (when abundance data is available)

Part 2. Process-based approaches

- B. Integrating local population dynamics

> The simplest approach possible is to take a patch occupancy model (e.g. Levins' model), and add a dynamical variable to describe local population density (e.g. logistic growth within each patch). This approach was taken for instance by Gyllenberg & Hanski (1992)

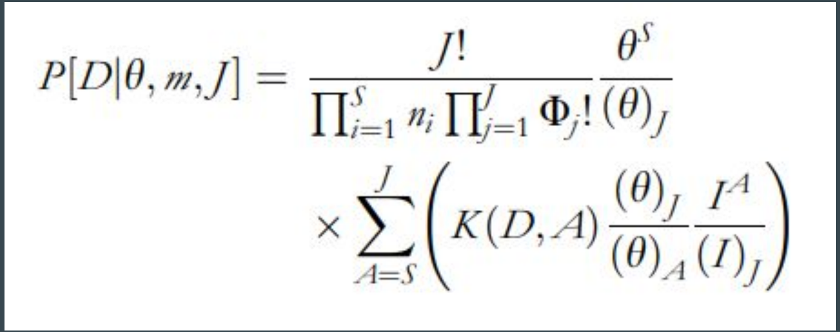
> Alternatively, one can simply distinguish "small" populations (i.e. recently colonized) from "large" populations (small populations that have grown). This adds a second equation to Levins' model, but remains quite simple (Hanski 1985)

This can cause **rescue effects** and **alternative stable states** (similar to an Allee effect at metapopulation level). It has implications for the response to perturbations (Eriksson et al. 2014)

Part 2. Process-based approaches

- B. Integrating local population dynamics

There are, again, many models that attempt to do this.
> Another example is Hubbell’s **neutral model of biodiversity** over several connected communities.
Owing to the fact that all species are assumed identical, the dynamics of local abundances (assuming some constant total abundance) is relatively easy to model.



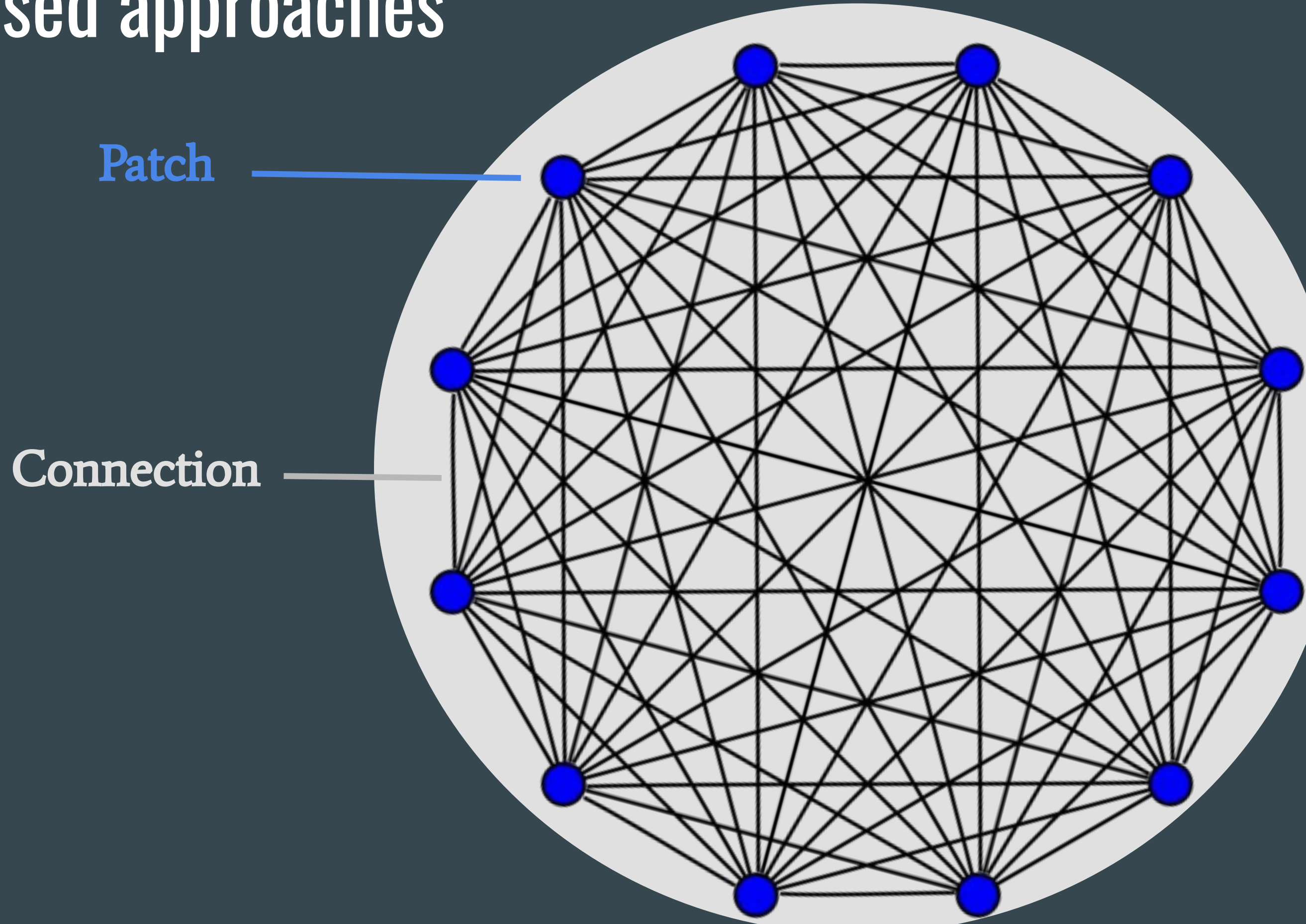
$$P[D|\theta, m, J] = \frac{J!}{\prod_{i=1}^{S} n_i \prod_{j=1}^{J} \Phi_j!} \frac{\theta^S}{(\theta)_J} \times \sum_{A=S}^{J} \left(K(D,A) \frac{(\theta)_J}{(\theta)_A} \frac{I^A}{(I)_J} \right)$$

