Courtesy V. Deblauwe

# Structure spatiale:

## des processus au conséquences dans les écoystèmes arides

**Sonia Kéfi**

SANTA FE INSTITUTE

Institut des Sciences de l'Evolution-Montpellier

http://photography.nationalgeographic.com/

http://photography.nationalgeographic.com/

http://photography.nationalgeographic.com/

http://photography.nationalgeographic.com/

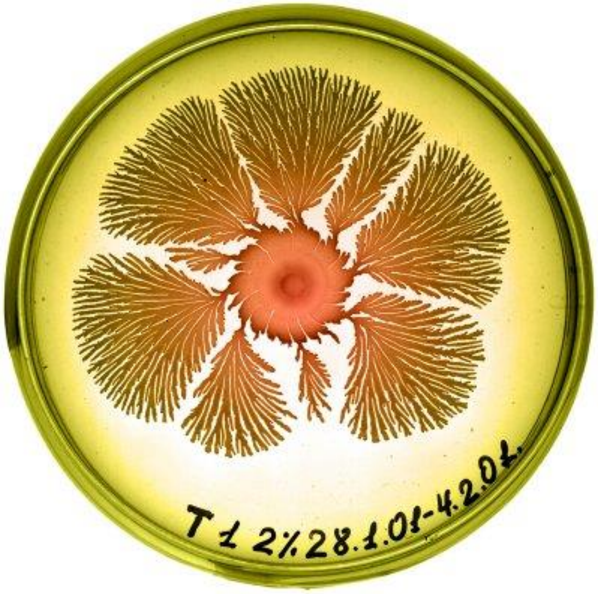

http://photography.nationalgeographic.com/

*“It is impossible not to be fascinated and enthralled with the wealth, diversity and beauty of pattern in biology”*

JD Murray

Mathematical Biology (2011)

# Colonies bactériennes

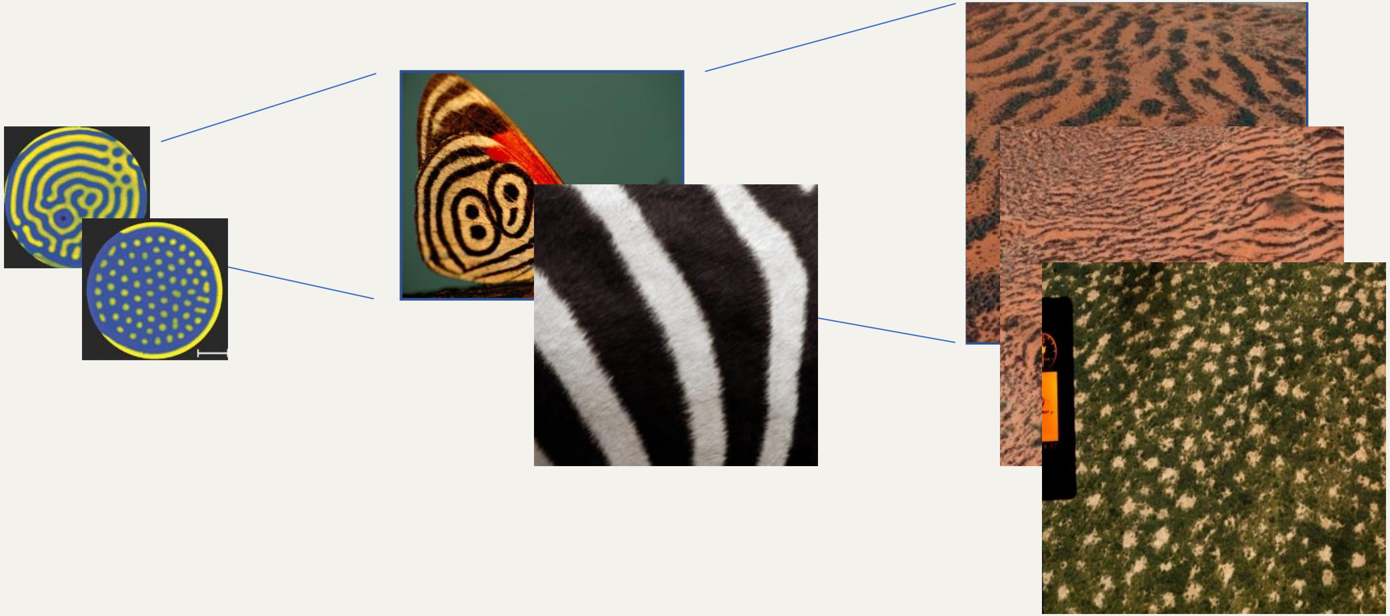



Fractal bacteria
http://star.tau.ac.il/~eshel/gallery.html


Van de Koppel et al., Science, 2008

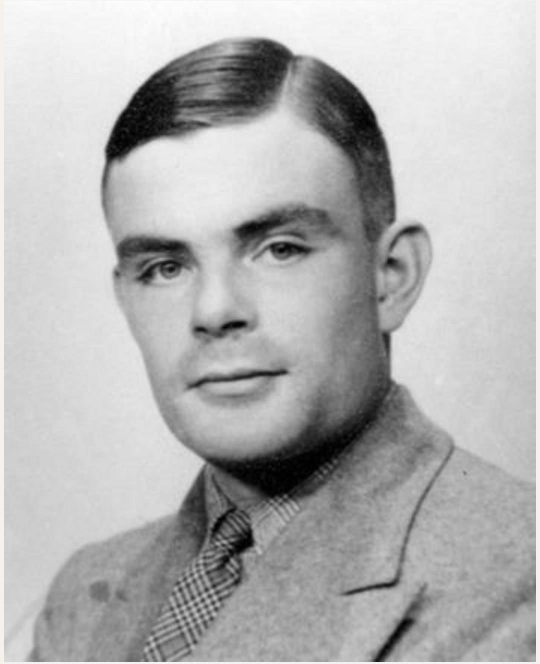

Courtesy J. van de Koppel

# Différentes formes
# Differentes échelles



Quels sont les mécanismes sous-jacents ?

# Alan Turing

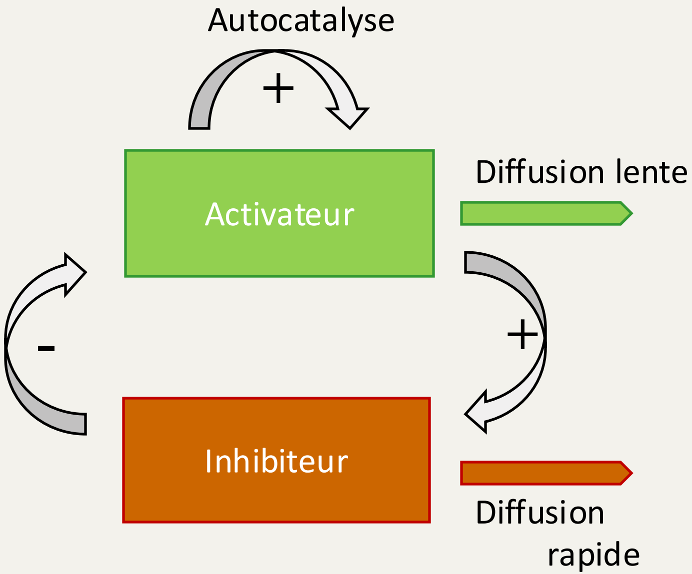


The chemical basis of morphogenesis, 1952

# Mécanisme d'activation-inhibition

Turing, 1952

"The chemical basis of morphogenesis"




Turing, Philos. Trans. Roy. Soc. London B, 1952

# Equations d'activation-inhibition

**Activateur** $$\frac{\partial a}{\partial t} = \frac{\rho a^2}{h} - \mu a + D_a \frac{\partial^2 a}{\partial x^2}$$

**Inhibiteur** $$\frac{\partial h}{\partial t} = \rho a^2 - \nu h + D_h \frac{\partial^2 h}{\partial x^2}$$

Meinhardt, 2008

# Equations d'activation-inhibition

Autocatalyse

**Activateur** $$\frac{\partial a}{\partial t} = \frac{\boxed{\rho a^2}}{h} - \mu a + D_a \frac{\partial^2 a}{\partial x^2}$$

**Inhibiteur** $$\frac{\partial h}{\partial t} = \rho a^2 - \nu h + D_h \frac{\partial^2 h}{\partial x^2}$$

Meinhardt, 2008

# Equations d'activation-inhibition

**Activateur** $$\frac{\partial a}{\partial t} = \frac{\rho a^2}{\boxed{h}} - \mu a + D_a \frac{\partial^2 a}{\partial x^2}$$

Ralentissement par h

**Inhibiteur** $$\frac{\partial h}{\partial t} = \rho a^2 - \nu h + D_h \frac{\partial^2 h}{\partial x^2}$$

Meinhardt, 2008

# Equations d'activation-inhibition

**Activateur** $$\frac{\partial a}{\partial t} = \frac{\rho a^2}{h} - \boxed{\mu a} + D_a \frac{\partial^2 a}{\partial x^2}$$

déclin

**Inhibiteur** $$\frac{\partial h}{\partial t} = \rho a^2 - \nu h + D_h \frac{\partial^2 h}{\partial x^2}$$

Meinhardt, 2008

# Equations d'activation-inhibition

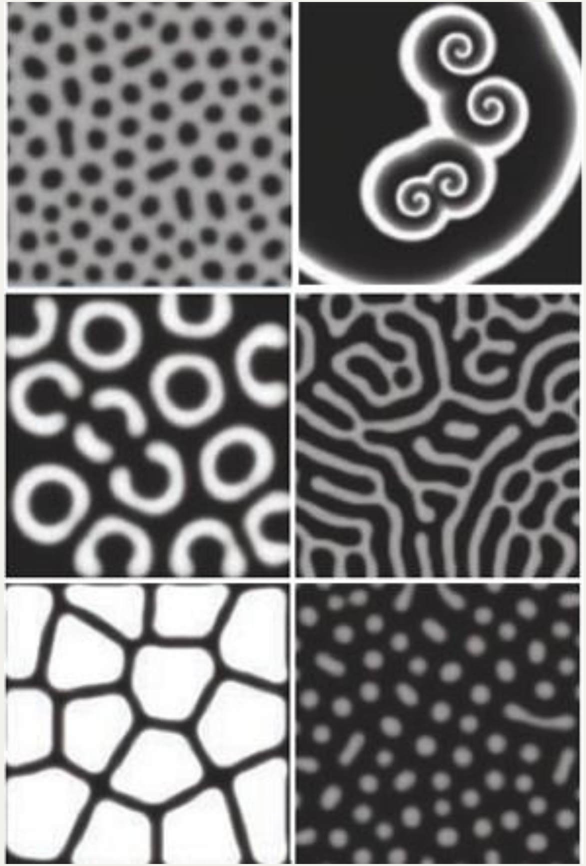
**Activateur** $$\frac{\partial a}{\partial t} = \frac{\rho a^2}{h} - \mu a + D_a \frac{\partial^2 a}{\partial x^2}$$

**Inhibiteur** $$\frac{\partial h}{\partial t} = \rho a^2 - \nu h + D_h \frac{\partial^2 h}{\partial x^2}$$

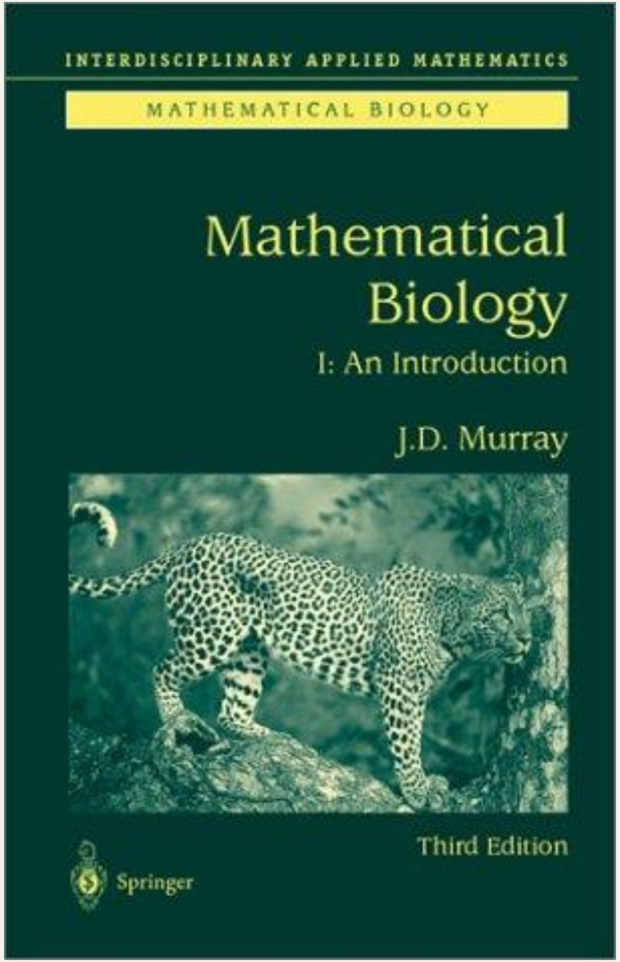
**Structuration spatiale si $D_a << D_h$**

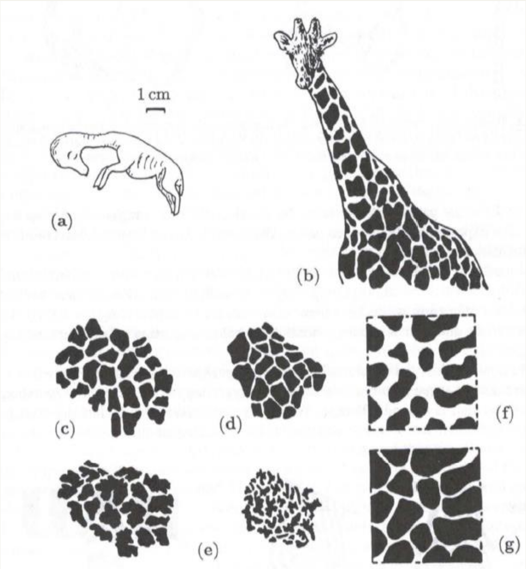
Meinhardt, 2008

# Equations d'activation-inhibition



http://www.fbs.osaka-u.ac.jp/labs/skondo/paper/watanabe2012.pdf


INTERDISCIPLINARY APPLIED MATHEMATICS
MATHEMATICAL BIOLOGY
Mathematical Biology
I: An Introduction
J.D. Murray
Third Edition
Springer


1 cm
(a)
(b)
(c)
(d)
(e)
(f)
(g)

# Transposition aux écosystèmes ?

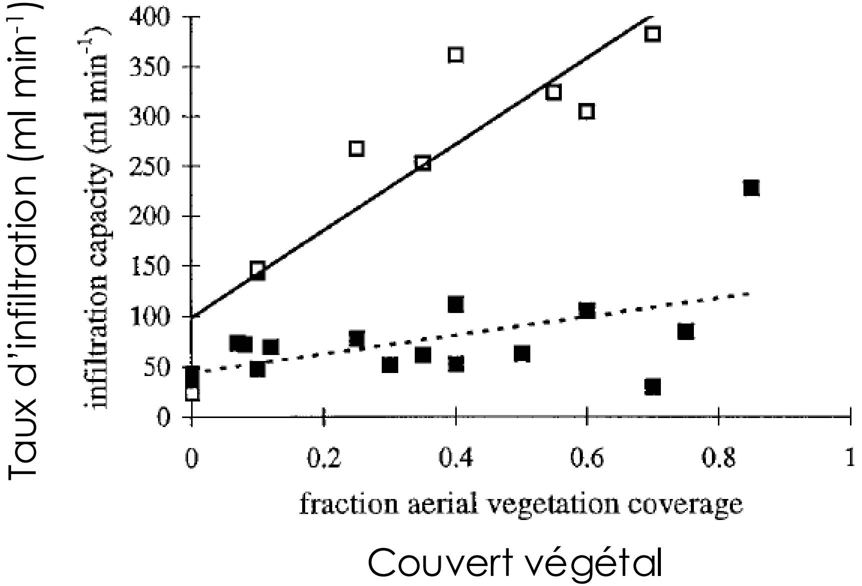
# Exemple des écosystèmes arides

Végétation

Eau de ruissellement

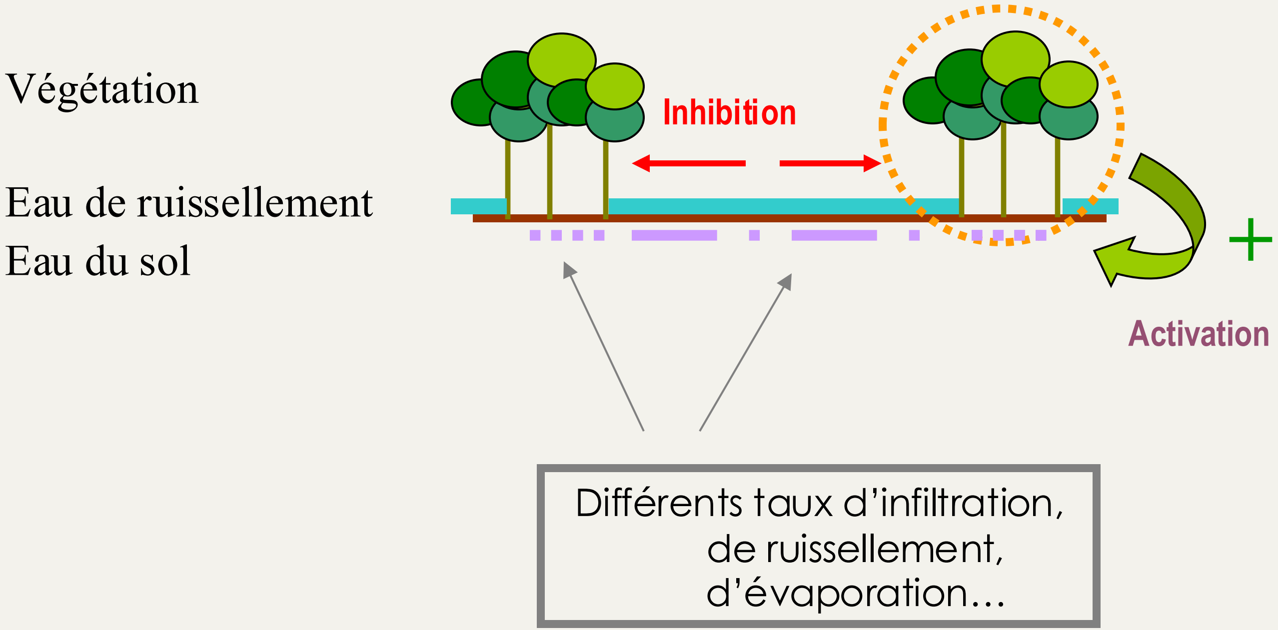
Eau du sol

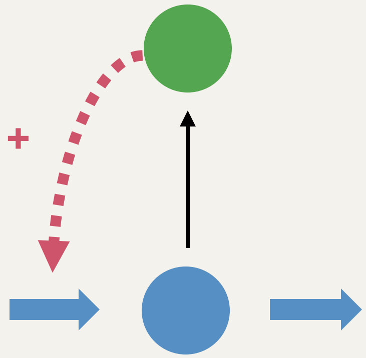
# Exemple des écosystèmes arides

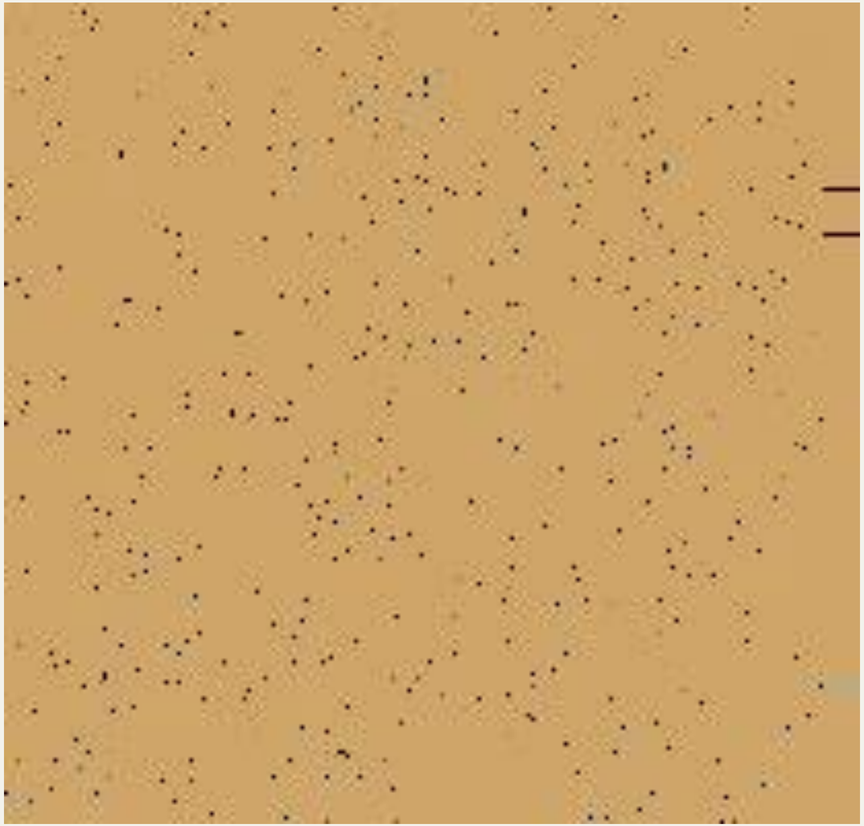



Rietkerk et al. 2000

# Exemple des écosystèmes arides





black: vegetation

brown: bare soil

Rietkerk et al. 2002 Am. Nat.

# Auto-organisation

# Mécanisme d'activation-épuisement

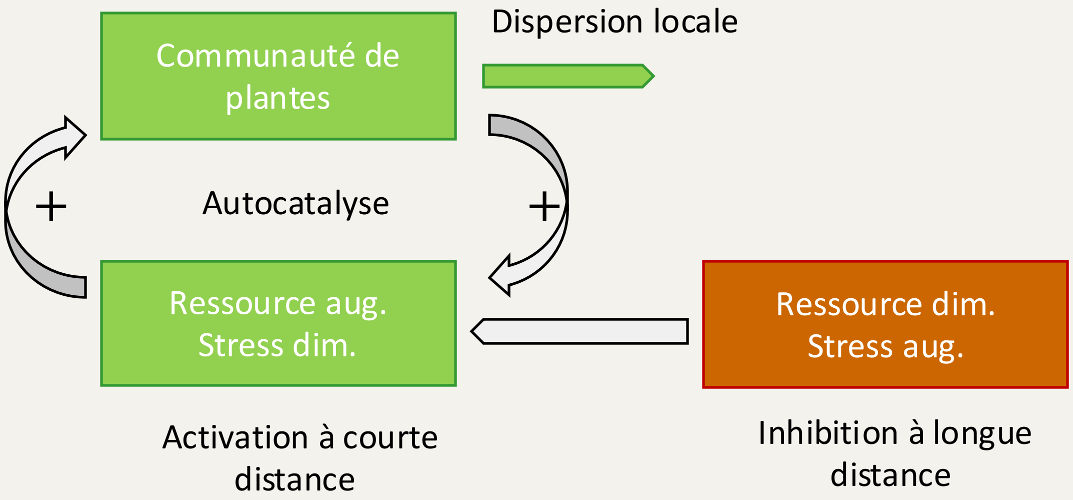



Fig. modifiée de Rietkerk et van de Koppel, TREE, 2008

# Scale-dependent feedback

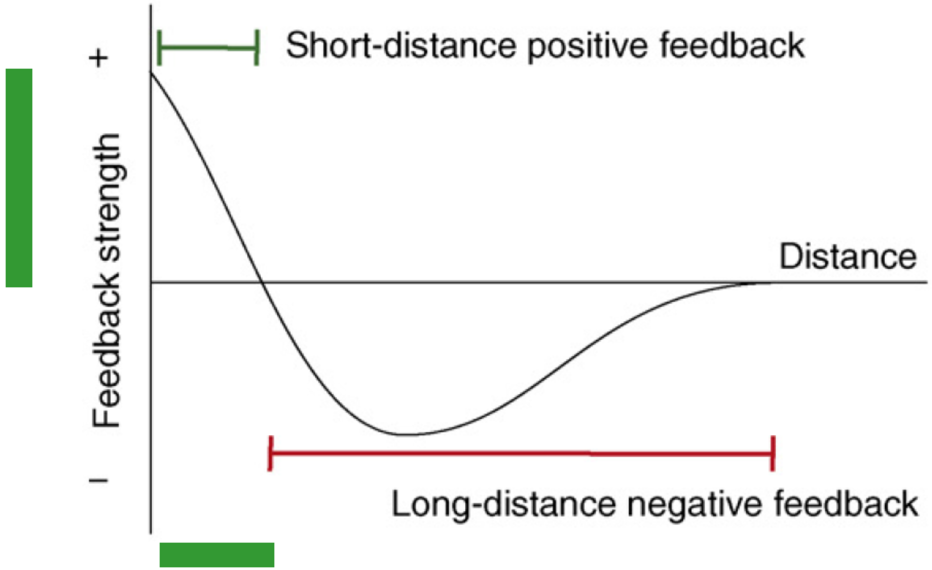
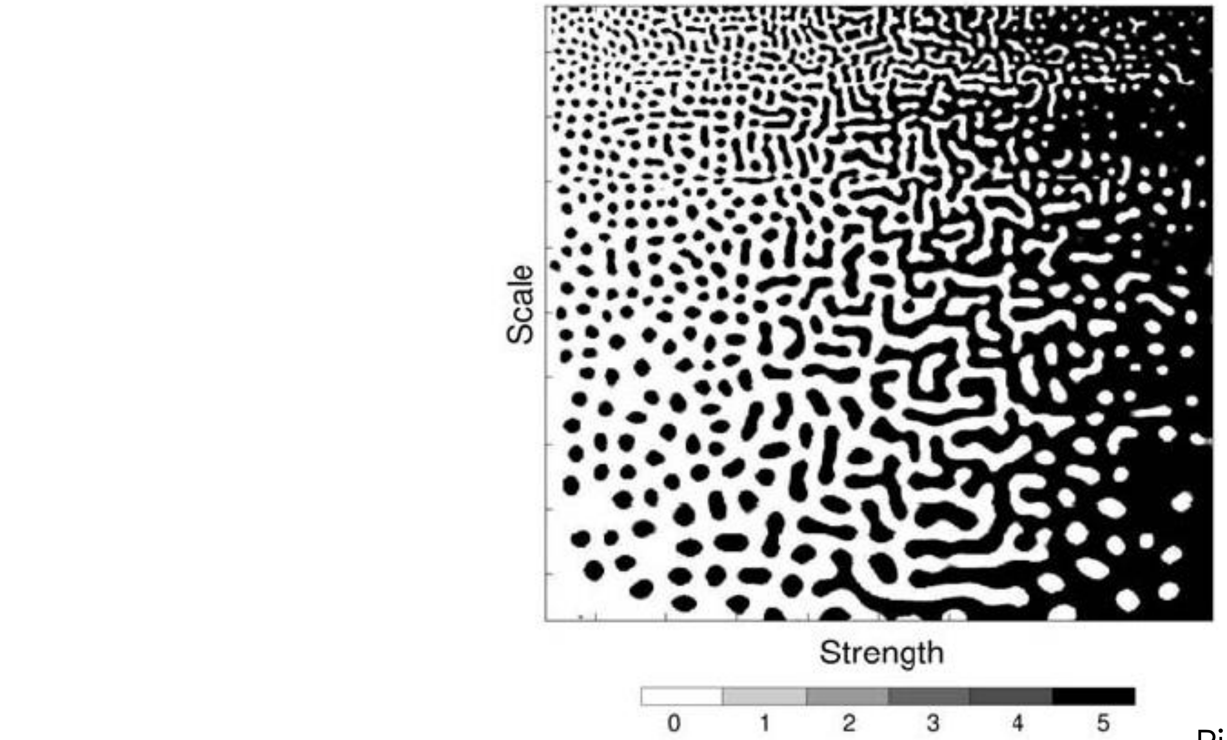



