

Structure et dynamique des communautés écologiques

(iii)

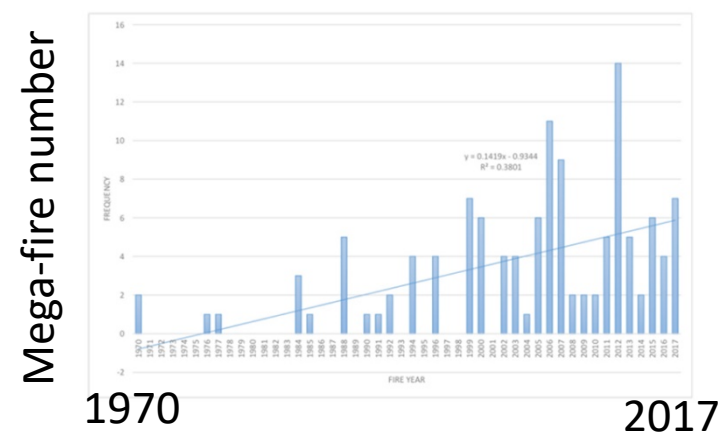
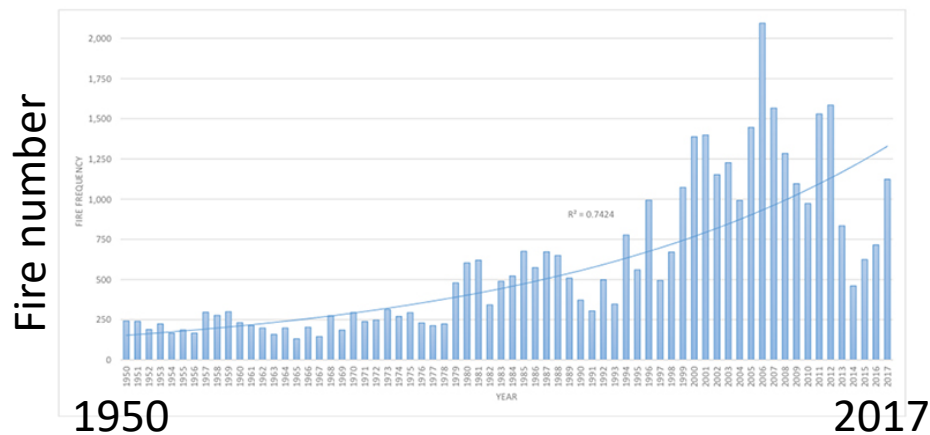
Stability of ecological communities

Colin Fontaine

Aussois 2021

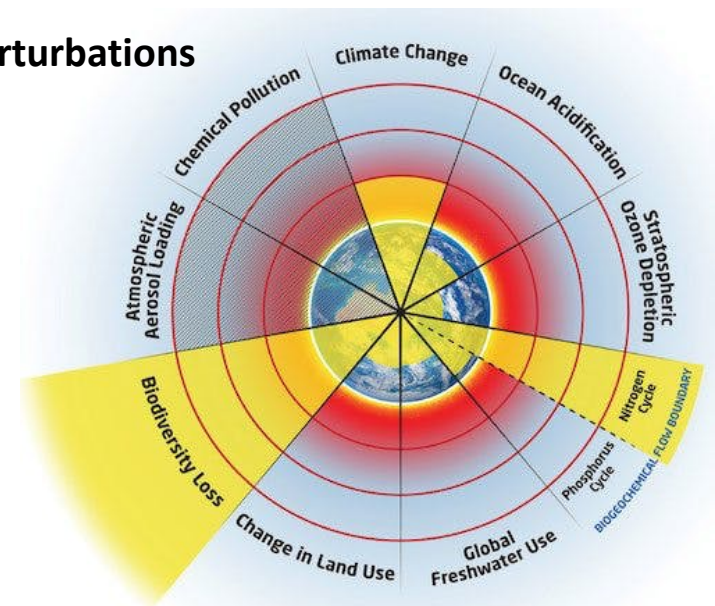
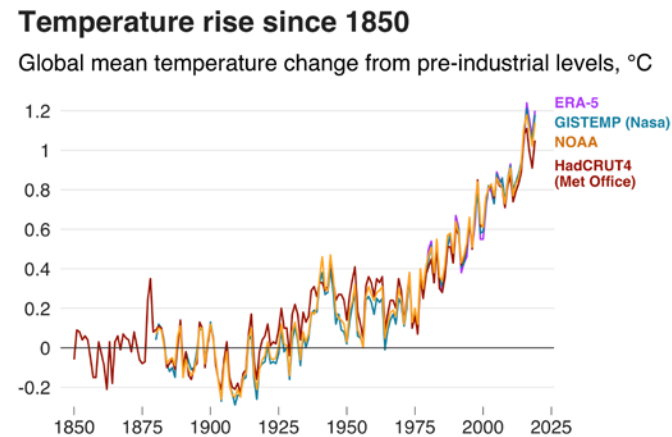
Stability of ecosystems

- Most ecologists describe ecosystem stability as the ability of an ecosystem to **maintain its structure and function** over long period of time and **despite disturbances**
- Natural ecosystems experience regular punctual environmental changes, or disturbances
 - Fire; flooding; storm; Insect outbreak...
- The Anthropocene is characterized by
 - An increase in the frequency and amplitude of **pulse perturbations**



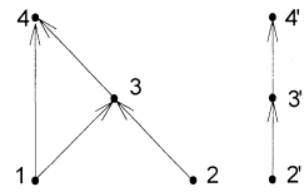
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- The Anthropocene is characterized by
 - An increase in the frequency and amplitude of **pulse perturbations**
 - An increase of system forcing/**press perturbations**



Complexity stability relationship

- Original idea:
 - Theoretical and experimental evidence that simple model ecosystems are inherently unstable
 - Observations suggest that diversity of species and interactions among them favor community stability



Odum E. 1950

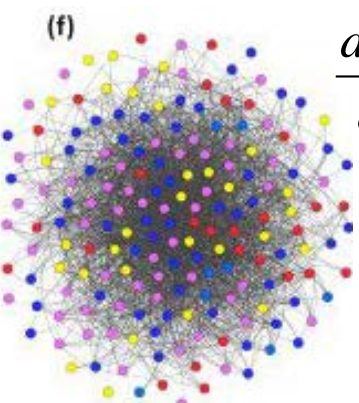


Elton C. S. 1958



MacArthur R. 1955

- Challenged by theory



$$\frac{dN_i}{dt} = F_i(N_1, \dots, N_k)$$

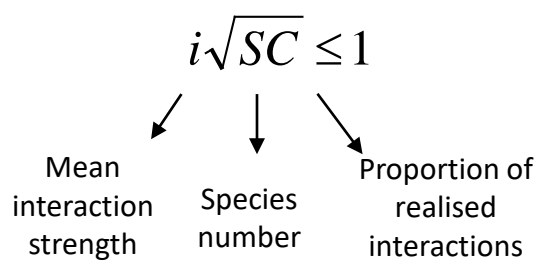
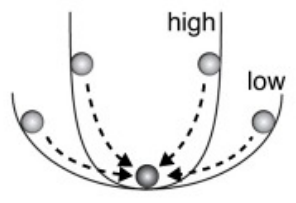
A = matrice de communauté

a_{ij} = force d'interaction

	1	2	n
1	■	■	■	■
2	■	■	■	■
...	■	■	■	■
n	■	■	■	■

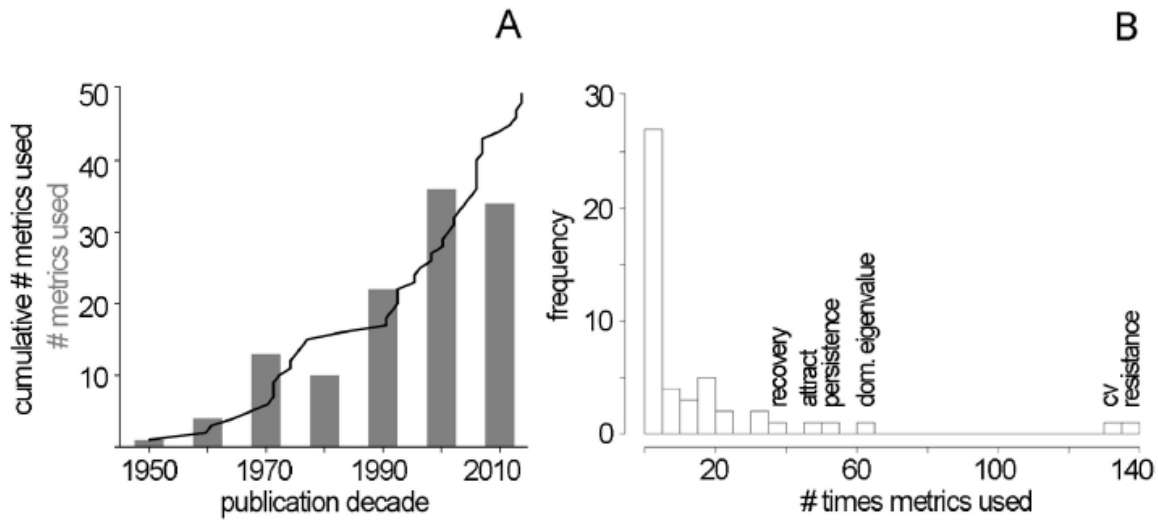
$$a_{ij} = \left(\frac{\partial F_i}{\partial N_j} \right)_{eq}$$

(a) Engineering resilience



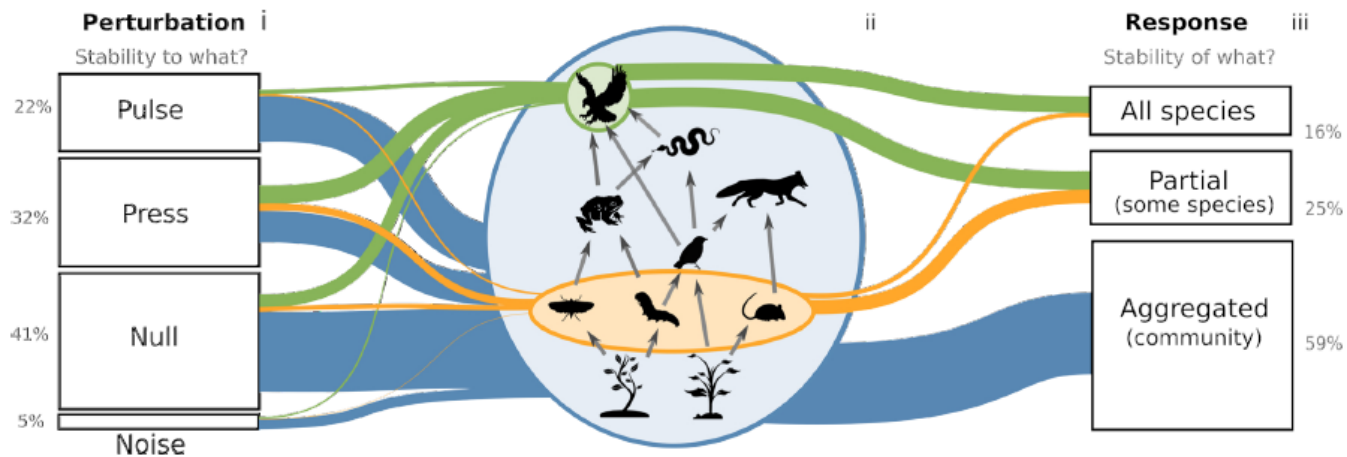
May R. 1971

Ecological stability: an expanding (messy) field



B

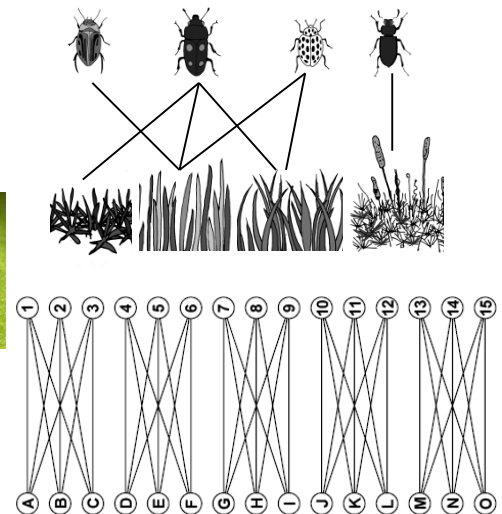
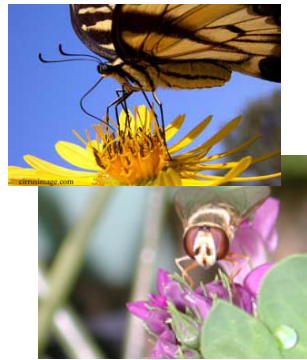
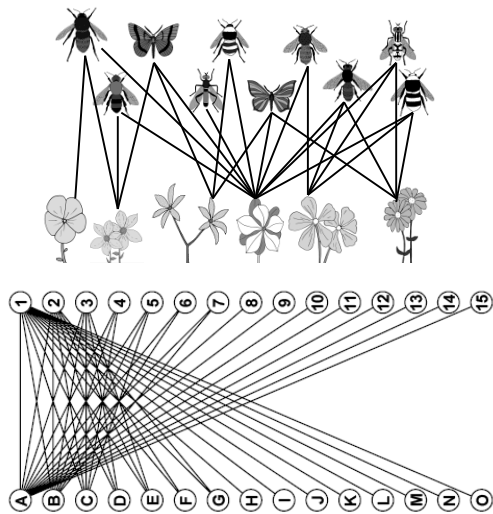
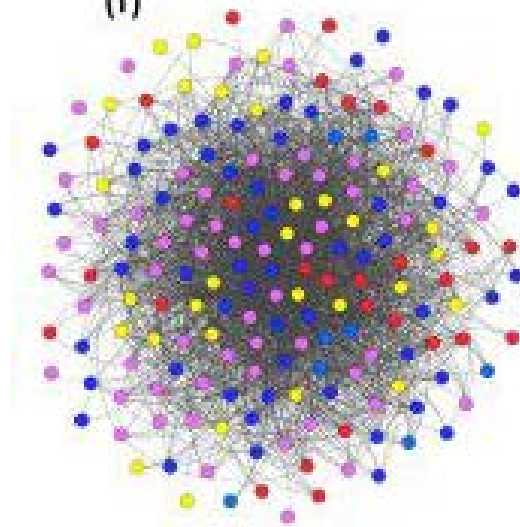
	Constancy	Recovery	Resistance	Dynamical Attractors
definition	variability (or lack thereof) of the dynamics of composition or structure of the system over time or space	whether and how fast the system recovers after a perturbation	how much the system changes after a perturbation	existence or changes between attractors/dynamical states (alternative stable states or stable to unstable/oscillation)
metric (example)	variability (cv, std) persistence permanence	engineering resilience recovery back to predisturbed state	resistance (eg deviation from reference) robustness	attractor type trends in variance/autocorrelation
	<p>a</p> <p>ecological state</p> <p>time</p> <p>change in variability</p>	<p>b</p> <p>ecological state</p> <p>time</p> <p>pulse</p> <p>recovery rate (slope)</p> <p>time to recover</p>	<p>c</p> <p>ecological state</p> <p>time</p> <p>press</p> <p>resistance</p>	<p>d</p> <p>ecological state</p> <p>time</p> <p>onset of oscillations</p>



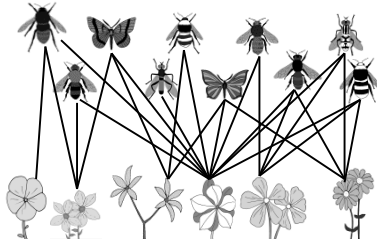
- How to reconcile May's results with the idea that complexity favors stability?
- Empirical approaches to ecological stability
- The dimensionality of ecological stability

Ecological interaction networks are not random

(f)



Network structure and community dynamic

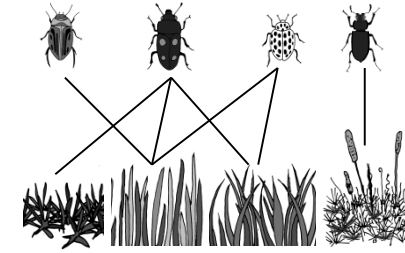


Mutualistic

$$\frac{dA_i}{dt} = r_{A_i} A_i - I_{A_i} A_i^2 + \sum_{j=1}^{N_p} \frac{c_{ji} A_i P_j}{\alpha_{ji}^{-1} + \sum_{P_k \in \text{mut}(A_i)} P_k}$$

$$\frac{dP_i}{dt} = r_{P_i} P_i - I_{P_i} P_i^2 + \sum_{j=1}^{N_a} \frac{c_{ij} A_j P_i}{\alpha_{ij}^{-1} + \sum_{A_k \in \text{mut}(P_i)} A_k}$$

- intrinsic growth rates
 r_P and $r_A < 0 \rightarrow$ obligate mutualism
- density dependence term
- interaction term
saturates with mutualistic partner densities