Etienne (2005)

Part 2. Process-based approaches

Connectivity graph

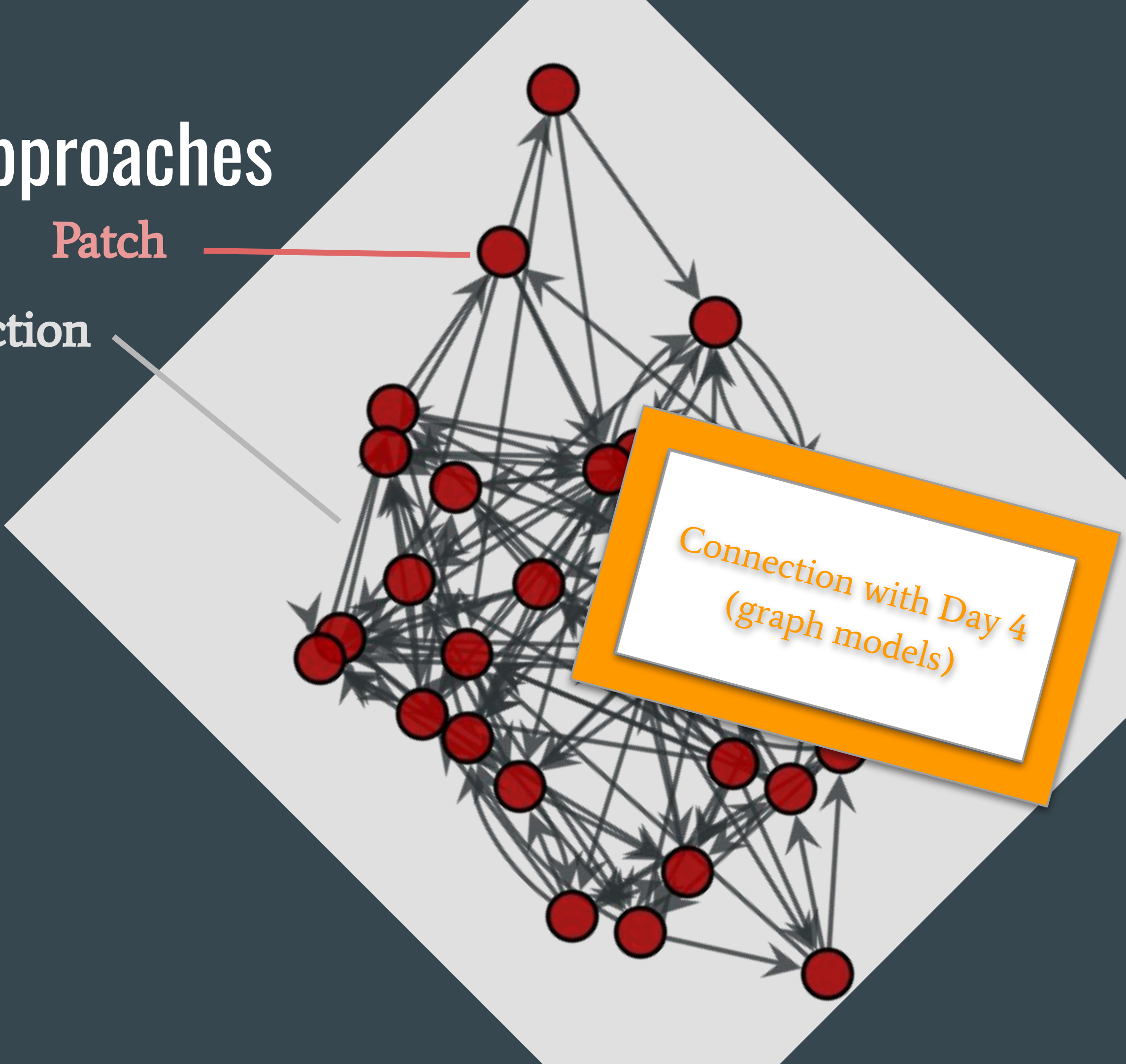
Fully connected
(complete)