Fig. de Rietkerk et van de Koppel, TREE, 2008

# Motifs réguliers




Rietkerk et al., Am Nat, 2002

Kéfi et al., Theor Ecol, 2010

# Motifs réguliers

650 m

800 m

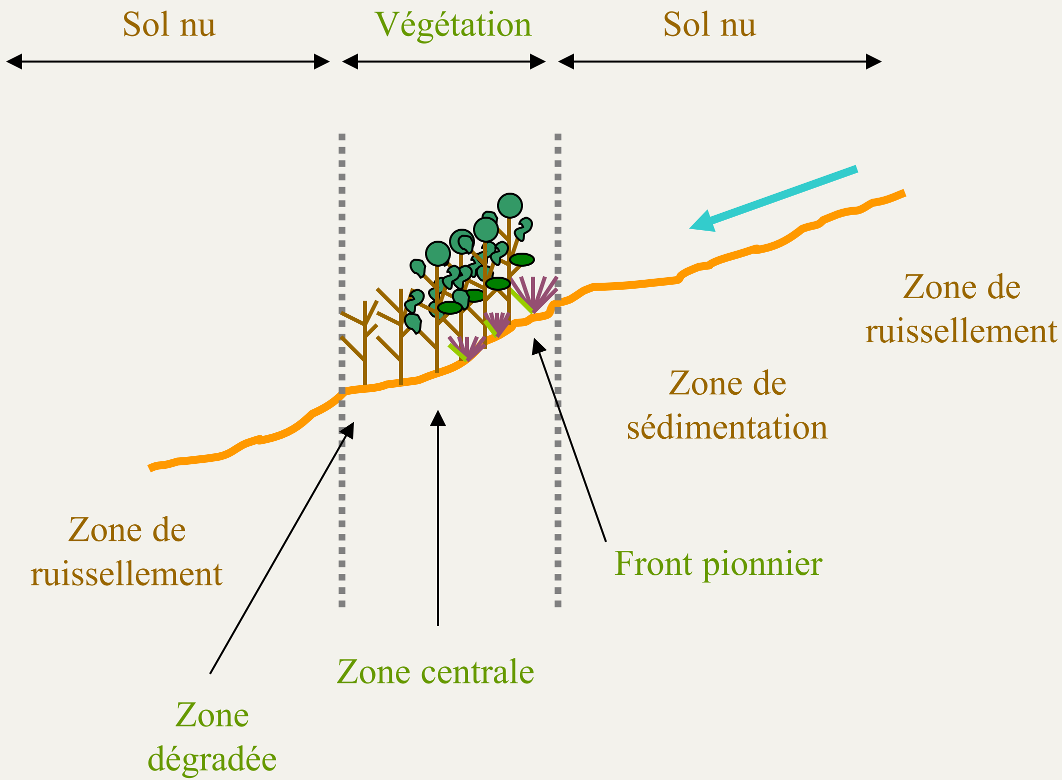
Courtesy S Prince
Univ of Maryland

# Motifs réguliers


Rietkerk et al., Am Nat, 2002

Kéfi et al., Theor Ecol, 2010

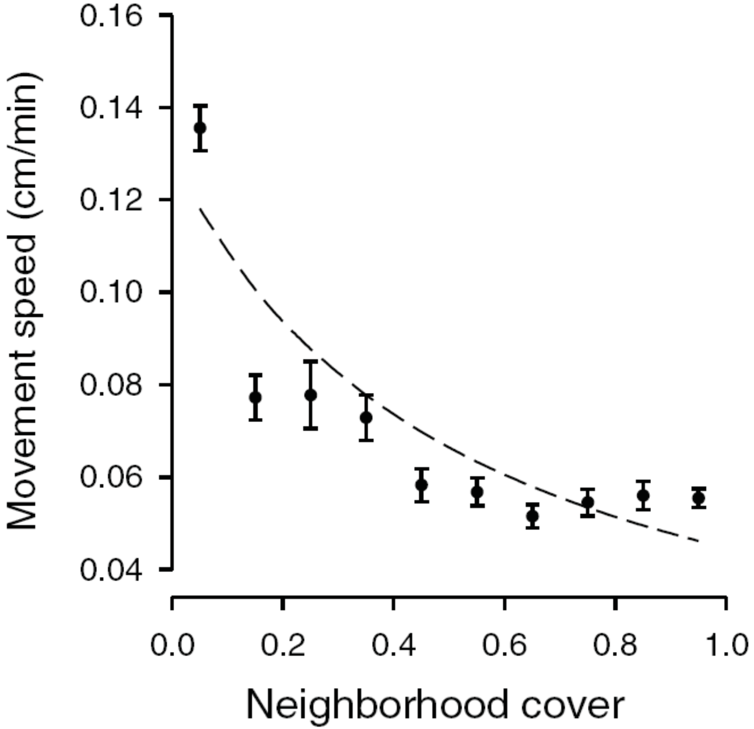
# Brousse tigrée

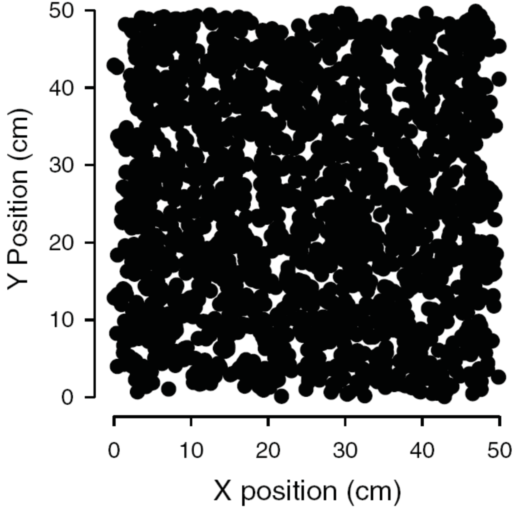


Preuve expérimentale ?


Van de Koppel et al., Science, 2008

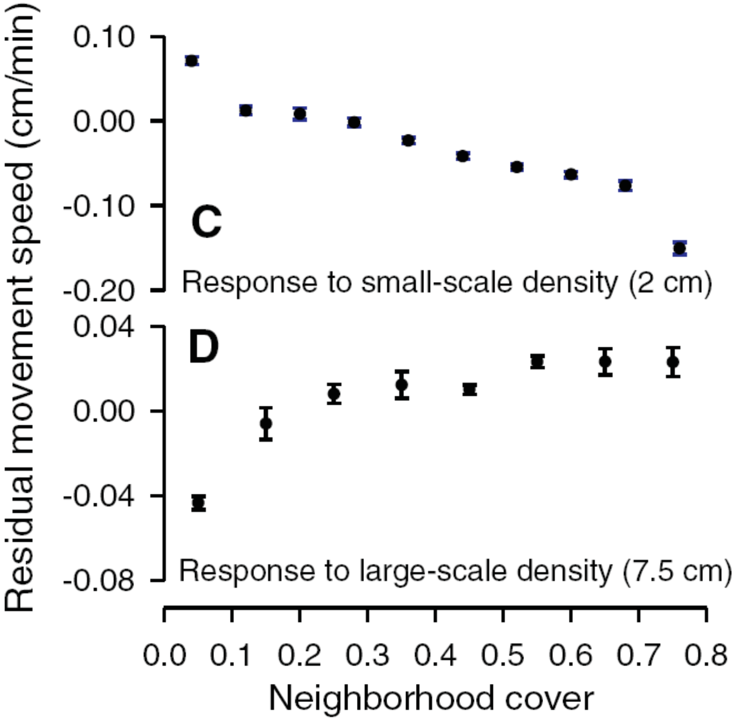
# Mécanismes sous-jacents

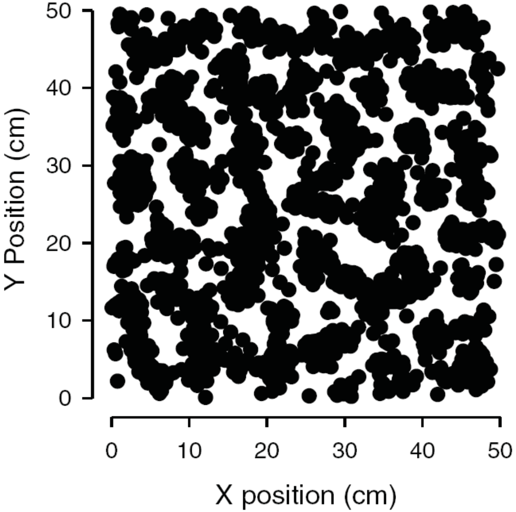



Van de Koppel et al., Science, 2008

# Mécanismes sous-jacents




Van de Koppel et al., *Science*, 2008

# Scale-dependent feedback

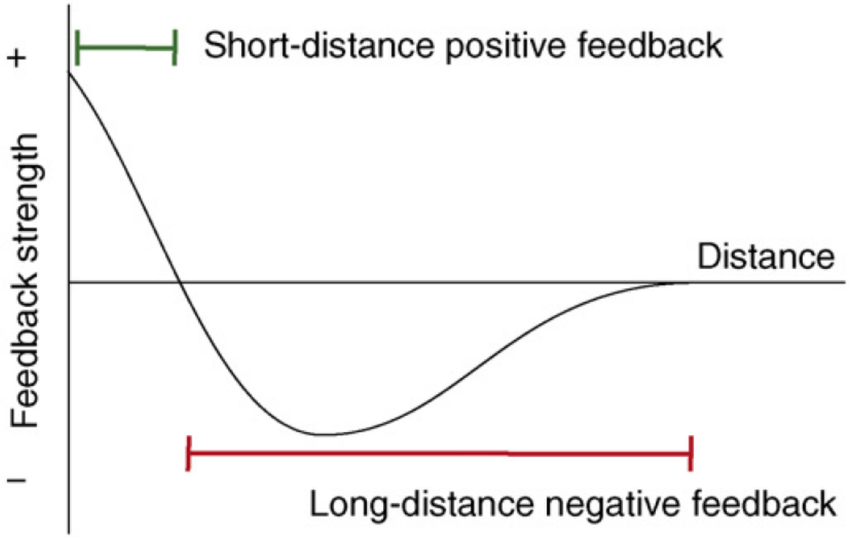


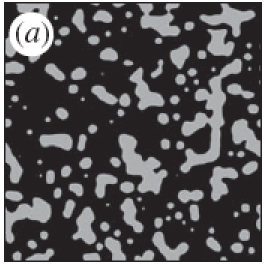

Fig. de Rietkerk et van de Koppel, TREE, 2008

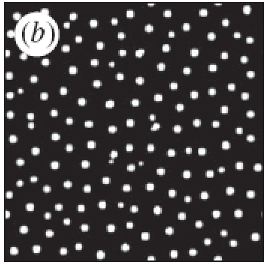
**Échelle de la facilitation** ⟷ **Échelle de la compétition**

Von Hardenberg, 10, proc B
Manor & Shnerb, 08, JTB
Kéfi et al. 2007, 2010

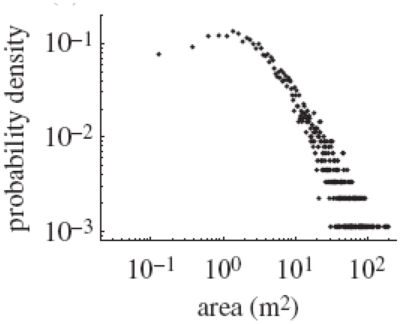
## Système dominé par la facilitation

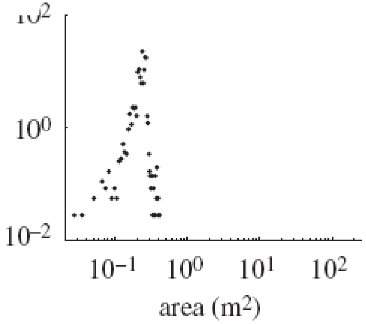
## Système dominé par la compétition




**Scale-free**



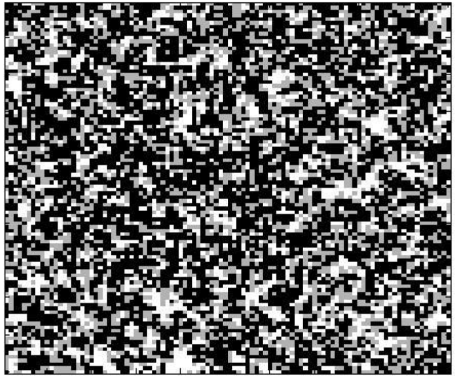

**Échelle charactéristique**
**Motifs périodiques, « de Turing »**

Von Hardenberg, 10, proc B
Manor & Shnerb, 08, JTB

# Motifs irréguliers

**States (σ):**

- degraded (-)
- empty (0)
- vegetated (+)



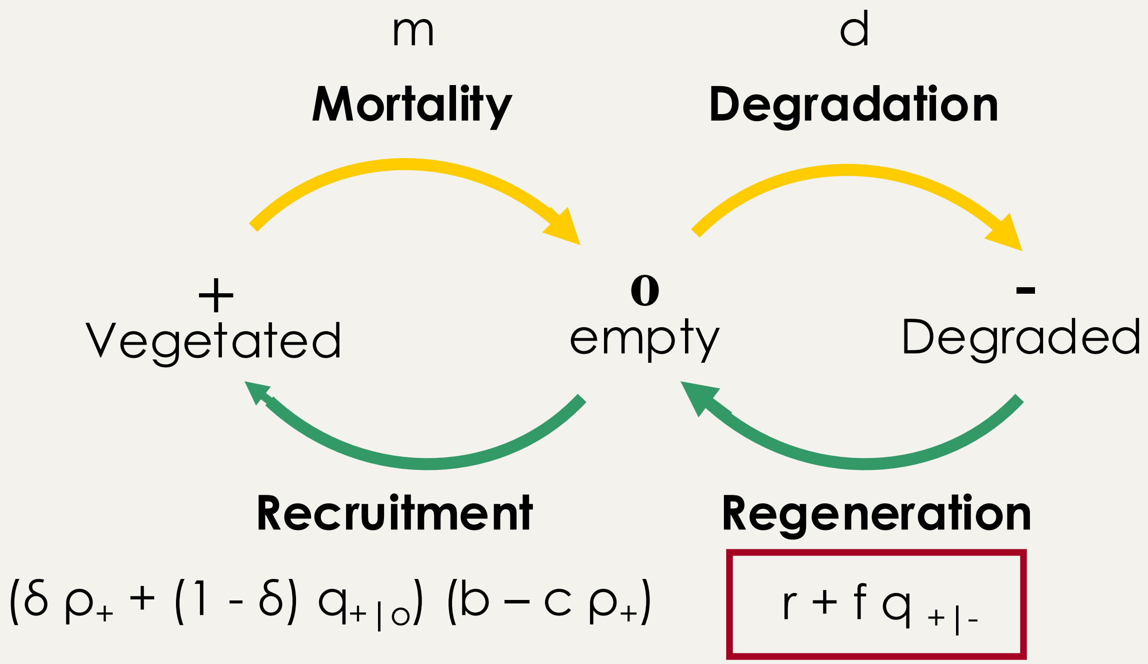
b=0.9 r=0.9

**Variables:**

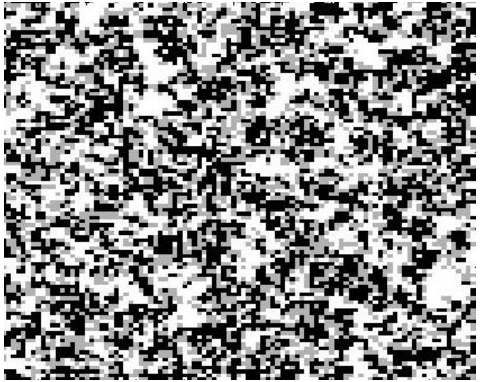
$\rho_\sigma$ : proportion of sites σ

$q_{\sigma|\sigma'}$ : proportion of sites σ in the neighborhood of a site σ'

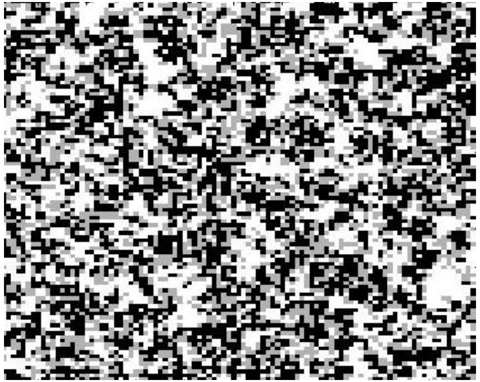
Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018



m
**Mortality**
d
**Degradation**
+
Vegetated
0
empty
-
Degraded
**Recruitment**
$(\delta \rho_{+} + (1 - \delta)\, q_{+|0})\, (b - c\, \rho_{+})$
**Regeneration**
$\boxed{r + f\, q_{+|-}}$

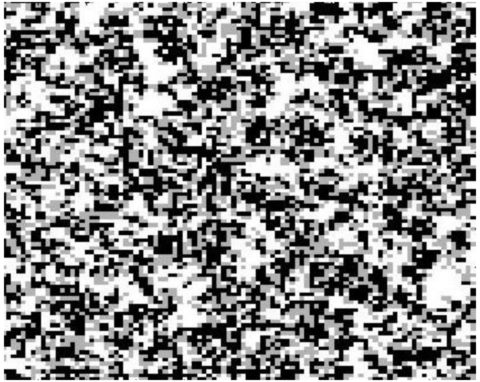


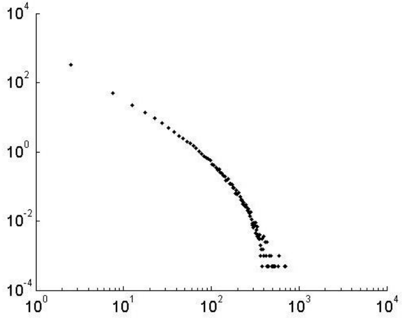
Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018



“Patch” = group of adjacent vegetated cells
(4 neighbors)

Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

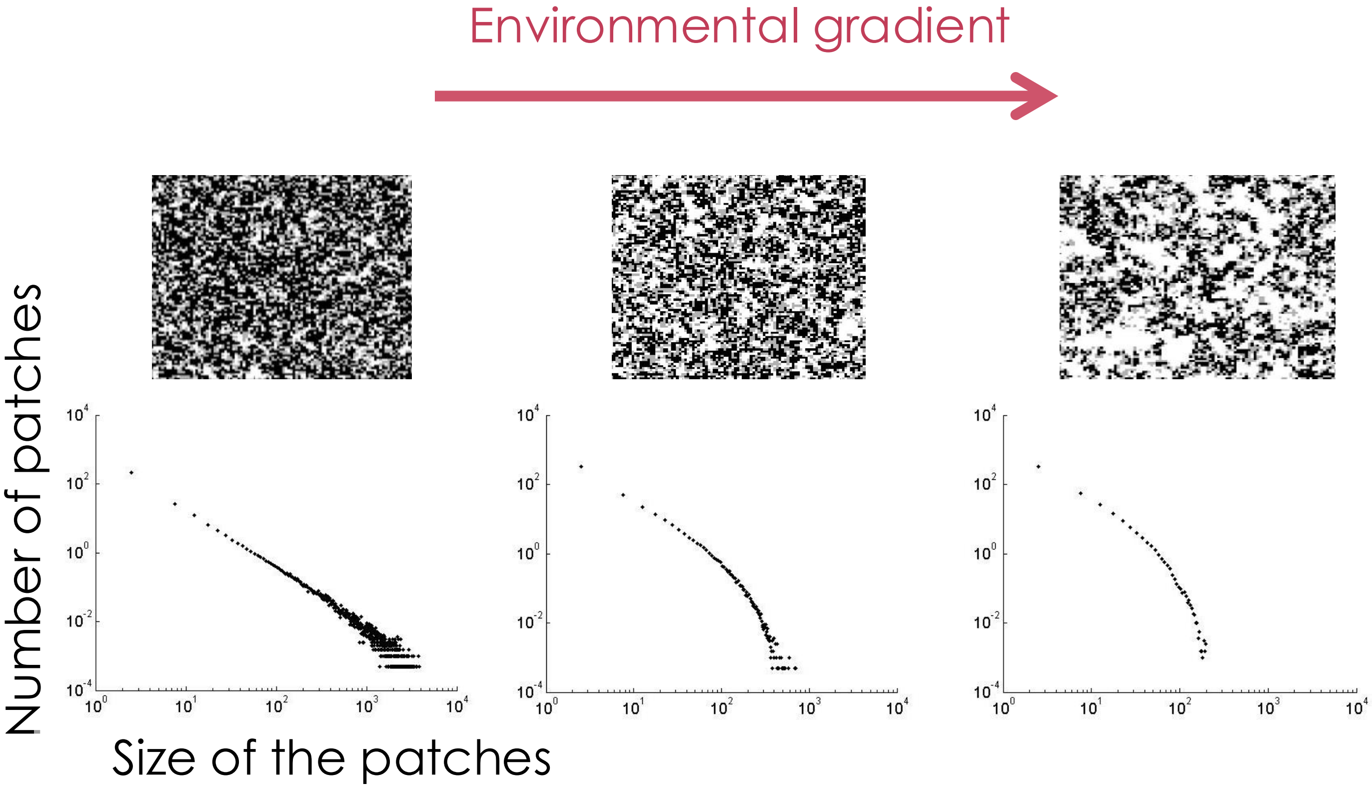





Number of patches

Size of the patches

Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018




Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

# Mécanismes → structure spatiale

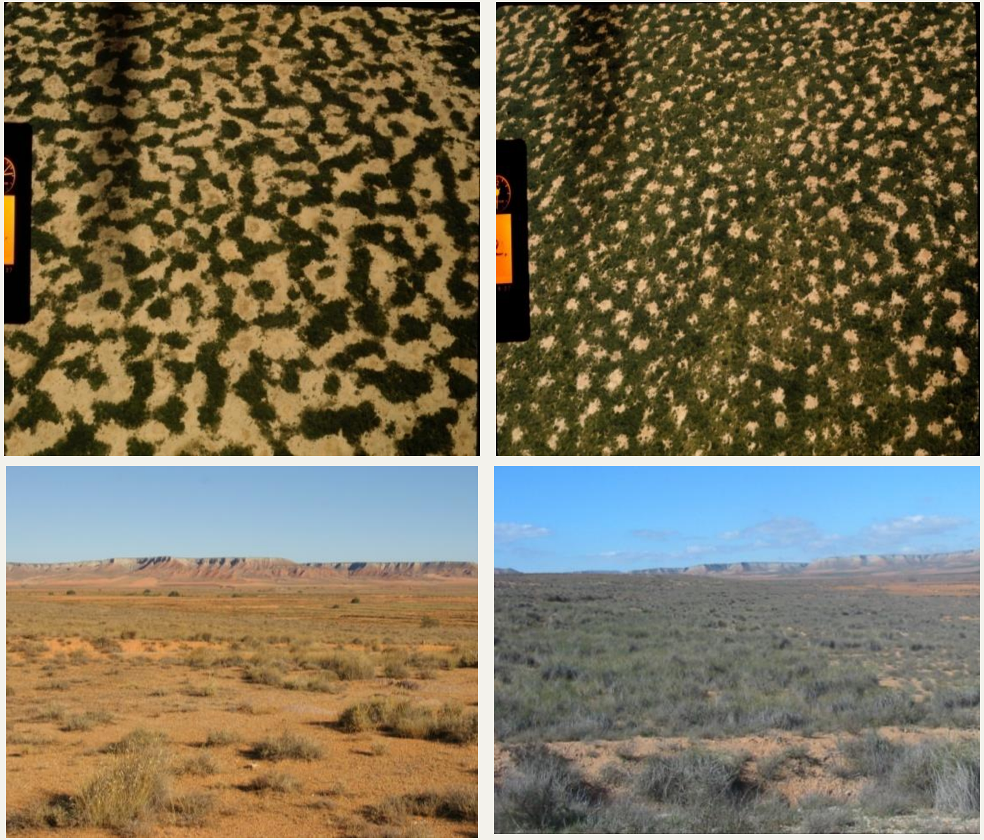
**Échelle de la facilitation** ↔ **Échelle de la compétition**

