Resilience and stability of ecological networks

Elisa Thébault
elisa.thebault@upmc.fr
Why study ecological interaction webs?
Why study ecological interaction webs?

Factors which determine interactions between species

Network structural patterns

Naisbit et al. 2012

Rezende et al. 2007
Why study ecological interaction webs?

Network structural patterns

Consequences on ecosystem functioning and stability

Dunne et al. (2004)
Why study ecological interaction webs?

Effects of global change on networks and consequences

Cavalheiro et al. (2008)
Before 1970s, the view is that complexity begets stability
Before 1970s, the view is that complexity begets stability

*Elton 1958*

Several arguments:

- Theoretical and experimental evidence that simple model ecosystems are inherently unstable

- Species-poor islands and artificial agricultural ecosystems are more prone to invasions by new species and pests than are their continental and natural counterparts.
Before 1970s, the view is that complexity begets stability

Several arguments:

- Theoretical and experimental evidence that simple model ecosystems are inherently unstable

- Species-poor islands and artificial agricultural ecosystems are more prone to invasions by new species and pests than are their continental and natural counterparts.
This traditional view is challenged in the early 1970s

A mathematical formulation

May 1972

– Consider a community of $k$ species with population density $N_i$
– Population dynamics can be described by:

$$\frac{dN_i}{dt} = F_i(N_1, \ldots, N_k)$$
This traditional view is challenged in the early 1970s

Near equilibrium, the behaviour of the community is related to the eigenvalues of the Jacobian of the system at this point

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

A = community matrix

$$a_{ij} = \text{interaction strength}$$
This traditional view is challenged in the early 1970s

– Near equilibrium, the behaviour of the community is related to the eigenvalues of the Jacobian of the system at this point

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

\[ A = \text{community matrix} \]

\[ a_{ij} = \text{interaction strength} \]

– For a random network with a proportion C of nonzero interaction strengths (connectance), and s the mean interaction strength, the condition for local stability is:

\[ s \sqrt{kC} < 1 \]
These contrasting views are at the origin of the complexity – stability debate.
These contrasting views are at the origin of the complexity – stability debate

Tackling this debate is fundamental to understand how the structure of ecological networks affect ecosystem resilience
These contrasting views are at the origin of the complexity – stability debate

Today we will focus on two questions from recent works in this field:

- New perspectives on this debate with different definitions of stability
- Going beyond May’s work: ecological networks are not random and new model assumptions
These contrasting views are at the origin of the complexity – stability debate

Today we will focus on two questions from recent works in this field:

- New perspectives on this debate with different definitions of stability
- Going beyond May’s work: ecological networks are not random and new model assumptions
Stability: a multifaceted concept …

Dynamic stability

Local stability: definition often used in theoretical studies
See May

Cycles and Chaos: Associated measures of stability:
Variability, amplitude of fluctuations, etc.
Stability: a multifaceted concept...

Dynamic stability

Resilience and resistance of the community, species persistence, ....
... in relation with many diversity-stability relationships

Model of randomly structured competitive communities:

\[ x_i(t + 1) = x_i(t) \exp \left( r - \sum_{j=1}^{n} b_{ij} x_j(t) + \varepsilon_i(t) \right) \]

Investigate 13 relationships between diversity and stability

Ives and Carpenter (2007)
... in relation with many diversity-stability relationships

Ives and Carpenter (2007)
... in relation with many diversity-stability relationships

\[ x_i(t + 1) = x_i(t) \exp \left( r - \sum_{j=1}^{n} b_{ij} x_j(t) + \varepsilon_i(t) \right) \]
... in relation with many diversity-stability relationships
Temporal variability of ecosystem functioning: a new perspective on the diversity-stability debate

Tilman et al. (2006)
Insurance hypothesis

Diversity decreases variability of ecosystem properties through asynchronous responses of species to environmental perturbation