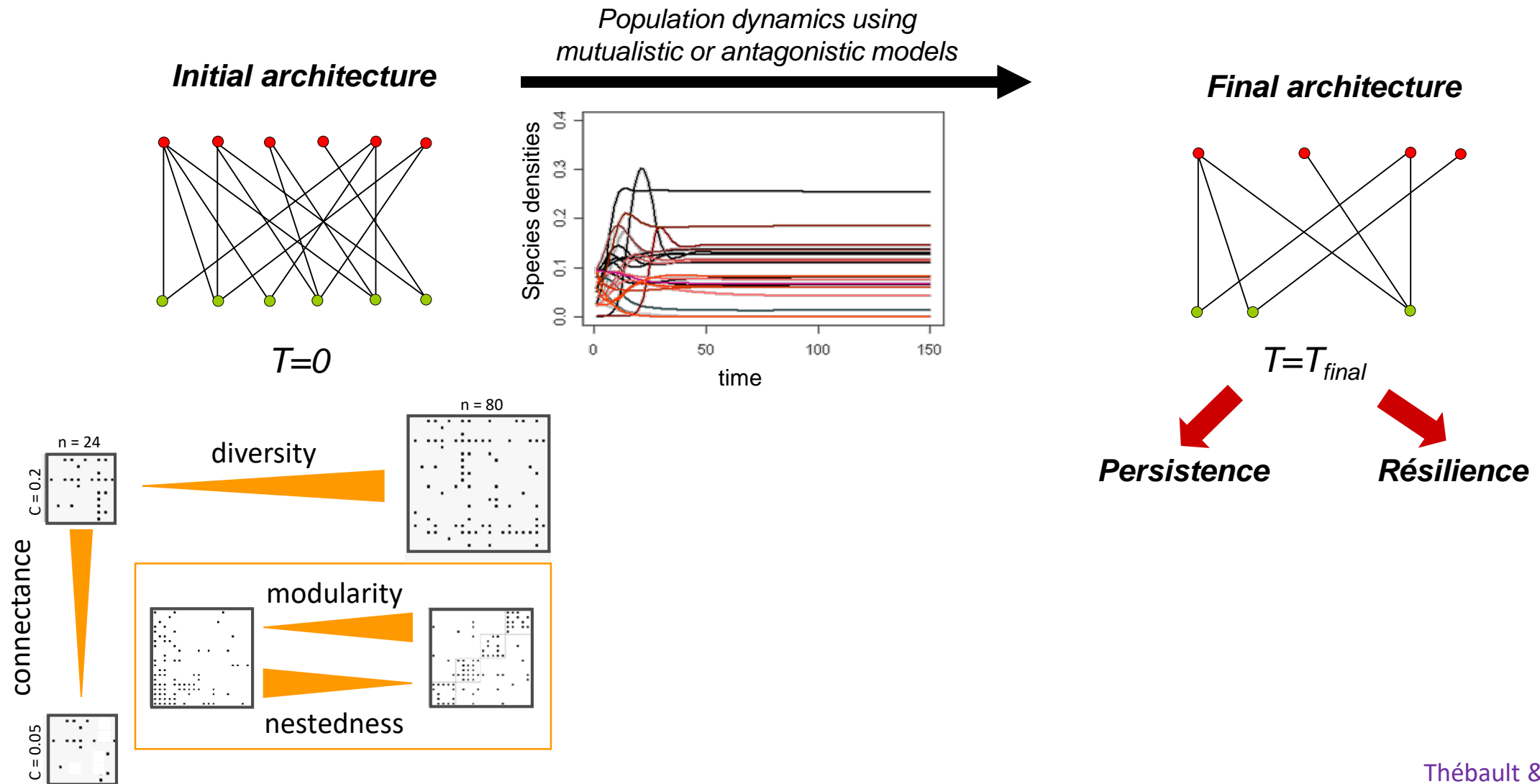
Trophic

$$\frac{dA_i}{dt} = r_{A_i} A_i - I_{A_i} A_i^2 + \sum_{j=1}^{N_p} \frac{c_{ji} A_i P_j}{\alpha_{ji}^{-1} + \sum_{P_k \in \text{prey}(A_i)} P_k}$$

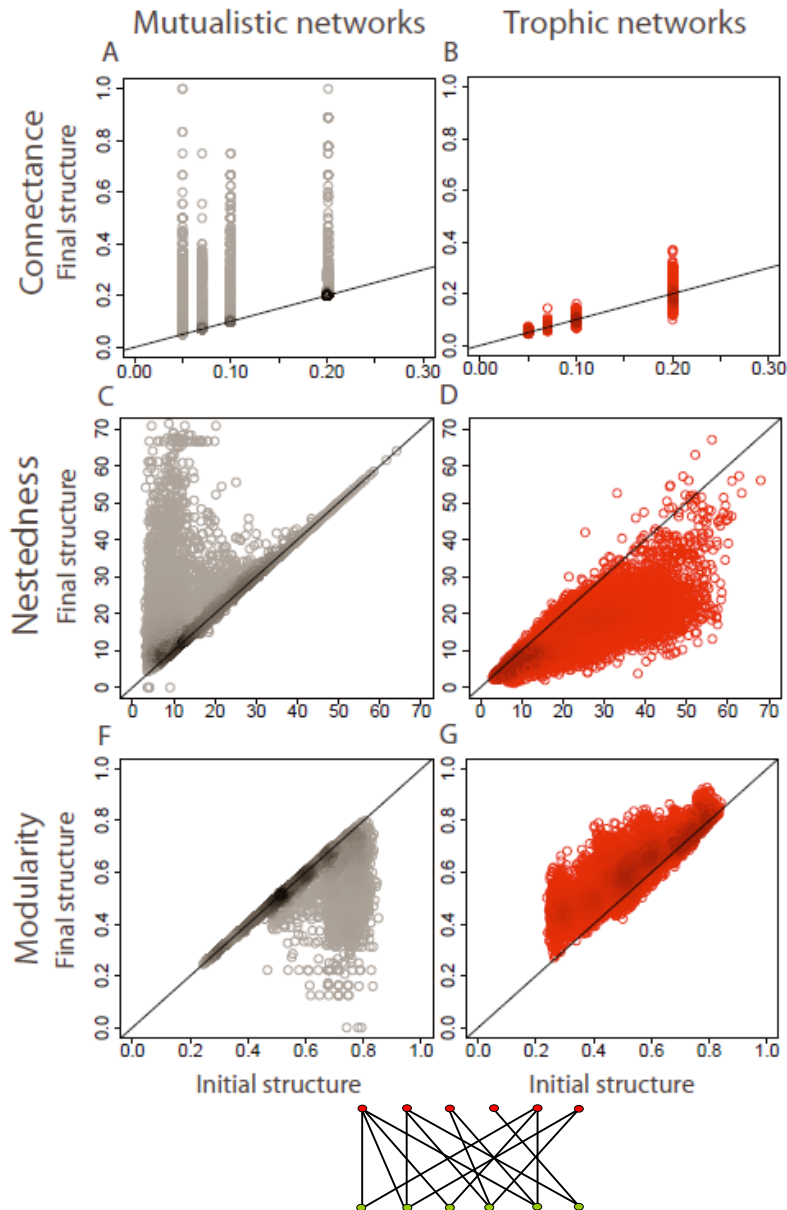
$$\frac{dP_i}{dt} = r_{P_i} P_i - I_{P_i} P_i^2 - \sum_{j=1}^{N_a} \frac{c_{ij} A_j P_i}{\alpha_{ij}^{-1} + \sum_{P_k \in \text{prey}(A_j)} P_k}$$

- intrinsic growth rates
 $r_P > 0$ and $r_A < 0$
- density dependence term
- interaction term
saturates with prey densities

Network structure and community dynamic



Network structure and community dynamic



Persistence

	réseau mutualiste	réseau trophique
diversité	+	-
connectance	+	-
emboitement		-
compartimentalisation	-	

Résilience

	réseau mutualiste	réseau trophique
diversité	+	-
connectance	+	-
emboitement	+	
compartimentalisation		+

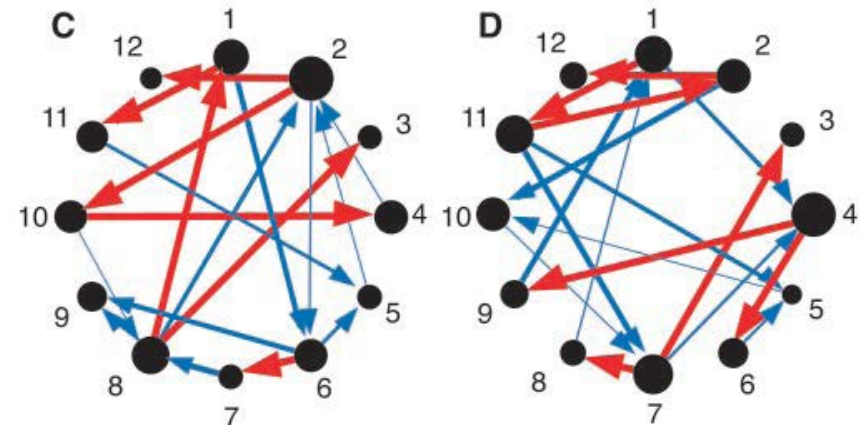
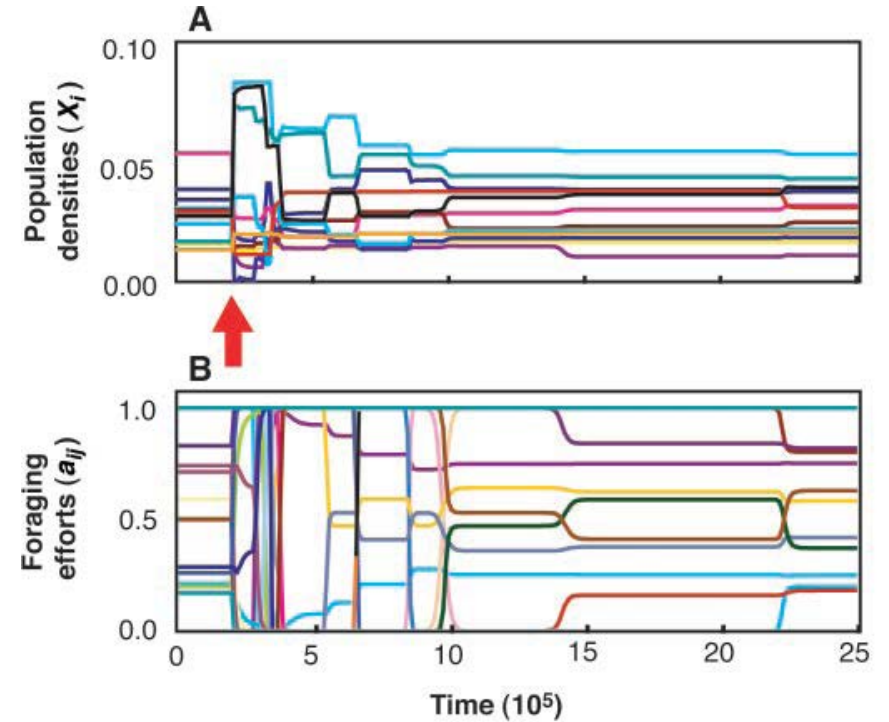
Considering effects of foraging adaptation

$$\frac{dX_i}{dt} = X_i \left(r_i - s_i X_i + \sum_{j \in \text{resources}} e_{ij} f_{ij} a_{ij} X_j - \sum_{j \in \text{consumers}} f_{ji} a_{ji} X_j \right) \quad (1)$$

Metabolic rate
 Foraging efficiency
 Attack rate

$$\frac{da_{ij}}{dt} = G_i a_{ij} \left(\underbrace{e_{ij} f_{ij} X_j}_{\text{Profitability of resource } j} - \sum_{k \in \text{resources}} \underbrace{a_{ik} e_{ik} f_{ik} X_k}_{\text{Profitability of other resources}} \right) \quad (2)$$

Adaptation rate



Considering effects of foraging adaptation

$$\frac{dX_i}{dt} = X_i \left(r_i - s_i X_i + \sum_{j \in \text{resources}} e_{ij} f_{ij} a_{ij} X_j - \sum_{j \in \text{consumers}} f_{ji} a_{ji} X_j \right) \quad (1)$$