Système dominé par la facilitation

**Motifs irréguliers**

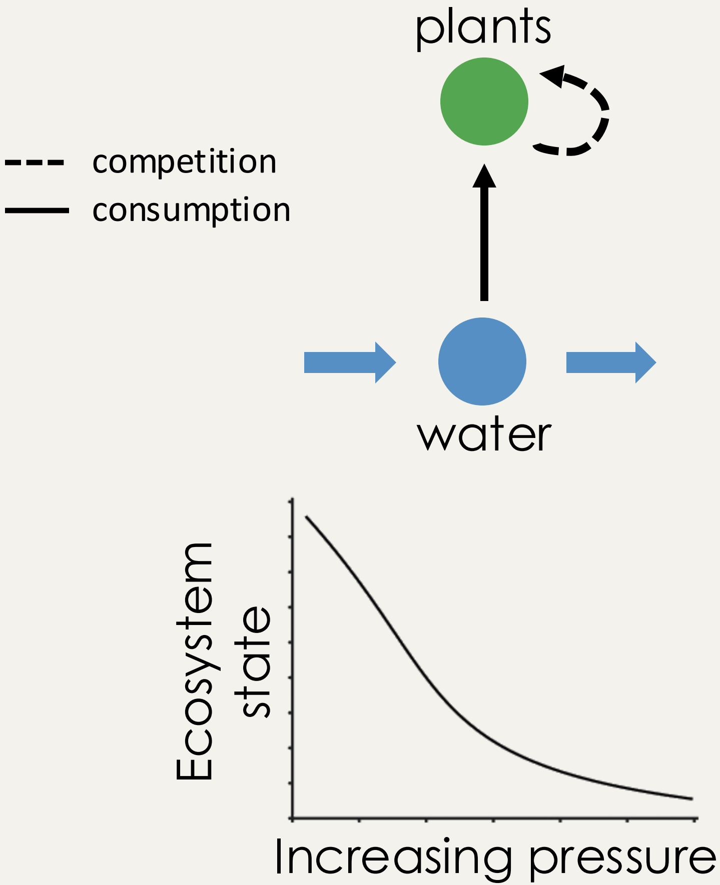
Système dominé par la compétition

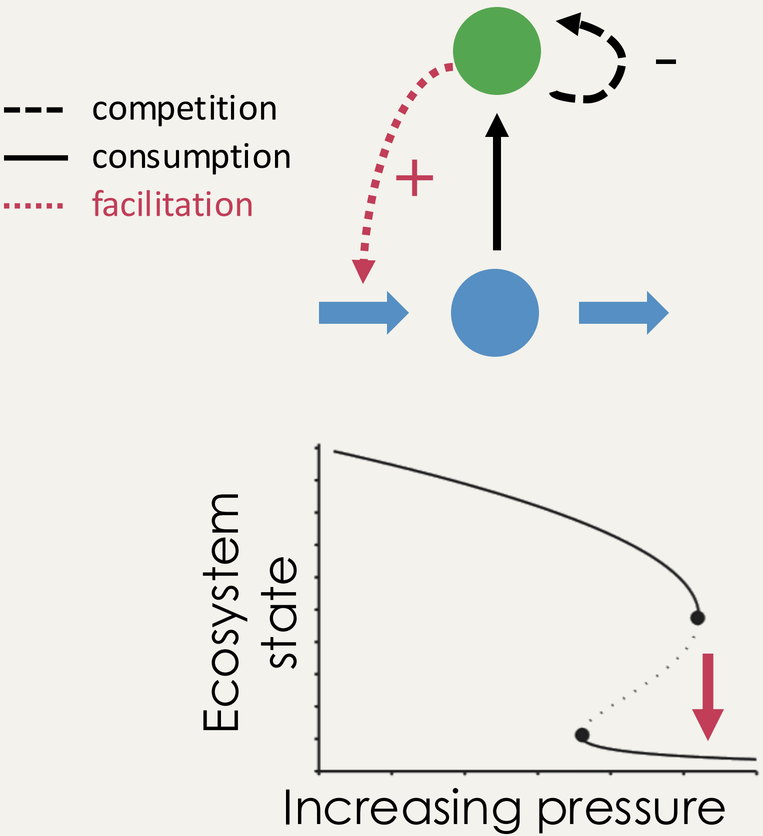
**Motifs réguliers**



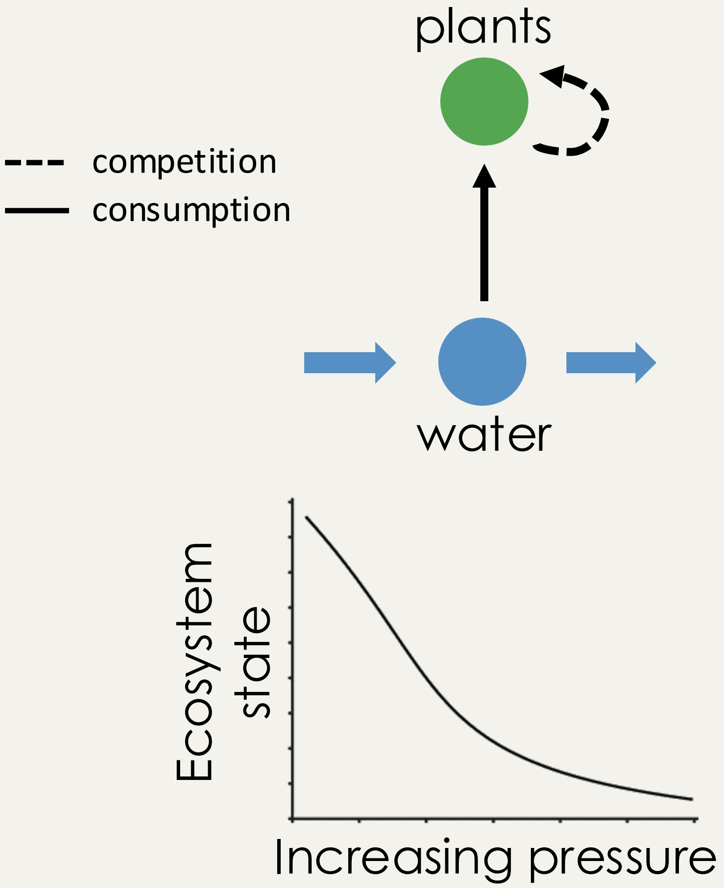
Courtesy S Prince, Univ of Maryland

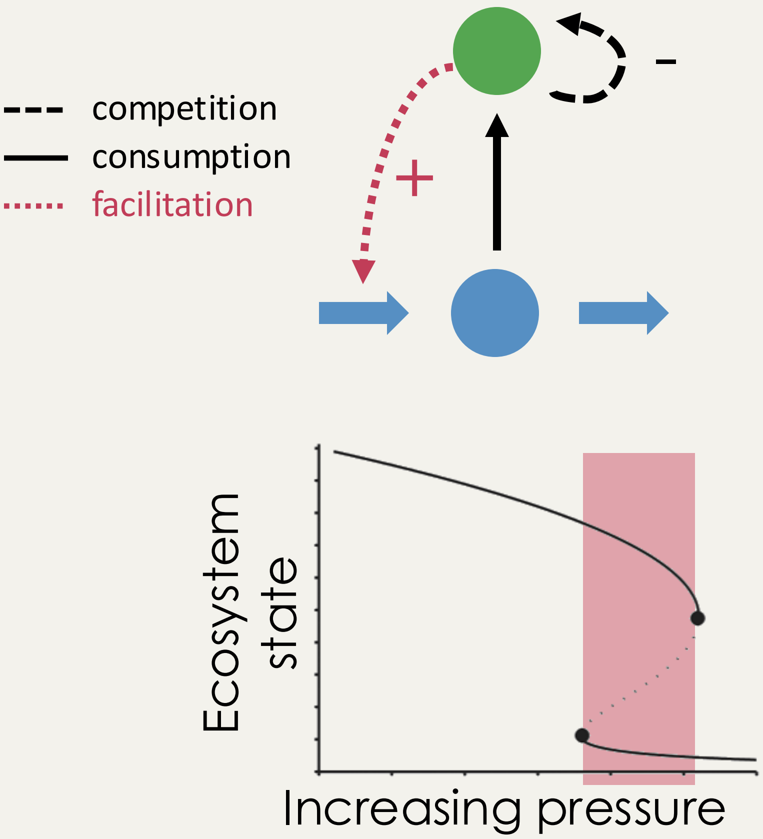
rôle clé de la facilitation pour la structure spatiale mais aussi : une autre conséquence



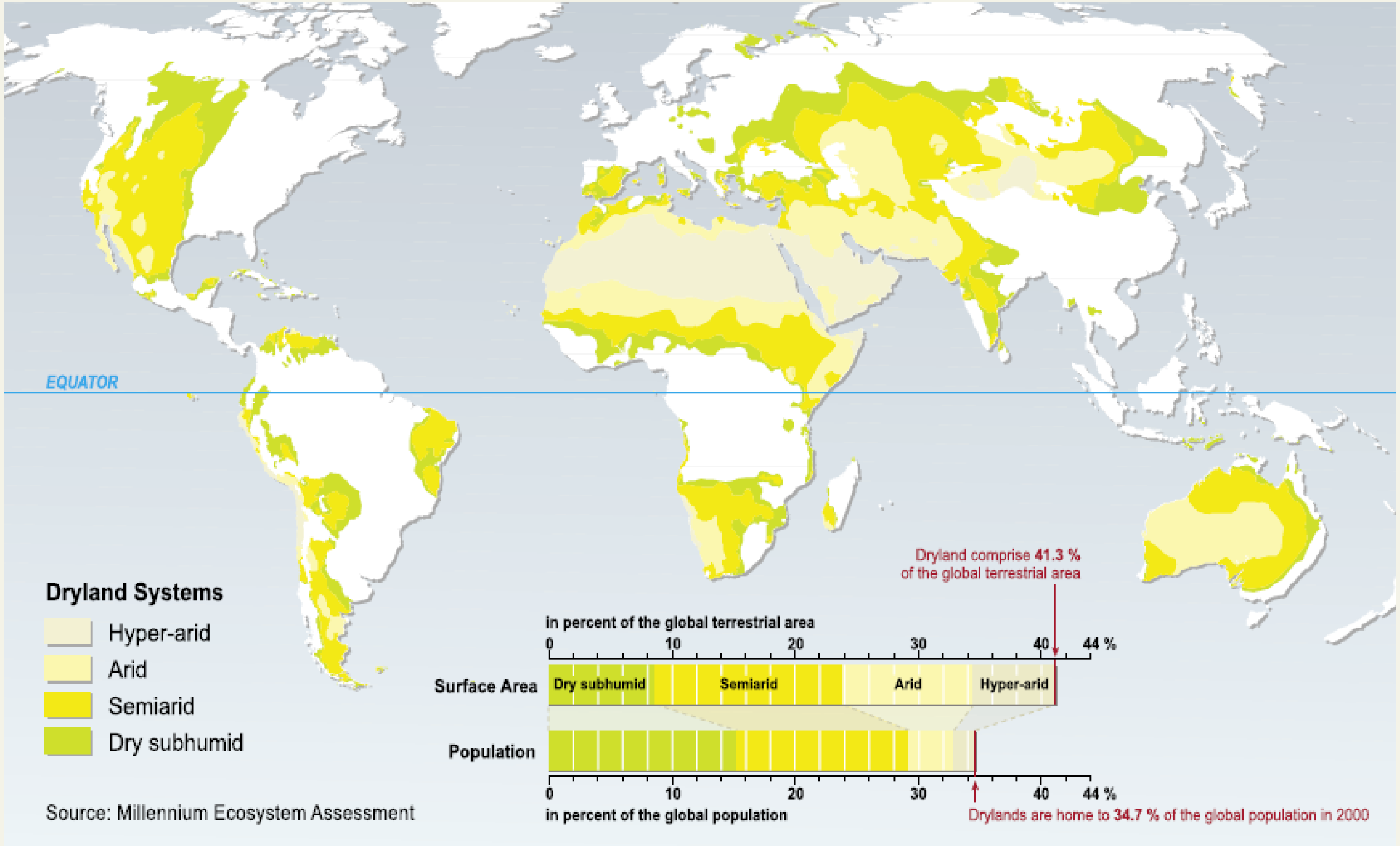

Rietkerk *et al.* 2002, Am Nat
Kéfi *et al.* 2007 TPB, Kéfi *et al.* 2010 TE




Rietkerk *et al.* 2002, Am Nat
Kéfi *et al.* 2007 TPB, Kéfi *et al.* 2010 TE

Les écosystèmes arides peuvent basculer




**41% of the Earth's land area**

**1/3 of the world population**

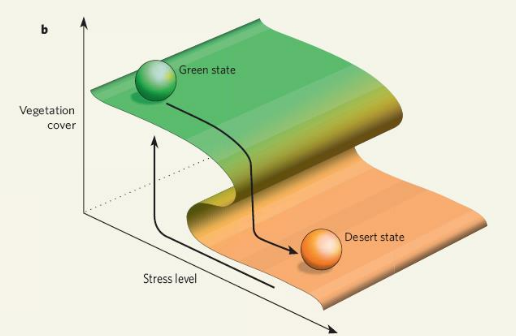
Identifier les zones fragiles ?

Facilitation

Shifts

?

Spatial organization




Rietkerk et al., Science, 2004

low pressure → high pressure

# Spatial structure changes along stress gradients

Von Hardenberg et al. 2001
Rietkerk et al. 2002, 2004
Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

# Spatial structure as an indicator of stress?

Von Hardenberg et al. 2001
Rietkerk et al. 2002, 2004
Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

# [break]

# [wrap up]

**Drylands show self-organized patterns**

Regular vs irregular patterns

Mecanisms: local facilitation + global competition

**Drylands can shift**: rapid, sometimes irreversible changes

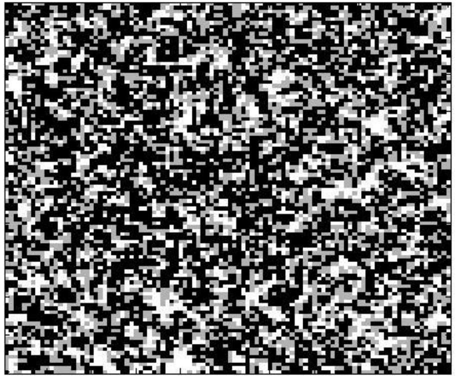
→ Can we find indicators?

→ Can spatial organisation help?

→ To design indicators, we need to learn how patterns change with stress.

**States (σ):**

- degraded **(-)**
- empty **(0)**
- vegetated **(+)**



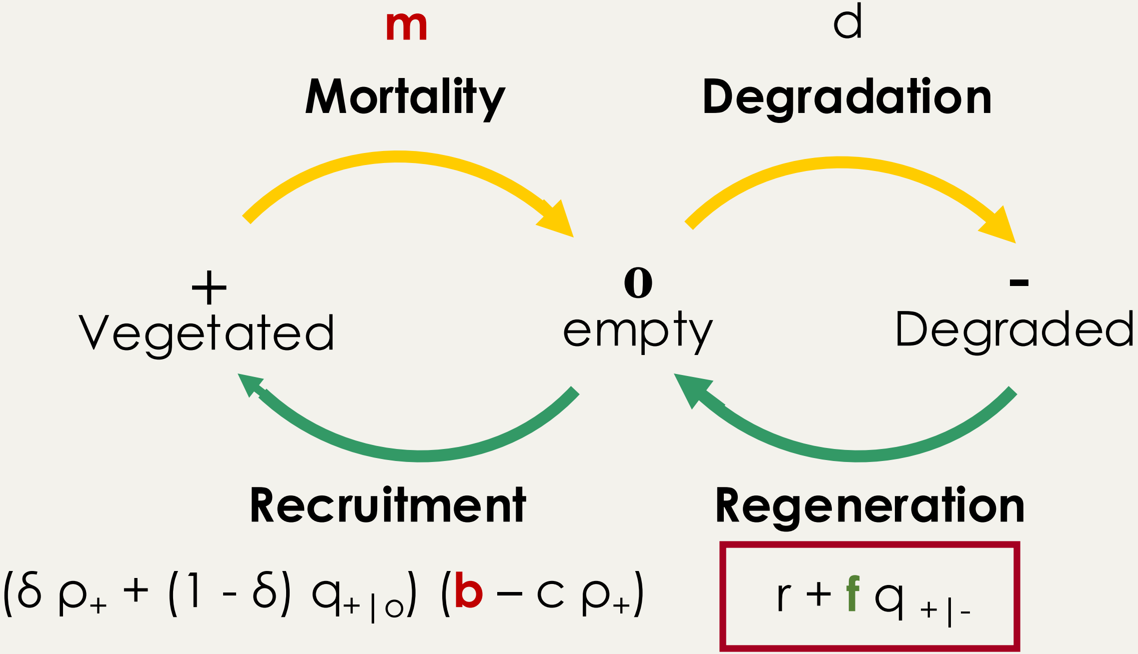
b=0.9 r=0.9

**Variables:**

$\rho_\sigma$ : proportion of sites σ

$q_{\sigma|\sigma'}$ : proportion of sites σ in the neighborhood of a site σ'

Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018




Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

Mean field approximation

Pair approximation

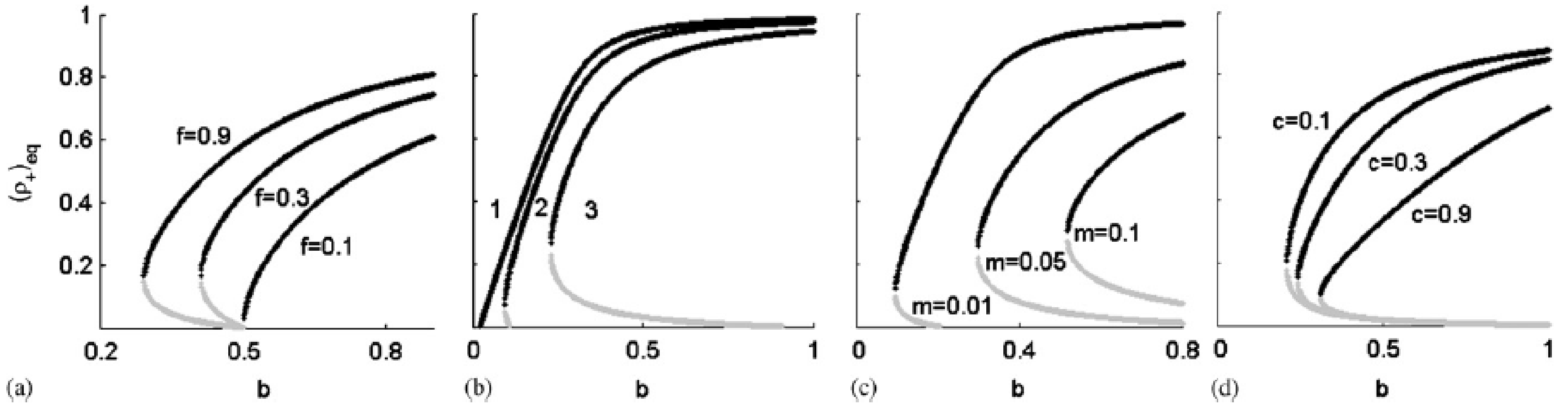
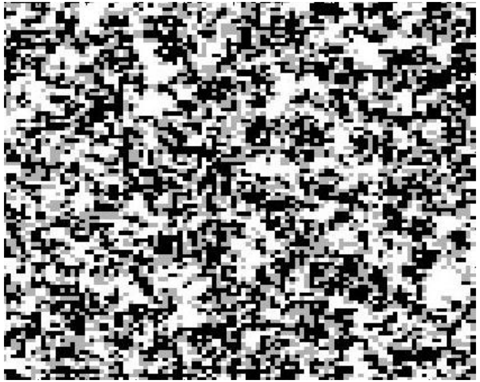
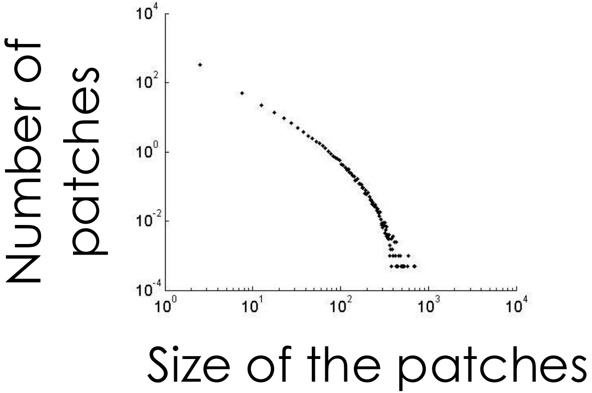



Fig. 1. Effects of the parameters on the bifurcation diagrams of the mean field model. On the ordinate, $(\rho_+)_{eq}$ is the global density of vegetation sites at equilibrium. For clarity, only non-trivial equilibria are traced. A lower $b$ value reflects more severe environmental conditions. In black: stable equilibria, in gray: unstable equilibria. The system is bistable for a certain range of environmental conditions. (a): Effect of facilitation ($f$). $m = 0.1$, $\delta = 0.1$, $c = 0.3$, $d = 0.2$, $r = 0.05$. (b): Effect of soil type ($r$ and $d$). $m = 0.01$, $c = 0.3$, $\delta = 0.1$, $f = 0.3$. 1: unsusceptible soil $r = 0.09$, $d = 0.1$, 2: $r = 0.03$, $d = 0.3$, 3: susceptible soil $r = 0.01$, $d = 0.9$. (c): Effect of mortality ($m$). $\delta = 0.1$, $r = 0.01$, $c = 0.3$, $d = 0.2$, $f = 0.3$. (d): Effect of competition intensity ($c$). $m = 0.1$, $d = 0.1$, $\delta = 0.1$, $r = 0.01$, $f = 0.9$. See Table 1 for the interpretation of the parameters that are not defined here.

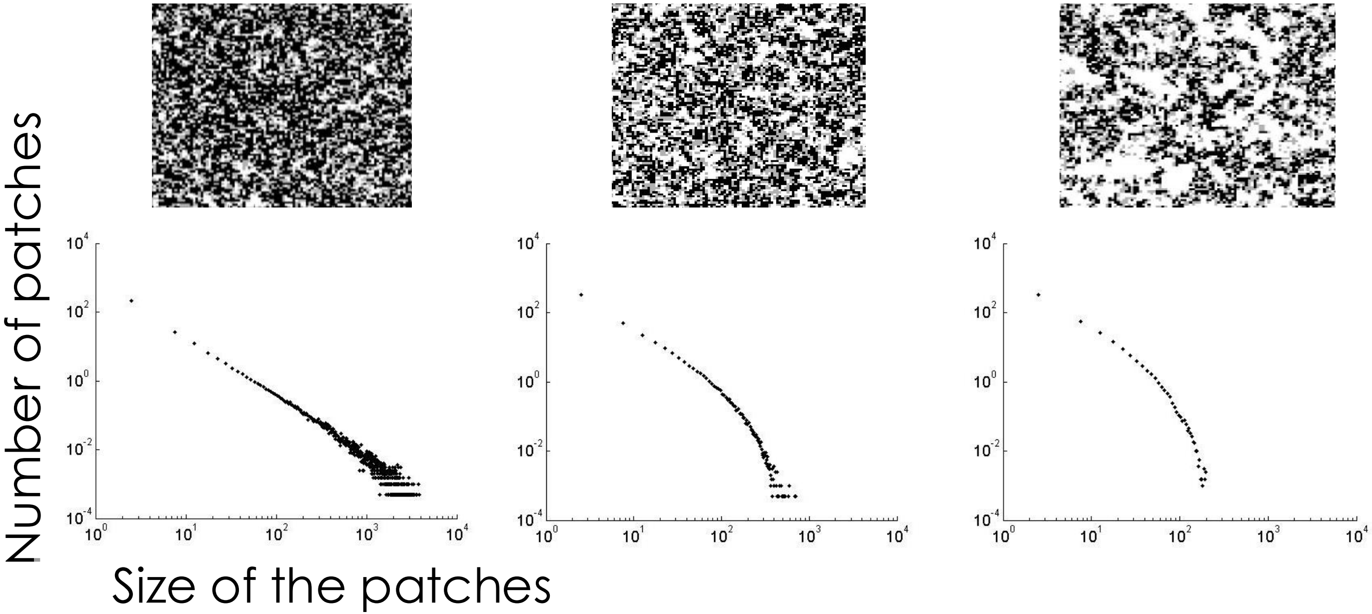
Kéfi et al. 2007, TPB






Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

Environmental gradient




Kéfi et al. 2007, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

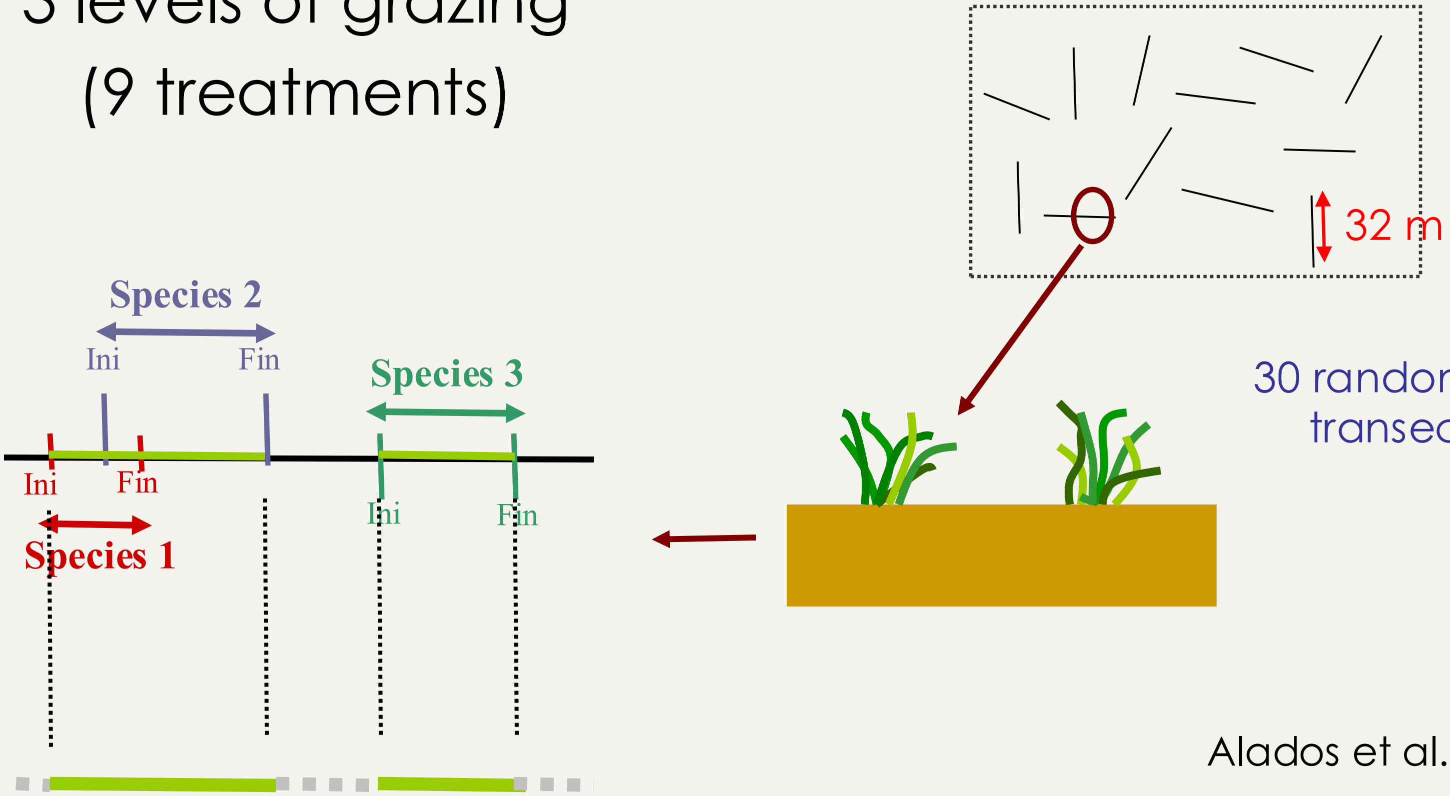
# Empirical validation?

| Spain | Greece | Marocco |
| --- | --- | --- |
|  |  |  |
| Cabo de Gata Natural park<br>Preserved since 1987 | Sithonia peninsula<br>Northern Greece | Middle Atlas<br>Ait Beni Yacoub |
| Scattered matorral (scrubland) | Dense matorral (shrubland) | High mountain grassland |
| R=200 mm<br>T=18°C<br>Altitude: 100m | R= 590 mm<br>T=16.2°C<br>Altitude: 50 m | R= 800 mm<br>T=22°C<br>Altitude: 1900 m |