Part 2. Process-based approaches

Connectivity graph

Random graph



Patch

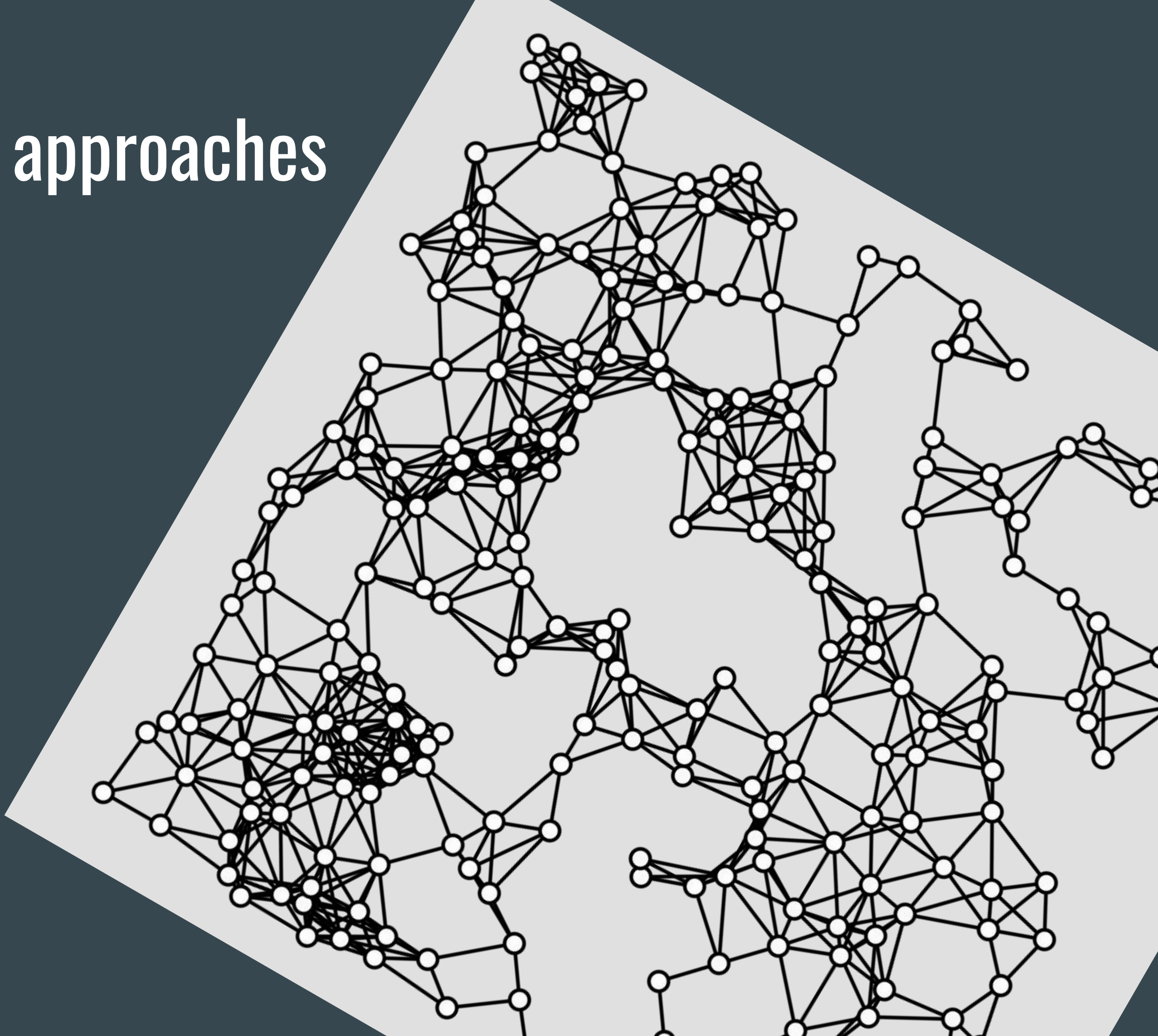
Connection

Connection with Day 4
(graph models)

