Petri nets for modelling and analysing Trophic networks

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Framework

Ecosystem = community of living organisms + nonliving components of the environment

A trophic network (or food web) is a representation of the feeding interactions in an ecosystem (what-eats-what)

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Let's employ Petri nets in this framework!

Trophic networks

They are represented as directed graphs where:

- each node represents a species or a group of species (compartment) with similar feeding behaviour;
- each arc denotes a flow of biomass or energy from the source node to the target one

They are usually open systems:

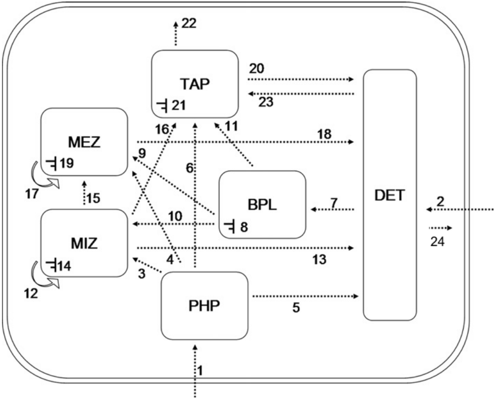
- input flows, e.g, primary production, immigration, incoming of detrital matter into the system
- output flows, e.g. respiration, emigration, harvesting by humans, exit of detrital matter from the system

Trophic networks

In a trophic network fluxes encompass some relevant organism-level processes such as:

- prey-predator fluxes
- non-predatory mortality
- defecation
- respiration

A simple planktonic trophic network of the Venice Lagoon



- TAP = *R. philippinarum*, a clam living on the bottom
- MEZ = "large" zooplankton
- MIZ = small zooplankton
- BPL = bacteria
- PHP = phytoplankton
- DET = detritus (dead organic matter)

Trophic networks: quantitative data

It is possible to add quantitative data:

- Some quantitative information can be derived from the literature or gained from field or laboratory studies (e.g. diet composition, information on consumption, information on primary production)

However, it is unfeasible to determine the magnitudes of all flows in the system directly

Trophic networks: estimating quantitative data

Widely accepted approach:

- Assuming the mass balance on all compartments
  - conservation of mass principle $\Rightarrow$ reasonable assumption if a sufficiently long period of time is considered
  - steady state snapshot of the flows, averaged over time
- Representing the trophic network as a system of equations
- Adding specific ecological constraints.

The resulting system is usually underspecified.

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By assuming linear dependencies, it is possible to solve the system using the linear inverse model approach: it finds a unique solution based on some optimisation criteria (i.e. minimising the sum of squared flows)

Analysis of trophic networks

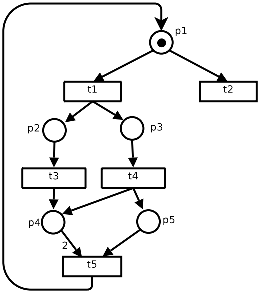
Many different analyses, both on the structural and quantitative level, have been defined in the ecological literature.

One of them is the degree of recycling (Ulanowicz, 1986), which is based on the determination of:

- all simple cycles
  - representing the internal recycling of matter
- all straight-through flows
  - representing the way energy/matter are provided by the environment, used by the network and then (partially) released back to the environment

Petri nets (PNs)

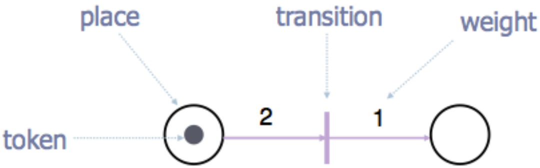
- First introduced in 1962 by Carl Adam Petri for describing chemical processes
- A diagrammatic tool to model concurrency and synchronisation in distributed systems
- Used as a visual communication aid to model the system behaviour
- Based on strong mathematical foundation



Components of a PN

A PN is a directed, weighted, bipartite graph, consisting of two types of nodes:

- places (states)
- transitions (events or actions)
- places marked with tokens (non-negative integer).