Alados et al., 2004

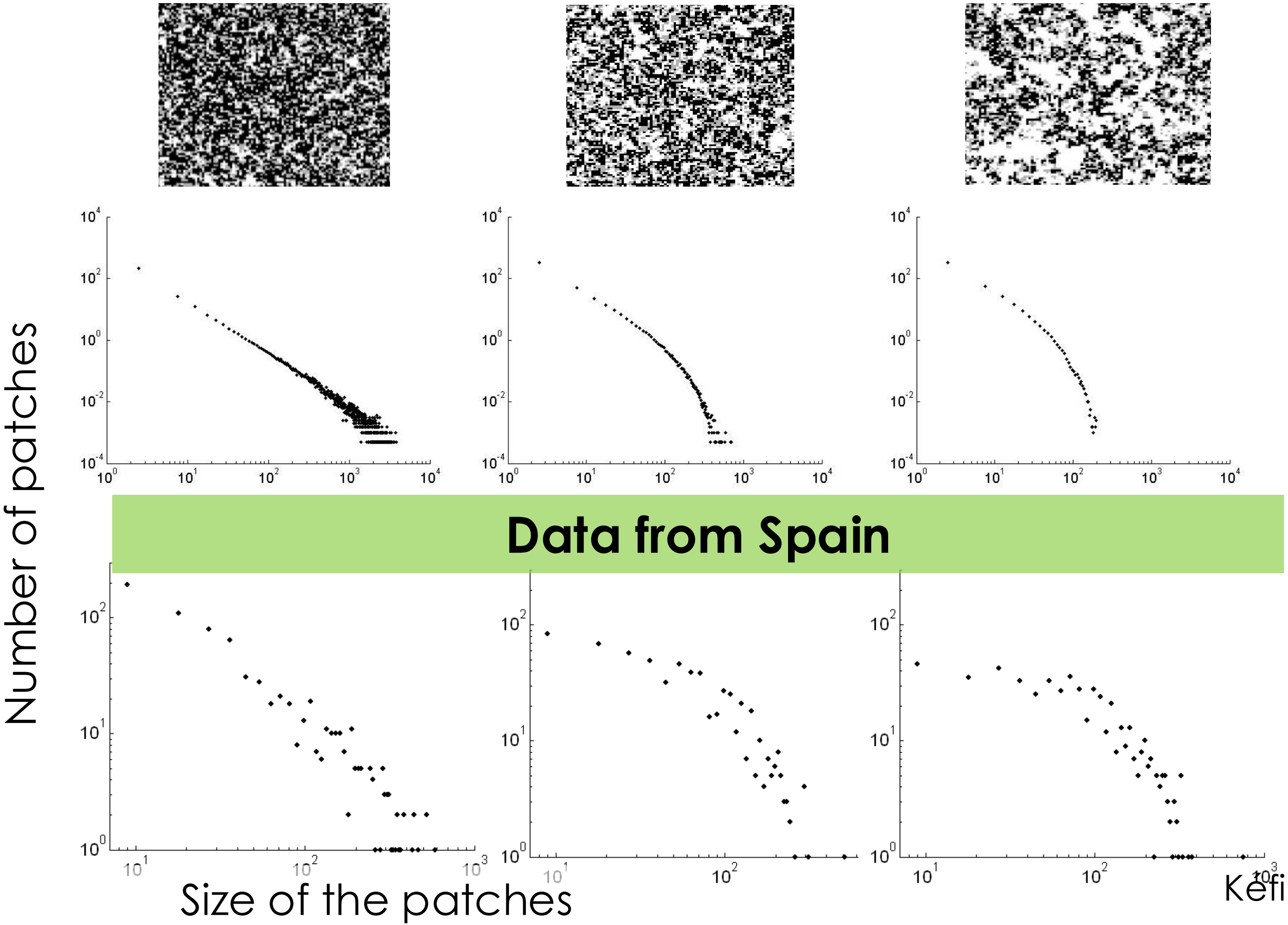
# 3 levels of grazing (9 treatments)

**For each treatment**




30 random transects

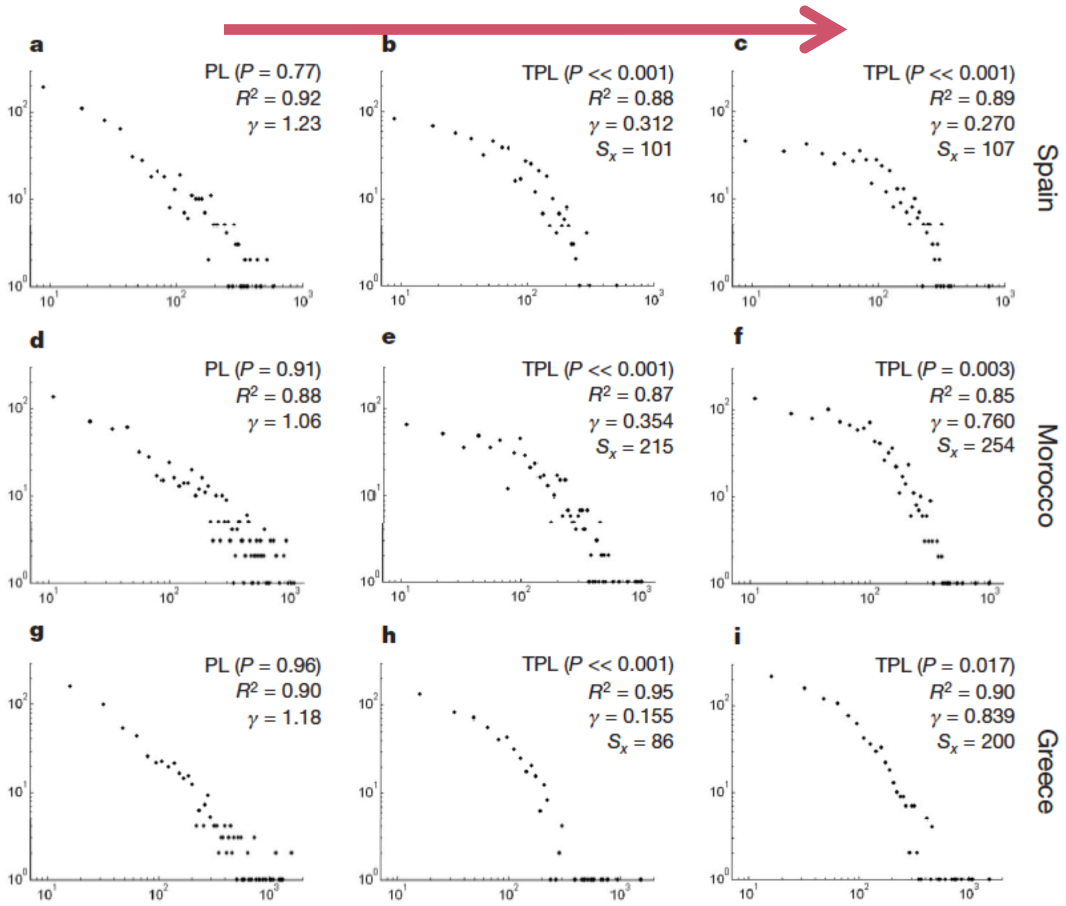
Alados et al., 2004




Kéfi et al. 2007

Grazing pressure

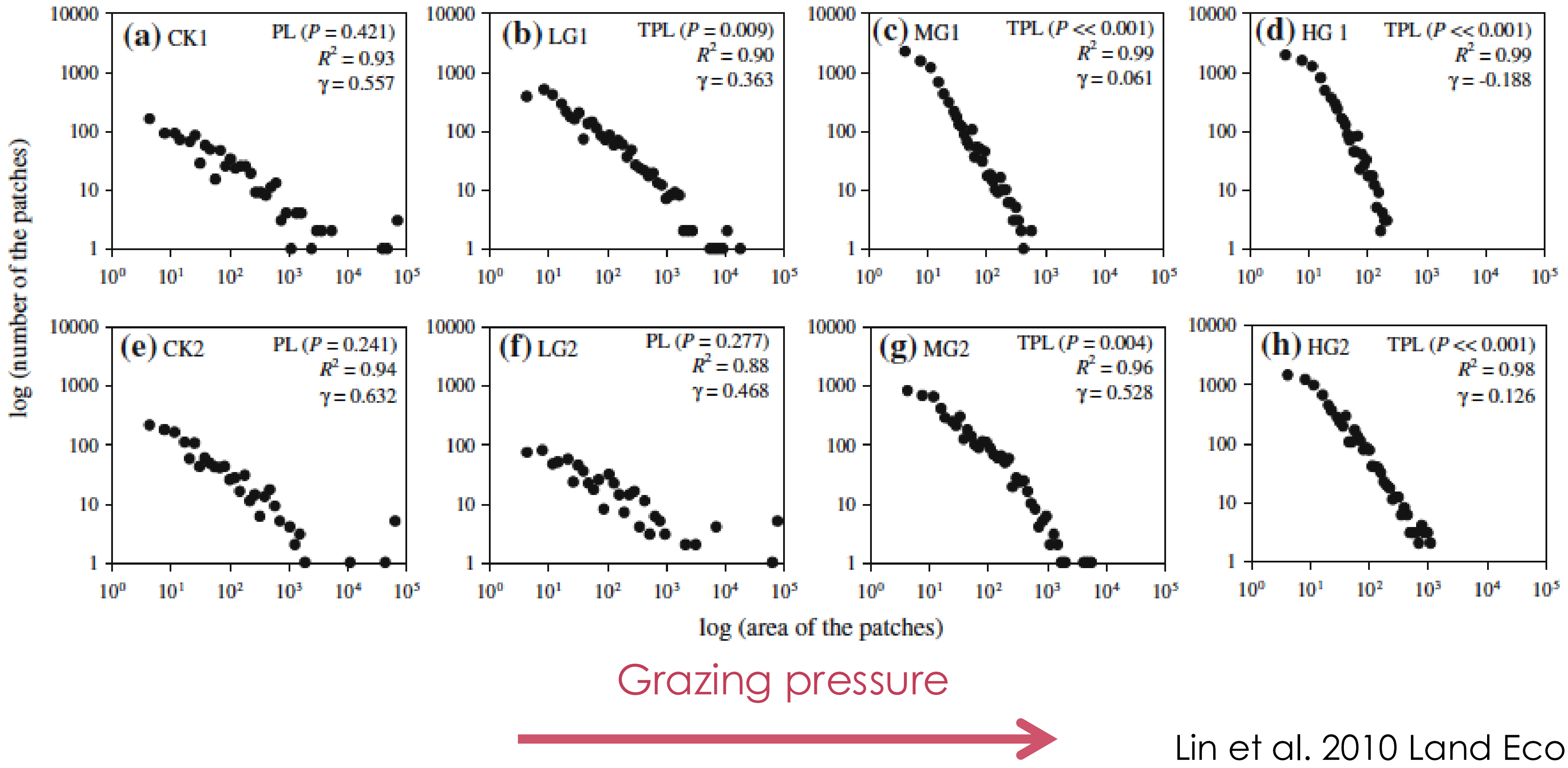
Number of patches




Size of the patches

Kéfi et al. 2007

# desert steppe, Mongolia



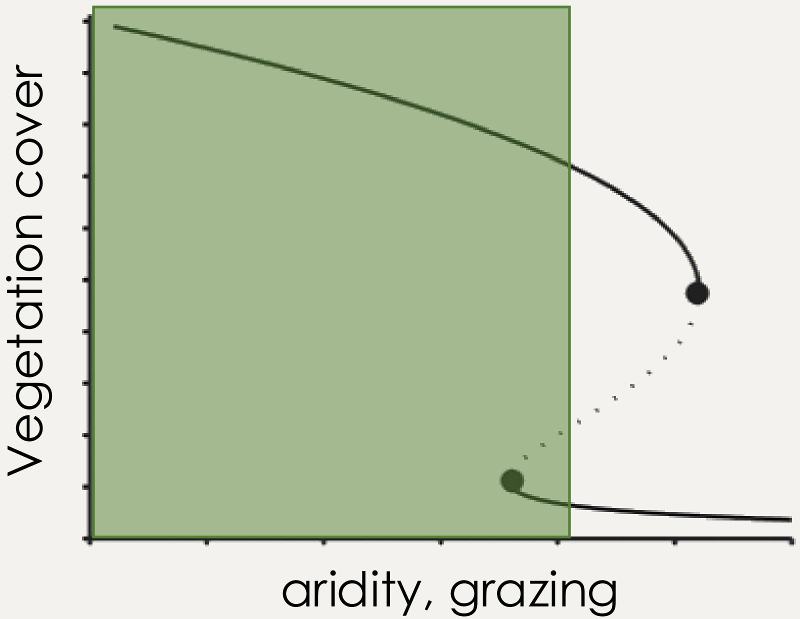

Lin et al. 2010 Land Ecol

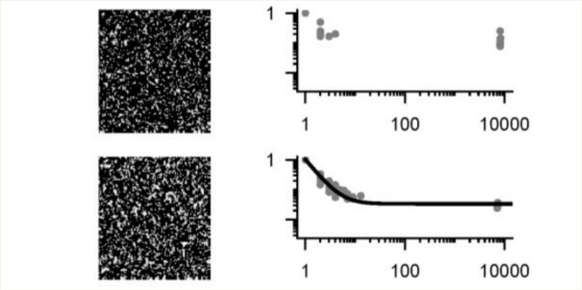
# Patch-size distributions change with stress level in drylands

Rietkerk et al. 2004
Kéfi et al. 2007, 2010, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

More precisely

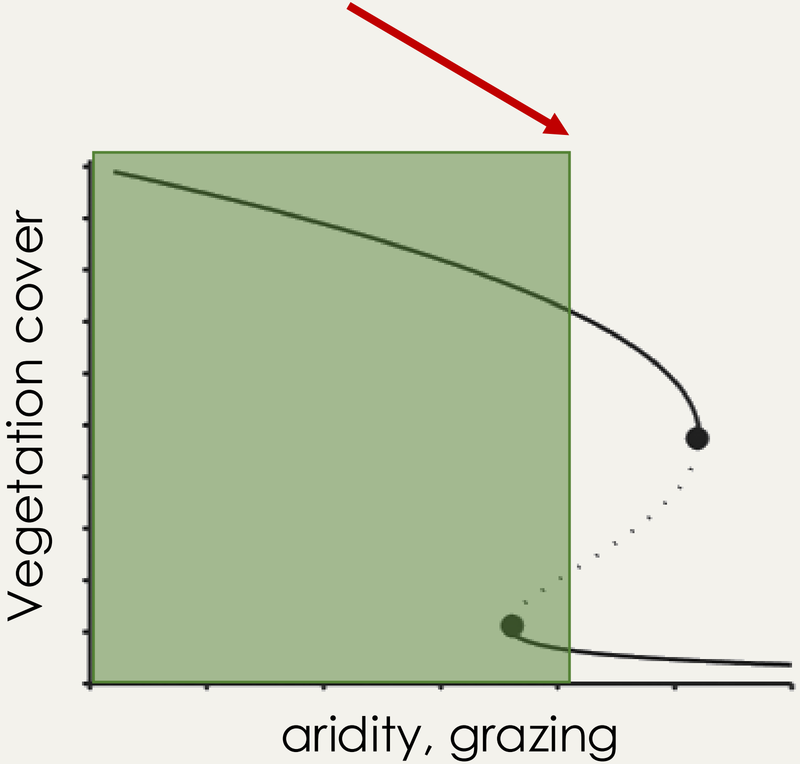

Kéfi et al. 2011

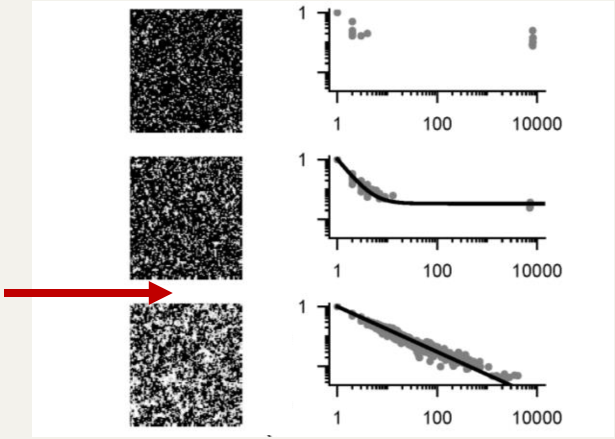


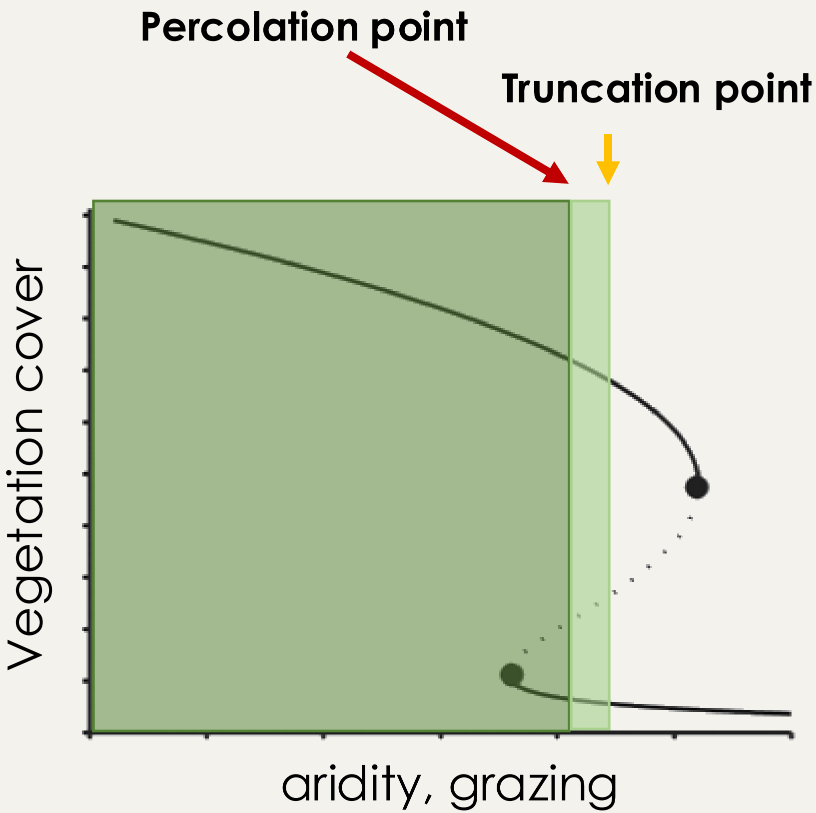

Kéfi et al. 2011

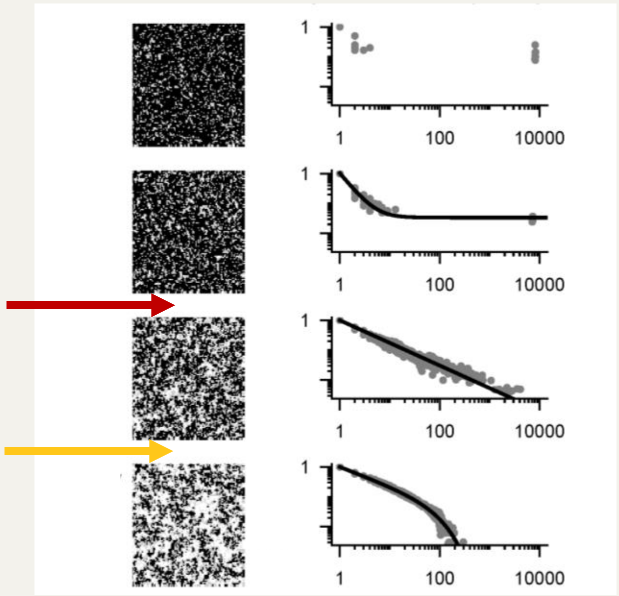
**Percolation point**



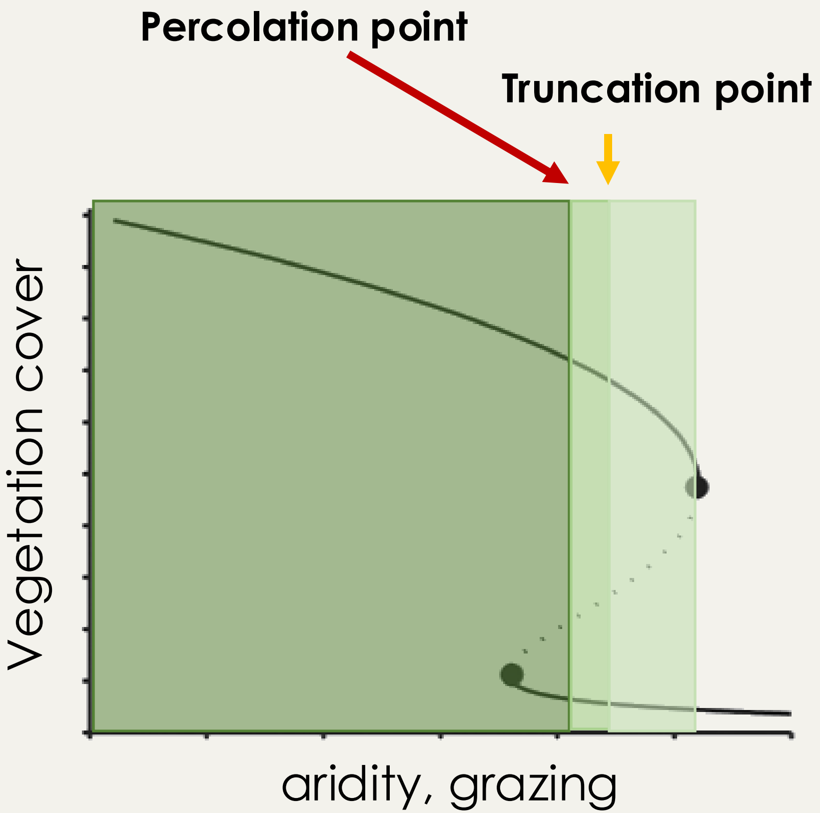



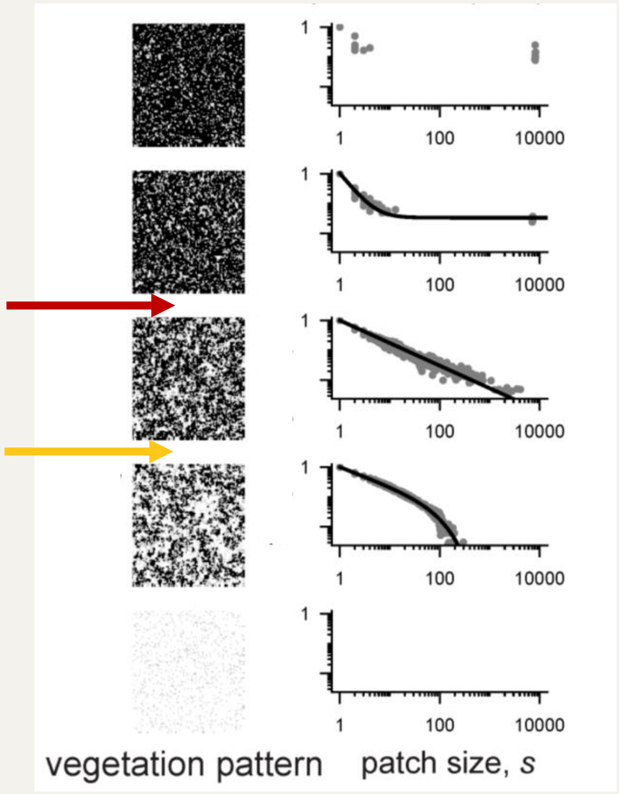

Kéfi et al. 2011



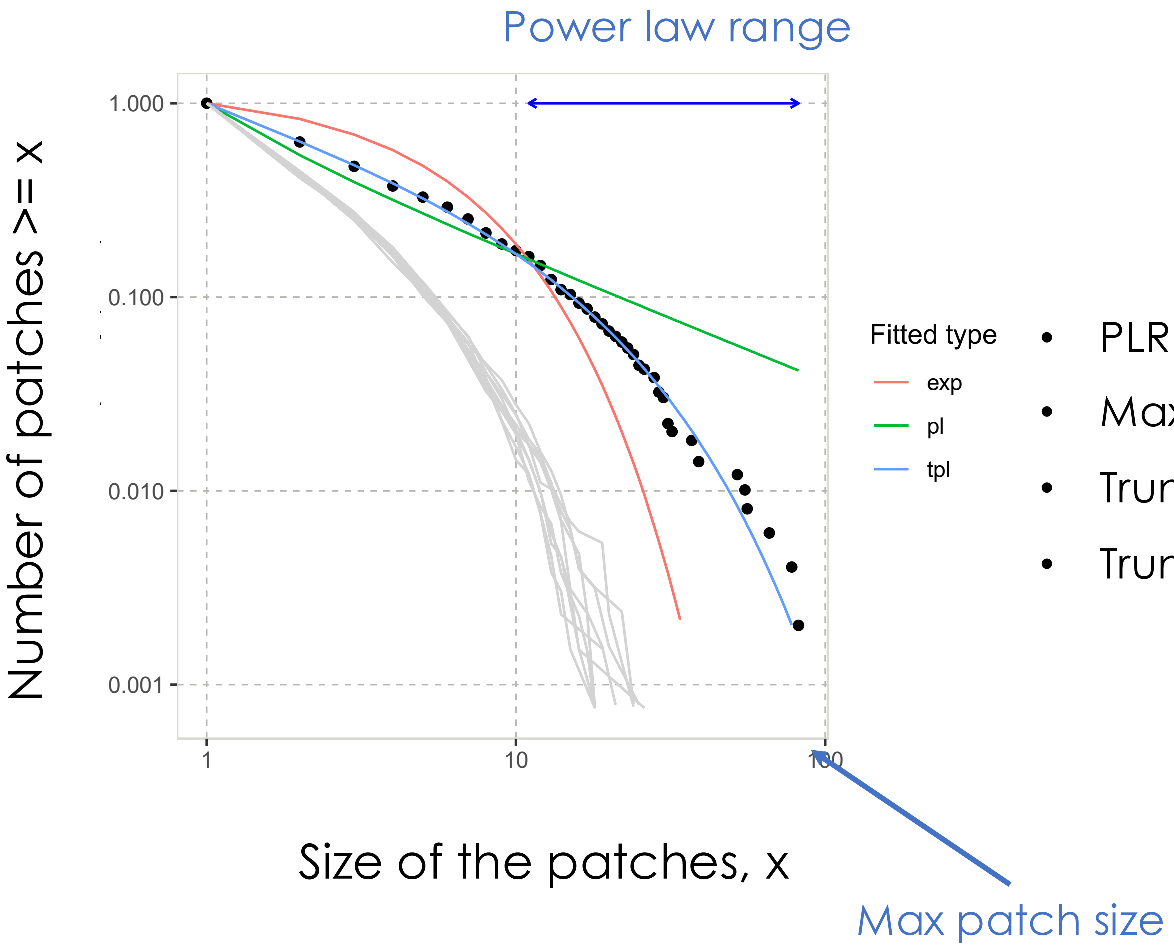




Kéfi et al. 2011



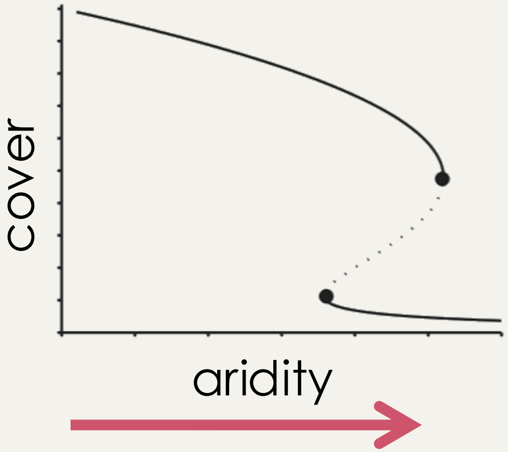



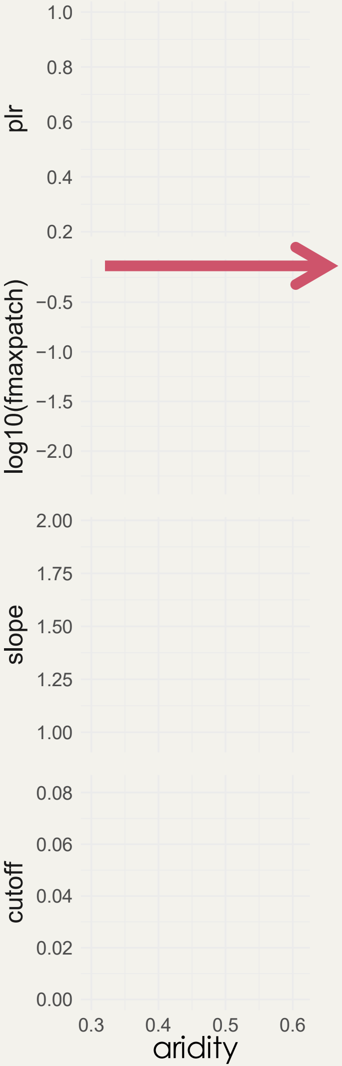

Kéfi et al. 2011




- PLR (power law range)
- Maximum patch size
- Truncated power law fit → slope a
- Truncated power law fit → cutoff b

$$F(x) = x^{-a} exp(-bx)$$

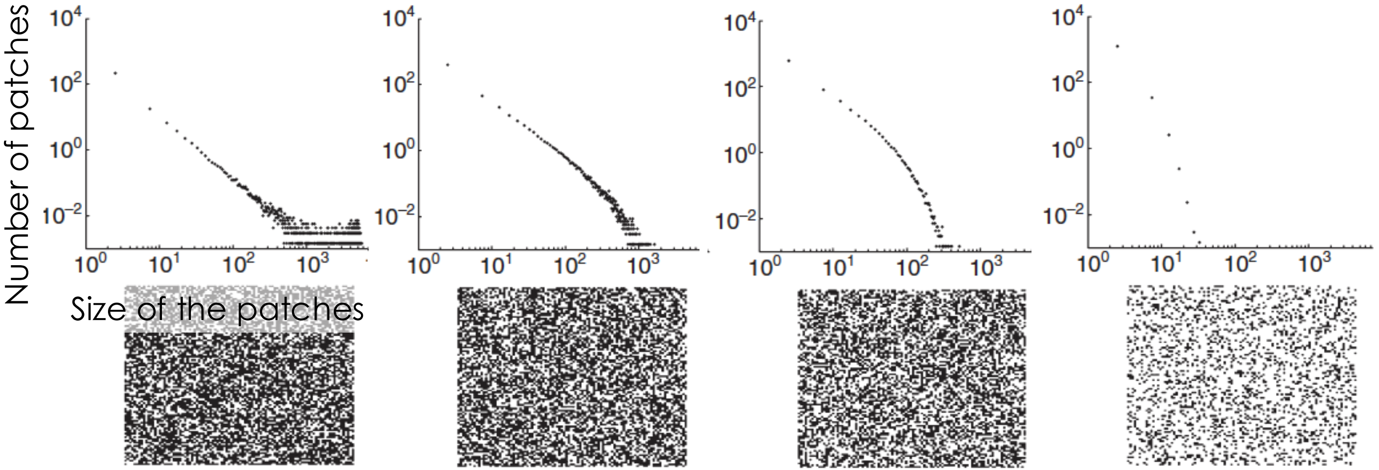

cover
aridity


plr
1.0
0.8
0.6
0.4
0.2
log10(fmaxpatch)
−0.5
−1.0
−1.5
−2.0
slope
2.00
1.75
1.50
1.25
1.00
cutoff
0.08
0.06
0.04
0.02
0.00
0.3
0.4
0.5
0.6
aridity

