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**.
Most ecologists describe ecosystem stability as the ability of an ecosystem to **maintain its structure and function** over long periods 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**
- 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

• Challenged by theory

\[
\frac{dN_i}{dt} = F_i(N_1, \ldots, N_k)
\]

A = matrice de communauté

\[
a_{ij} = \text{force d’interaction}
\]

(a) Engineering resilience

\[i \sqrt{SC} \leq 1\]

Mean interaction strength Species number Proportion of realised interactions
Ecological stability: an expending (messy) field

Kéfi et al. 2020
• 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
Network structure and community dynamic

Mutualistic

\[
\frac{dA_i}{dt} = r_{Ai}A_i - I_{Ai}A_i^2 + \sum_{j=1}^{N_p} c_{ji}A_jP_j - \sum_{P_k \in \text{mut}(A_i)} P_k \\
\frac{dP_i}{dt} = r_{Pi}P_i - I_{Pi}P_i^2 + \sum_{j=1}^{N_a} c_{ij}A_jP_i - \sum_{A_k \in \text{mut}(P_i)} A_k
\]

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

Trophic

\[
\frac{dA_i}{dt} = r_{Ai}A_i - I_{Ai}A_i^2 + \sum_{j=1}^{N_p} c_{ji}A_jP_j - \sum_{P_k \in \text{prey}(A_i)} P_k \\
\frac{dP_i}{dt} = r_{Pi}P_i - I_{Pi}P_i^2 + \sum_{j=1}^{N_a} c_{ij}A_jP_i - \sum_{A_k \in \text{prey}(P_i)} A_k
\]

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

Thébault & Fontaine 2010
Network structure and community dynamic

Initial architecture

Population dynamics using mutualistic or antagonistic models

Final architecture

Persistence

Résilience

Thébault & Fontaine 2010

Connectance

Modularity

Nestedness

Species densities

Time

Initial architecture

Final architecture

T=0

T=T_{final}
Network structure and community dynamic

Persistence

<table>
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<tr>
<th></th>
<th>réseau mutualiste</th>
<th>réseau trophique</th>
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<tr>
<td>diversité</td>
<td>+</td>
<td>-</td>
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<tr>
<td>connectance</td>
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<td>-</td>
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<td>emboitement</td>
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<td>-</td>
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<td>compartimentalisation</td>
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Résilience

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Thébault & Fontaine 2010
Considering effects of foraging adaptation

\[
\frac{dX_j}{dt} = r_j - s_jX_j + \sum_{f \in \text{resources}} e_{ij} f_{ij} a_{ij} X_j - \sum_{f \in \text{consumers}} f_{ij} a_{ij} X_j
\]

(1)

\[
\frac{da_{ij}}{dt} = G_{ij} a_{ij} (e_{ij} f_{ij} X_j - \sum_{k \in \text{resources}} a_{ik} e_{ik} f_{ik} X_k)
\]

(2)

Dynamics:
- Metabolic rate
- Foraging efficiency
- Attack rate
- Profitability of other resources
- Profitability of resource $j$
- Adaptation rate
Considering effects of foraging adaptation

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

\[
\frac{da_{ij}}{dt} = G_i a_{ij} \left( e_{ij} f_{ij} X_j - \sum_{k \in \text{resources}} a_{ik} e_{ik} f_{ik} X_k \right) \tag{2}
\]

Foraging efficiency
Metabolic rate
Attack rate
Profitability of other resources
Profitability of resource \( j \)
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

Diversity decreases variability of ecosystem properties through:

- Asynchronous responses of species to environmental perturbation
Evolutionary history of species and the temporal stability of biomass production

Cadotte et al. 2012
Resitance, resilience and variability of primary production to climatic extrems

- In addition to warming, current climat change lead to a increase in the frequency of extrem climatic events
- Both resitance and resilence 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?

Perturbations → diversity loss → lower stability

Hautier et al. (2015)
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

Olivier et al. 2020
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

Olivier et al. 2020
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

\[ CV = \sqrt{\varphi CV_w} \quad \text{with} \quad \varphi = \frac{\sigma^2}{(\sum_i \sigma_i)^2} \quad \text{and} \quad CV_w = \sum_i \frac{\mu_i}{\mu} \times \frac{\sigma_i}{\mu_i} = \frac{\sum_i \sigma_i}{\mu} \]

Loreau & de Mazancourt (2008)
Thibaut & Connolly et al. (2013)
Results: relation between diversity and community stability

Olivier et al. 2020
Results: relation between land use and community stability

Olivier et al. 2020
Results: disentangling the effects of land use and diversity on community stability
Results: disentangling the effects of land use and diversity on community stability