State and state changing

- places are the possible states
- a global state is constituted by all the places
- a marking is a vector listing the number of tokens in each place of the net

- A change of state is achieved by a movement of token(s) from place(s) to place(s) and is caused by the firing of a transition
- The firing represents an occurrence of the event or an action taken

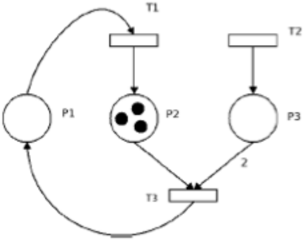
Behaviour

- a transition may fire when it is enabled
- a transition is enabled when each of its input places contain at least as many tokens as the weight of the corresponding input arc
- firing depends only on the local state of input places (pre-condition) and it affects the local state of input and output places (pos-tcondition)
- firing is atomic, namely it is a non-interruptible step
- firing is immediate in basic Petri nets

- An enabled transition may or may not fire (nondeterminism).

Incidence Matrix

The Incidence Matrix of a PN is a matrix with a row for each place and a column for each transition. The k-th matrix column is the vector representing the marking change when Tk fires.



$$A=\begin{bmatrix} -1 & 0 & 1 \\ 1 & 0 & -1 \\ 0 & 1 & -2 \end{bmatrix}$$

Analysis of Petri nets

PNs used for modelling and analysing complex systems

- Analysis allows for model validation and for studying properties of the modelled system
- Analysis can be performed at different levels
  - structural analysis
    structural properties only depend on the net topology
  - behavioural analysis
    behavioural properties depend on the evolution of the net from an initial state (marking)
  - simulation
    allows for running the network

Structural analysis of PNs: T-invariants

A T-invariant of a Petri net N is an m-dimensional vector in which each component represents the number of times that a transition should fire to take the net from a state M back to M itself. It can be obtained as a solution of the following equation:

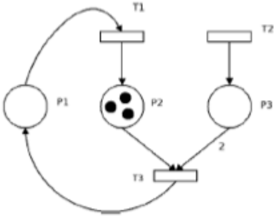
$$A_N X = 0$$

where $X = (x_1, \ldots, x_m)^T$ and x_i natural number for $\mathrm{i} = 1 \ldots \mathrm{m}$

A T-invariant $X \neq 0$ indicates that the system can cycle on a state M enabling the cycle.

The presence of a T-invariant in a PN can reveal the presence of a steady state in the involved subnet.

Structural analysis of PNs: T-invariants



A T-invariant of the net is $X_1 = (1, 2, 1)$

$$\begin{bmatrix} -1 & 0 & 1 \\ 1 & 0 & -1 \\ 0 & 1 & -2 \end{bmatrix} \begin{bmatrix} 1 \\ 2 \\ 1 \end{bmatrix} = 0$$

- In general a PN admits more than one T- invariant
- A T-invariant is minimum if there does not exist a different invariant whose support (non-zero components) is a subset of the given T-invariant.
- A linear combination of invariants is still an invariant.

The set of minimal T-invariants of a PN is called Hilbert Basis.

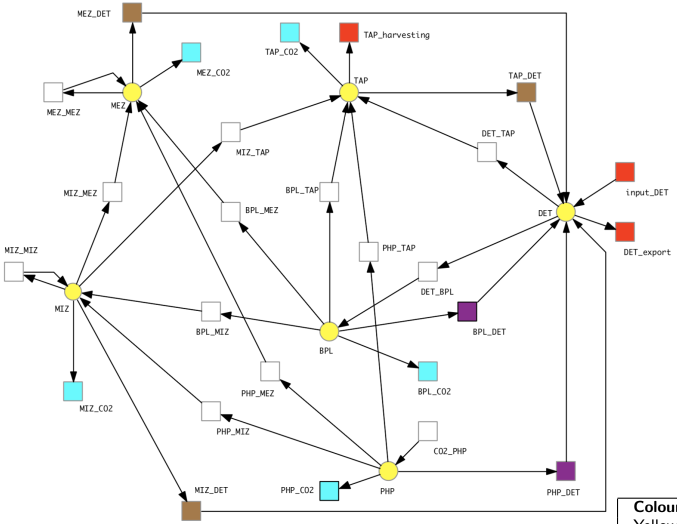
Modelling trophic networks as Petri nets

A structural Petri net model of a trophic network $\mathcal{T}$ is the net $N_s(\mathcal{T})$ where

- any species (or compartment) becomes a place;
- any flow between two species S_1 and S_2 becomes a transition having S_1 as a pre-condition and S_2 as a post-condition;
- any outgoing flow from a species S_1 to the external environment becomes a transition with empty post-condition and pre-condition S_1;
- any incoming flow from the environment to a species S_2 becomes a transition with empty pre-condition and post-condition S_2.