# Changes in patch-based metrics reflect changes in stress level in drylands

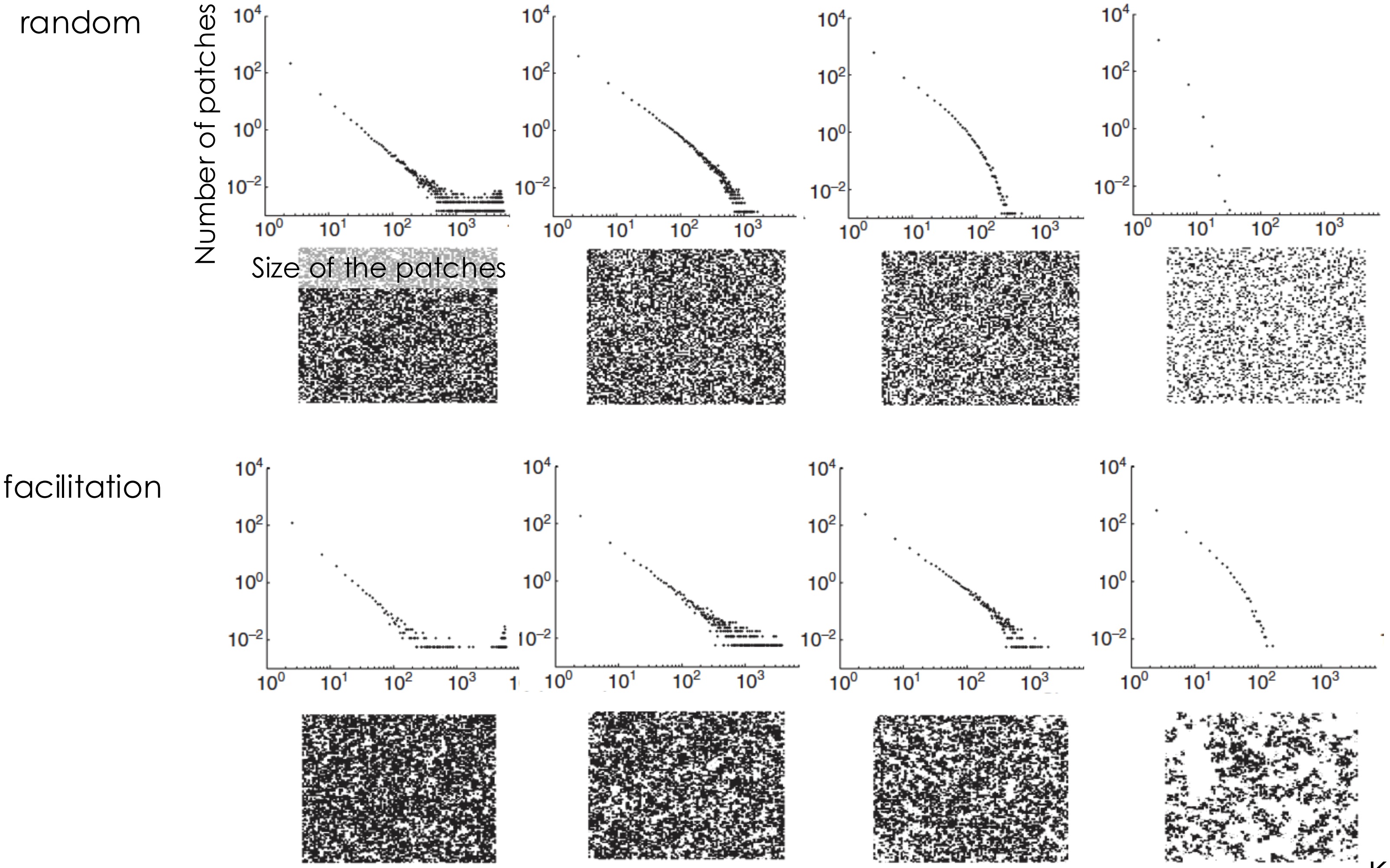
Rietkerk et al. 2004
Kéfi et al. 2007, 2010, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

The same succession of patterns happens in a randomly filled matrix random

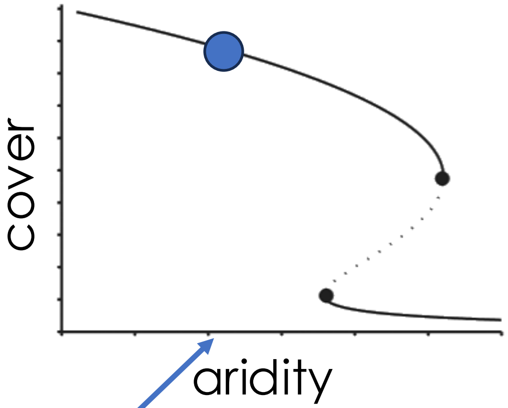


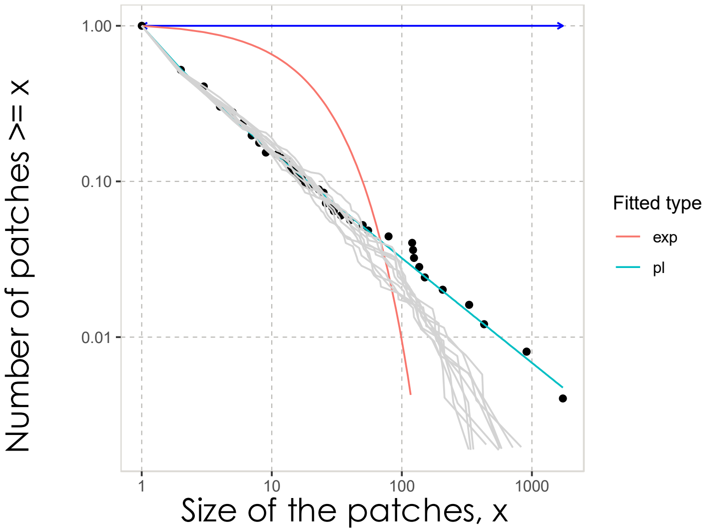

Cover decreases

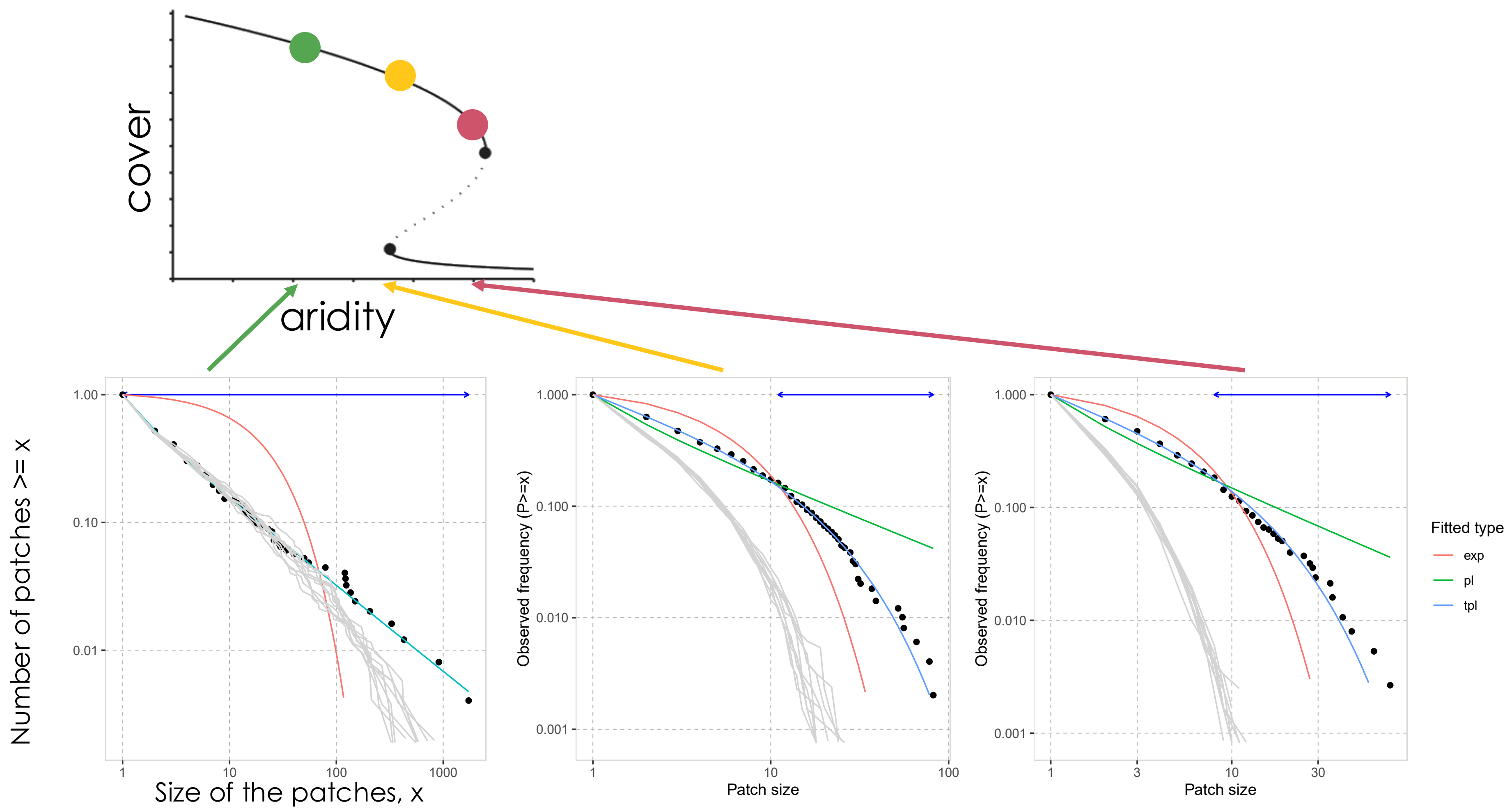
Kéfi et al. 2011




Kéfi et al. 2011


cover
aridity


Number of patches >= x
Size of the patches, x
1.00
0.10
0.01
1
10
100
1000
Fitted type
exp
pl



cover
aridity
Number of patches >= x
Size of the patches, x
1.00
0.10
0.01
1
10
100
1000
Observed frequency (P>=x)
Patch size
1.000
0.100
0.010
0.001
1
10
100
Observed frequency (P>=x)
Patch size
1.000
0.100
0.010
0.001
1
3
10
30
Fitted type
exp
pl
tpl

# Spatial structure changes slower than expected in a null model

Rietkerk et al. 2004
Kéfi et al. 2007, 2010, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

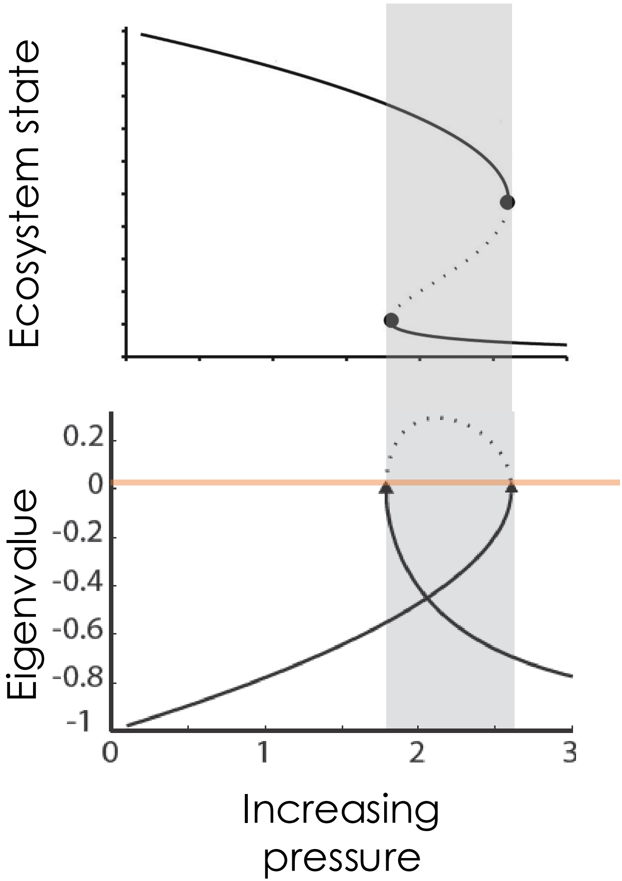
Spatial structure changes slower than expected in a null model

→ resilience of spatial structure to stress due to facilitation

Rietkerk et al. 2004
Kéfi et al. 2007, 2010, 2011, 2014
Schneider and Kéfi 2016
Génin et al. 2018

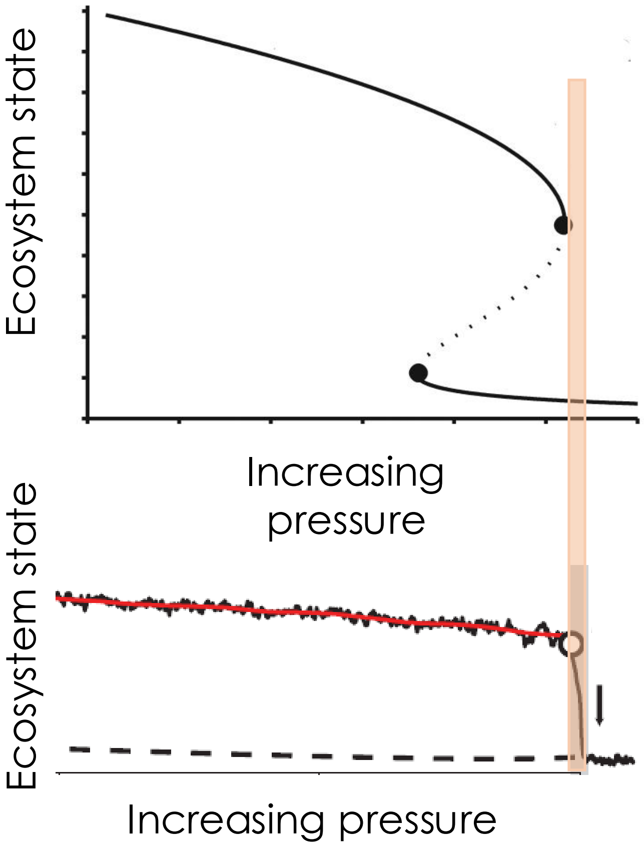
Also…

# Critical slowing down

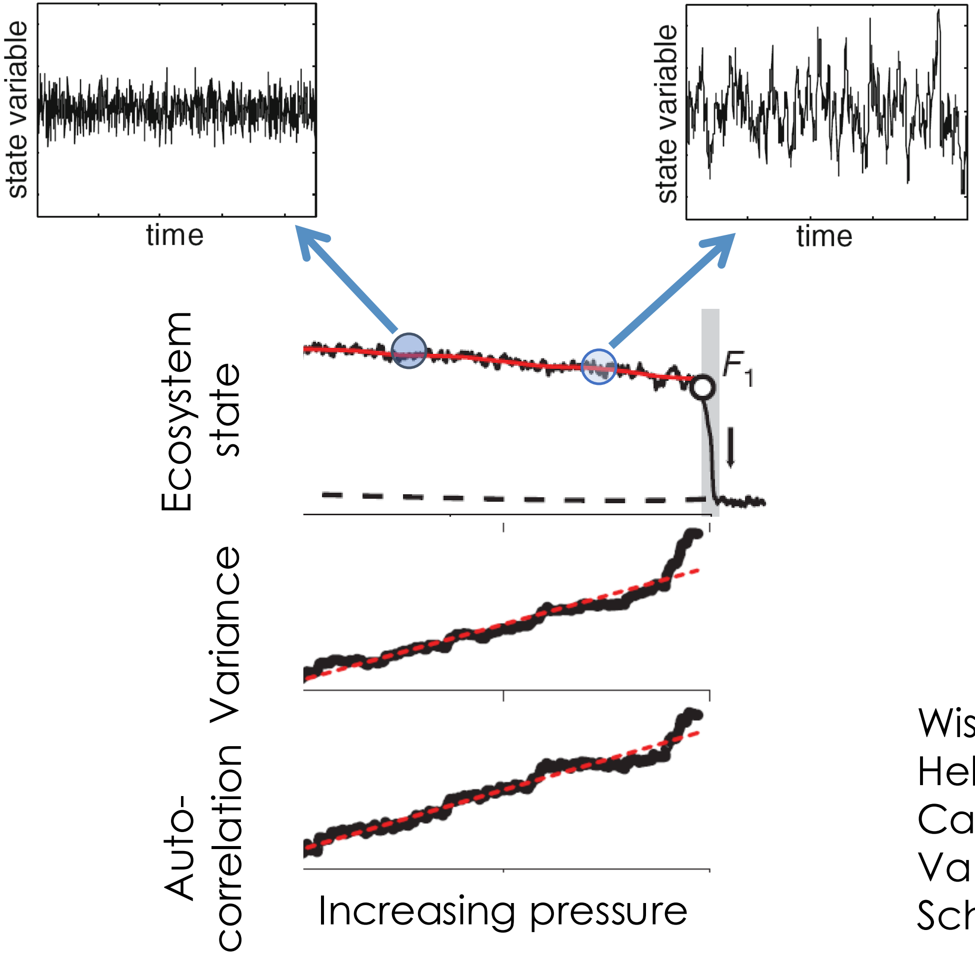



Wissel 1984
Strogatz 1994

# Critical slowing down

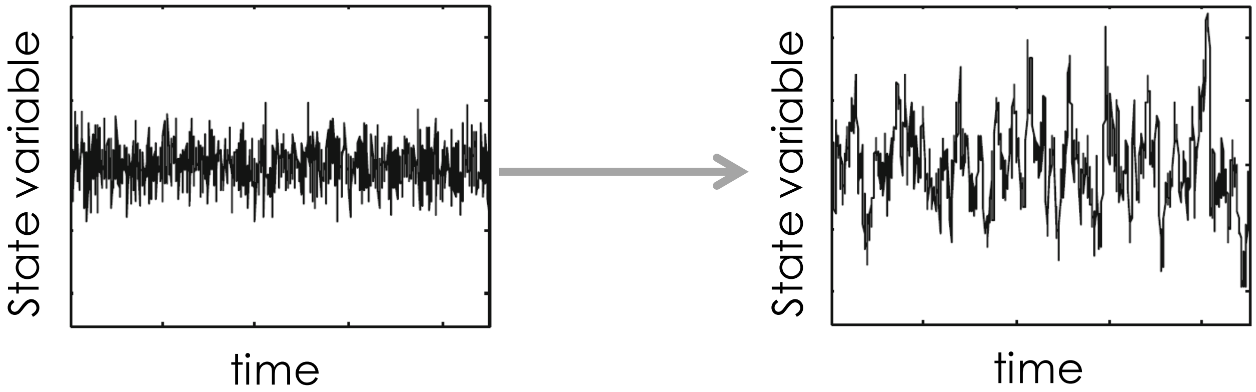



Wissel 1984
Strogatz 1994




Wissel 1984
Held and Kleinen 2004
Carpenter and Brock 2006
Van Nes and Scheffer 2007
Scheffer et al. 2009

# Generic early-warning signals




Variance ↗
Autocorrelation at lag 1 ↗

Scheffer et al. 2009

LETTER

doi:10.1038/nature10723

## Recovery rates reflect distance to a tipping point in a living system

Annelies J. Veraart[1], Elisabeth J. Faassen[1], Vasilis Dakos[1], Egbert H. van Nes[1], Miquel Lürling[1,2] & Marten Scheffer[1]

LETTERS

## Early warning signals of extinction in deteriorating environments

John M. Drake[1] & Blaine D. Griffen[2]

LETTER

doi:10.1038/nature12071

## Slower recovery in space before collapse of connected populations

Lei Dai[1], Kirill S. Korolev[1] & Jeff Gore[1]

## Generic Indicators for Loss of Resilience Before a Tipping Point Leading to Population Collapse

Lei Dai,[1*] Daan Vorselen,[2*] Kirill S. Korolev,[1] Jeff Gore[1]†

## Anticipating Critical Transitions

Marten Scheffer,[1,2*] Stephen R. Carpenter,[3] Timothy M. Lenton,[4] Jordi Bascompte,[5] William Brock,[6] Vasilis Dakos,[1,5] Johan van de Koppel,[7,8] Ingrid A. van de Leemput,[1] Simon A. Levin,[9] Egbert H. van Nes,[1] Mercedes Pascual,[10,11] John Vandermeer[10]

## Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment

S. R. Carpenter,[1*] J. J. Cole,[2] M. L. Pace,[3] R. Batt,[1] W. A. Brock,[4] T. Cline,[1] J. Coloso,[3] J. R. Hodgson,[5] J. F. Kitchell,[1] D. A. Seekell,[3] L. Smith,[1] B. Weidel[1]

## Foreseeing tipping points

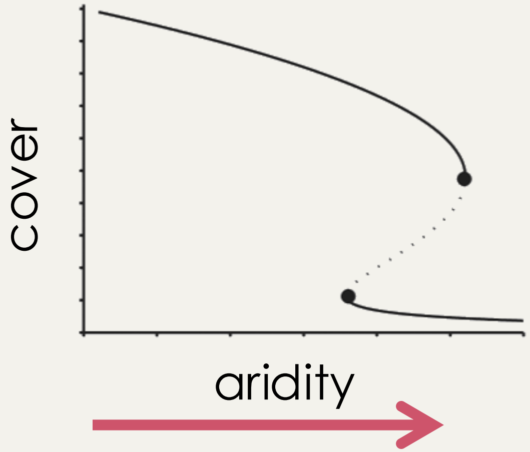
**Theory suggests that the risk of critical transitions in complex systems can be revealed by generic indicators. A lab study of extinction in plankton populations provides experimental support for that principle.** SEE LETTER P. 456

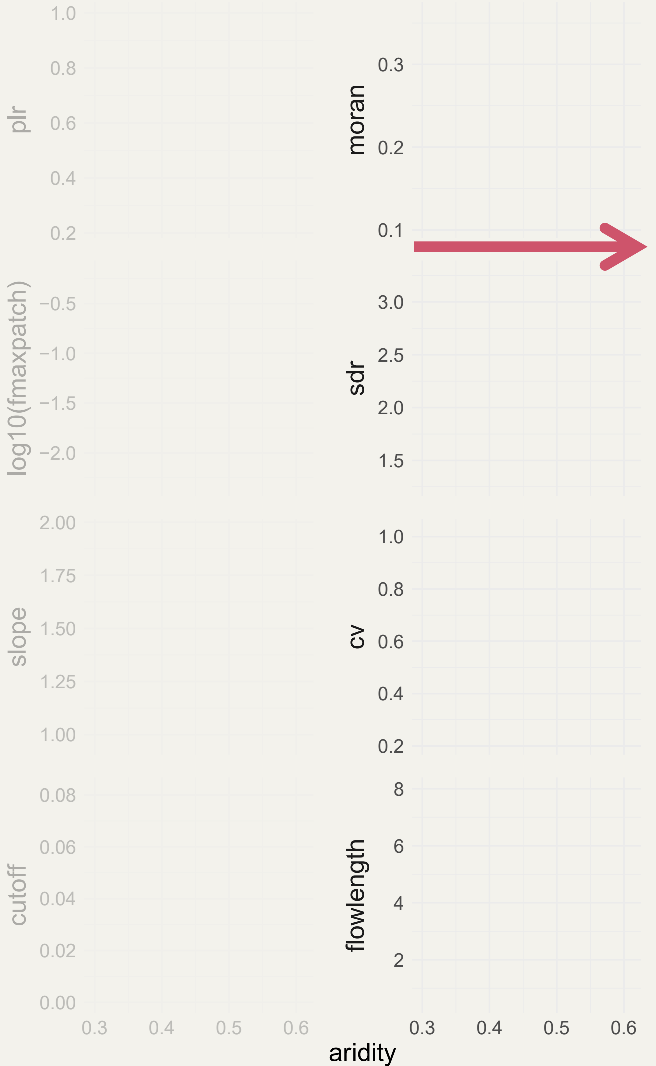
What about their spatial equivalent?