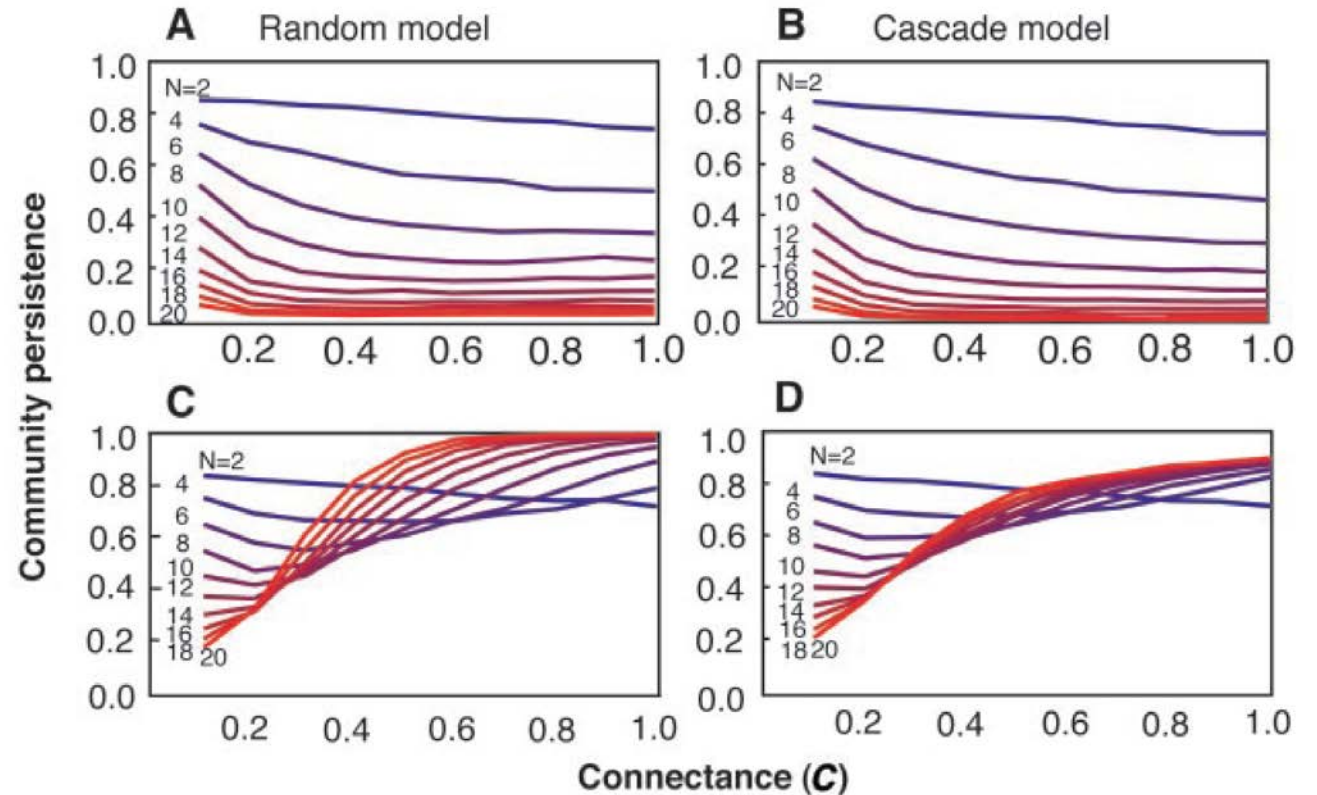
Metabolic rate

Foraging efficiency

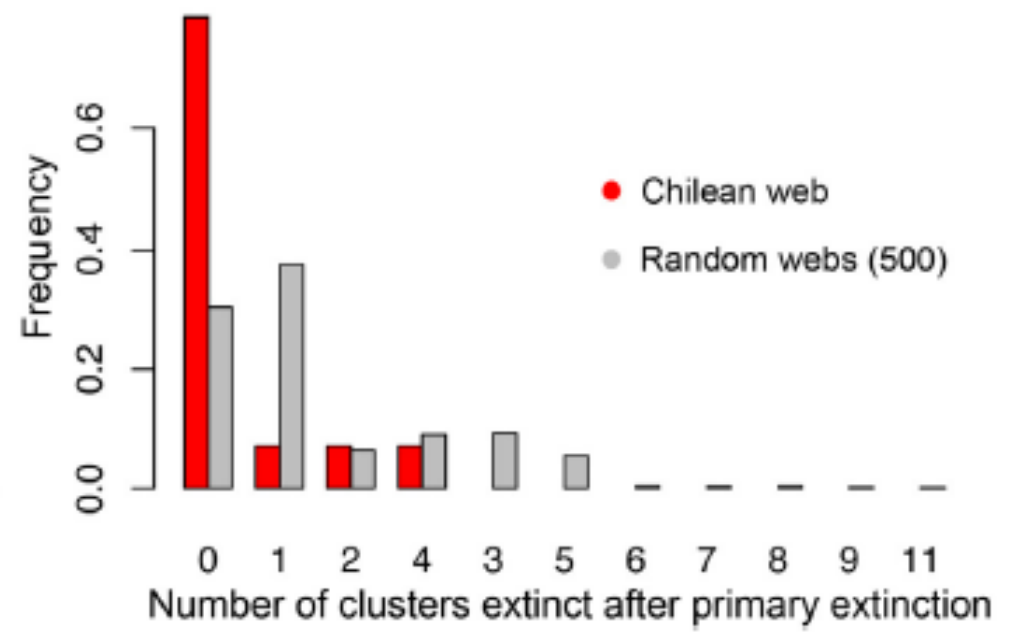
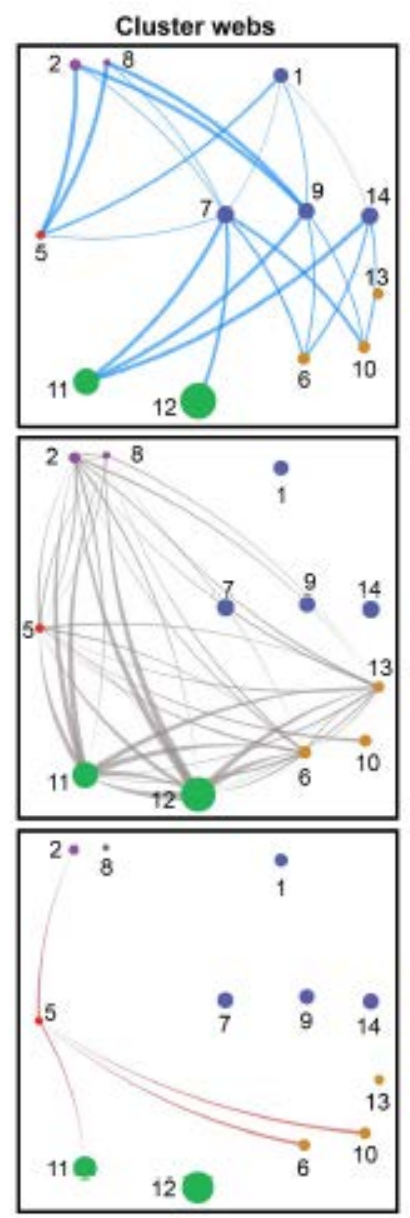
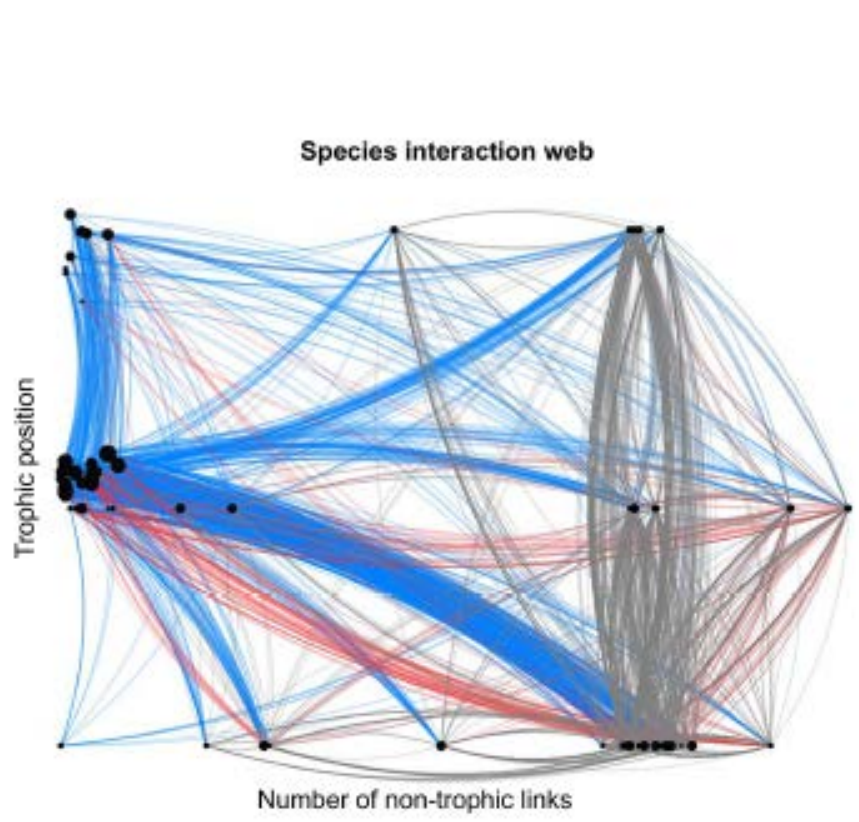
Attack rate

$$\frac{da_{ij}}{dt} = G_i a_{ij} \left(\underbrace{e_{ij} f_{ij} X_j}_{\text{Profitability of resource } j} - \sum_{k \in \text{resources}} \underbrace{a_{ik} e_{ik} f_{ik} X_k}_{\text{Profitability of other resources}} \right) \quad (2)$$

Adaptation rate



Stability of networks integrating different interaction types

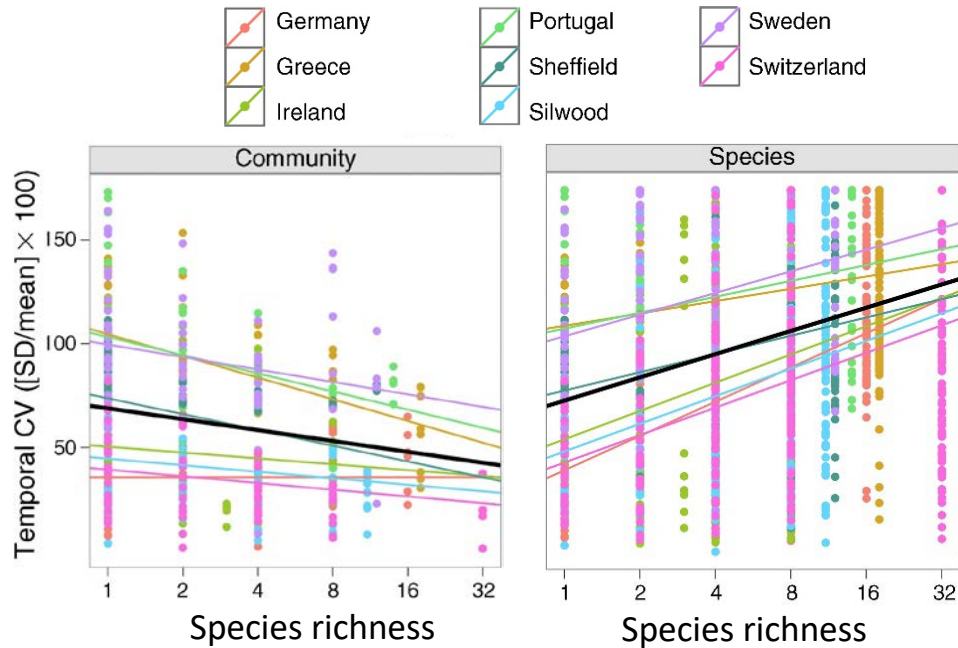


- How to reconcile May's results with the idea that complexity favors stability?
- Empirical approaches to ecological stability
- The dimensionality of ecological stability

The relationship between diversity and temporal stability of communities



The relationship between diversity and temporal stability of communities

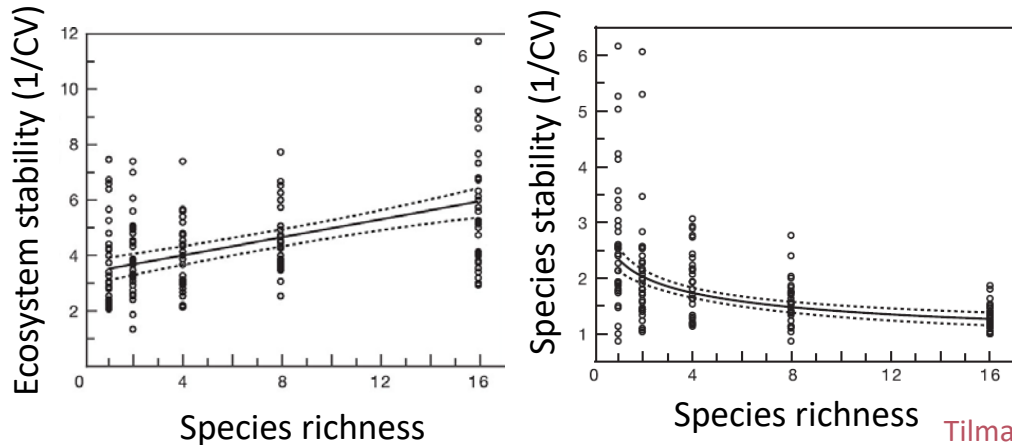


Hector et al. (2010)

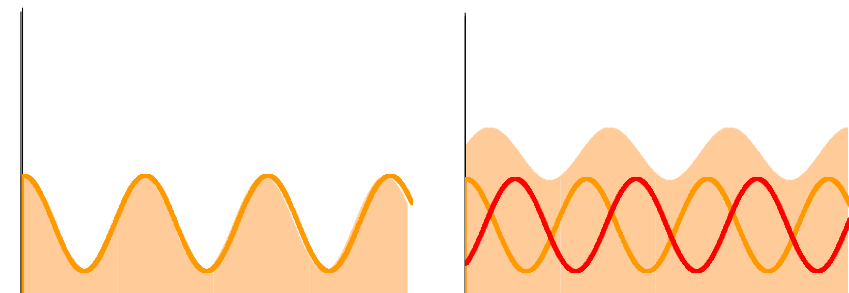


Diversity decreases variability of ecosystem properties through:

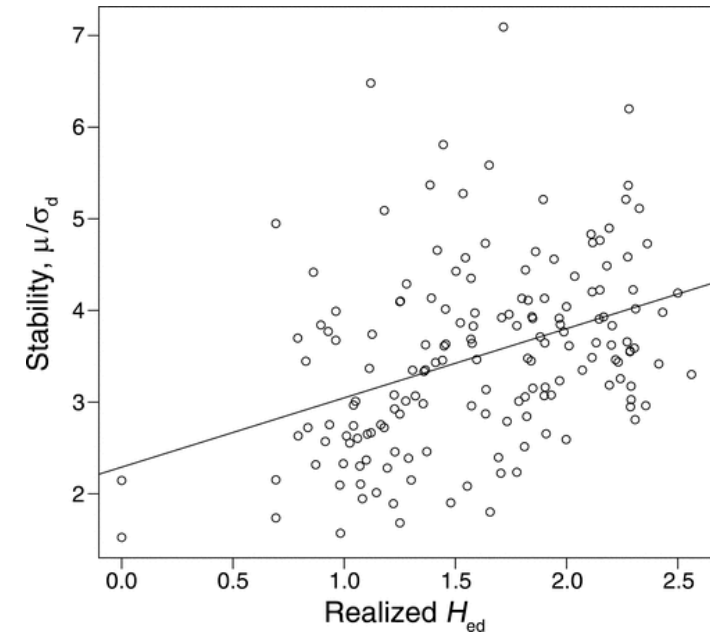
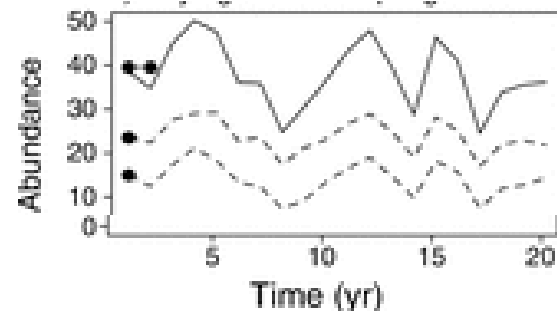
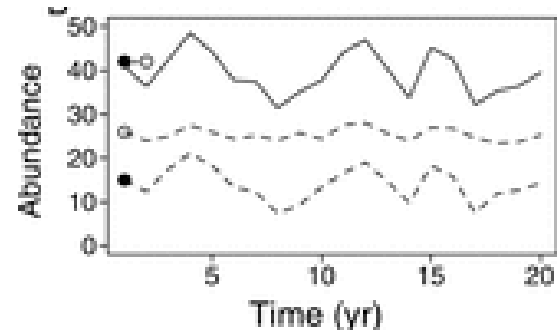
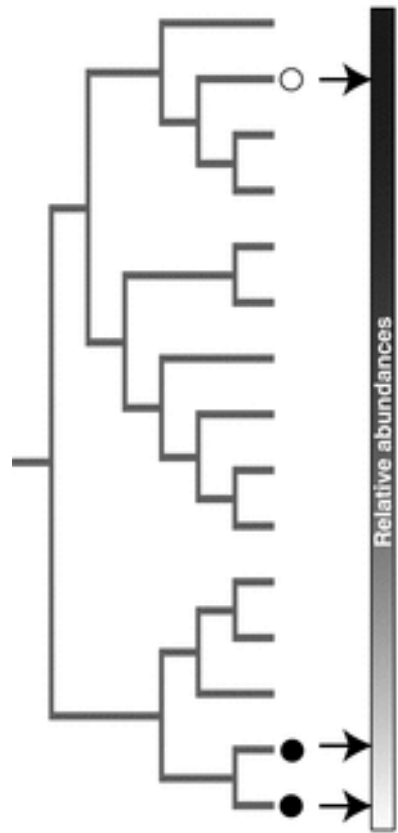
- Asynchronous responses of species to environmental perturbation



Tilman et al. (2006)

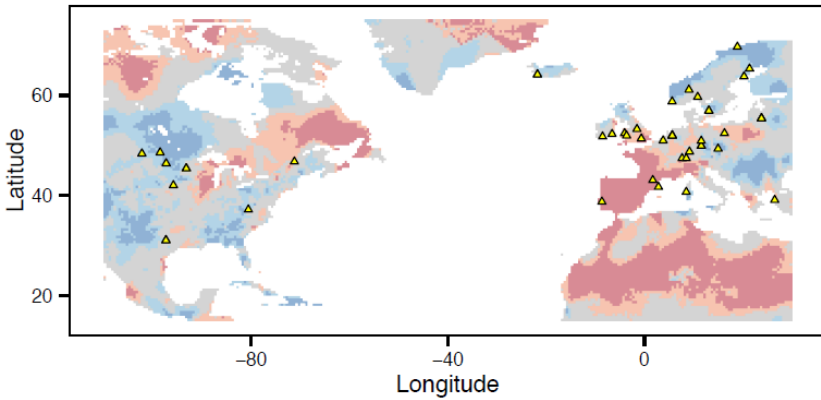


Evolutionary history of species and the temporal stability of biomass production

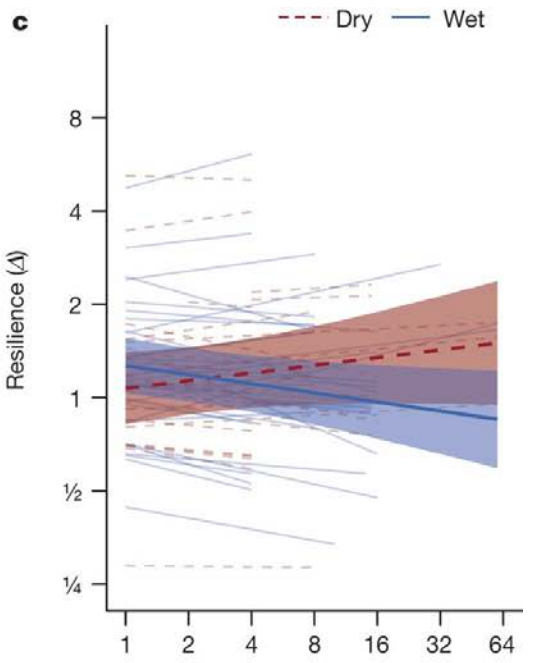
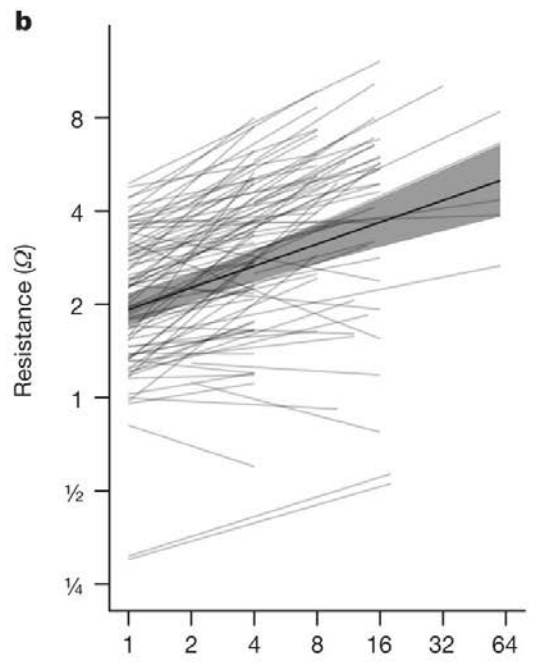
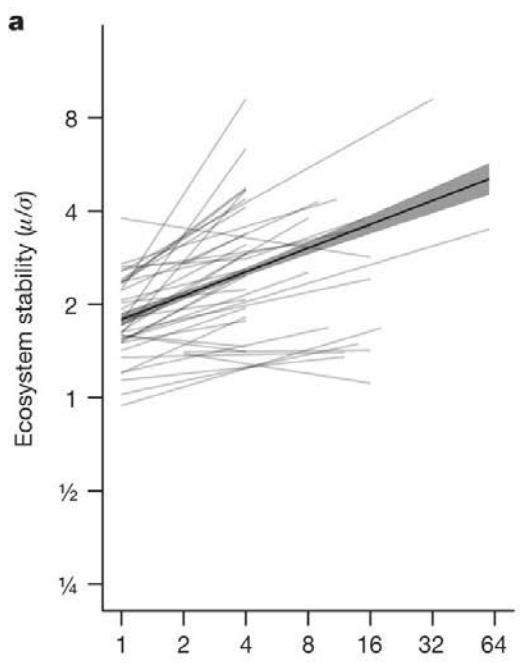
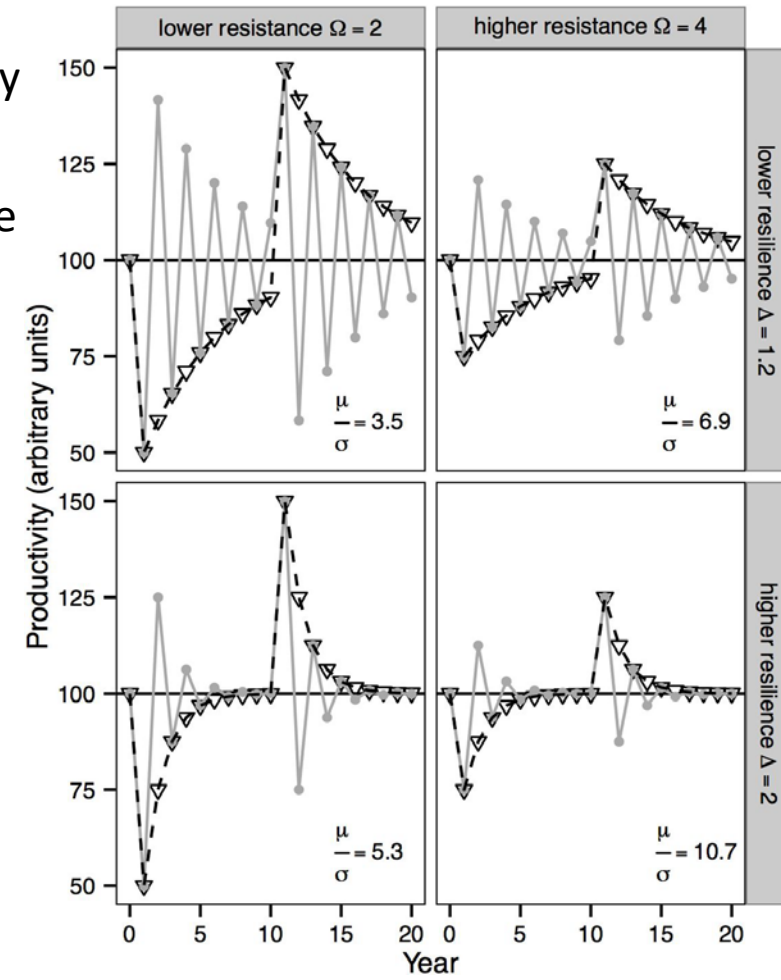