In absence of any information regarding the fluxes, all weights are set to one

The Petri net of the Venice Lagoon



Colours legend:
Yellow places = Compartments
Red transitions = Interface flows
Light blue transitions = Respiration flows
Brown transitions = Defecation flows
Purple transitions = Death flows
White transitions = Consumption flows

Analysis of trophic networks represented as Petri nets

Given a trophic network $\mathcal{T}$, consider the corresponding Hilbert basis $\mathcal{B}(N_s(\mathcal{T}))$. For any T-invariant of the basis:

- Minimal internal invariants are simple cycles, involving only internal transitions
  $\Rightarrow$ correspond to Ulanowicz simple cycles
- Minimal I/O invariants are acyclic paths, connecting two interface transitions
  $\Rightarrow$ correspond to Ulanowicz straight-through flows

The Petri net model of the Venice Lagoon has 69 minimal T-invariants: nine internal and sixty I/O invariants.

Continuous Petri net model of a trophic network

We refine the structural Petri net model turning it into a continuous Petri net model

- derived from the network topology by exploiting the minimal T-invariants in a way similar to what is done in (Popova-Zeugmann, Heiner, and Koch, 2005)

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The structural Petri net model of a trophic network is covered by T-invariants

- under the assumption that any place has at least one incoming and one outgoing transition

Continuous Petri net model of a trophic network

Two approaches for inducing rates keeping the model in a steady state:

- Uniform activation of all minimal subsystems
- Minimal activation of subsystems

We examine them in detail...

First Continuous Petri net model of a trophic network

Uniform activation of all minimal subsystems: each subsystem corresponding to a minimal T-invariant

- is active
  $\Rightarrow$ reasonable assumption from an ecological viewpoint
- performs all its transitions once per time unit
  $\Rightarrow$ rather strong and unrealistic assumption

Uniform Continuous Petri net model of a trophic network

The uniform continuous Petri net model $N_c(\mathcal{T})$ is the continuous Petri net obtained by

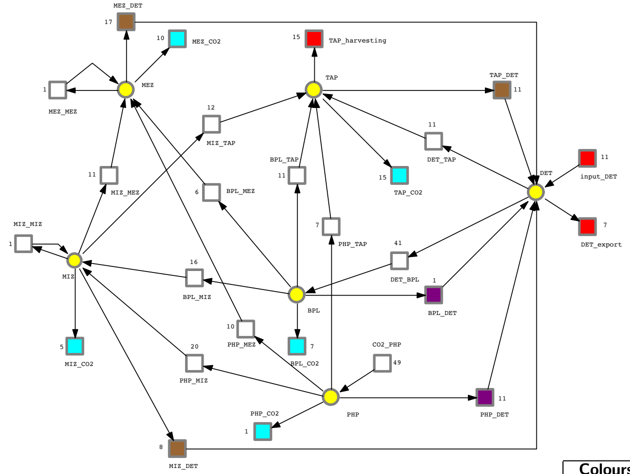
- considering the structural model $N_s(\mathcal{T})$ as underlying Petri net
- associating to each transition t a constant rate given by:

$$rate(t) = |\{I_i | I_i \in \mathcal{B}(N_s(\mathcal{T})) \ \wedge \ t \in I_i\}|.$$

Then:

- all the transitions in all the invariants in $N_c(\mathcal{T})$ are performed once in one time unit and the system is in a steady state;
- since all transition arcs are 1-weighted, rates and flows per time unit coincide;
- for each compartment the sum of incoming and outgoing fluxes coincide, i.e. the mass balance assumption is satisfied

Uniform continuous Petri net of the Venice Lagoon



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Ecological validation of the uniform continuous Venice Lagoon model

For each compartment, we consider some basic ecological processes:

- throughput: total amount of flux flowing per time unit
- consumption: total amount of ingested food per time unit
- assimilation: total amount of ingested food minus amount of feaces, per time unit
- respiration