Part 2. Process-based approaches

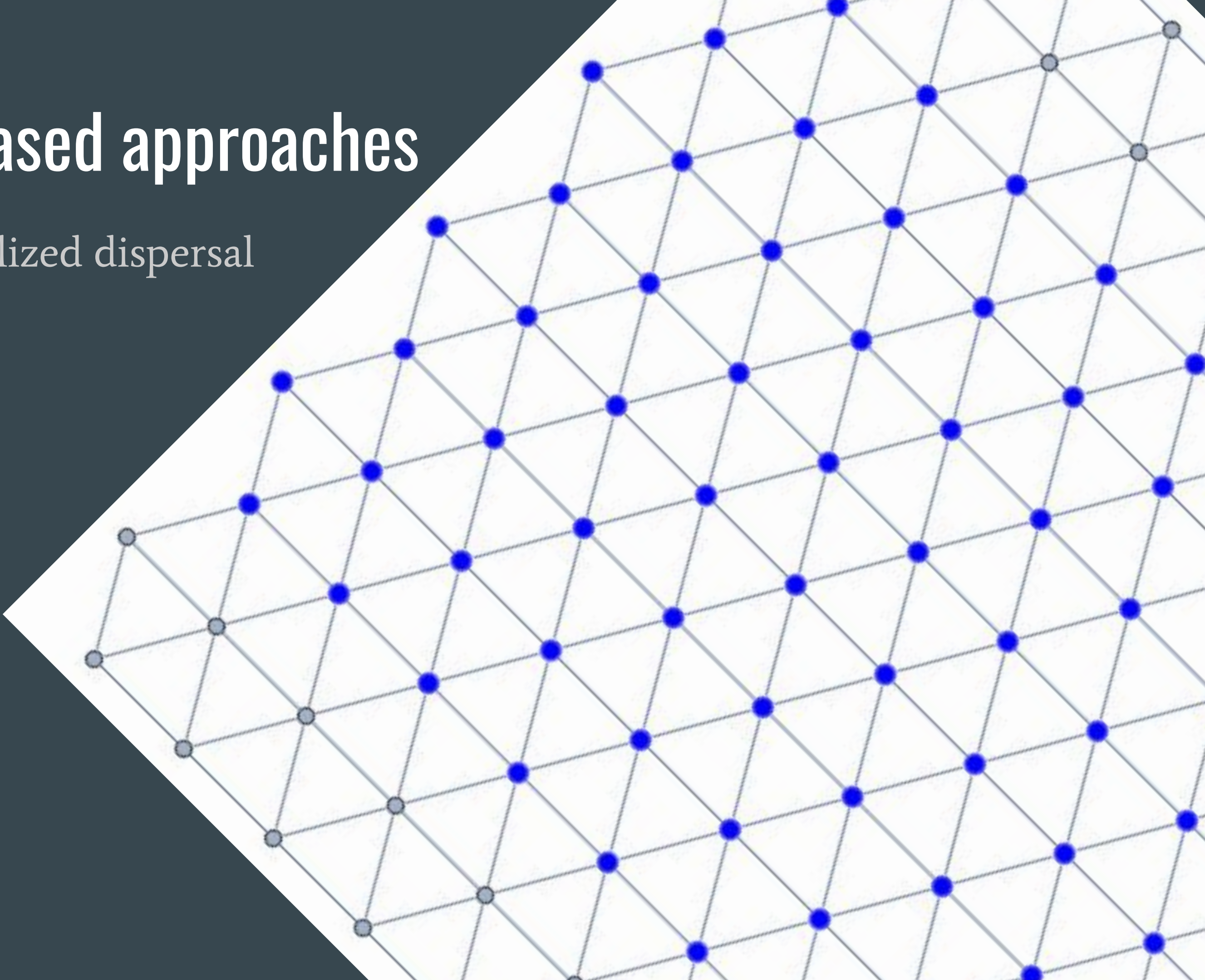
Connectivity graph

Planar graph



Part 2. Process-based approaches

- C. Models with localized dispersal

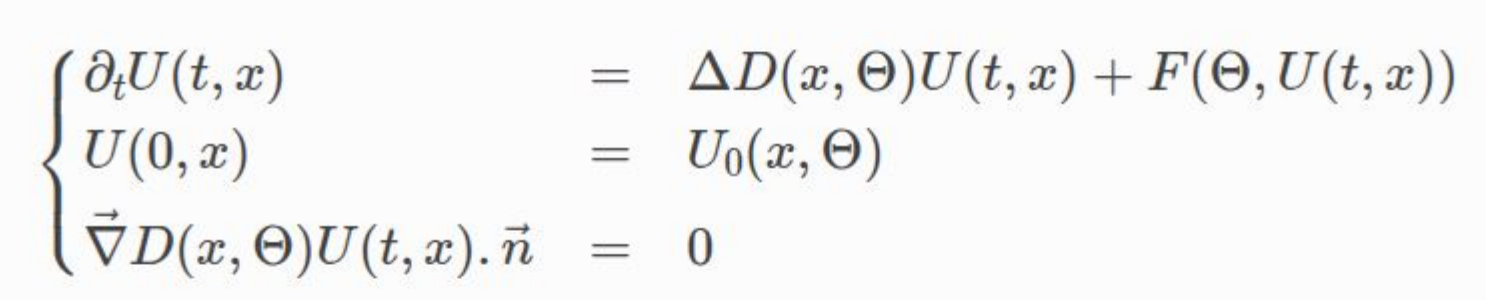


Lattice (grid) graph

Part 2. Process-based approaches

- C. Models with localized dispersal

> **Reaction-diffusion models** are a convenient framework to model the spatial spread of species, combining local dispersal (diffusion) and local population dynamics (reaction)



$$\begin{cases} \partial_t U(t,x) & = & \Delta D(x,\Theta)U(t,x) + F(\Theta, U(t,x)) \\ U(0,x) & = & U_0(x,\Theta) \\ \vec{\nabla} D(x,\Theta)U(t,x).\vec{n} & = & 0 \end{cases}$$