# What about their spatial equivalent?

Spatial variance ↗
Near-neigh. correlation ↗

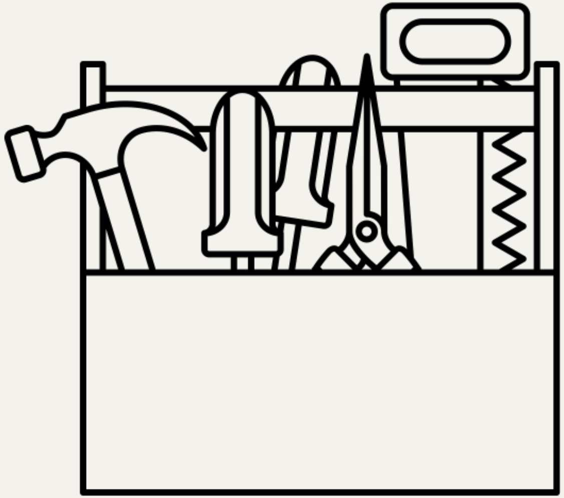
Guttal et al. 2009
Dakos et al. 2010
Dakos et al. 2011

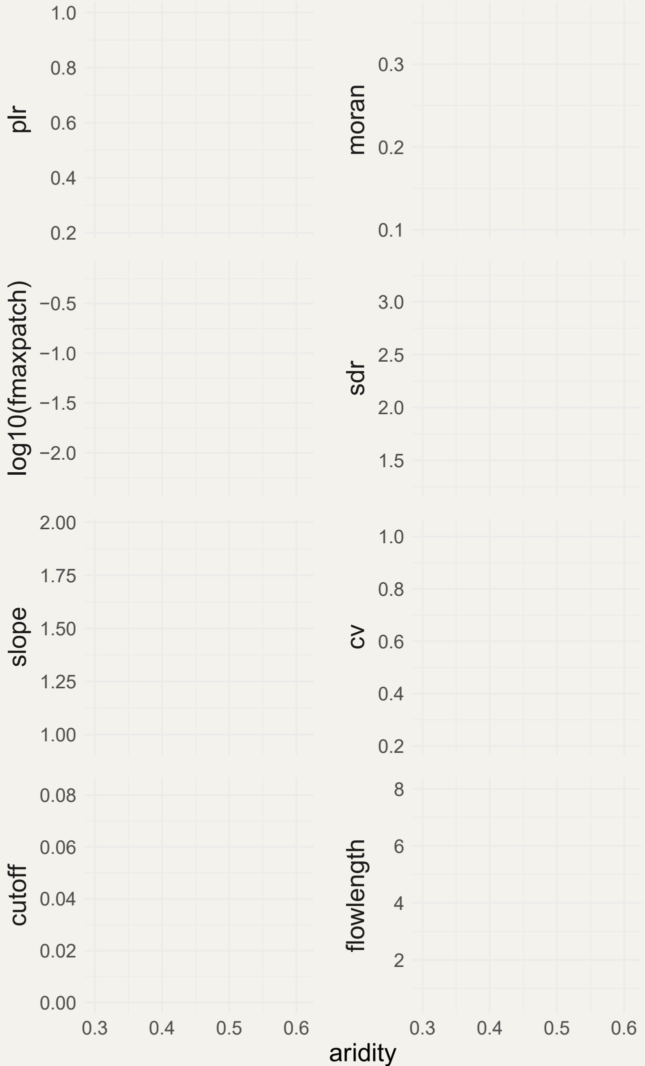


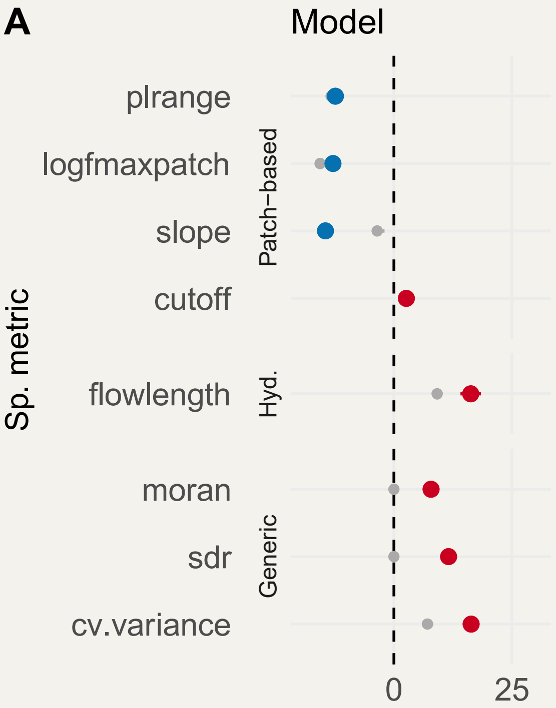

Dakos, Kéfi et al. 2011
Kéfi et al. 2014

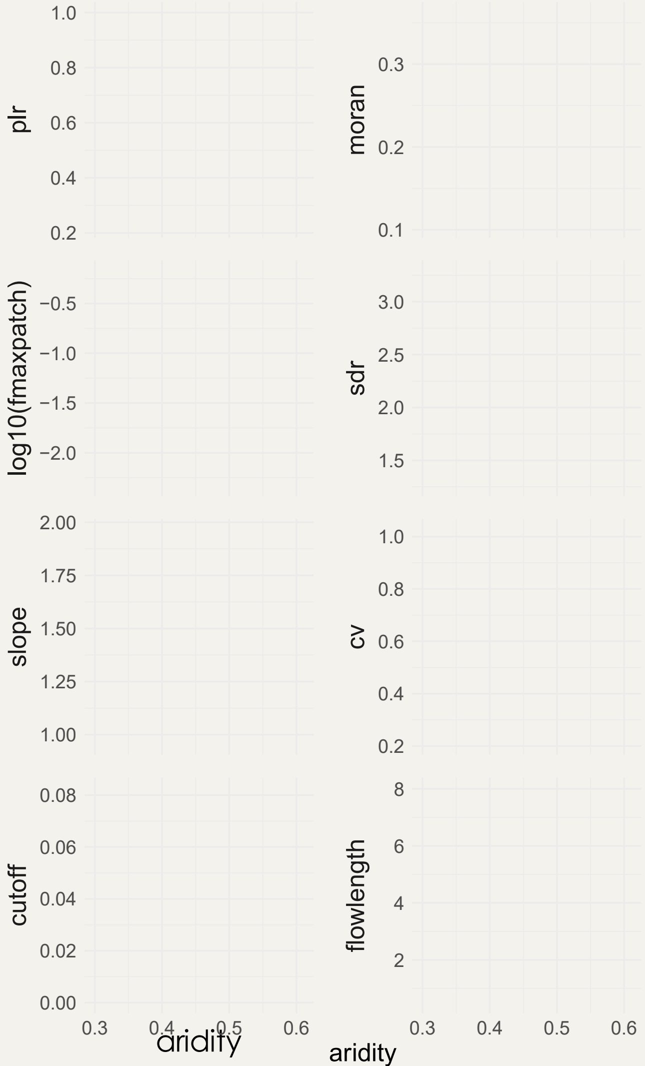
# Indicator toolbox



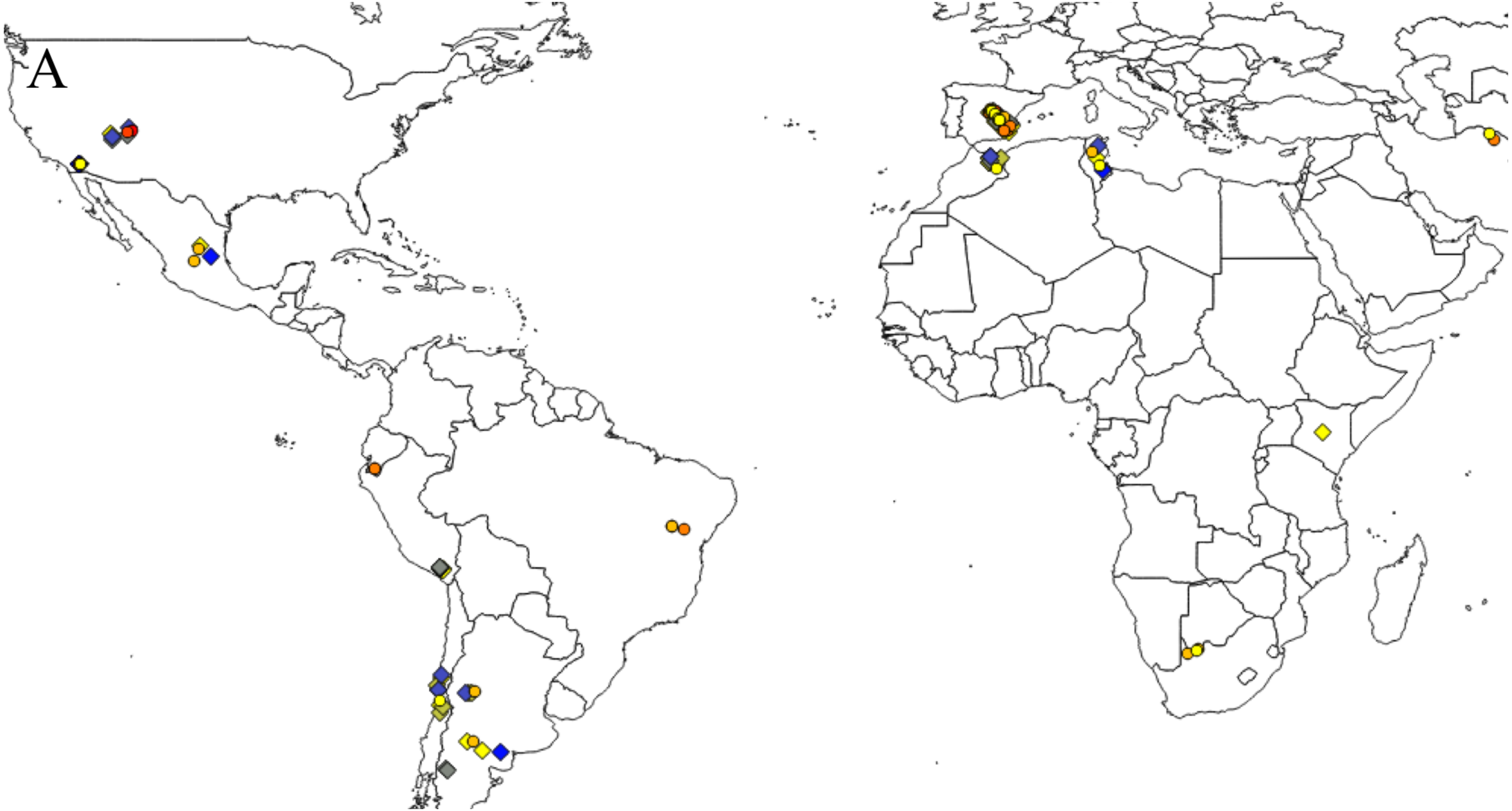



Kéfi et al. 2011, 2014 ; Génin et al. 2018

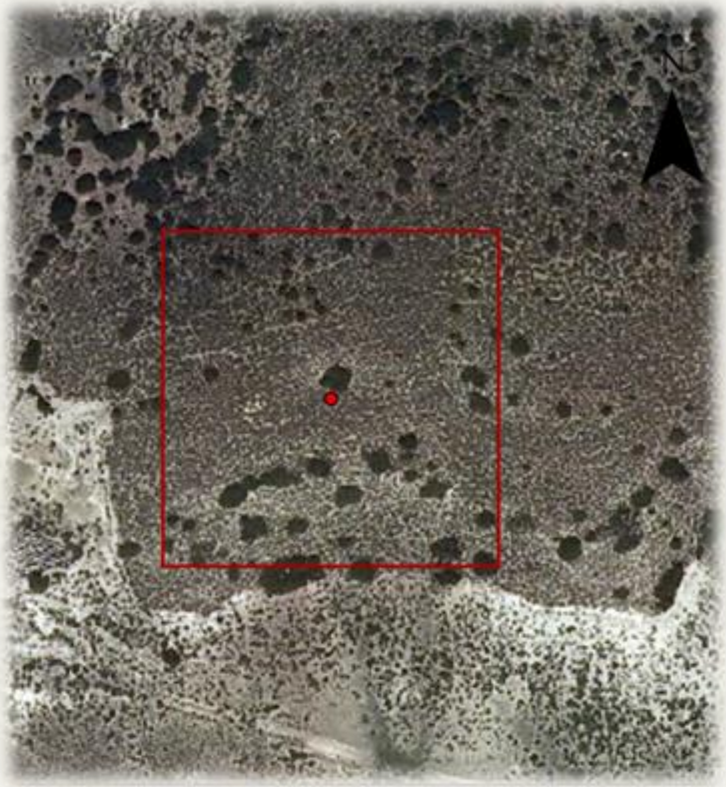

A
Model
Sp. metric
plrange
logfmaxpatch
slope
cutoff
flowlength
moran
sdr
cv.variance
Patch−based
Hyd.
Generic
0
25


plr
1.0
0.8
0.6
0.4
0.2
moran
0.3
0.2
0.1
log10(fmaxpatch)
−0.5
−1.0
−1.5
−2.0
sdr
3.0
2.5
2.0
1.5
slope
2.00
1.75
1.50
1.25
1.00
cv
1.0
0.8
0.6
0.4
0.2
cutoff
0.08
0.06
0.04
0.02
0.00
flowlength
8
6
4
2
0.3
0.4
0.5
0.6
aridity
0.3
0.4
0.5
0.6
aridity

# Empirical validation?




Biocom project
115 sites worldwide
(Maestre et al. 2012)



**For each site:**

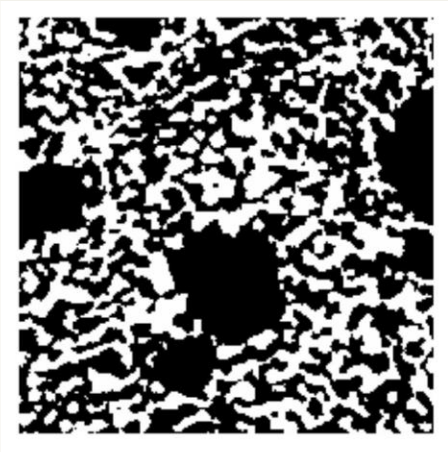
→Aridity
→Multifunctionality
→Vegetation cover

Field data

→3 times 50x50 m plots

Aerial image data

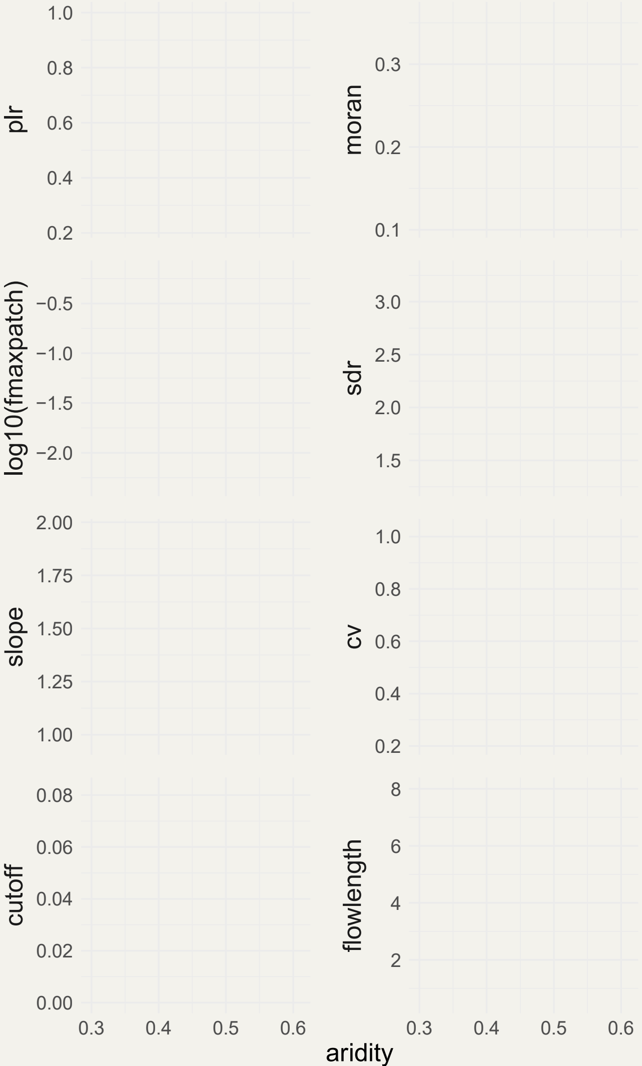
Berdugo et al. 2017 NEE

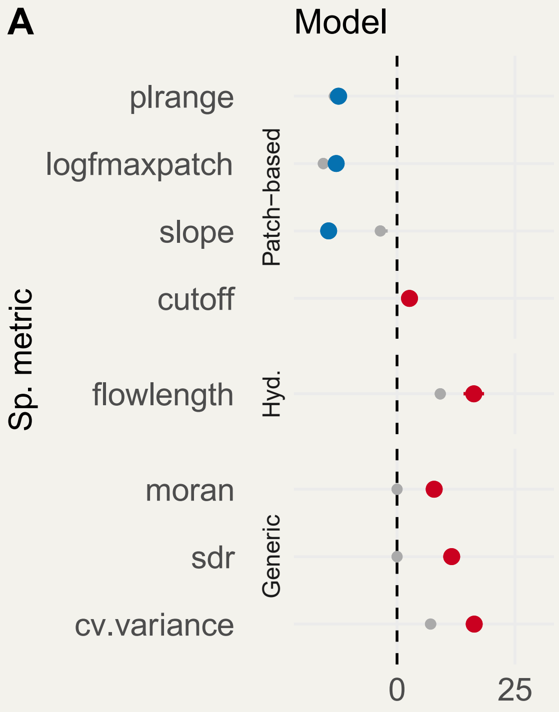


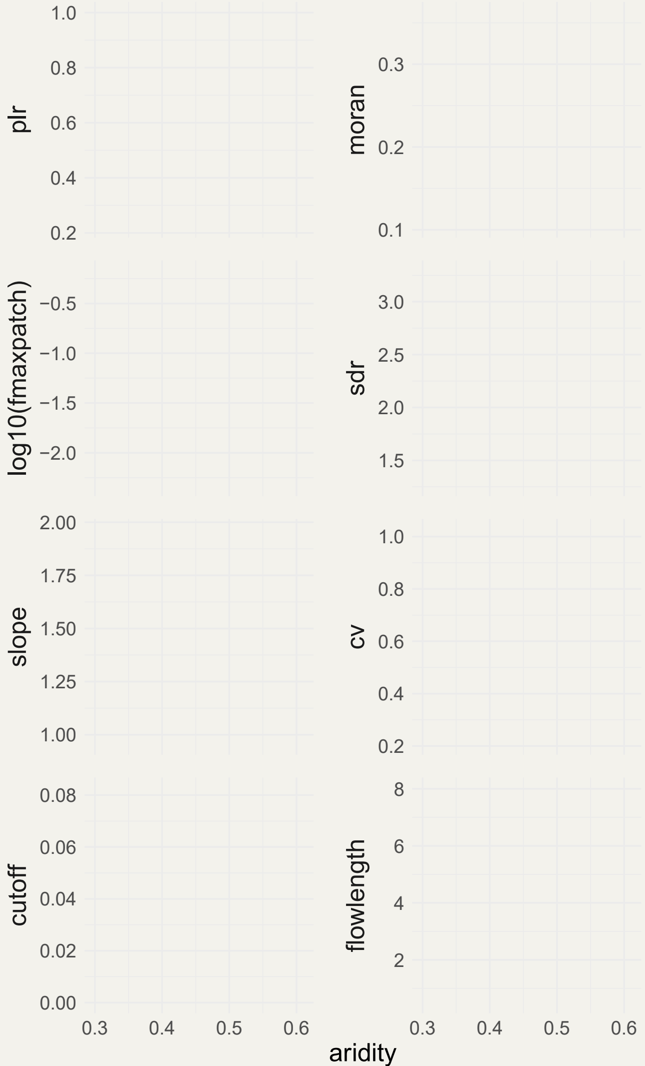
?

Spatial metrics

# Model expectations

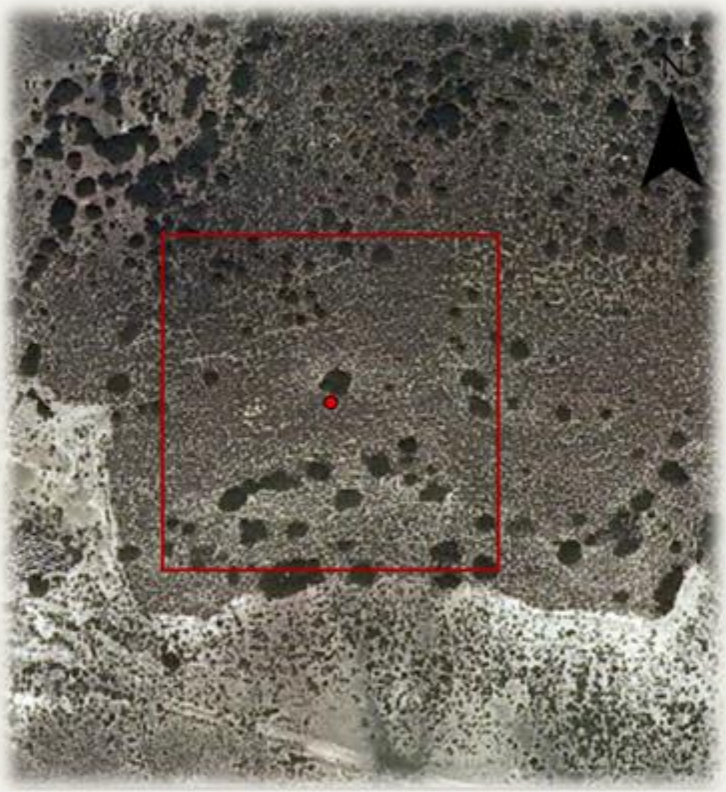



A
Model
Sp. metric
plrange
logfmaxpatch
slope
cutoff
flowlength
moran
sdr
cv.variance
Patch−based
Hyd.
Generic
0
25


plr
moran
log10(fmaxpatch)
sdr
slope
cv
cutoff
flowlength
aridity
0.3
0.4
0.5
0.6


All metrics show significant trends along the aridity gradient

Kéfi et al. 2024




**For each site:**

→Aridity
→**Multifunctionality**
→**Vegetation cover**

→3 times 50x50 m plots

Field data

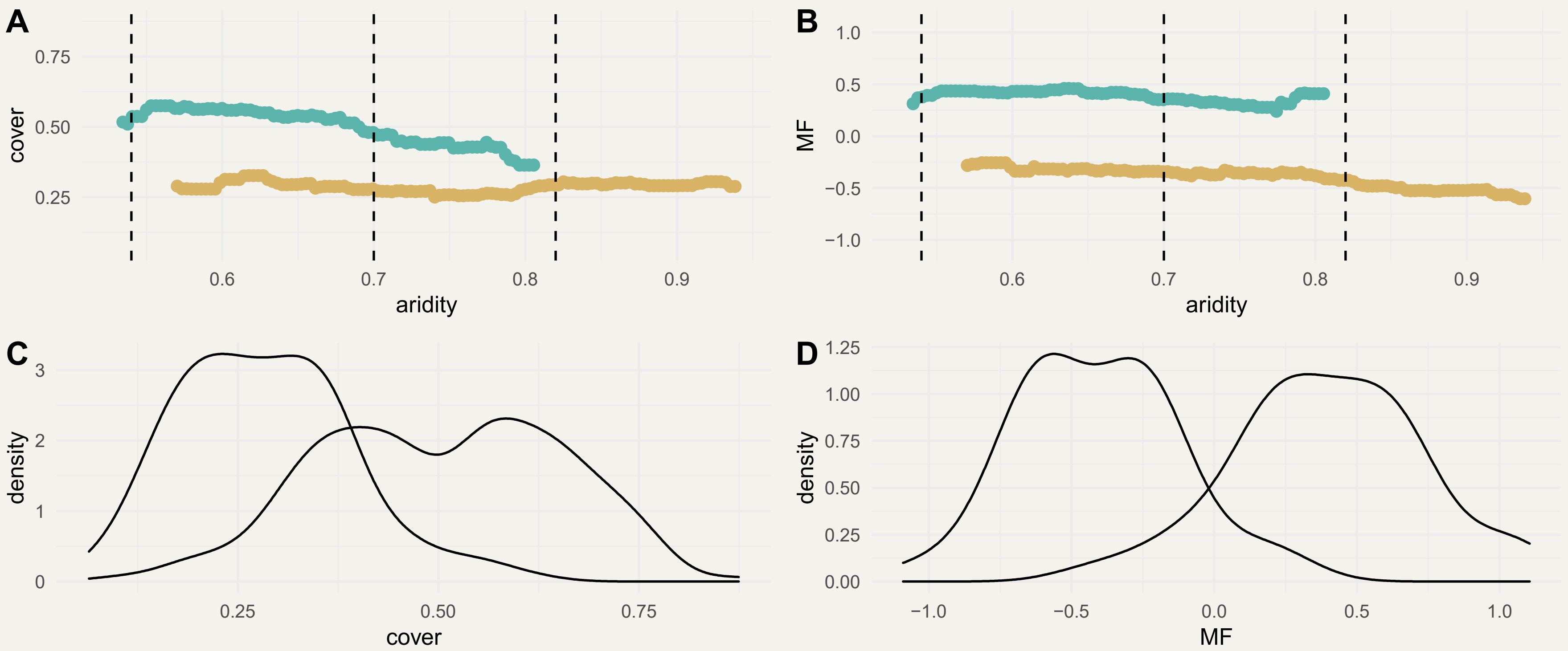
Aerial image data

Kéfi et al. 2024

**Ecosystem functions** → **Z-score (for each function)** → **Multifunctionality (sum of z-scores)**

| | | |
|---|---|---|
| NITROGEN CYCLE | Nitrate | Nitrates concentration in the soil |
| | Amonium | Amonium concentration in the soil |
| | Nitrogen | Total nitrogen |
| | PotNtransf | Potential Nitrogen transformation rate |
| | aa | aminoacids |
| | Prots | Proteins |
| CARBON CYCLE | Carbon | Total carbon |
| | Pentoses | Pentoses |
| | Hexoses | Hexoses |
| | Arom | Aromaci compounds |
| | Phenols | Phenols |
| | beta | activity of beta glucosidase enzime |
| PHOSPHOROUS CYCLE | AVP | Available phosphorous |
| | phos | activity of phosphatase enzime |
| | P_HCL | Inorganic phosphorous |
| | TP | Total phosphorous |