We check their plausibility from an ecological point of view

Ecological validation of the uniform continuous Venice Lagoon model

Compartment	throughput	Literature values	Model values
TAP	41	Respiration $\geq$ 20% 37% $\leq$ Assimilation $\leq$ 70%	Respiration = 36% Assimilation = 73% Defecation and Mortality = 27%
MEZ	28	Respiration $\geq$ 20% 40% $\leq$ Assimilation $\leq$ 80%	Respiration = 37% Assimilation = 39% Defecation and Mortality = 61%
MIZ	37	Respiration $\geq$ 20% 40% $\leq$ Assimilation $\leq$ 80%	Respiration = 14% Assimilation = 78% Defecation and Mortality = 22%
BPL	41	Respiration $\geq$ 20% Assimilation = Consumption	Respiration = 17% Assimilation = Consumption Mortality = 2,4%
PHP	49	10% $\leq$ Respiration $\leq$ 30% Assimilation = Consumption	Respiration = 2% Assimilation = Consumption Mortality = 22%
DET	58	not relevant	not relevant

Throughput: DET > PHP > BPL = TAP > MIZ > MEZ

Second Continuous Petri net model of a trophic network

Minimal activation of subsystems:

- some subsystems are active ensuring that all the flows of the system are active, while minimising their sum
  $\Rightarrow$ maximal parsimony assumption

It correspond to solve the following system of linear equations:

minimise	$\Sigma_{i=1}^{m} x_i$
subject to	$A_N \cdot X = 0$
and	$X \geq 1$

where $X = (x_1, \ldots, x_m)^T$

A solution $K = (k_1, \ldots, k_m)$ defines the transitions rates.

Minimal Continuous Petri net model of a trophic network

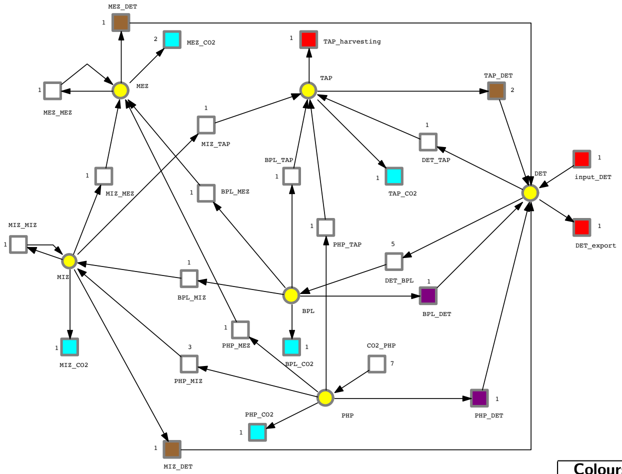
Given a solution $K = (k_1, \ldots, k_m)$, a minimal continuous Petri net model $N_c(\mathcal{T})$ is the continuous Petri net obtained by

- considering the structural model $N_s(\mathcal{T})$ as underlying Petri net
- associating to each transition t_i a constant rate k_i, for $i \in \{1, \ldots, m\}$.

Note again that:

- since all transition arcs are 1-weighted, rates and flows per time unit coincide;
- for each compartment the sum of incoming and outgoing fluxes coincide, i.e. the mass balance assumption is satisfied

Minimal continuous Petri net of the Venice Lagoon



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Ecological validation of the minimal continuous Venice Lagoon model

Compartment	throughput	Literature values	Model values
TAP	4	Respiration $\geq$ 20% 37% $\leq$ Assimilation $\leq$ 70%	Respiration = 25% Assimilation = 50% Defecation and Mortality = 50%
MEZ	4	Respiration $\geq$ 20% 40% $\leq$ Assimilation $\leq$ 80%	Respiration = 50% Assimilation = 75% Defecation and Mortality = 25%
MIZ	5	Respiration $\geq$ 20% 40% $\leq$ Assimilation $\leq$ 80%	Respiration = 20% Assimilation = 80% Defecation and Mortality = 20%
BPL	5	Respiration $\geq$ 20% Assimilation = Consumption	Respiration = 20% Assimilation = Consumption Mortality = 20%
PHP	7	10% $\leq$ Respiration $\leq$ 30% Assimilation = Consumption	Respiration = 14% Assimilation = Consumption Mortality = 14%
DET	7	not relevant	not relevant

Throughput: DET=PHP>BPL=MIZ>MEZ=TAP

Embedding ecological contraints in a continuous model

Usually some ecological knowledge is available on a species, such as:

- its metabolism
- its diet

Idea: making a continuous model closer to real trophic networks by embedding the additional knowledge in the system

That is, by imposing some constraints on the transitions' rates

Including constraints in a continuous model

Embedding in the continuous model additional information expressed as linear constraints

e.g. MIZ_CO2 $\geq$ 0.2 (PHP_MIZ + BPL_MIZ)

We are interested in the minimal T-invariant satisfying the additional constraints

They can be obtained as solutions of a system of inequalities:

$$\begin{array}{lcl} A_N \cdot X & = & 0 \\ C \cdot X & \geq & 0 \end{array}$$

where A_N is the incidence matrix of $N_s(\mathcal{T})$

The solutions of the above system define the constrained Hilbert basis $\mathcal{B}_C(N_s(\mathcal{T}))$.