Part 2. Process-based approaches

- C. Models with localized dispersal

> **Reaction-diffusion models** are a convenient framework to model the spatial spread of species, combining local dispersal (diffusion) and local population dynamics (reaction)

$$\frac{\partial u}{\partial t} - D\frac{\partial^2 u}{\partial x^2} = ru(1-u).$$

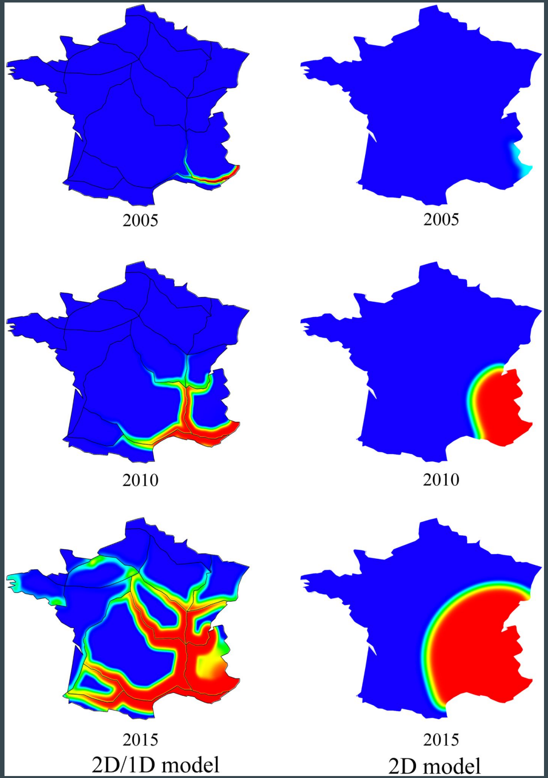
Fisher KPP in 1D

Part 2. Process-based approaches

- B. Models with local population dynamics

Can be simulated and fitted to data (Roques & Bonnefond 2016)