Resistance, resilience and variability of primary production to climatic extremes

extreme dry moderate dry normal moderate wet extreme wet



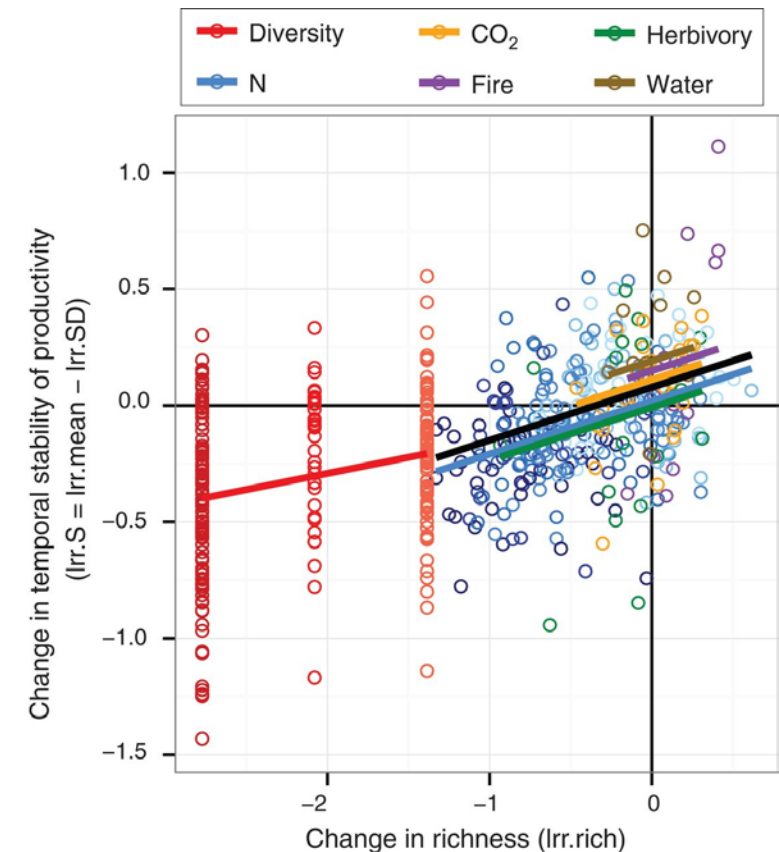
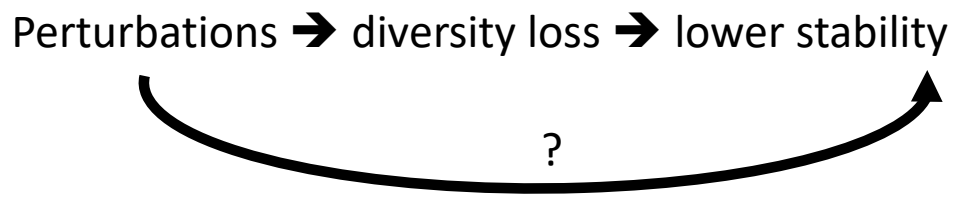
- In addition to warming, current climate change leads to an increase in the frequency of extreme climatic events
- Both resistance and resilience can affect the variability of primary production
- Plant diversity mainly affects resistance



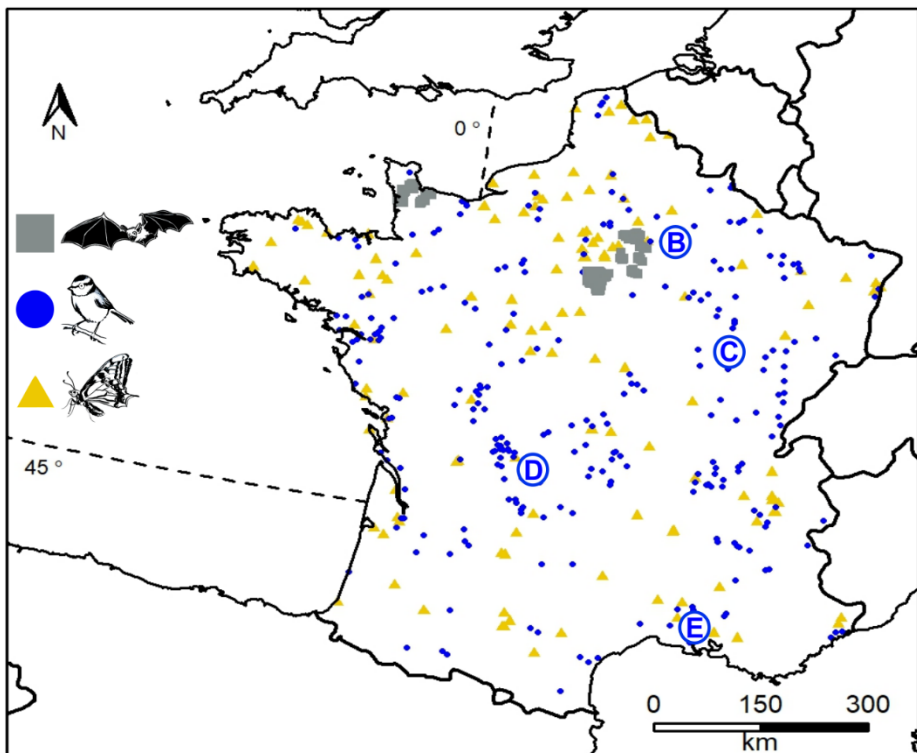
The relationship between diversity and temporal stability of communities: Limits of existing empirical studies



- Mostly comes from plant experimental communities
 - diversity - stability relationship for other taxa?
 - Effects of non-random species loss?
- Effects of anthropogenic perturbations other than species loss on community and ecosystem stability?



Data from citizen science programs to investigate the links between land uses, species diversity and community stability



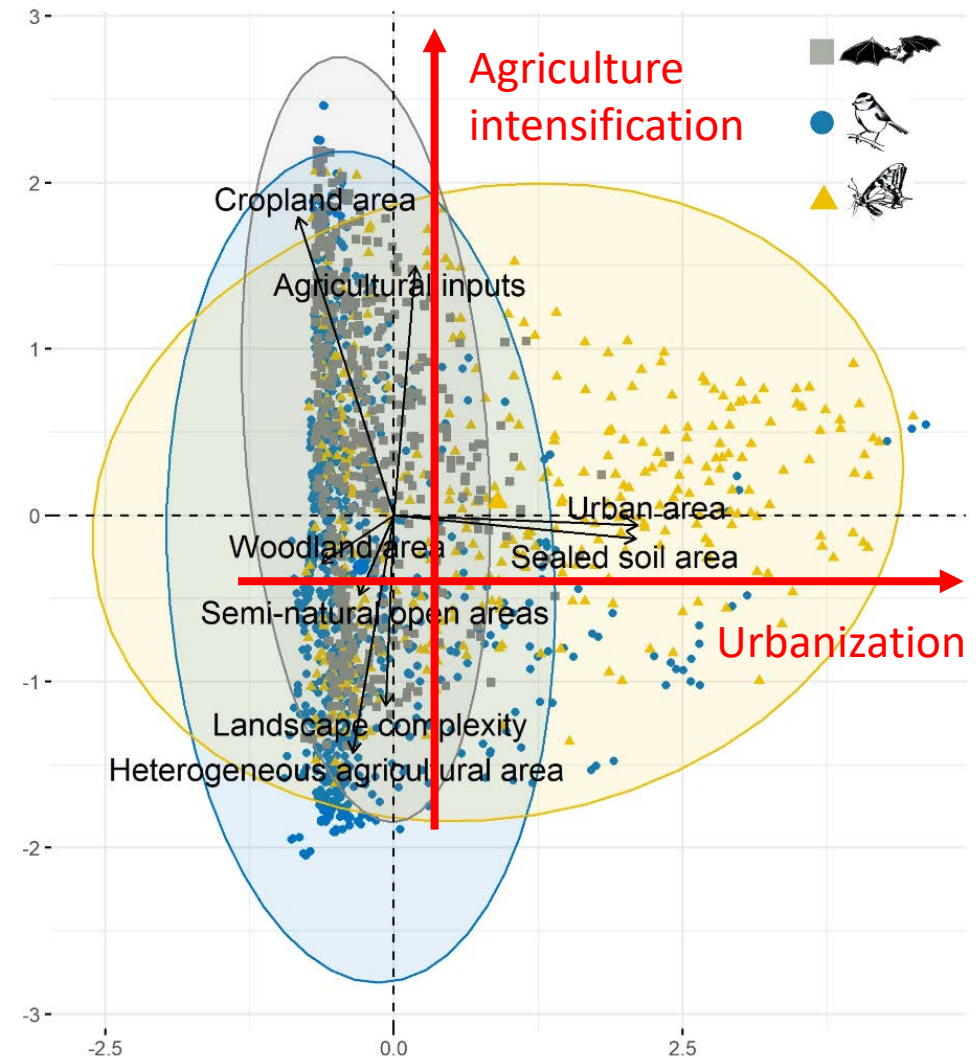
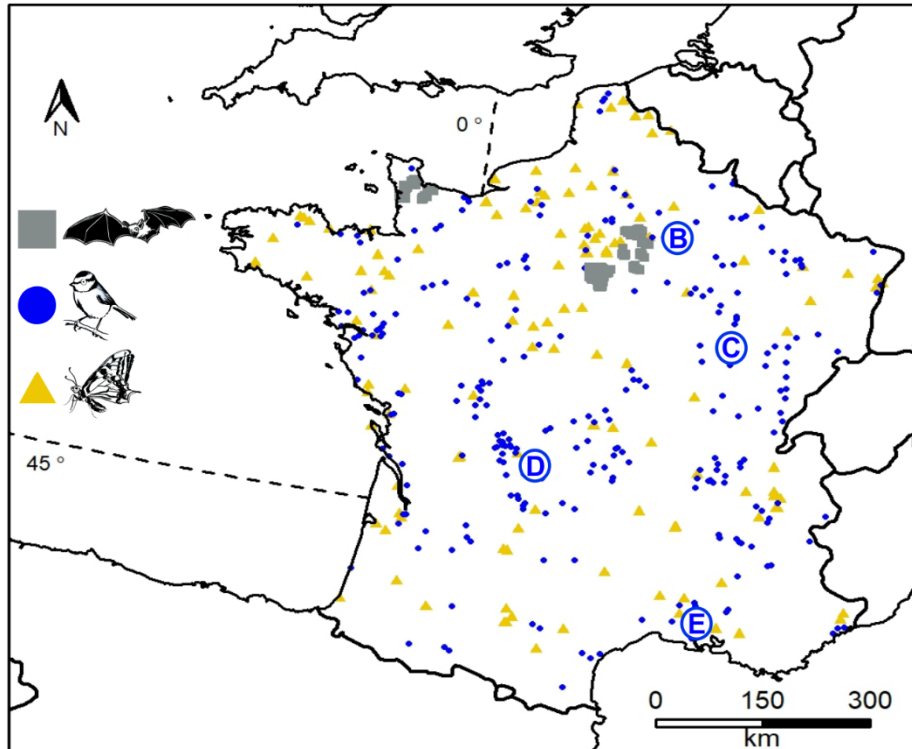
Annual abundances of communities:
161 bat communities for 4 year
269 bird communities for 8 years
130 butterfly communities for 7 years