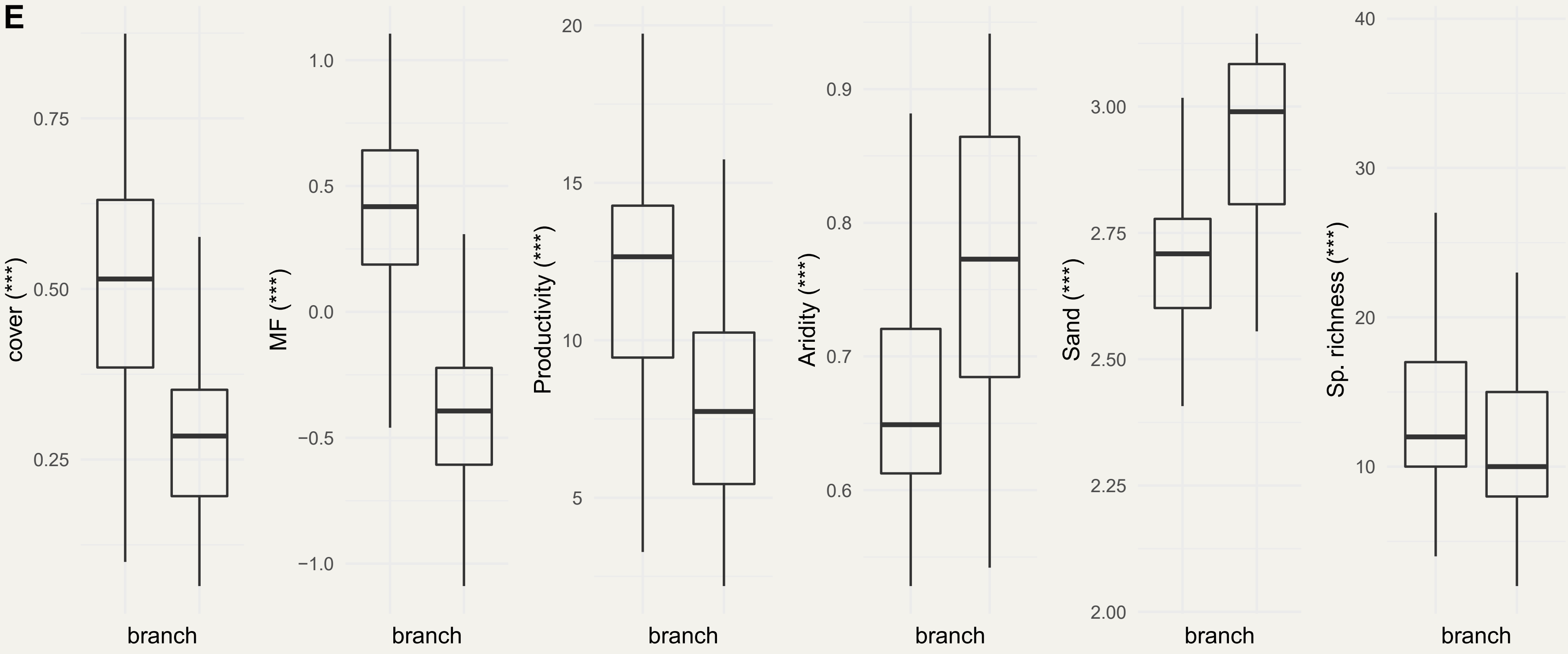
Maestre et al. 2012




2D clustering on MF + cover = 2 groups of sites

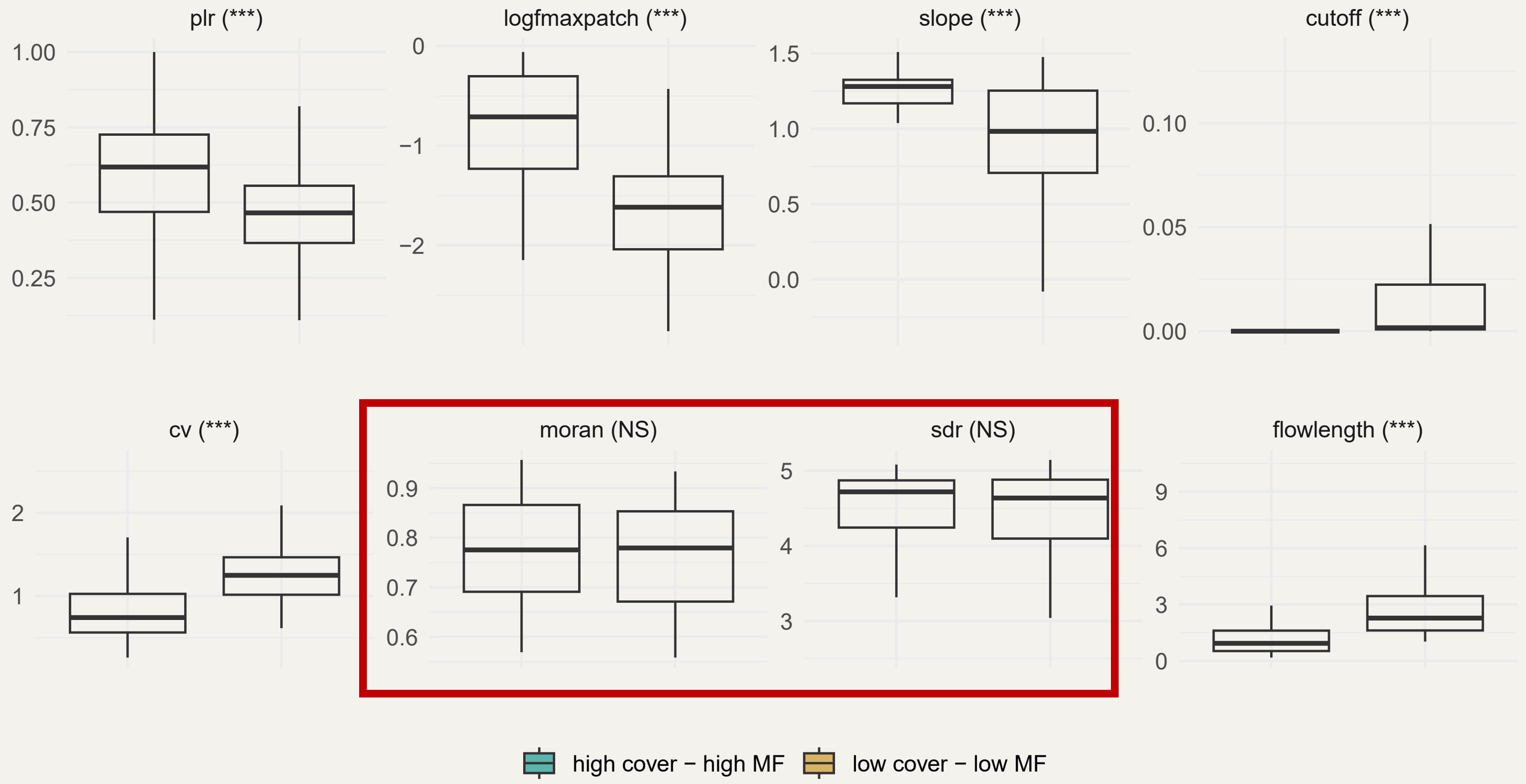
Kéfi et al. 2024

Two groups of dryland sites
globally in terms of functioning + cover



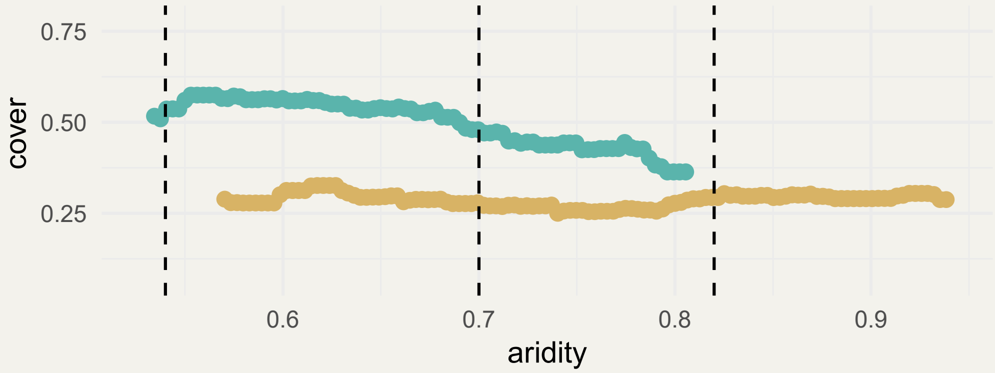

Kéfi et al. 2024

What about the spatial structure ?

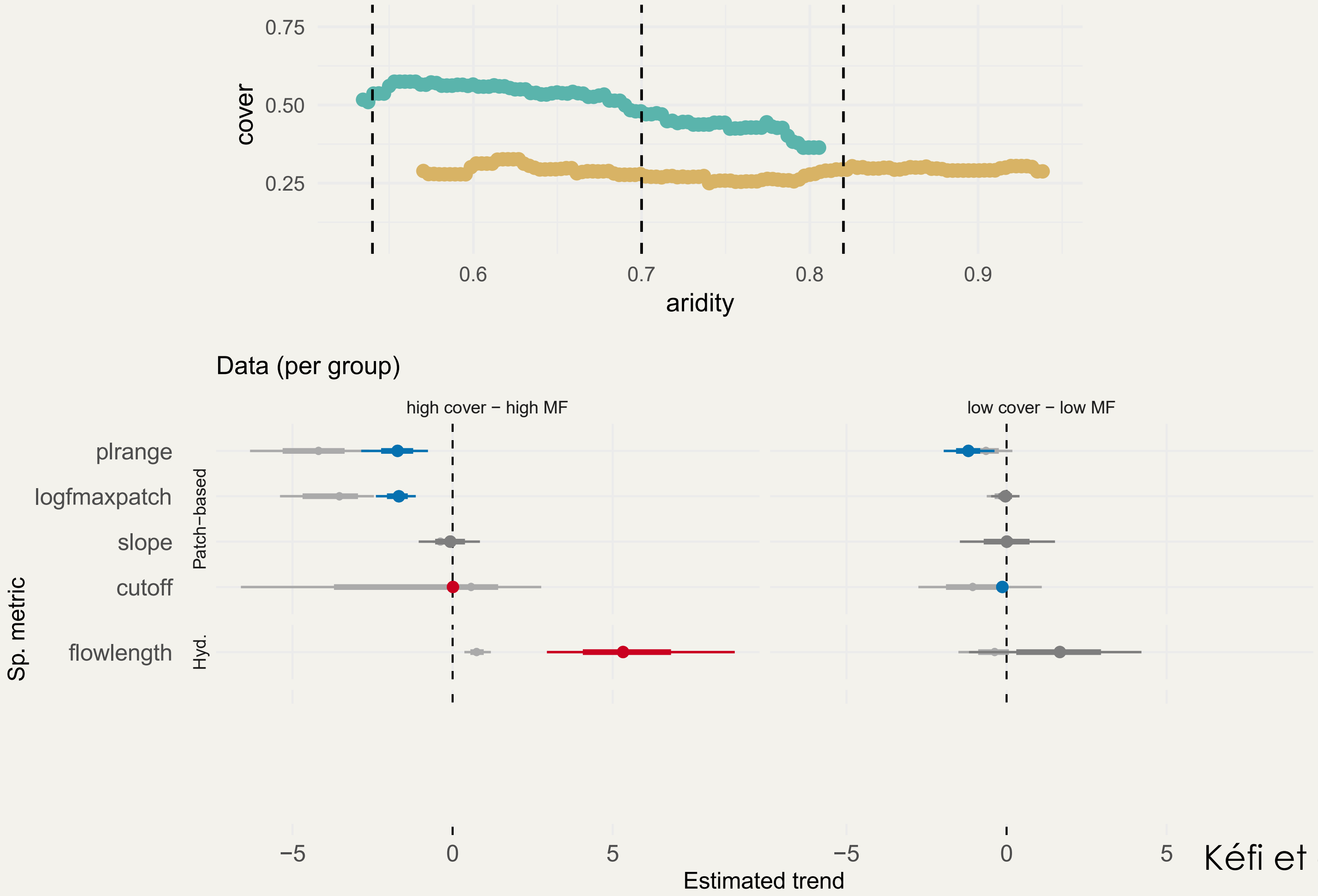



Kéfi et al. 2024

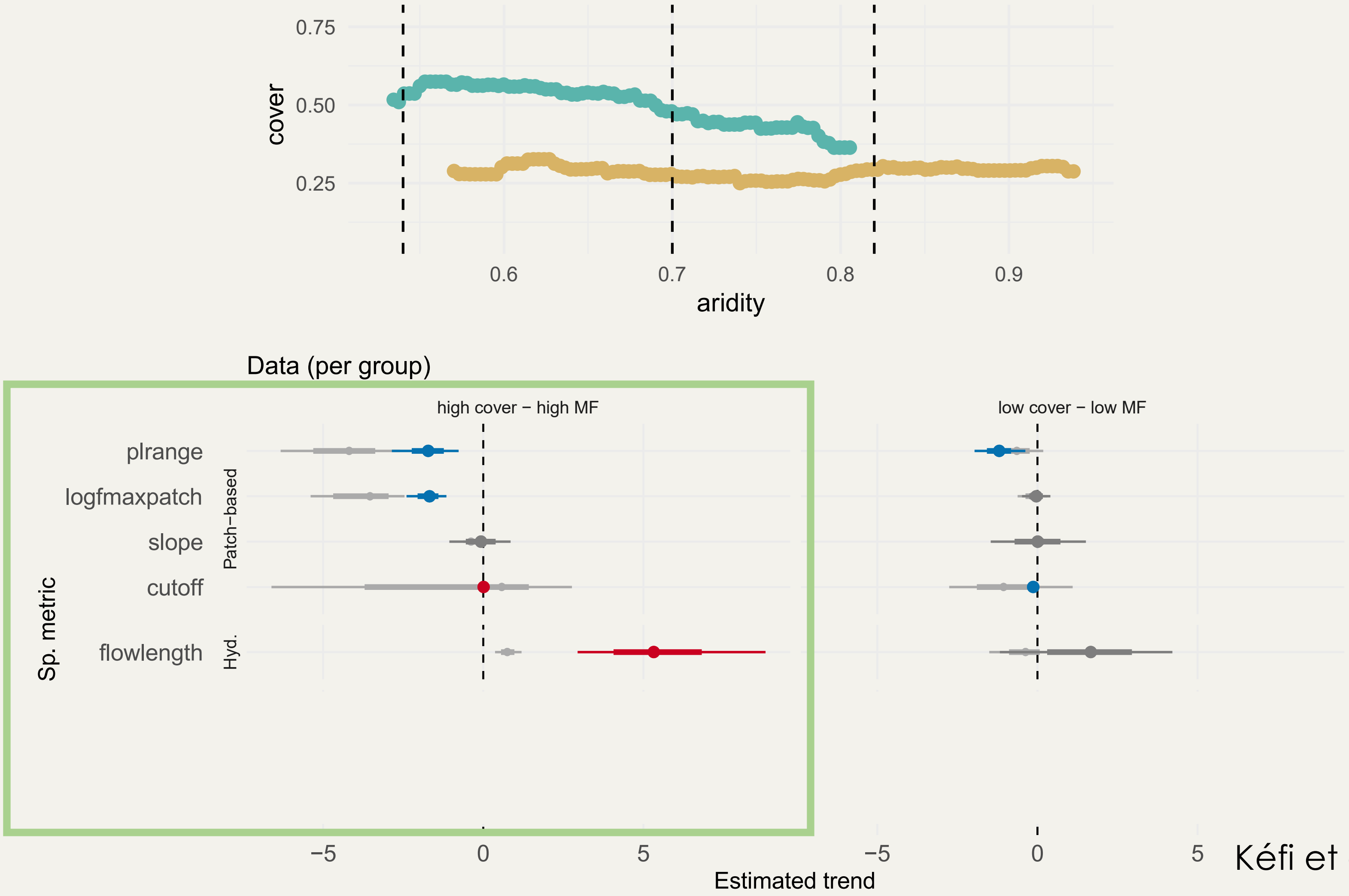
The 2 groups of functioning are characterized by different spatial structure



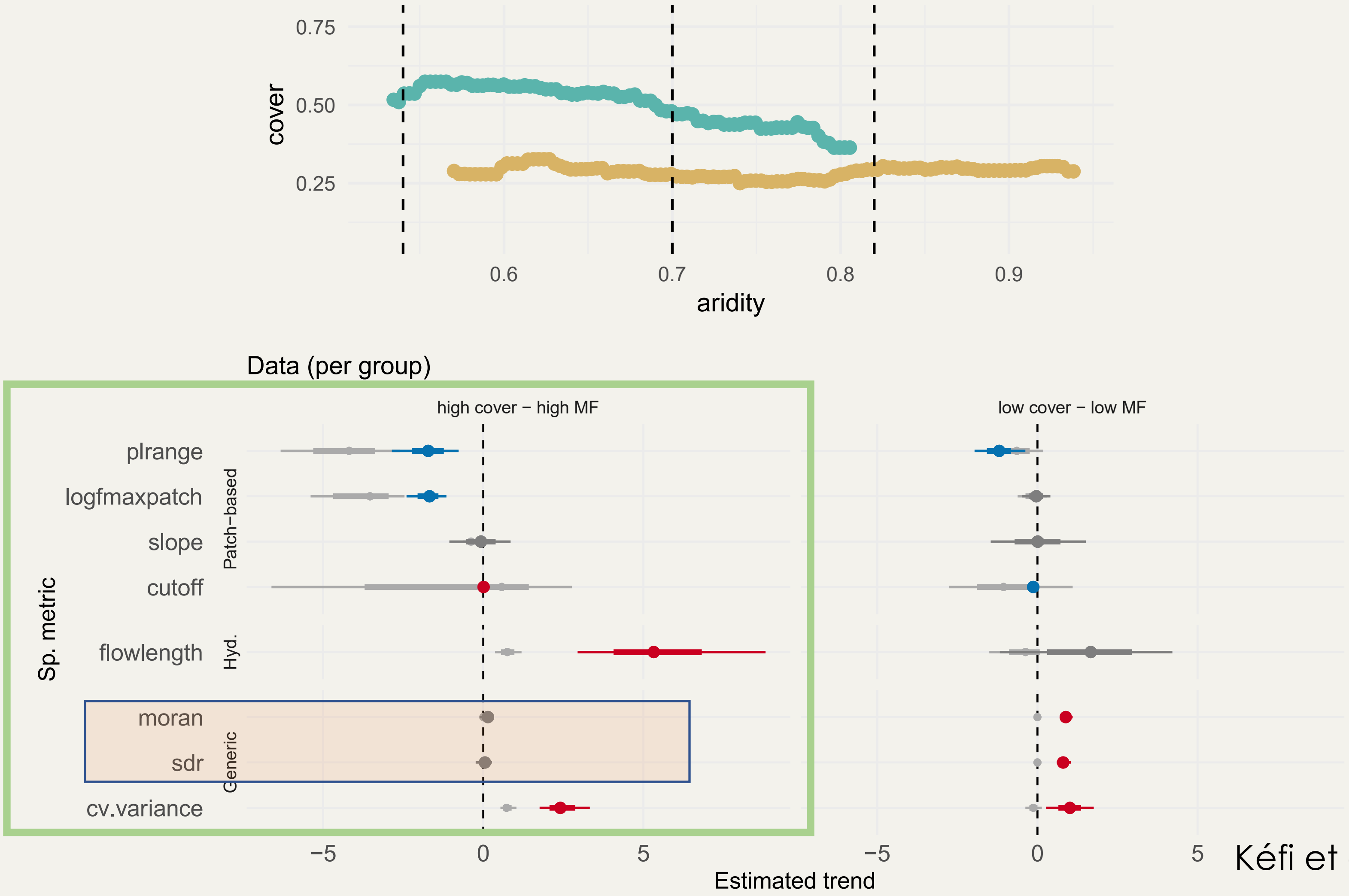

Kéfi et al. 2024



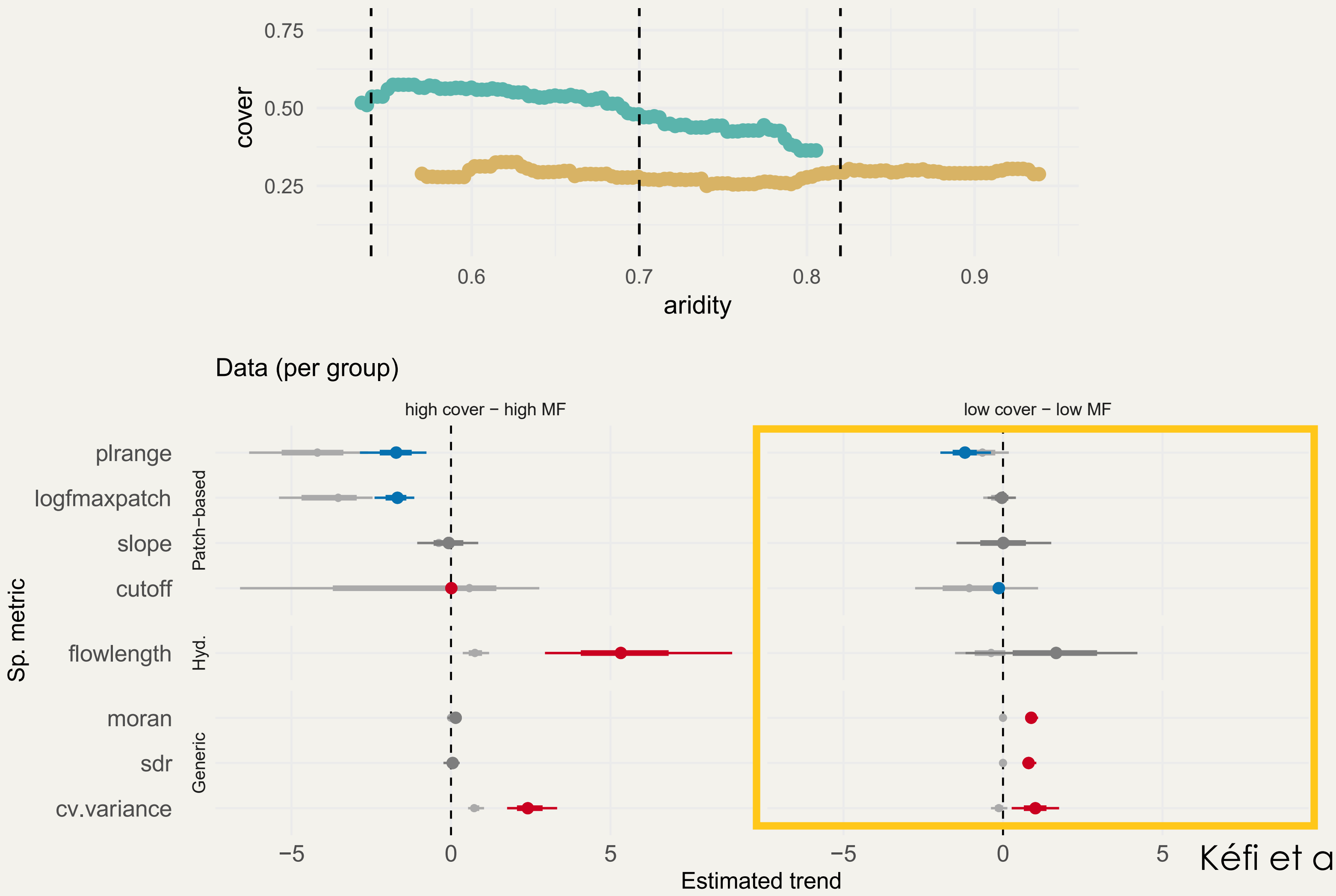

Kéfi et al. 2024



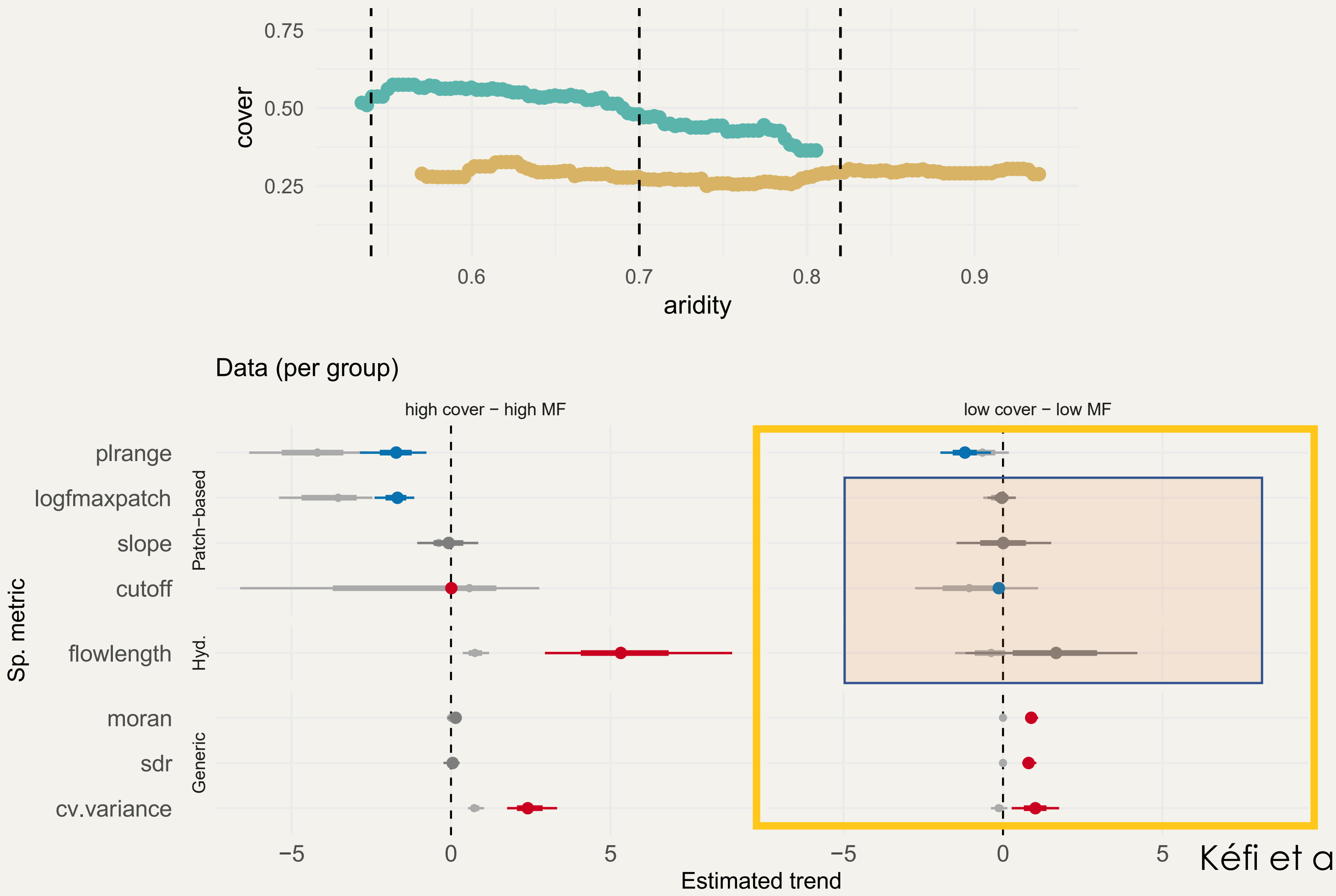

Kéfi et al. 2024



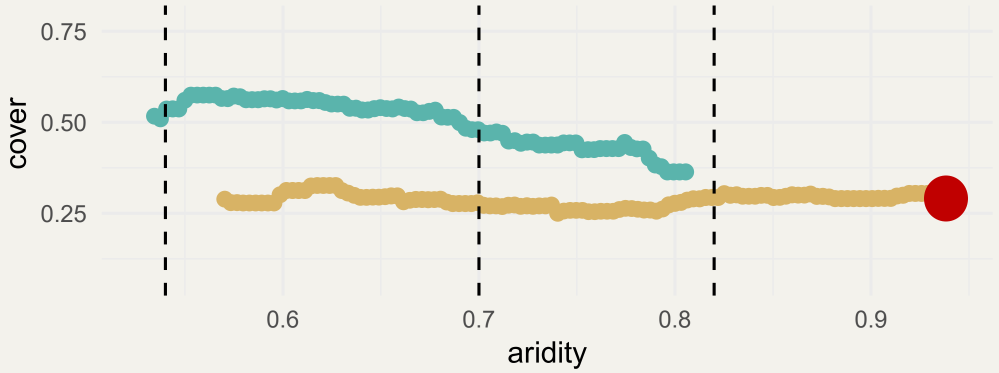

Kéfi et al. 2024

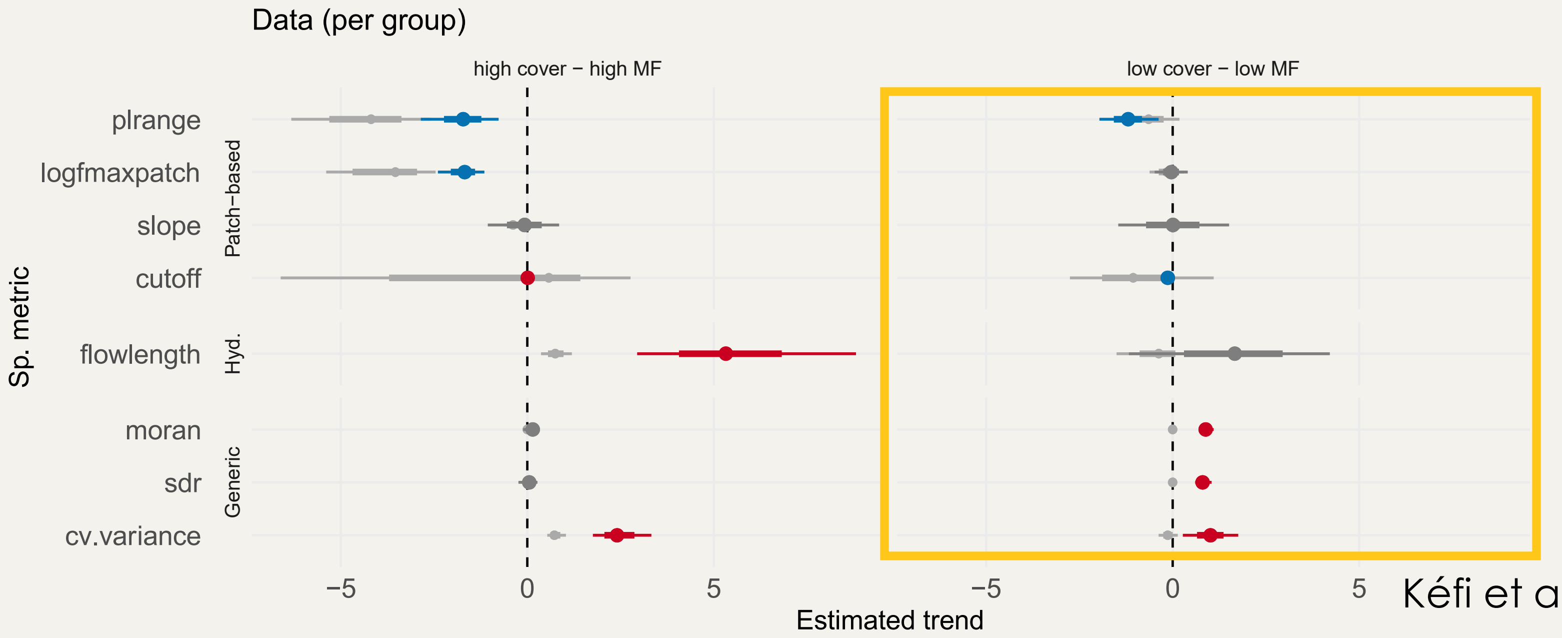



Kéfi et al. 2024




Kéfi et al. 2024




Kéfi et al. 2024

Two groups of dryland sites
with different responses to aridity

# Self-organisation as a mechanism of resilience

Degradation drivers?