Yachi & Loreau (1999)
Insurance hypothesis and interactions between species

Environmental fluctuations

Plants and herbivores mortality rates $m$

Degree of niche differentiation

Thébault & Loreau (2005)
Insurance hypothesis and interactions between species

Specialist herbivores

\[ H_I \rightarrow P_I \]
\[ H_{n-I} \rightarrow P_{n-I} \]
\[ H_n \rightarrow P_n \]

CV of plant and herbivore biomass

Plant diversity

- synchronous responses
- asynchronous responses
- highly asynchronous responses

Higher degree of niche differentiation

Thébault & Loreau (2005)
Insurance hypothesis and interactions between species

Thébault & Loreau (2005)
Insurance hypothesis and interactions between species

Plant diversity

CV of total plant biomass

CV of total herbivore biomass

synchronous responses
asynchronous responses
highly asynchronous responses

Thebault & Loreau (2005)
Insurance hypothesis and interactions between species

Thébault & Loreau (2005)
Insurance hypothesis and interactions between species

Plant diversity

CV of plant and herbivore biomass

0
0,1
0,2
0,3
0,4
0,5
0,6
0,7
0,8
0,9
1

1
2
4
8
16

synchronous responses
asynchronous responses
highly asynchronous responses

CV of plant biomass

CV of total herbivore biomass

0
0,1
0,2
0,3
0,4
0,5
0,6
0,7
0,8

1
2
4
8
16

Thébault & Loreau (2005)
Diversity promotes ecosystem stability

Jiang et al. 2009

Haddad et al. 2010


Community stability (cv−1)

- Predator richness
- Herbivore richness

Population stability (cv−1)

- Specialist aphids
- Generalist leafhopper

Effect size at the community level

- Experimental
- Observational
- Terrestrial
- Aquatic
- Single-trophic
- Multi-trophic

Effect size at the population level

- Experimental
- Observational
- Terrestrial
- Aquatic
- Single-trophic
- Multi-trophic
These contrasting views are at the origin of the complexity – stability debate

Today we will focus on two questions from recent works in this field:

- Going beyond May’s work: ecological networks are not random and new model assumptions
  - effects of interaction type and network structure
  - importance of foraging adaptation
A diversity of interaction networks

Food web

Host-parasitoid network

Plant-pollinator network
A focus on food webs

Proportions of papers on ecological networks published in the last 50 years that were related to food webs, mutualistic webs and parasitic webs.

- 94% food webs
- 1% mutualistic webs
- 4% parasitic webs
A focus on food webs

Schmid-Araya et al. 2002
A focus on food webs

Trophic groups

Modules

Gauzens et al. 2015
Food web structure and stability

Gross et al. (2009)

Stouffer et al. (2011)
A growing number of studies on mutualistic webs

- Seed dispersal
- Pollination

**Nested structure**

- Continuum between specialist and generalist species
- Presence of a core of highly connected species
- Asymmetrical specialization

Bascompte et al. 2003
A growing number of studies on mutualistic webs

Finding NEMO: nestedness engendered by mutualistic organization in anemonefish and their hosts
Jeff Ollerton, Duncan McCollin, Daphne G. Fautin and Gerald R. Allen

The Nested Assembly of Plant Facilitation Networks Prevents Species Extinctions
Miguel Verde and Alfonso Valiente-Banuet

Low specificity and nested subset structure characterize mycorrhizal associations in five closely related species of the genus Orchis
HANS JACQUEMYN, OLIVIER HONNAY, BRUNO P. A. CAMMUE, REIN BEYS and BART
Nestedness of mutualistic webs and stability

Okuyama & Holland (2008)