Standardized protocols in fixed sites

Non-lethal monitoring

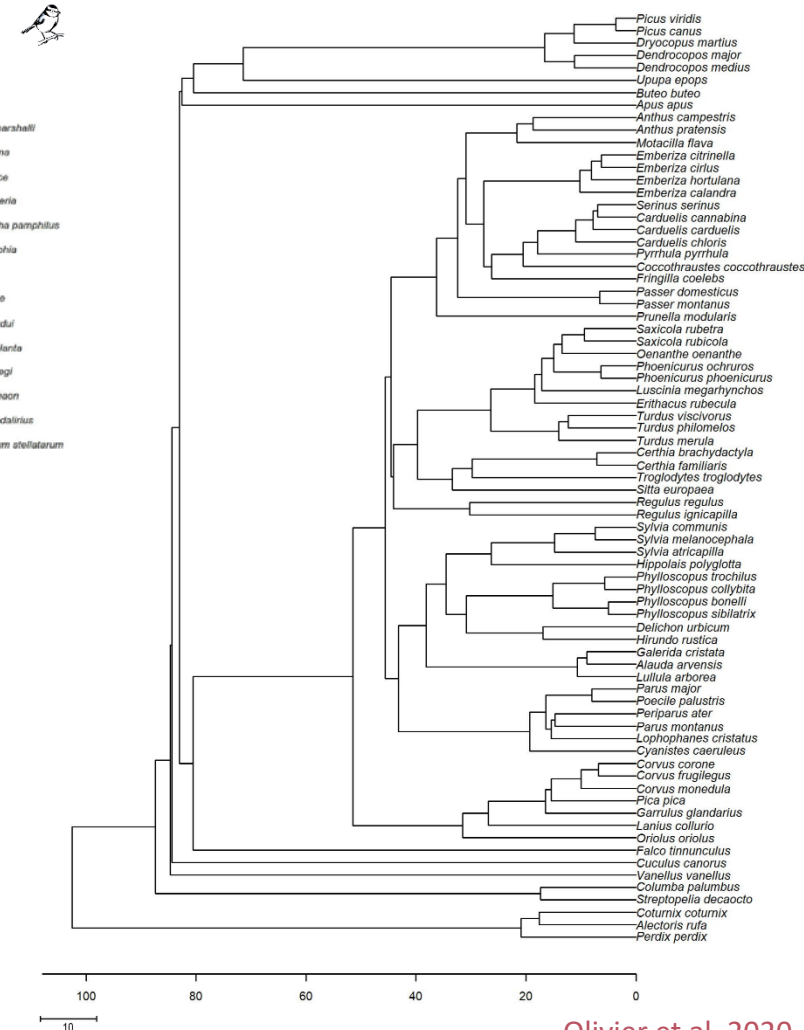
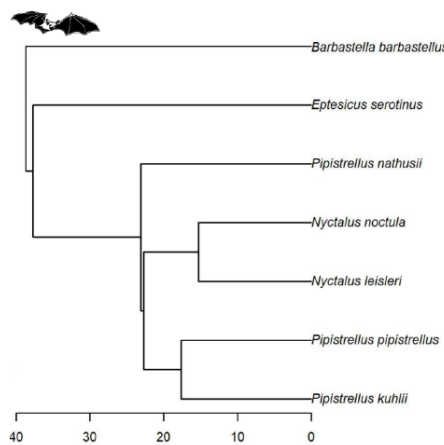
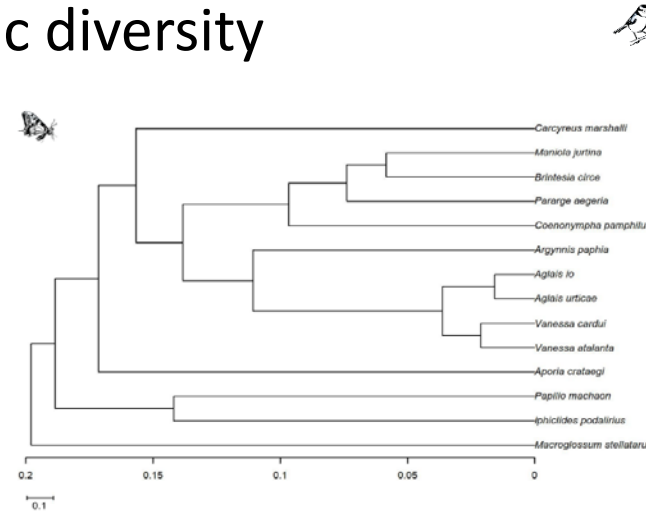
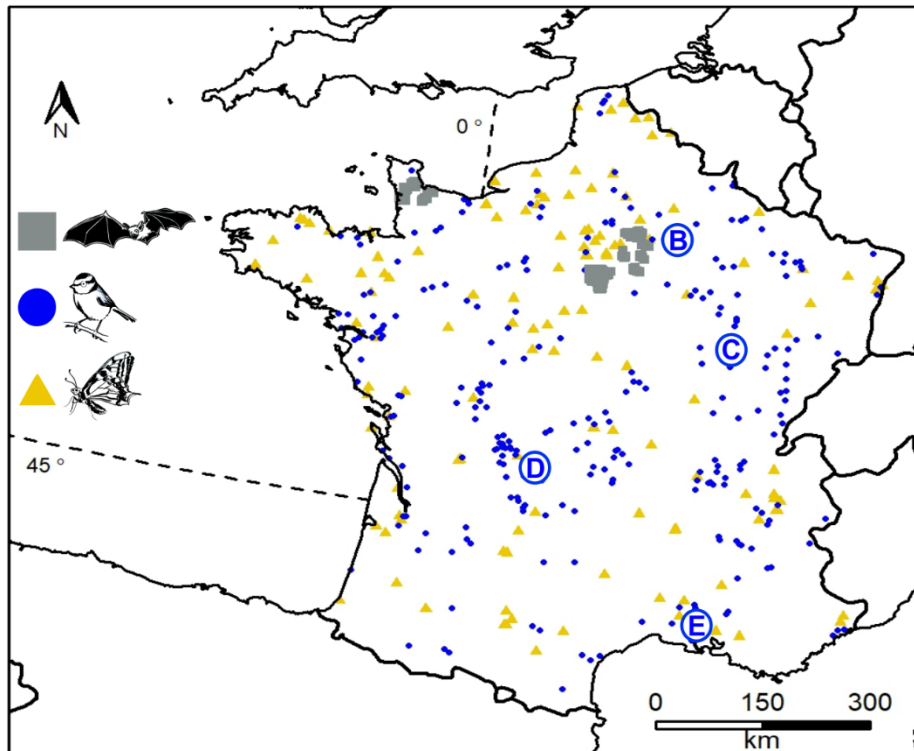
Assessing the links among: land uses, species diversity and community stability

- 8 landscape variables



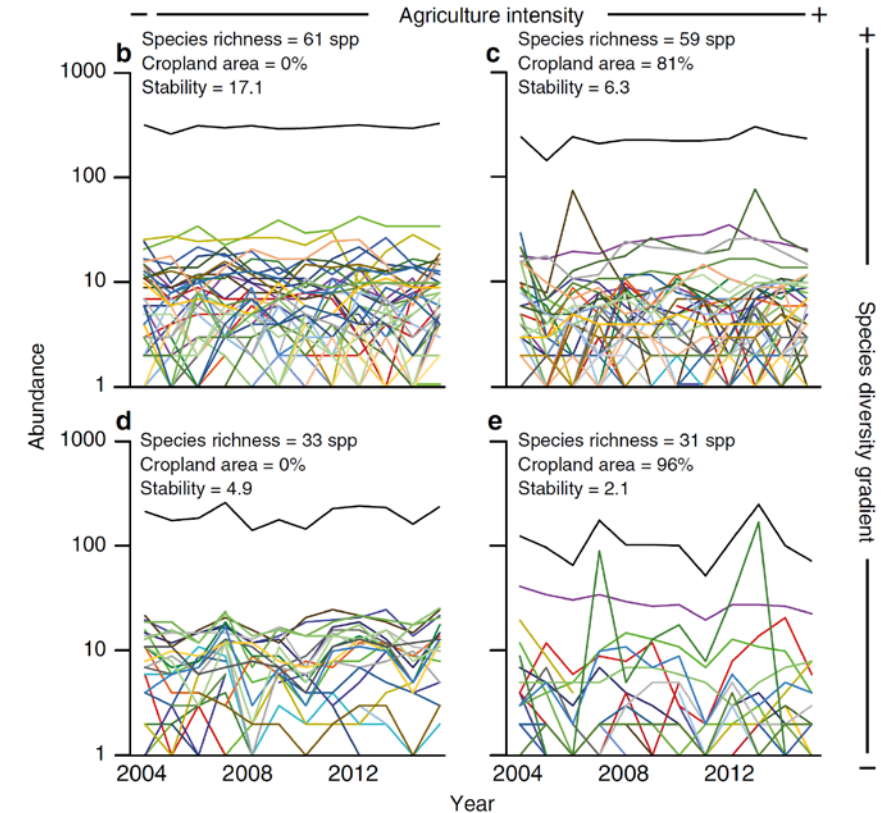
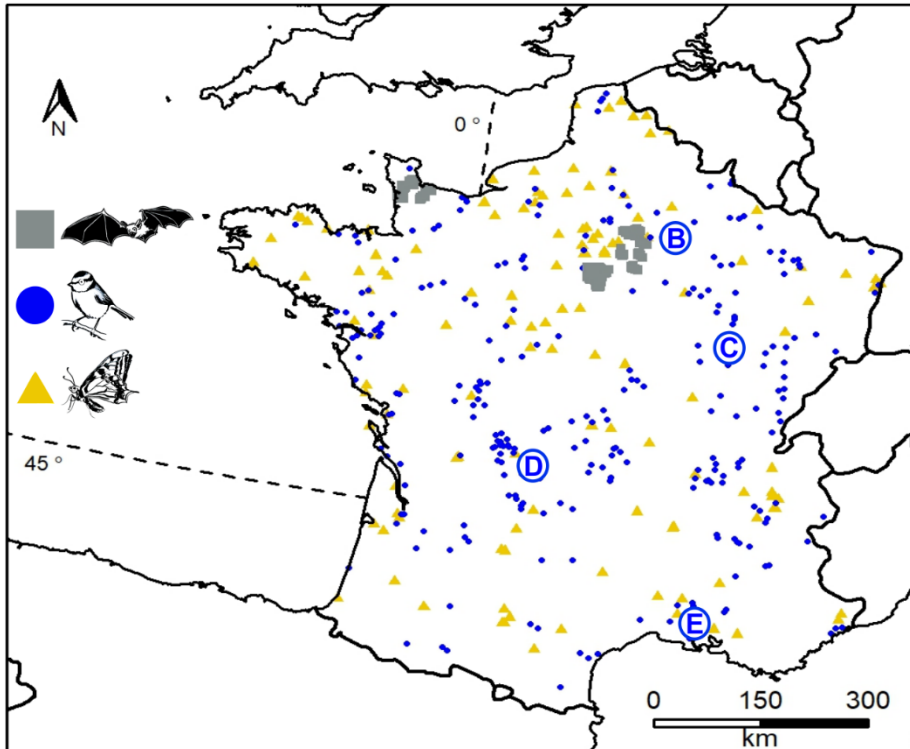
Assessing the links among: land uses, species diversity and community stability

- 8 landscape variables
- Species richness and phylogenetic diversity



Assessing the links among: land uses, species diversity and community stability

- 8 landscape variables
- Species richness and phylogenetic diversity
- Community stability/variability as a function of population stability/variability and asynchrony



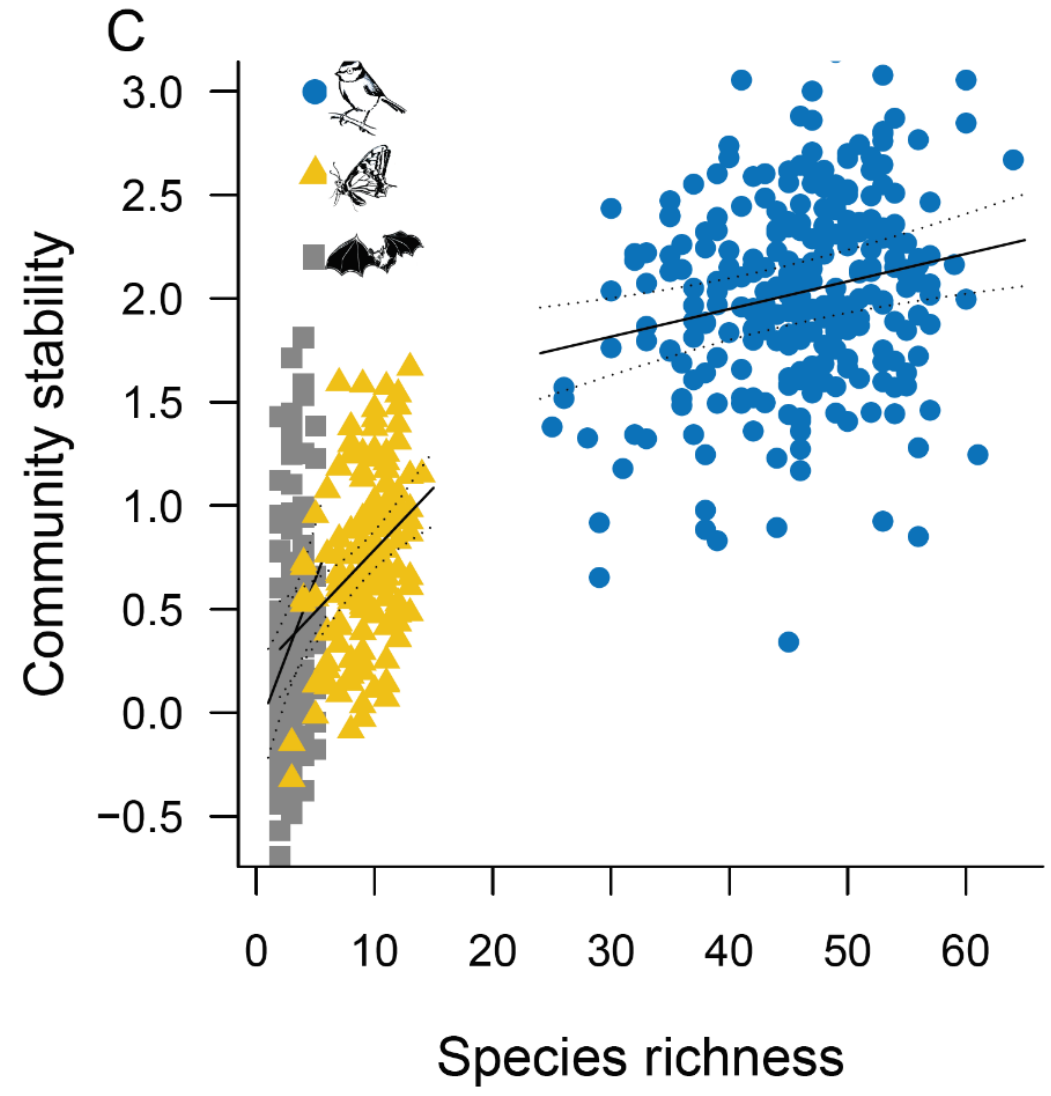
$$CV = \sqrt{\varphi \overline{CV}_w} \quad \text{with} \quad \varphi = \frac{\sigma^2}{(\sum_i \sigma_i)^2} \quad \text{and} \quad \overline{CV}_w = \sum_i \frac{\mu_i}{\mu} \times \frac{\sigma_i}{\mu_i} = \frac{\sum_i \sigma_i}{\mu}$$

community variability synchrony weighted mean population variability

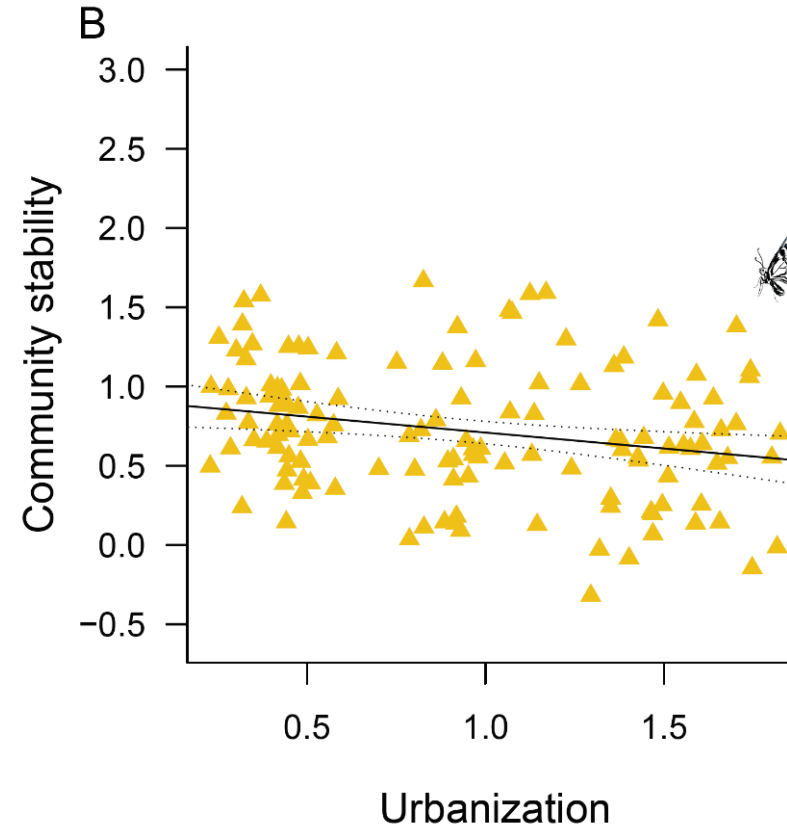
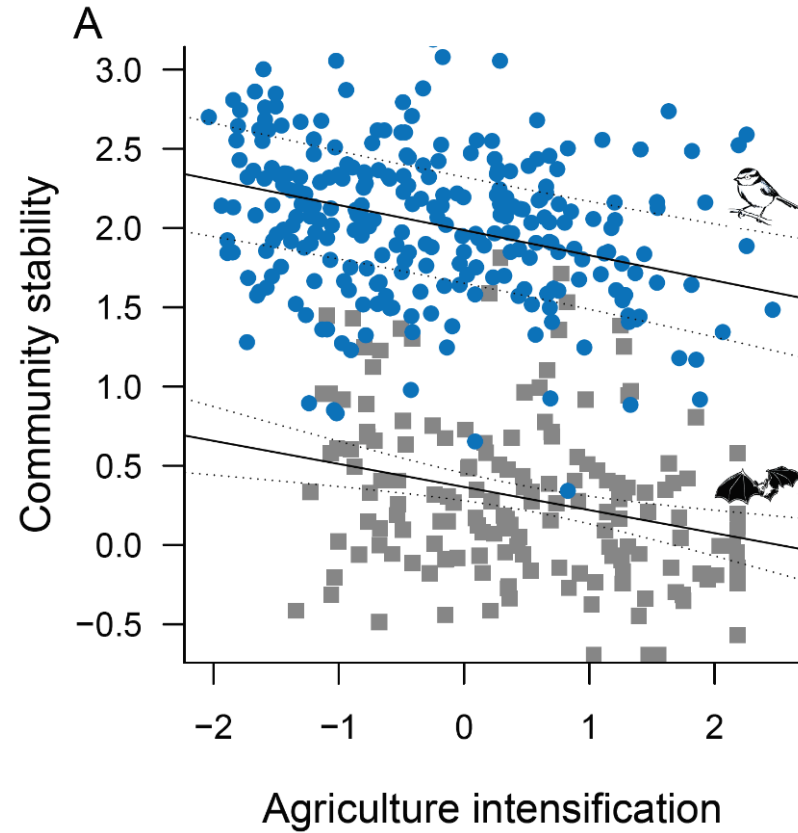
Loreau & de Mazancourt (2008)

Thibaut & Connolly et al. (2013)