CASCADE

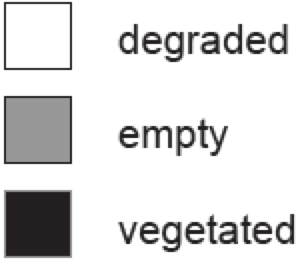
Catastrophic shifts in drylands

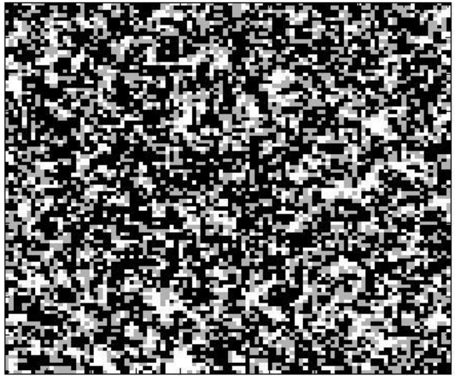

20.03.2014

b=0.9 r=0.9

Schneider and Kéfi 2016 TE

# + spatially explicit stressor



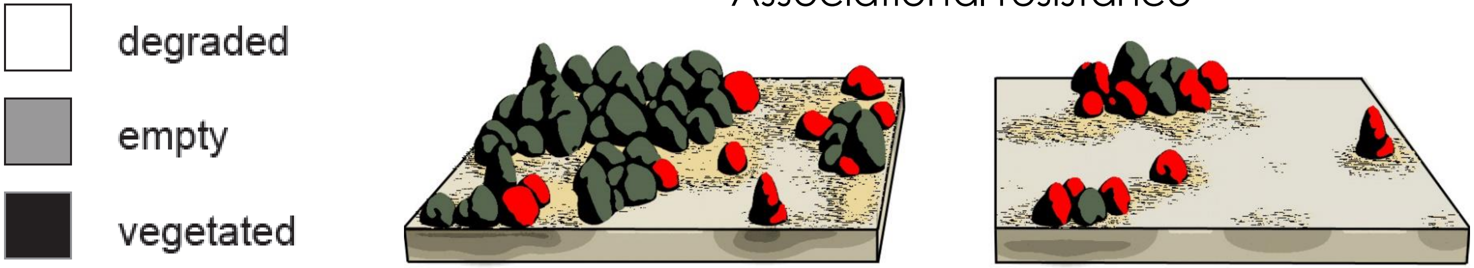



b=0.9 r=0.9

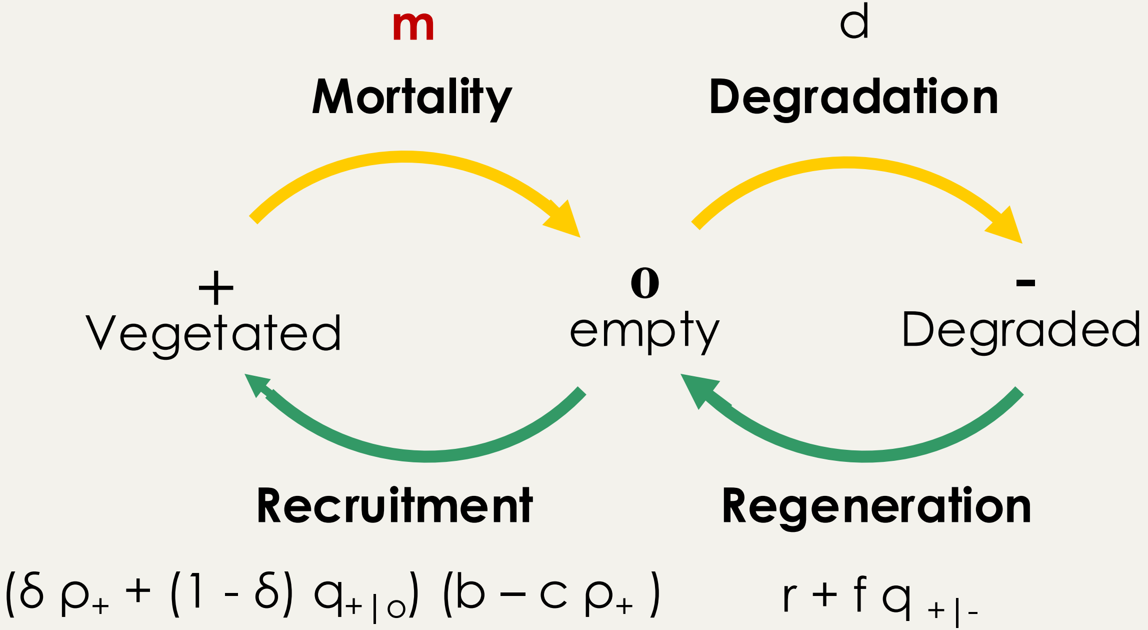
Schneider and Kéfi 2016 TE

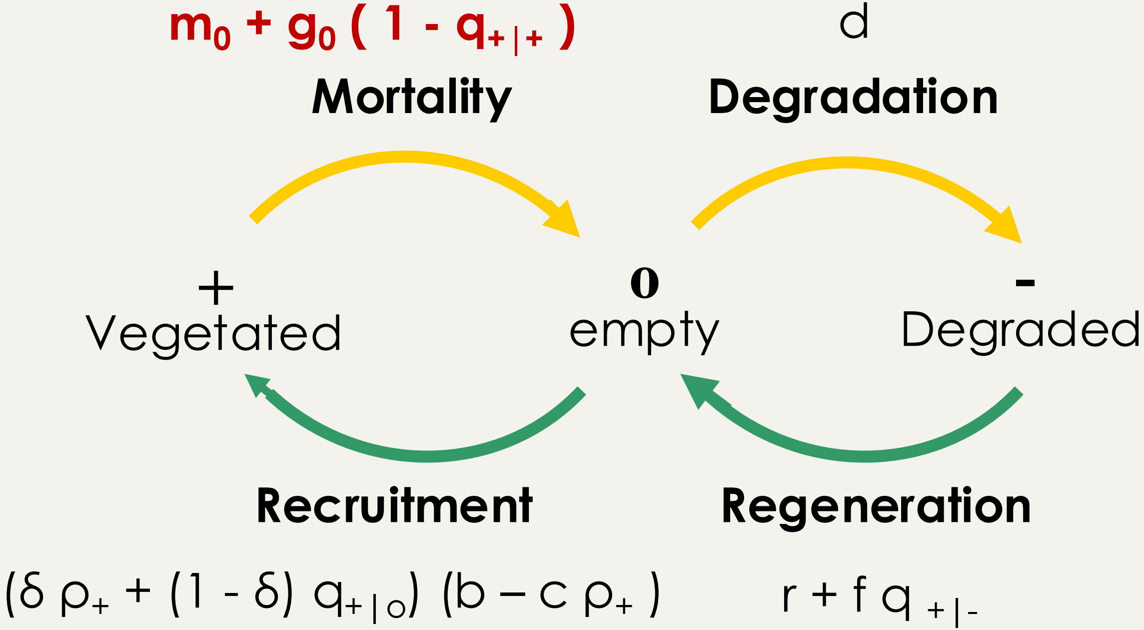
# + spatially explicit stressor

Associational resistance

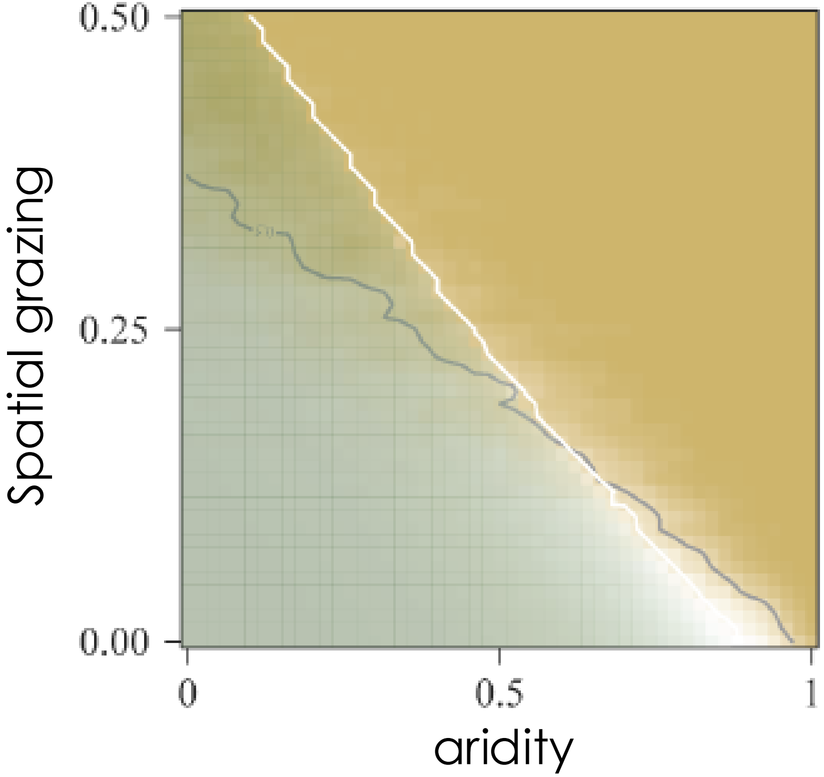



Schneider and Kéfi 2016 TE

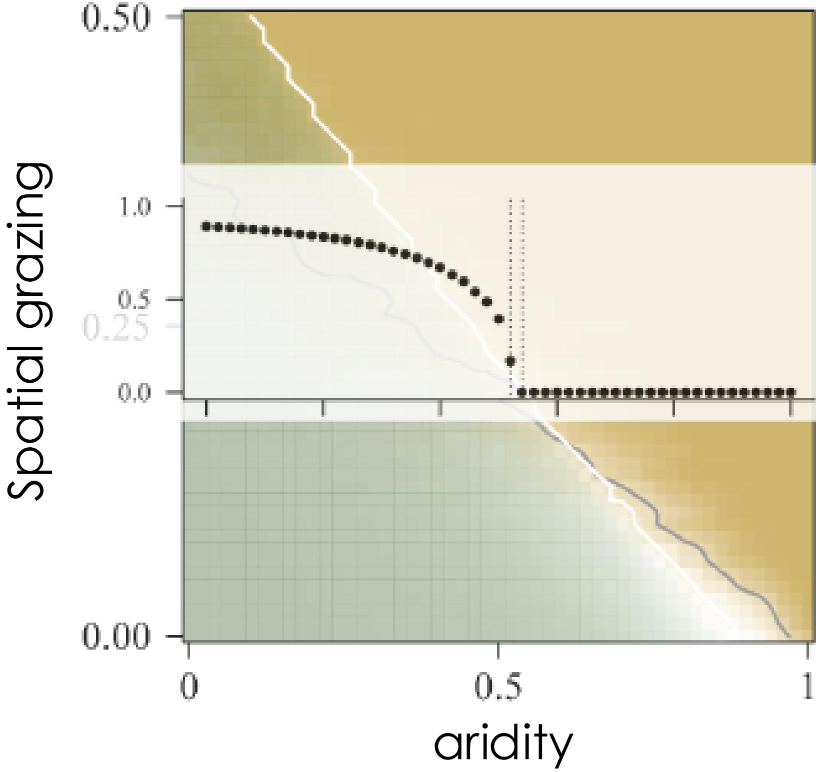

m
Mortality
d
Degradation
+
Vegetated
0
empty
-
Degraded
Recruitment
$(\delta \rho_+ + (1 - \delta)\, q_{+|0})\, (b - c\, \rho_+)$
Regeneration
$r + f\, q_{+|-}$



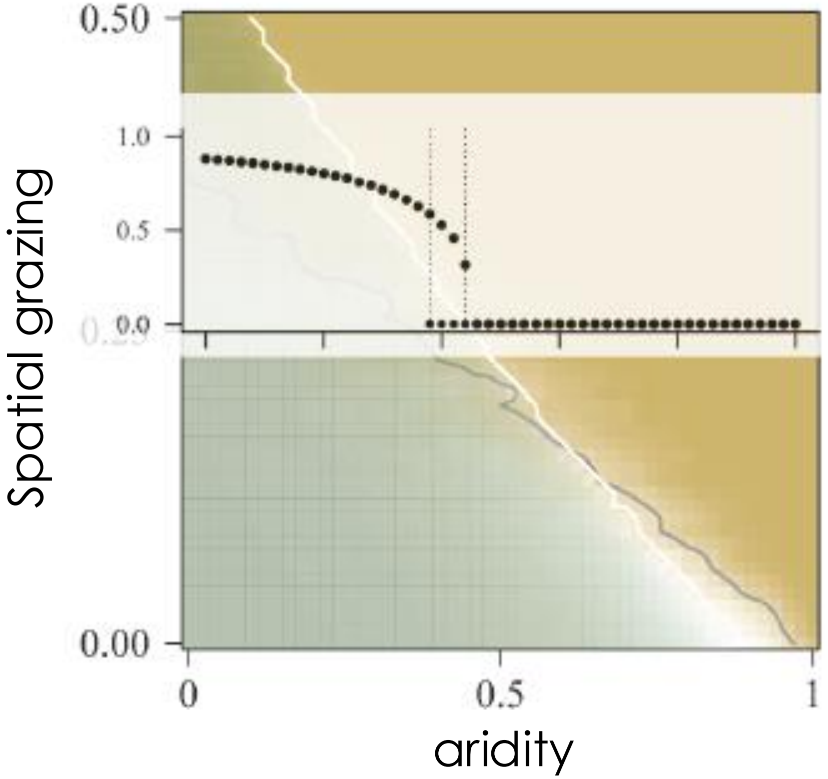

Schneider and Kéfi 2016 TE



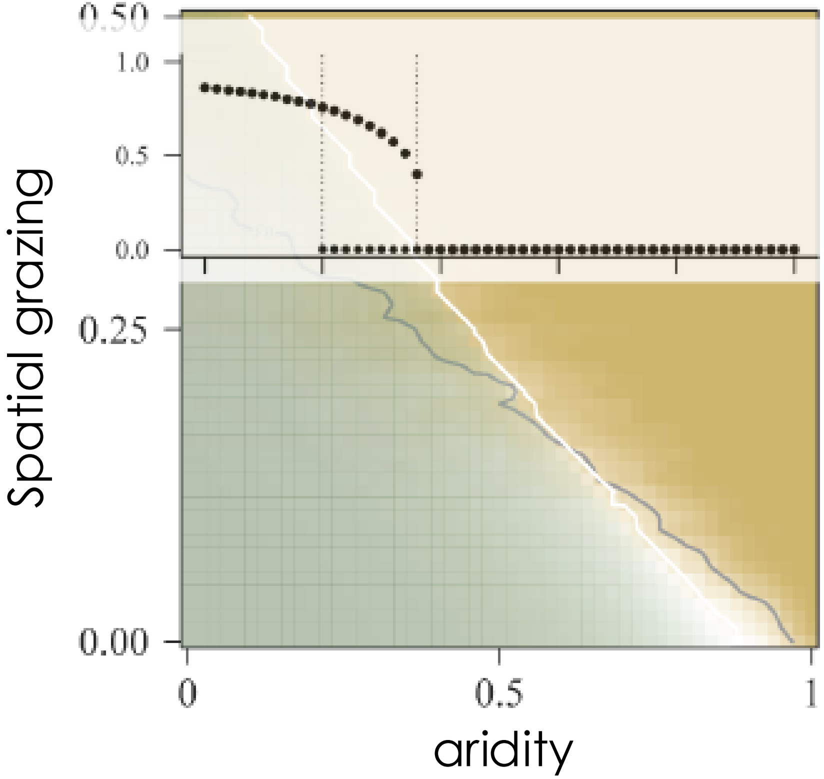

Schneider and Kéfi 2016 TE




Schneider and Kéfi 2016 TE




Schneider and Kéfi 2016 TE

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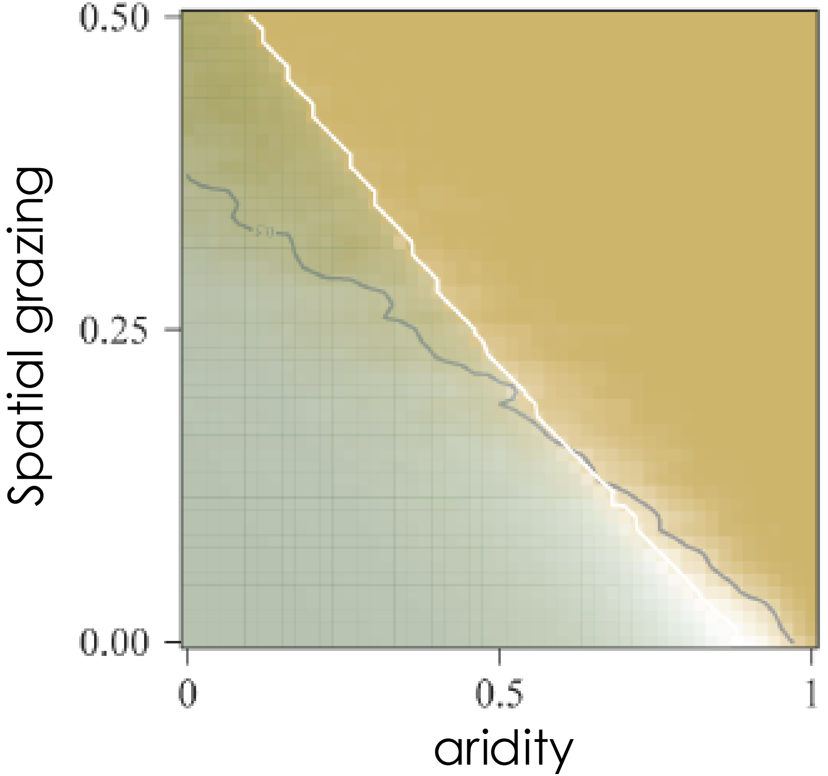
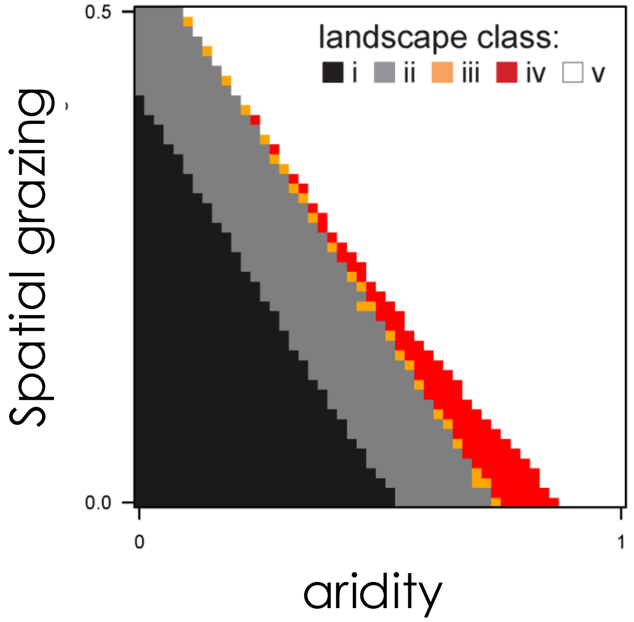
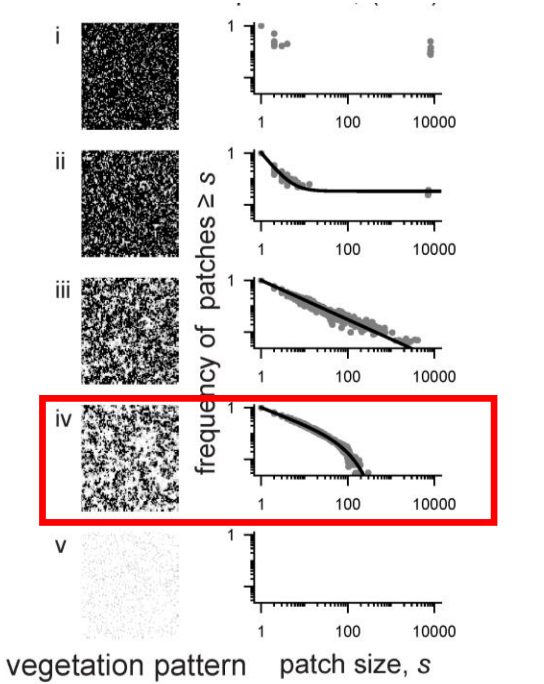



The bistability domain becomes wider with increasing grazing pressure.

Schneider and Kéfi 2016 TE




Schneider and Kéfi 2016 TE

Spatial stressors can affect:

ecosystem resilience

the interpretation of spatial indicators

# Conclusion

an apparence of stability and resilience

Jonathan Jimenez, 'Naturalia: Reclaimed by Nature' but dramatic, irreversible ecosystem responses as well

# The shape and size of the patterns:

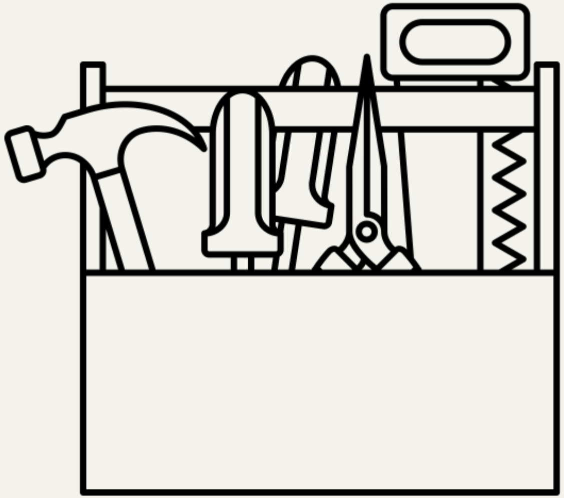
→ provide information about the underlying mechanisms

→ reveal their role of the patterns for ecosystem functioning and resilience

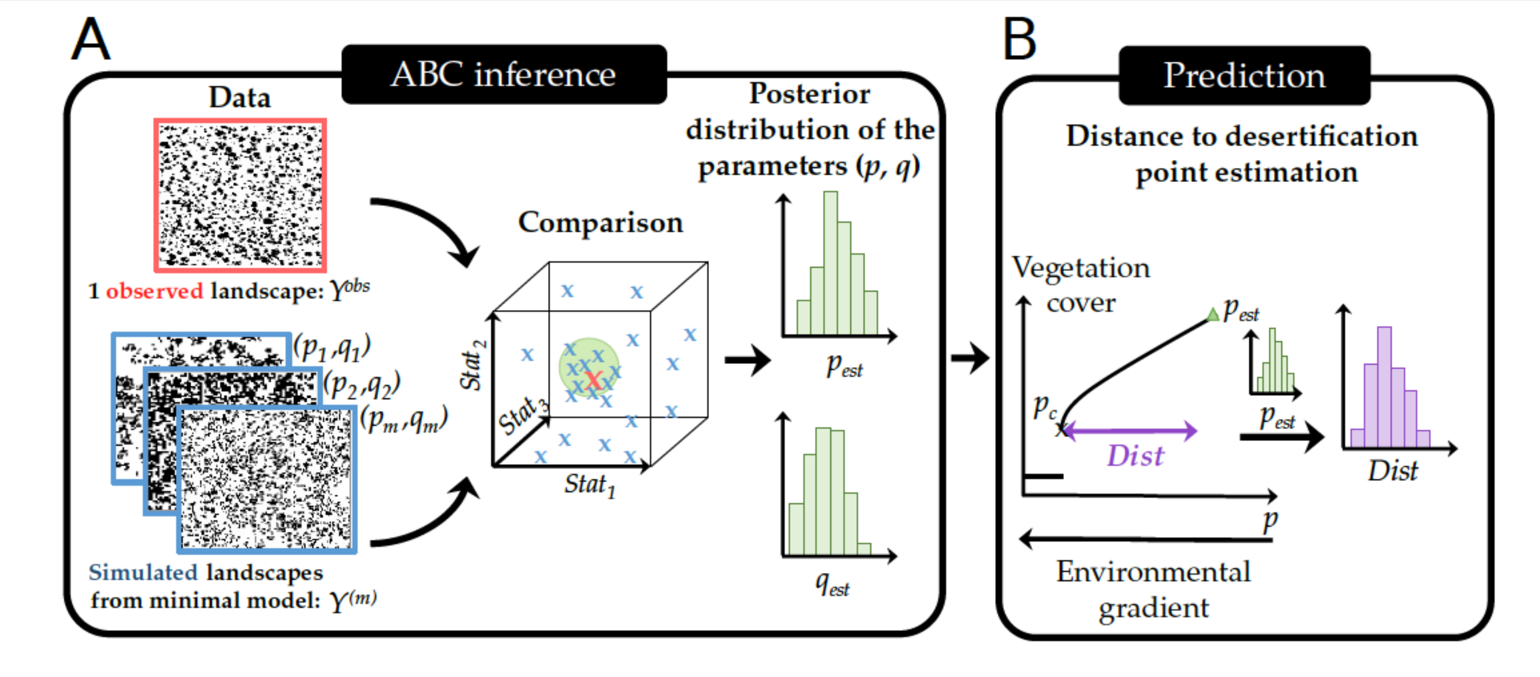
→ inform about the indicators to look at

So far, spatial indicators suggest trends

Indicator toolbox



model ⟷ data




Pichon et al., en cours

# Map areas vulnerable to increasing stress


N
Patterned peatland, Finland
199 m
Image © 2007 DigitalGlobe
©2007 Google™


N
Medium-scale patterning, Bunker Reef
171 m
Google


Courtesy J. van de Koppel

# Thanks

My co-authors and collaborators

All of you for your attention

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