Roques & Bonnefon 2016

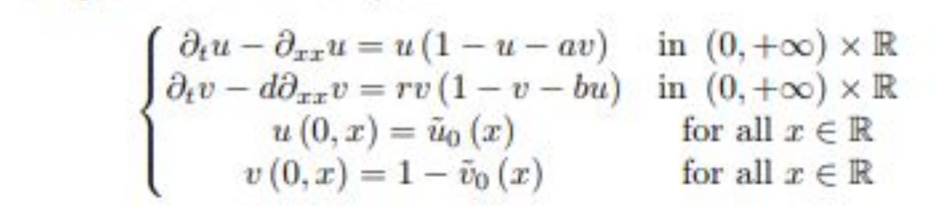


Aedes albopictus @Wikipedia

Part 2. Process-based approaches

- B. Models with local population dynamics

Can be extended to several interacting species



$$\begin{cases} \partial_t u - \partial_{xx} u = u\,(1 - u - av) & \text{in } (0,+\infty)\times\mathbb{R} \\ \partial_t v - d\partial_{xx} v = rv\,(1 - v - bu) & \text{in } (0,+\infty)\times\mathbb{R} \\ u\,(0,x) = \tilde{u}_0\,(x) & \text{for all } x\in\mathbb{R} \\ v\,(0,x) = 1 - \tilde{v}_0\,(x) & \text{for all } x\in\mathbb{R} \end{cases}$$

Girardin & Lam (2010)
(two species-competition-diffusion)

Predator-prey diffusion

Part 2. Process-based approaches

- B. Models with local population dynamics

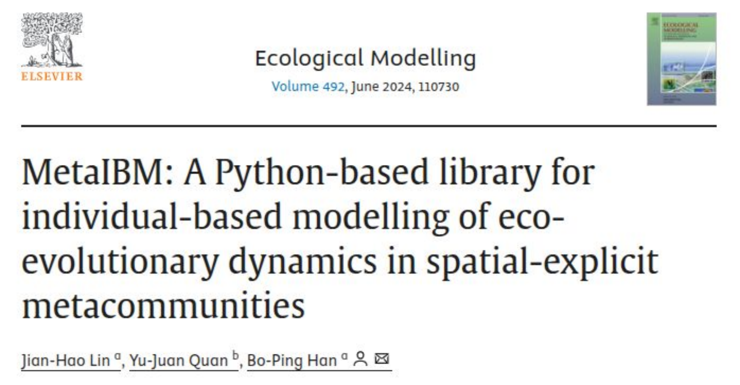
Describing the local population dynamics with several interacting species quickly becomes **too complicated** to be usefully modelled with simple mathematical models.

In this case, we usually turn to **stochastic simulation models**.

Part 2. Process-based approaches

- C. Stochastic simulation models

Various environments are now available to simulate spatial data



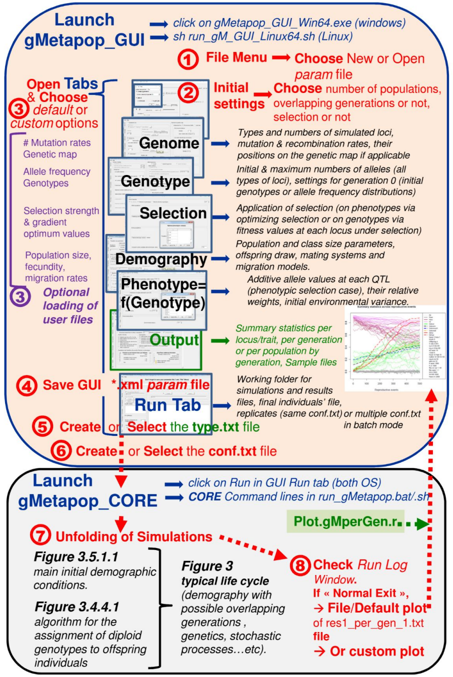
ELSEVIER

Ecological Modelling
Volume 492, June 2024, 110730

MetaIBM: A Python-based library for individual-based modelling of eco-evolutionary dynamics in spatial-explicit metacommunities