<table>
<thead>
<tr>
<th>Effects on community stability</th>
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<tbody>
<tr>
<td>Diversity:</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Total effects</td>
<td>0.433</td>
<td>0.224</td>
<td>0.513</td>
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<tr>
<td>Richness effects</td>
<td>0.195</td>
<td>0.139</td>
<td>0.347</td>
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<tr>
<td>Phylogenetic diversity effects</td>
<td>0.238</td>
<td>0.085</td>
<td>0.166</td>
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<tr>
<td>Effects via population stability</td>
<td>NS</td>
<td>-0.076</td>
<td>0.172</td>
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<tr>
<td>Effects via population asynchrony</td>
<td>0.433</td>
<td>0.299</td>
<td>0.341</td>
</tr>
</tbody>
</table>

Negative effects of habitat degradation on community stability mediated through decreased population stability

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

Olivier et al. 2020
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

- Standardized monitoring of river fish communities (ONEMA/OFB)
Stability of empirical multitrophic communities

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

A: Map of France showing river locations
B: Principal component analysis (PCA) with axes: Temperature and Enrichment, River size, and Altitude
C: Graph showing biomass density (g/m²) over time with stability and synchrony values
D: Graph showing biomass density (g/m²) over time with stability and synchrony values

Trophic species diet inference and fish-fish interactions diagram
Stability of empirical multitrophic communities

<table>
<thead>
<tr>
<th>Variable</th>
<th>Direct</th>
<th>Indirect effects via</th>
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<tr>
<td></td>
<td></td>
<td>Species richness</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Connectance</td>
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<tr>
<td></td>
<td></td>
<td>Avg trophic level</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CVsp</td>
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<tr>
<td></td>
<td></td>
<td>Synchrony</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total effect</td>
</tr>
<tr>
<td>PCA1 Avg stream size</td>
<td>NA</td>
<td>-0.10 0.00 0.12 0.00 0.00 0.00 0.02</td>
</tr>
<tr>
<td>PCA2 Avg temperature &amp; Avg BOD</td>
<td>NA</td>
<td>-0.17 0.00 0.09 -0.33 0.00 -0.41</td>
</tr>
<tr>
<td>Species richness</td>
<td>NA</td>
<td>NA 0.00 -0.09 -0.62 0.40 -0.31</td>
</tr>
<tr>
<td>Connectance</td>
<td>NA</td>
<td>NA NA NA NA 0.00 0.00 0.00</td>
</tr>
<tr>
<td>Avg trophic level</td>
<td>NA</td>
<td>NA NA NA NA 0.35 0.00 0.35</td>
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• 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

![Diagram of ecological network structure](image)

Bioenergetic model to simulate population dynamics

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

Logistic growth rate

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

Holling-type functional response

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

Conversion efficiency Metabolic demand Death rate

Three type of perturbations:
- pulse (e.g. mortality events)
- press (e.g. increased mortality rate, extinctions)
- environmental stochasticity (e.g. white noise)

Twenty seven stability metrics

Domingues-Garcia et al. 2019
What is the dimensionality of ecological stability?

Modularity analysis on the spearman correlation coefficients among stability metrics

Domingues-Garcia et al. 2019
Effect of perturbations on the dimensionality of stability

Perturbation treatments:
Insecticide x Herbicide x nutrients

Pollazo et al. 2021
Effect of perturbations on the dimensionality of stability

Pollazo et al. 2021
Effect of perturbations on the dimensionality of stability

Pollazo et al. 2021
Species contribution to different components of stability

White et al. (2020)
Species contribution to different components of stability

White et al. (2020)
Mathematical relationship among stability new metrics

<table>
<thead>
<tr>
<th>Stability measure</th>
<th>Interpretation</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptotic</td>
<td>Slowest asympt. rate of return to equilibrium after a shock.</td>
<td>$R_\infty = -\Re(\lambda_{\text{dom}}(A))$ (a)</td>
</tr>
<tr>
<td>Deterministic</td>
<td>Inverse of maximal response amplitude to periodic forcing.</td>
<td>$I_D = (\sup_\omega</td>
</tr>
<tr>
<td>Stochastic</td>
<td>Inverse of maximal response variance to white-noise.</td>
<td>$I_S = \frac{1}{2}</td>
</tr>
<tr>
<td>Initial</td>
<td>Slowest initial rate of return to equilibrium after a shock.</td>
<td>$R_0 = -\frac{1}{2}\lambda_{\text{dom}}(A + A^T)$ (d)</td>
</tr>
</tbody>
</table>

(a) $\lambda_{\text{dom}}$ 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) $\hat{A} = A \otimes I + I \otimes A$ where $I$ is the identity matrix; $\otimes$ is the Kronecker product.
(d) $A^T$ is the transpose of $A$.

$R_0 \leq I_S \leq I_D \leq R_\infty$