Including constraints in a continuous model

A continuous Petri net model $N_c(\mathcal{T}, \mathcal{C})$ for the trophic network $\mathcal{T}$ satisfying the constraints $\mathcal{C}$ is defined as follows:

- the underlying Petri net is $N_s(\mathcal{T})$
- each transition t is associate with a constant rate depending on the model (uniform or minimal) and on the minimal T-invariants in $\mathcal{B}_C(N_s(\mathcal{T}))$.

For the Venice Lagoon continuous model we obtain a constrained Hilbert basis with 993 minimal T-invariants

Main characteristics of the continuous models

All the continuous models proposed so far:

- rely only on the network topology
  $\Rightarrow$ transition rates are determined through the minimal T-invariants
- provide a static view of the trophic network
  $\Rightarrow$ constant transition rates does not allow for a sensible dynamic simulation and analysis of the system
- amounts of biomass of the compartments at steady state do not play any role
  $\Rightarrow$ when estimations of biomasses are available a more realistic dynamic model can be derived

A continuous PN model with mass dependent rates

Law of mass action

- for a prey-predator flow

$$rate_1 = k_1 \cdot M_{prey} \cdot M_{predator}$$

- for a respiration or defecation flow of a compartment C

$$rate_2 = k_2 \cdot M_C$$

Given a continuous model of a trophic network:

- a constant rate value is associated to each transition t at steady state BUT
- we assume now that the rate of t is regulated by the law of mass action

Application to the Venice lagoon minimal continuous model: increasing the TAP harvesting

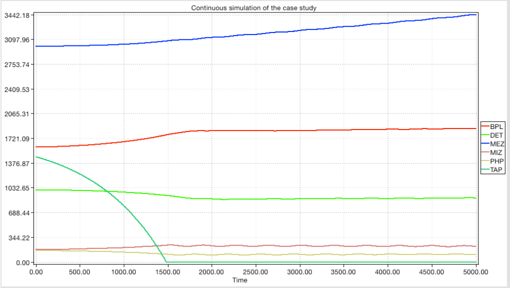
We associate

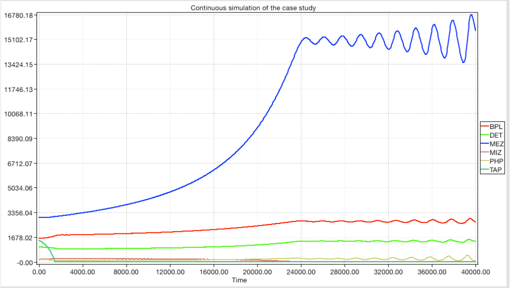
- mass-dependent rates to internal transitions
- constant rates to boundary transitions (*input_DET*, *DET_output* and *TAP_harvesting*)

Four tests case have been analysed corresponding to:

- pus/minus 30% of *TAP_harvesting* $\Rightarrow$ testing the systems on the basis of the fishing pressure for TAP
- pus/minus 30% of *input_DET* $\Rightarrow$ understanding the degree of dependence of TAP production in a given area on the larger lagoon environment

Application to the Venice lagoon minimal continuous model: increasing the TAP harvesting





Conclusions and future work

Exploring the use of Petri nets for representing and analysing trophic networks:

- natural representation as structural Petri nets
- classical trophic network concepts and analyses are recovered
- structural model turned into continuous models (uniform and minimal)
  - system at steady state with all fluxes balanced
- refinement of the continuous models by embedding ecological knowledge (constrained continuous models)
- further refinement of continuous models to represent the dynamic behaviour of the system

Conclusions and future work

- All the concepts and models have been applied to the Venice Lagoon trophic network
  - behaviour of the dynamic model reasonable from an ecological point of view and in agreement with the expectations based on the available knowledge
- Future work: further experiments with different and possibly larger trophic networks for
  - a better validation of our approach
  - indicating further extension