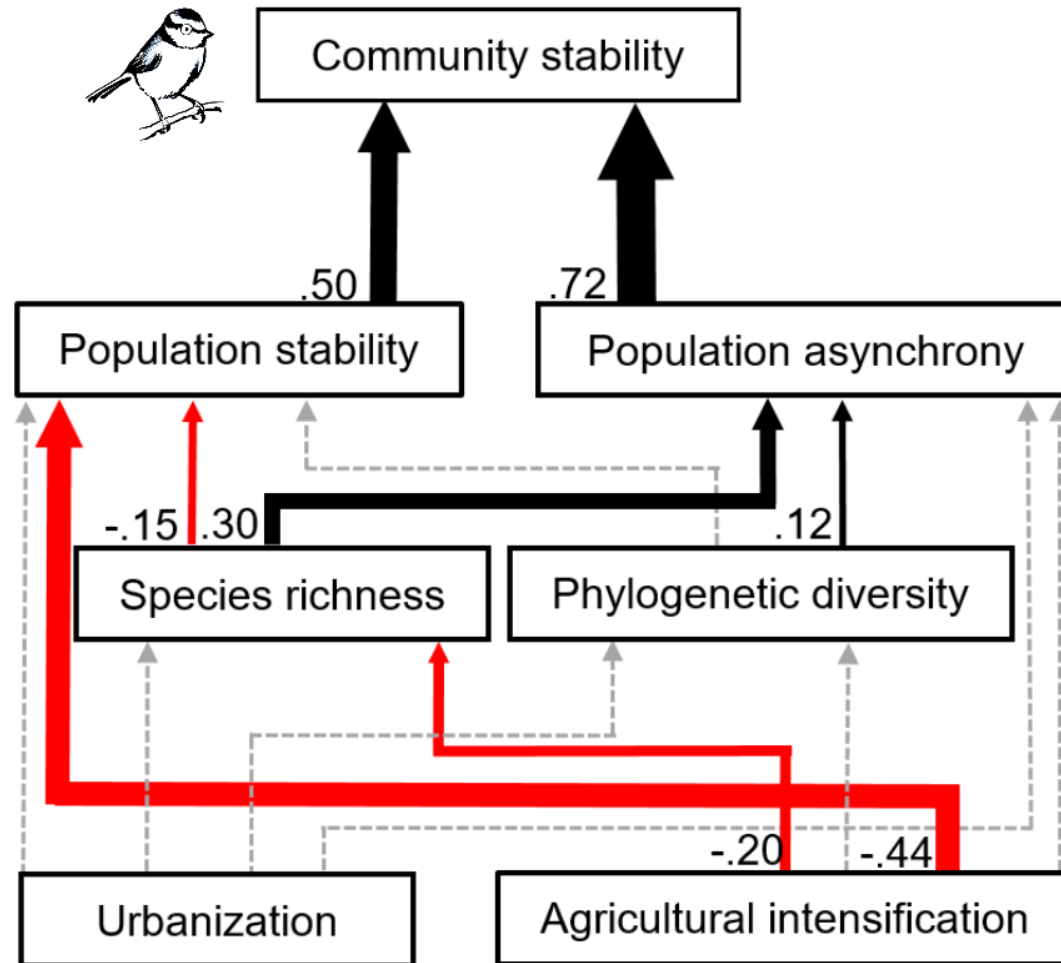
Results: relation between diversity and community stability






Results: relation between land use and community stability



Results: disentangling the effects of land use and diversity on community stability



Results: disentangling the effects of land use and diversity on community stability

Effects on community stability			
Diversity:			
Total effects	0.433	0.224	0.513
Richness effects	0.195	0.139	0.347
Phylogenetic diversity effects	0.238	0.085	0.166
Effects via population stability	NS	-0.076	0.172
Effects via population asynchrony	0.433	0.299	0.341

} Negative effects of diversity loss on community stability mainly mediated through decreased population asynchrony

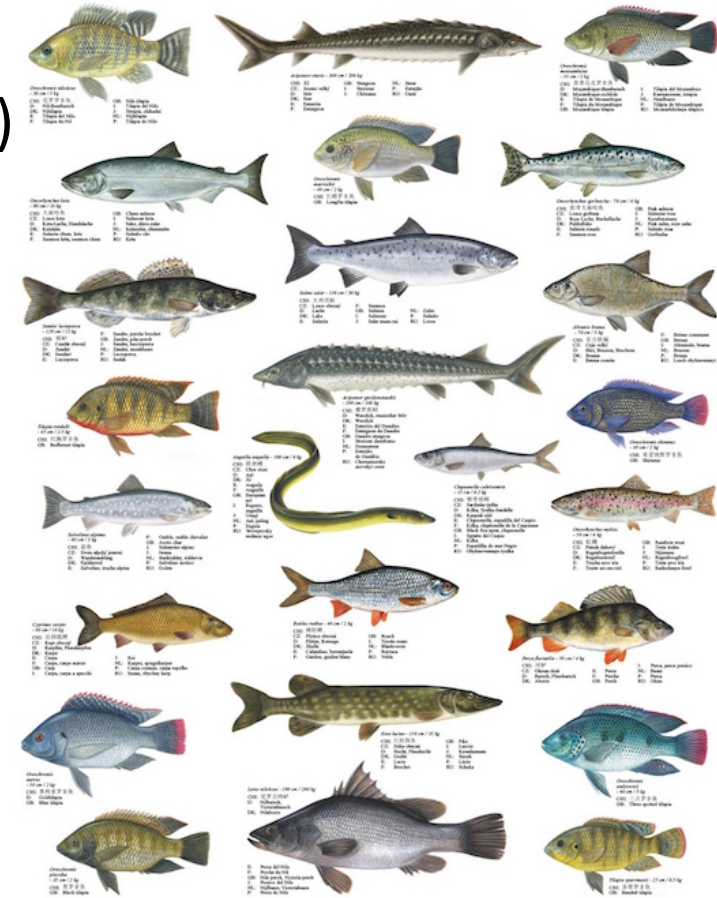
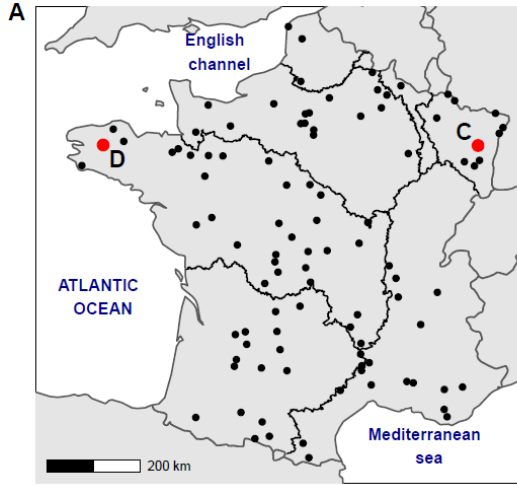
Effects of habitat degradation and diversity loss on community stability

Conclusion

- Anthropogenic habitat degradation and species diversity loss have both destabilizing effects at community level
- While the stabilizing effects of diversity are mediated by greater population asynchrony, the destabilizing effects of habitat degradation are mainly channeled by lower population stability
- These results suggest that classical studies on the diversity-stability relationship might miss a critical determinant of natural community stability by not including perturbations into the framework

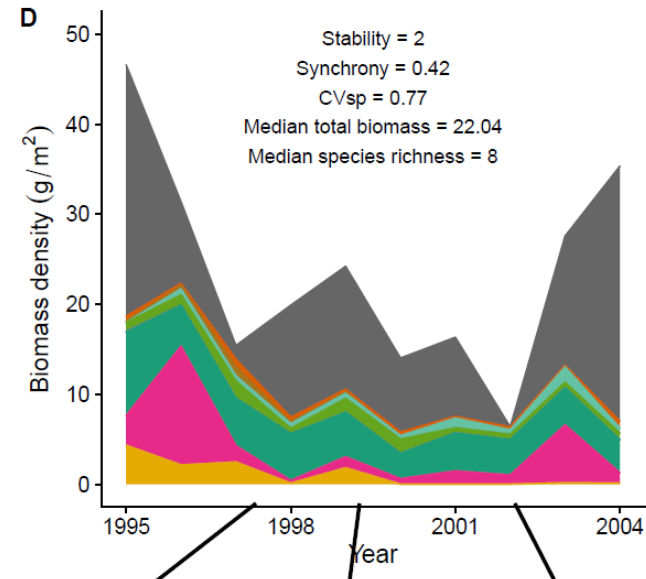
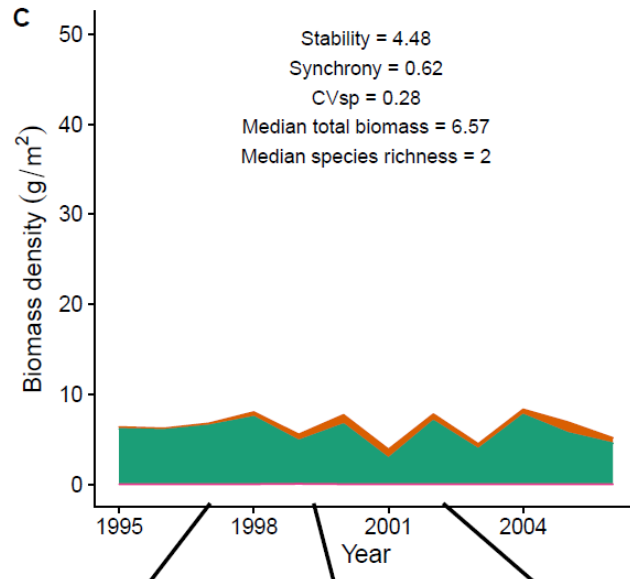
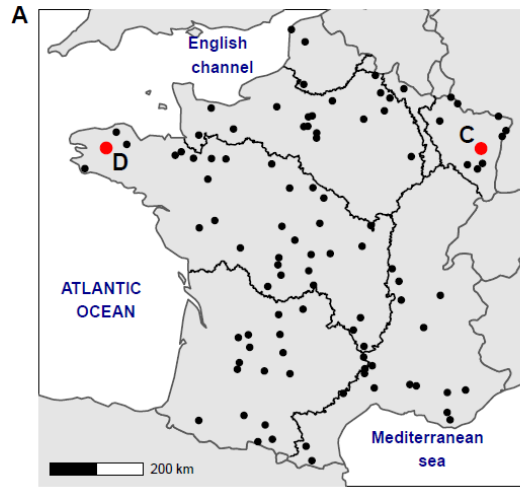
Stability of empirical multitrophic communities

➤ Standardized monitoring of river fish communities (ONEMA/OFB)



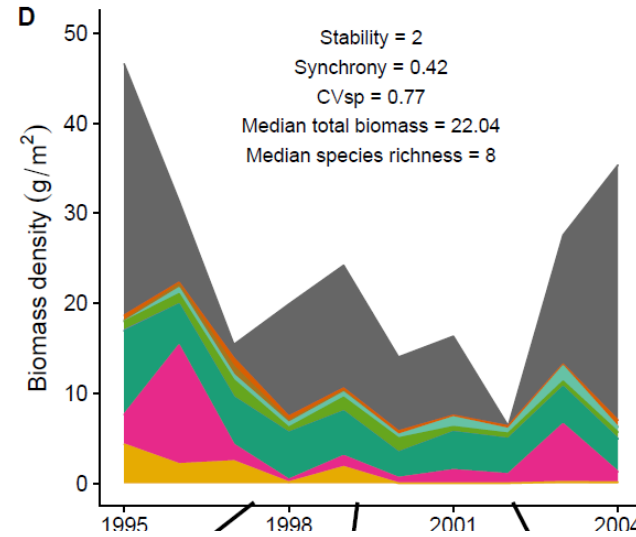
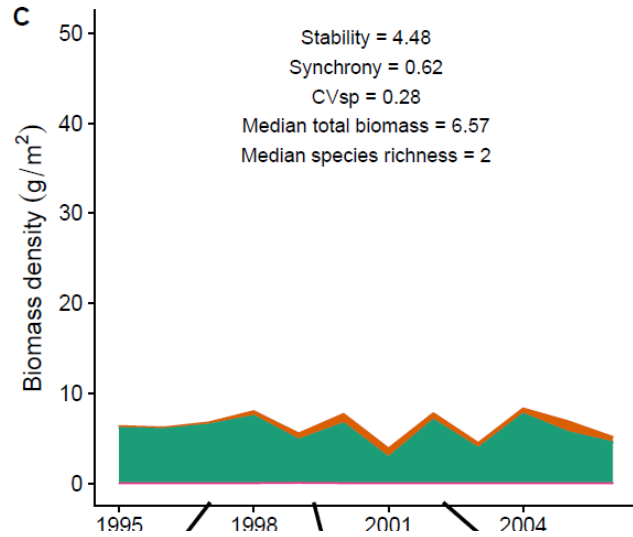
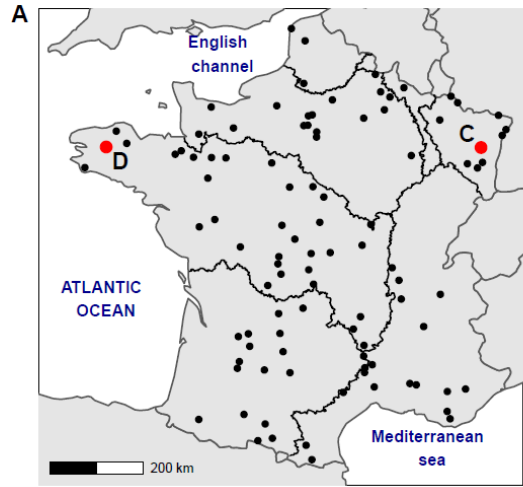
Stability of empirical multitrophic communities

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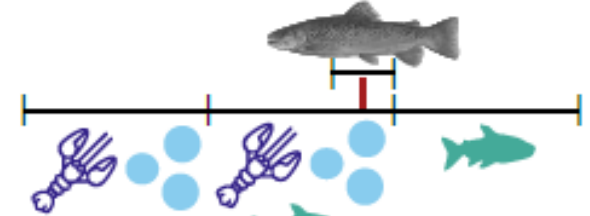


Stability of empirical multitrophic communities

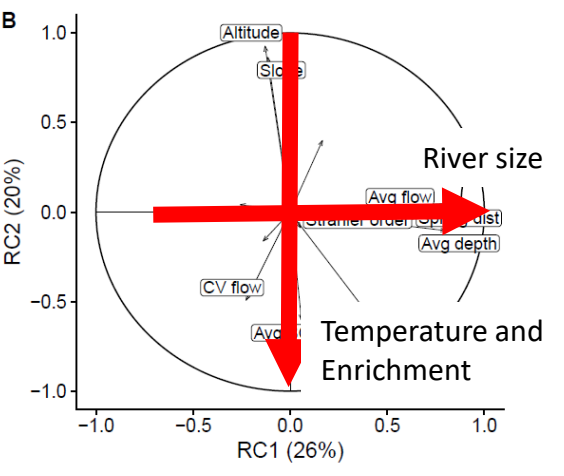
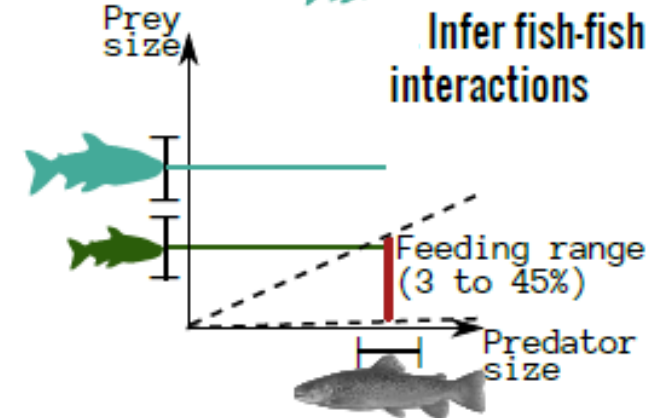
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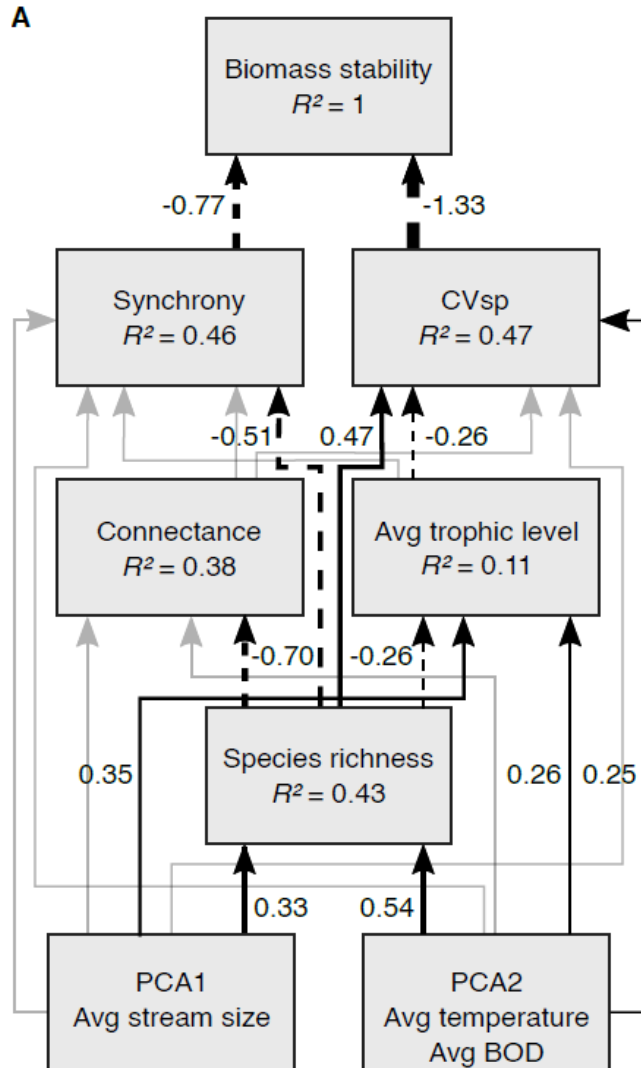
Trophic species diet inference



Infer fish-fish interactions



Stability of empirical multitrophic communities

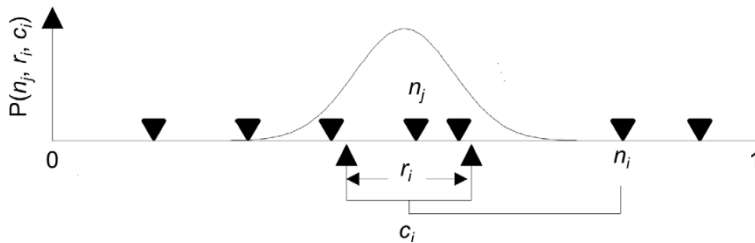


Variable	Direct	Indirect effects via					Total effect
		Species richness	Connectance	Avg trophic level	CVsp	Synchrony	
PCA1 Avg stream size	NA	-0.10	0.00	0.12	0.00	0.00	0.02
PCA2 Avg temperature & Avg BOD	NA	-0.17	0.00	0.09	-0.33	0.00	-0.41
Species richness	NA	NA	0.00	-0.09	-0.62	0.40	-0.31
Connectance	NA	NA	NA	NA	0.00	0.00	0.00
Avg trophic level	NA	NA	NA	NA	0.35	0.00	0.35

- How to reconcile May's results with the idea that complexity favors stability?
- Empirical approaches to ecological stability
- The dimensionality of ecological stability

What is the dimensionality of ecological stability?