Rohr et al. (2014)
The links between network structure and stability

The model: dynamics of mutualistic and trophic webs

Mutualistic

\[
\frac{dA_i}{dt} = r_{Ai} A_i - I_{Ai} A_i^2 + \sum_{j=1}^{Np} \frac{c_{ji} A_i P_j}{\alpha_{ji}^{-1} + \sum_{k \in \text{mut}(A_i)} P_k}
\]

\[
\frac{dP_i}{dt} = r_{Pi} P_i - I_{Pi} P_i^2 + \sum_{j=1}^{Na} \frac{c_{ij} A_j P_i}{\alpha_{ij}^{-1} + \sum_{k \in \text{mut}(P_i)} A_k}
\]

- intrinsic growth rates 
  \( r_P \) and \( r_A < 0 \) \( \Rightarrow \) obligate mutualism

- density dependence term

- interaction term
  saturates with mutualistic partner densities

Antagonistic

\[
\frac{dA_i}{dt} = r_{Ai} A_i - I_{Ai} A_i^2 + \sum_{j=1}^{Np} \frac{c_{ji} A_i P_j}{\alpha_{ji}^{-1} + \sum_{k \in \text{prey}(A_i)} P_k}
\]

\[
\frac{dP_i}{dt} = r_{Pi} P_i - I_{Pi} P_i^2 - \sum_{j=1}^{Na} \frac{c_{ij} A_j P_i}{\alpha_{ij}^{-1} + \sum_{k \in \text{prey}(A_i)} P_k}
\]

- intrinsic growth rates 
  \( r_P > 0 \) and \( r_A < 0 \)

- density dependence term

- interaction term
  saturates with prey densities
The model: network structure and stability

Species densities

diversity

modularity

nestedness

Connectance:
- \( c = 0.05 \)
- \( c = 0.2 \)

Network structure:
- \( n = 24 \)
- \( n = 80 \)
The model: network structure and stability

- Persistence: proportion of species persisting at the equilibrium
- Resilience: measure of the speed at which a system returns to its original state after a perturbation
Results: impact of network structure on species persistence

**Mutualistic networks**

- Connectance vs. Diversity
- Modularity vs. Nestedness

**Antagonistic networks**

- Connectance vs. Diversity
- Modularity vs. Nestedness

Thébault & Fontaine 2010
Results: impact of network structure on species persistence

- opposite effect of network structure on the persistence of mutualistic and trophic networks

Thébault & Fontaine 2010
Results: impact of network structure on species persistence

Mutualistic

- Persistence
  - Modularity: -0.53
  - Diversity: 0.31
- Nestedness
  - Connectance: -0.87

Diversity

Indirect effect: 0.40

Antagonistic

- Persistence
  - Modularity: -0.01
  - Diversity: 0.89
- Nestedness
  - Connectance: 0.86

Diversity

Indirect effect: -0.76

➢ Importance of nestedness and modularity for network stability

Thébault & Fontaine 2010
Results: impact of network structure on resilience

*opposite effect of network structure on the resilience of mutualistic and trophic networks*

Thébault & Fontaine 2010
Results: network structure at equilibrium

Thébault & Fontaine 2010
The relation between structure and stability strongly differ between mutualistic and antagonistic webs.

Observed differences between herbivory and pollination networks suggest that network structure might differ between mutualistic and antagonistic interactions.

Importance of the particular architecture of interaction networks in determining their stability.
Importance of foraging adaptation

Consumers can’t consume different resource species simultaneously because of the prey’s patchy distribution, the capturing strategy for different preys, consumer’s sensory and cognitive constraints for discriminating between preys.

Bernays and Funk 1999
Importance of foraging adaptation

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

(1)

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

(2)
Importance of foraging adaptation

Kondoh 2003
Take home message
Resilience, stability and the structure of ecological networks

➢ The relationship between network structure and stability depends on the definition of stability and on the mechanisms that determine species interactions

➢ Need to be very careful about stability measures and model assumptions when you consider a study
Take home message

Resilience, stability and the structure of ecological networks

➢ Is resilience the most appropriate measure to assess the stability of ecological networks and their response to perturbations?
Thank you for your attention