Jian-Hao Lin [a], Yu-Juan Quan [b], Bo-Ping Han [a]

MetaIBM (2024)



Launch gMetapop_GUI → *click on gMetapop_GUI_Win64.exe (windows)*
→ *sh run_gM_GUI_Linux64.sh (Linux)*

① **File Menu** → **Choose** New or Open *param* file

② **Initial settings** → **Choose** number of populations, overlapping generations or not, selection or not

Open Tabs & Choose ③ *default* or *custom* options

Genome → *Types and numbers of simulated loci, mutation & recombination rates, their positions on the genetic map if applicable*

Genotype → *Initial & maximum numbers of alleles (all types of loci), settings for generation 0 (initial genotypes or allele frequency distributions)*

Selection → *Application of selection (on phenotypes via optimizing selection or on genotypes via fitness values at each locus under selection)*

Demography → *Population and class size parameters, offspring draw, mating systems and migration models.*

Phenotype= f(Genotype) → *Additive allele values at each QTL (phenotypic selection case), their relative weights, initial environmental variance.*

Output → *Summary statistics per locus/trait, per generation or per population by generation, Sample files*

Mutation rates
Genetic map

Allele frequency
Genotypes

Selection strength
& gradient
optimum values

Population size,
fecundity,
migration rates

③ ***Optional loading of user files***

④ **Save GUI** *.xml ***param*** **file**

Run Tab → *Working folder for simulations and results files, final individuals' file, replicates (same conf.txt) or multiple conf.txt in batch mode*

⑤ **Create** or **Select** the **type.txt** file

⑥ **Create** or **Select** the **conf.txt** file

Launch gMetapop_CORE → *click on Run in GUI Run tab (both OS)*
→ ***CORE*** *Command lines in run_gMetapop.bat/.sh*

Plot.gMperGen.r

⑦ **Unfolding of Simulations**

Figure 3.5.1.1
main initial demographic conditions.

Figure 3.4.4.1
algorithm for the assignment of diploid genotypes to offspring individuals

Figure 3
typical life cycle
(demography with possible overlapping generations , genetics, stochastic processes…etc).

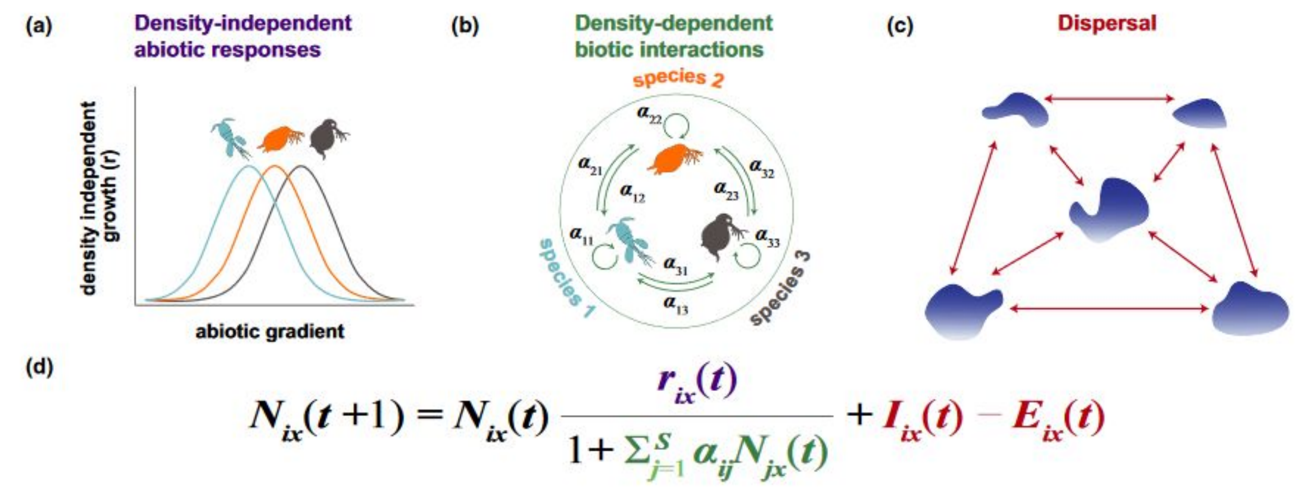
⑧ **Check** *Run Log Window***.**
If « Normal Exit »,
→ **File/Default plot** of res1_per_gen_1.txt **file**
→ **Or custom plot**

gMetapop (2024)