Niche model to define network structure



Three type of perturbations:

- pulse (e.g. mortality events)
- press (e.g. increased mortality rate, extinctions)
- environmental stochasticity (e.g. white noise)

Bioenergetic model to simulate population dynamics

$$\frac{dB_i}{dt} = r_i G_i B_i + B_i \sum_{j \in \text{prey}} e_{0j} F_{ij} - \sum_{k \in \text{pred}} B_k F_{ki} - x_i B_i - d_i B_i$$

Conversion efficiency
Metabolic demand
Death rate

$G_i = \left(1 - \frac{B_i}{K_i}\right)$

Logistic growth rate

$F_{ij} = \frac{w_i a_{ij} B_j^{1+q}}{m_i \left(1 + w_i \sum_{k \in \text{prey}} a_{ik} h_{ik} B_k^{1+q}\right)}$

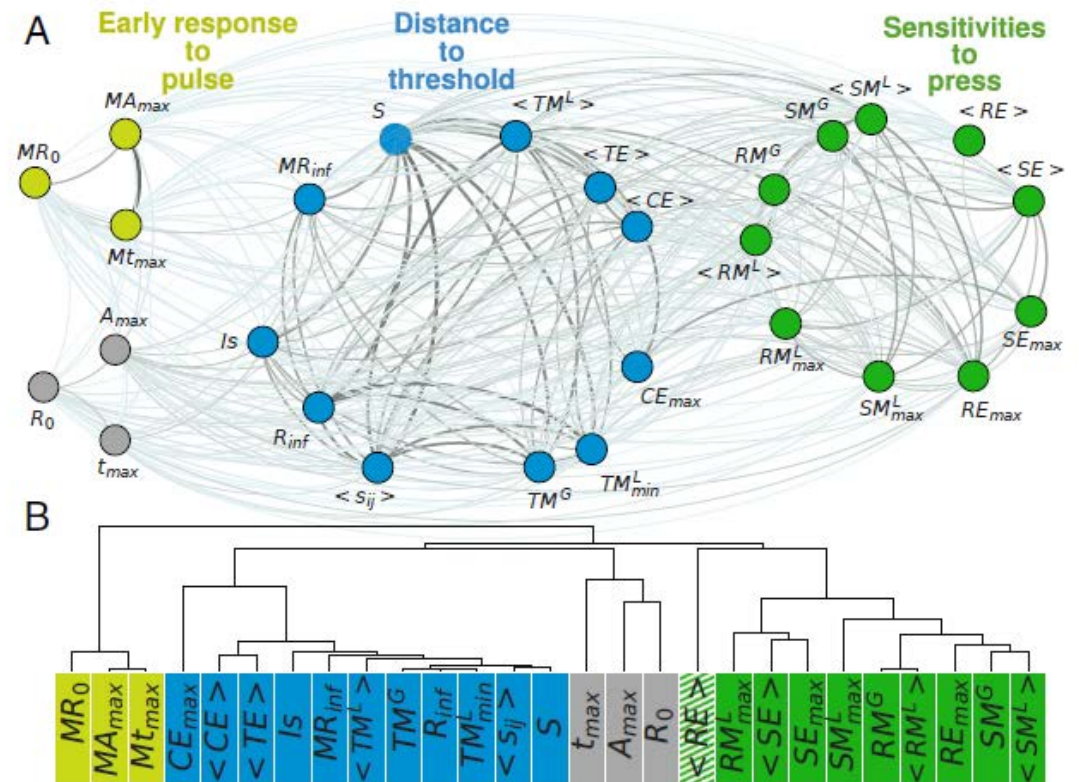
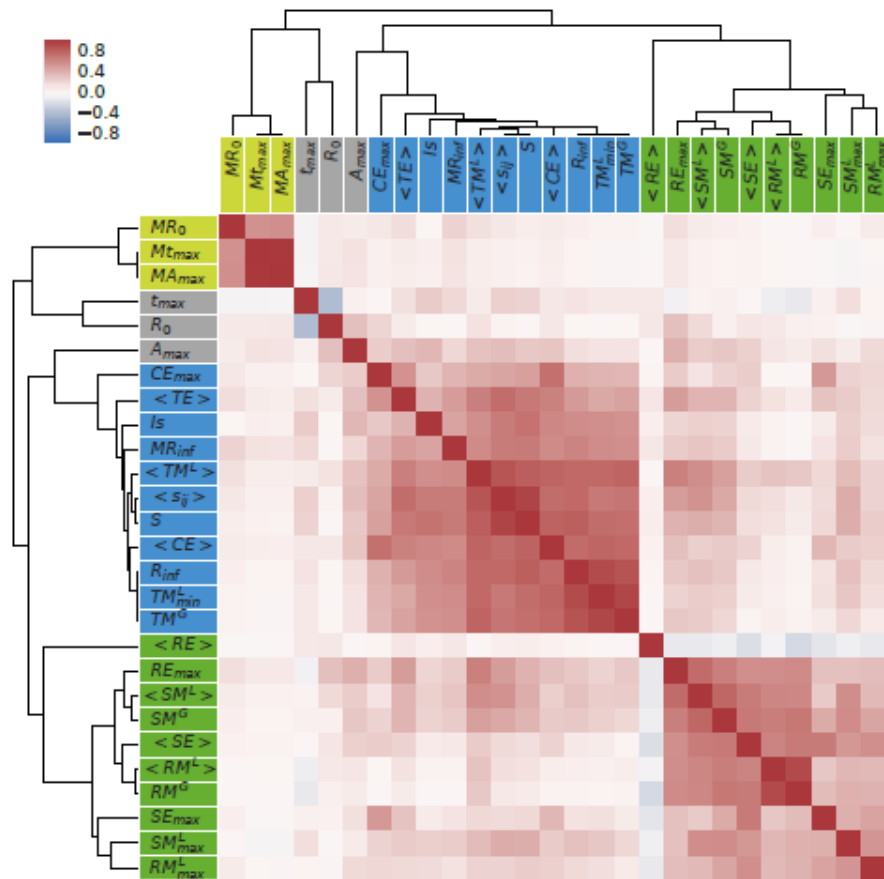
Holling-type functional response

Twenty seven stability metrics

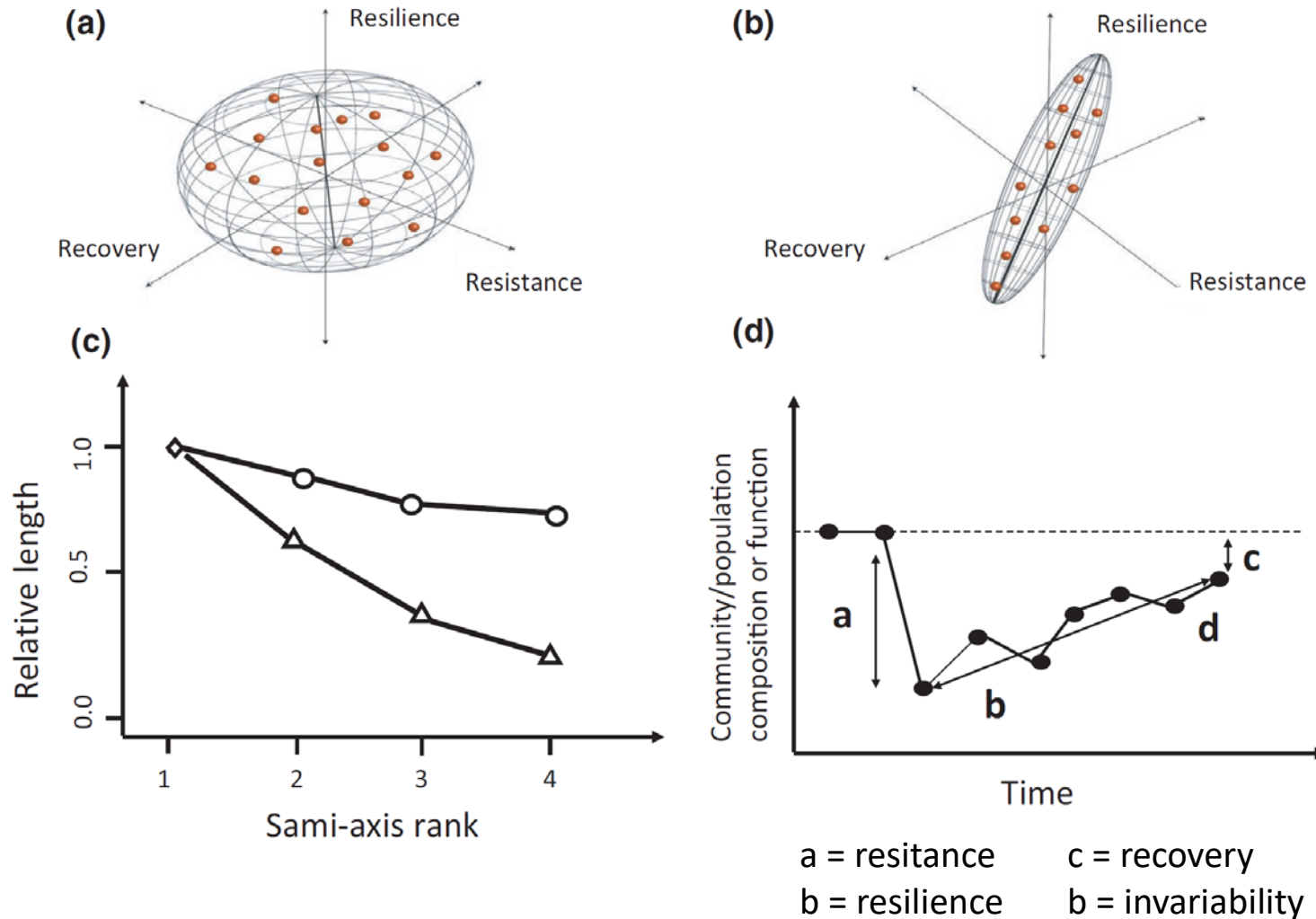
Name (time scale)	Acronym [equation in SI Appendix, section 10]	Name (time scale)	Acronym [equation in SI Appendix, section 10]
Reactivity (initial)	R_0 [6], MR_0 [11]	Resistance of total biomass (long-term): To mortality	RM^G [18]
Maximum amplification (transient)	A_{max} [9], MA_{max} [12]	To extinctions	$\langle RM^L \rangle$, RM_{max}^L
Time to maximum amplification (transient)	t_{max} , Mt_{max}	Cascading extinctions (long-term)	$\langle CE \rangle$, CE_{max}
Resilience (long-term)	R_{inf} [10], MR_{inf} [13]	Sensitivity of species' biomass (long-term): To mortality	SM^G [19]
Stochastic invariability (long-term)	I_s [14]	To extinctions	$\langle SM^L \rangle$, SM_{max}^L
Sensitivity matrix (long-term)	$\langle s_{ij} \rangle$ [16], S [15]	To extinctions	$\langle SE \rangle$ [21], SE_{max}
Tolerance (long-term): To mortality	TM^G [17]		
To extinctions	$\langle TM^L \rangle$, TM_{min}^L		
	$\langle TE \rangle$		

What is the dimensionality of ecological stability?

Modularity analysis on the spearman correlation coefficients among stability metrics

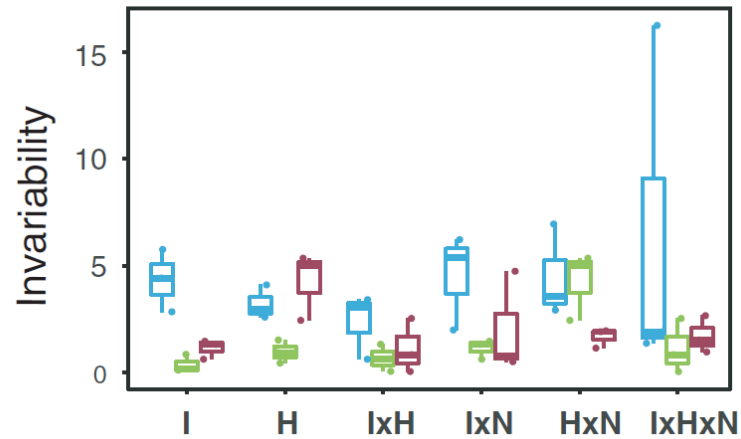
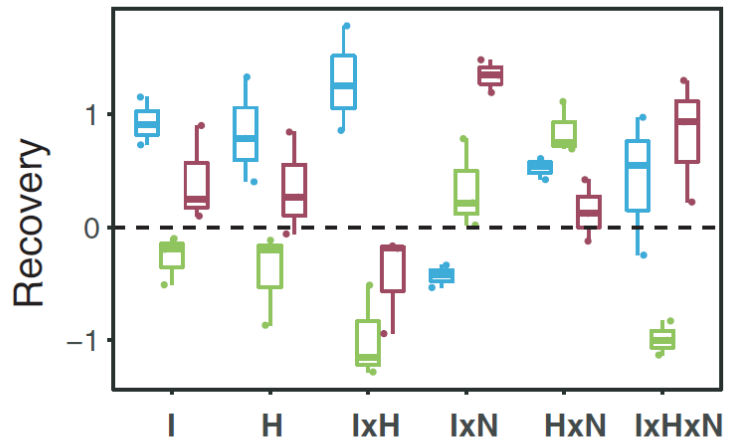
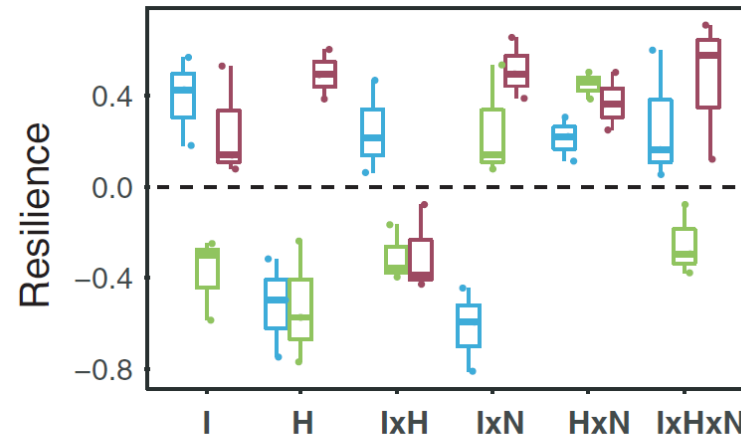
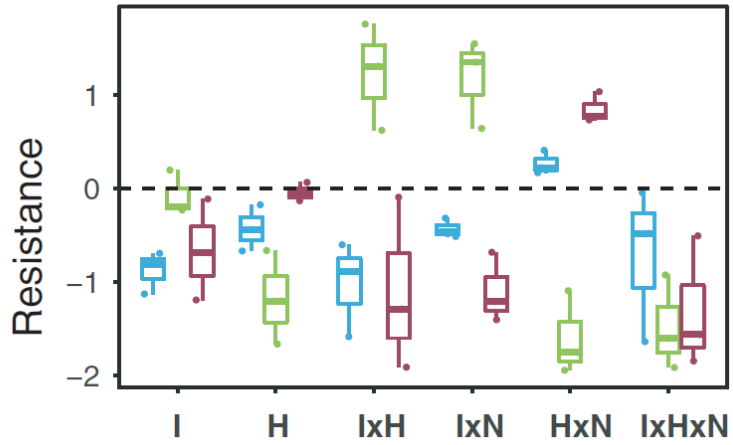