Part 2. Process-based approaches

- C. Stochastic simulation models

One relatively general metacommunity model has been proposed by Thompson et al. (2020)



$$N_{ix}(t+1) = N_{ix}(t)\frac{r_{ix}(t)}{1+\sum_{j=1}^{S}\alpha_{ij}N_{jx}(t)} + I_{ix}(t) - E_{ix}(t)$$

Stochasticity is modelled as the random draw of the values of E(t) and N(t)

Conclusion

Ordination methods

Pros:

- Very large litterature
- Widely used/applicable
- Able to work on (very) large datasets

Cons:

- Links with theory unclear
- So many methods
- Sometimes controversial

JSDMs

Pros:

- Sophisticated models with will for linking components to processes
- Very flexible
- Can assess relationship between species traits/phylo. and 'niche'

Cons:

- Still SDMs with residual correlation as criterion
- Results interpretation not always clear

Process-based models

Pros:

- Explicit processes and link to theory
- Can be customized to specific system based on knowledge
- Can address 'what if' questions

Cons:

- Greedy in data & comp. ressources
- Limited in the number of species they can handle
- Highly parametric

Conclusion

- So what?

Conclusion

- So what?

  So, no good method!

  “In conclusion, we find no reason why a proponent of either of the two extremes of correlative and process-based species distribution modelling should hold the moral high ground.‘ Correlationists’ should be humble: their model’s success maybe due to spurious correlations. ‘Mechanists’ should be unassertive about their approach, because they will only find effects of processes that they included. Either approach must comply with nature, statistically or mechanistically, and be aware of the kinds of questions they are best suited to answer.” Dormann et al. 2012

To go further

Main reference textbooks:

Legendre & Legendre. **2012**. *Numerical Ecology.*

Vellend. **2016**. *The Theory of Ecological Communities.*

Leibold & Chase. **2018**. *Metacommunity Ecology.*

Mittelbach & McGill. **2019**. *Community Ecology.*

Ovaskainen & Abrego. **2020**. *Joint Species Distribution Modelling*

Ready for practicals?

- questions on morning session

Afternoon: practicals

1. Simulate data/test methods

Simulate with the following code:

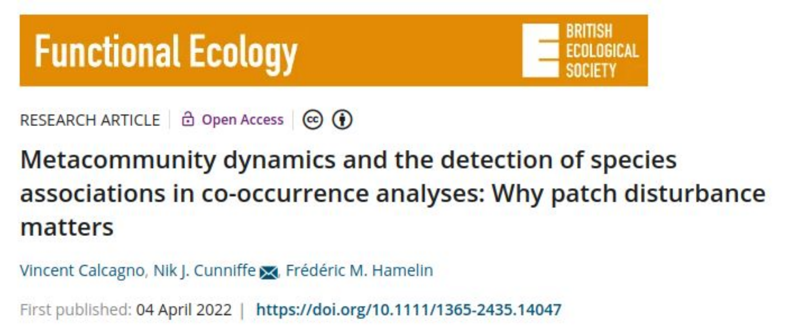
https://github.com/mxdub/TMDSpatial

Try different analyses
→Does it work?

To install : JAGS
R packages : vegan, R2jags, Hmsc
And
devtools::install_github('mxdub/TMDSpatial')

2. The effects of patch disturbance

Article walkthrough:



Functional Ecology

BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE | Open Access | 🅭 ⓘ

Metacommunity dynamics and the detection of species associations in co-occurrence analyses: Why patch disturbance matters

Vincent Calcagno, Nik J. Cunniffe ✉, Frédéric M. Hamelin

First published: 04 April 2022 | https://doi.org/10.1111/1365-2435.14047

Go fetch the R markdown at:
https://github.com/nikcunniffe/MetacommunityDynamics

Practical 2: the effects of patch disturbance

1. What is patch disturbance?

2. How do you include it in Levins' metapopulation model?

   (write down the equations)

   (walk through model formulation: pach age, equilibrium...)

3. What consequences for species co-occurrence patterns?

4. Test the expectations/predictions