Effect of perturbations on the dimensionality of stability



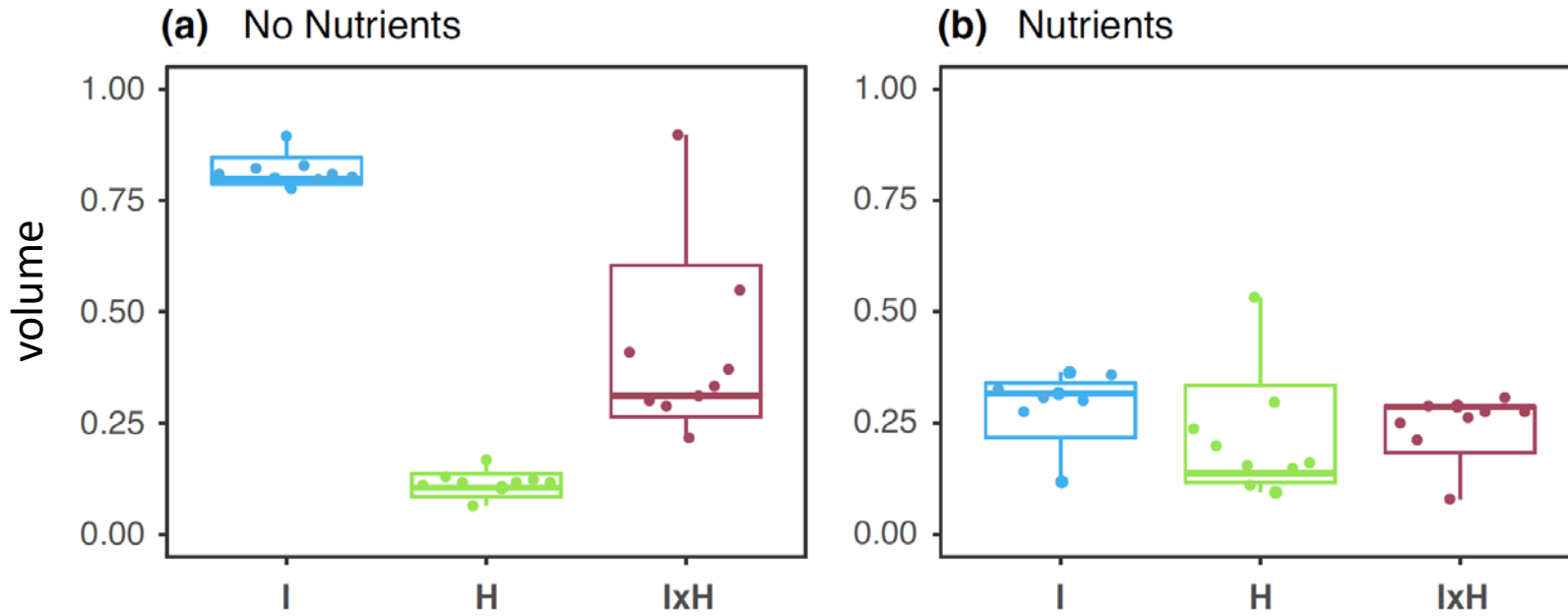
Perturbation treatments:
Insecticide x Herbicide x nutrients

Effect of perturbations on the dimensionality of stability

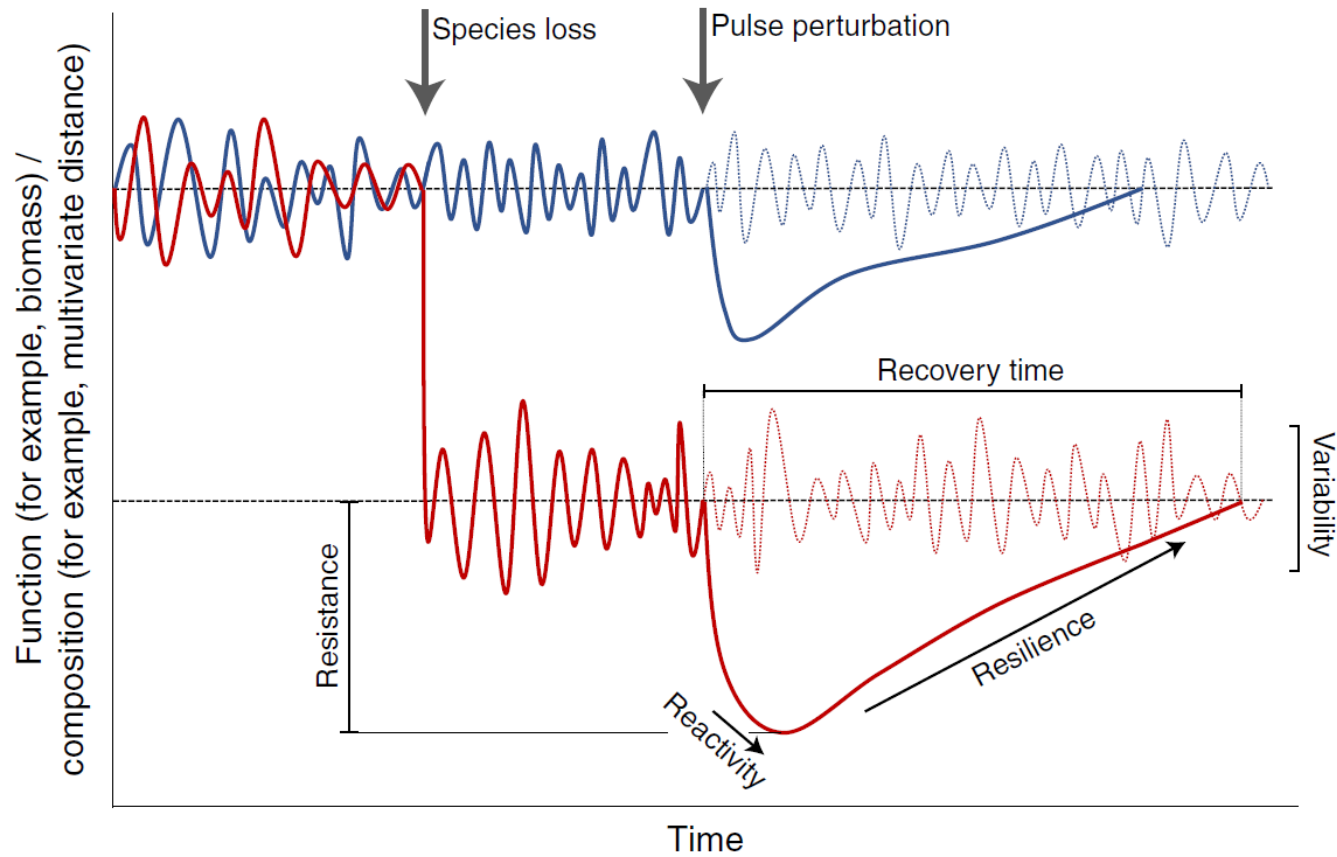


Macroinvertebrates Phytoplankton Zooplankton

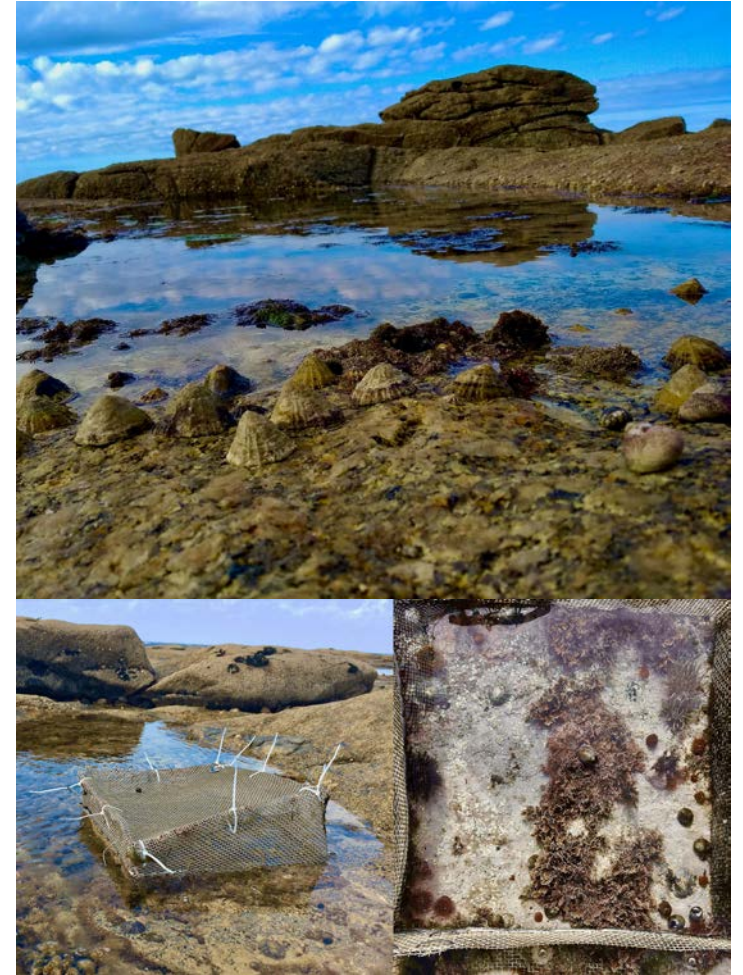
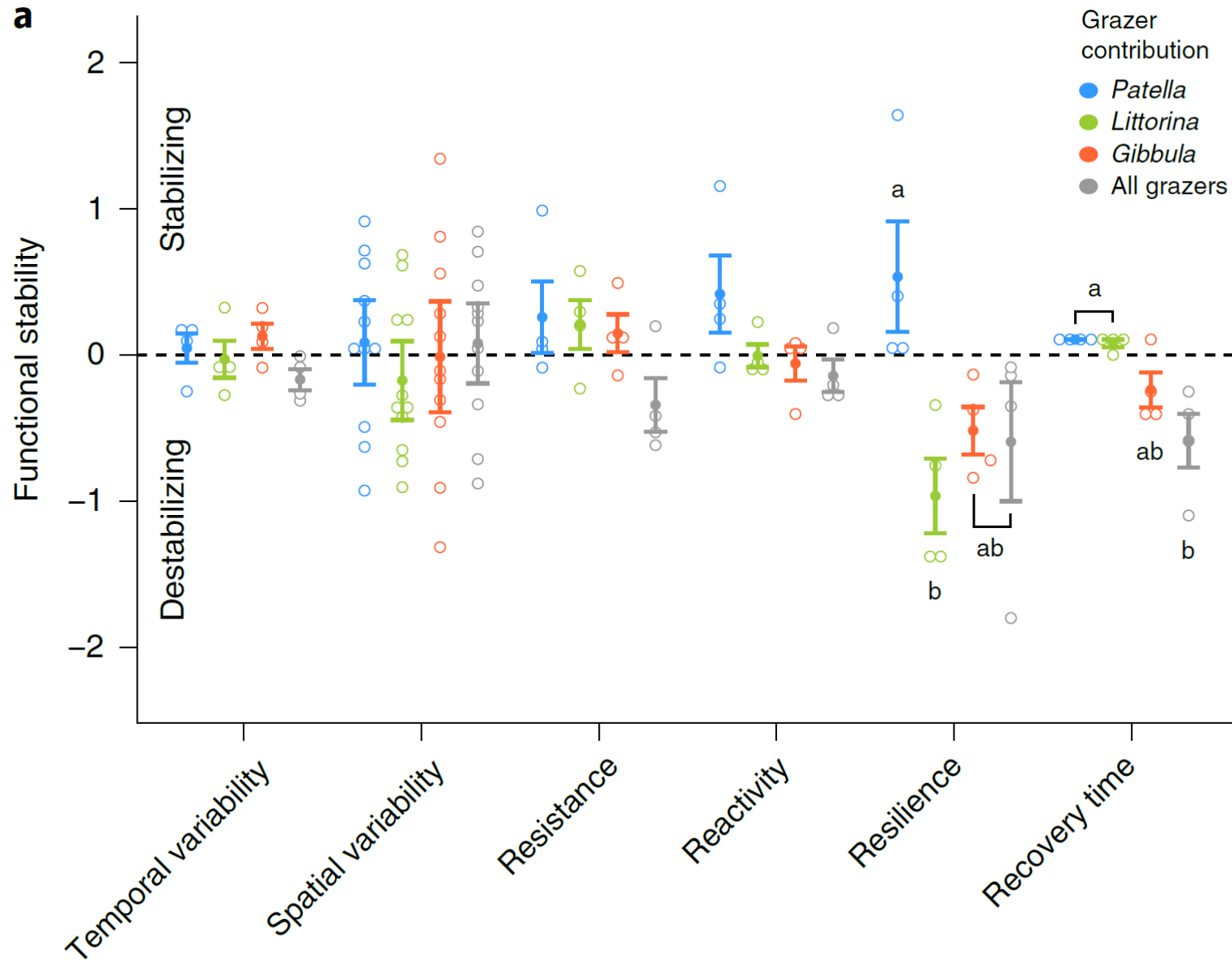
Effect of perturbations on the dimensionality of stability



Species contribution to different components of stability

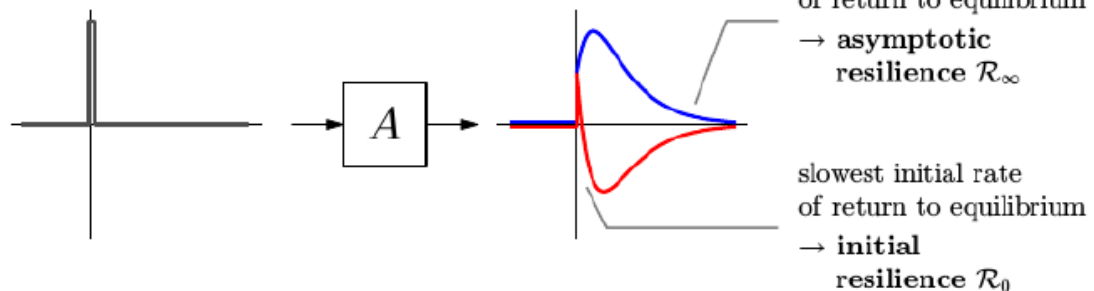


Species contribution to different components of stability

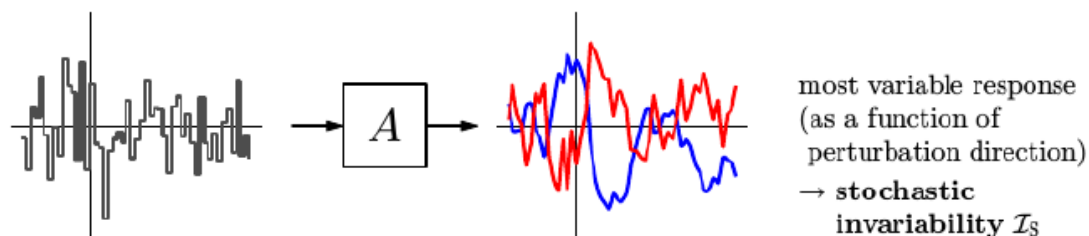


Mathematical relationship among stability new metrics

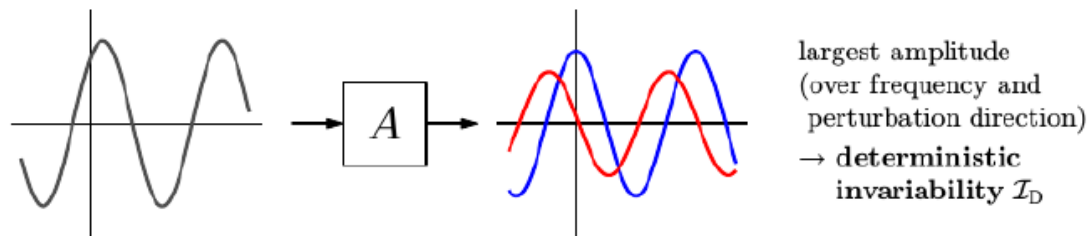
Pulse perturbation



Persistent perturbation – white noise



Persistent perturbation – single frequency



Stability measure	Interpretation	Formula
Asymptotic resilience	Slowest asympt. rate of return to equilibrium after a shock.	$\mathcal{R}_\infty = -\Re(\lambda_{\text{dom}}(A))$ ^(a)
Deterministic invariability	Inverse of maximal response amplitude to periodic forcing.	$\mathcal{I}_D = (\sup_{\omega} \ (i\omega - A)^{-1}\)^{-1}$ ^(b)
Stochastic invariability	Inverse of maximal response variance to white-noise.	$\mathcal{I}_S = \frac{1}{2} \ \hat{A}^{-1}\ ^{-1}$ ^(c)
Initial resilience	Slowest initial rate of return to equilibrium after a shock.	$\mathcal{R}_0 = -\frac{1}{2} \lambda_{\text{dom}}(A + A^T)$ ^(d)

^(a) λ_{dom} is the eigenvalue of community matrix A with maximal real part $\Re(\lambda_{\text{dom}})$.

^(b) i is the imaginary unit and $\omega \geq 0$. $\|\cdot\|$ is the spectral norm of matrices.

^(c) $\hat{A} = A \otimes \mathbb{I} + \mathbb{I} \otimes A$ where \mathbb{I} is the identity matrix; \otimes is the Kronecker product.

^(d) A^T is the transpose of A .

$$\mathcal{R}_0 \leq \mathcal{I}_S \leq \mathcal{I}_D \leq \mathcal{R}_\infty$$