Petri nets for modelling and analysing Trophic networks

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Framework

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

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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:

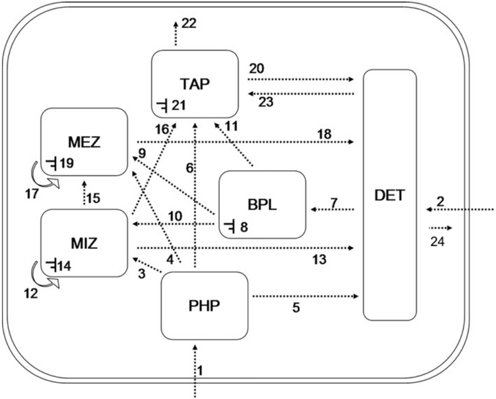
- input flows, e.g, primary production, immigration, incoming of detrital matter into the system
- output flows, e.g. respiration, emigration, harvesting by humans, exit of detrital matter from the system

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

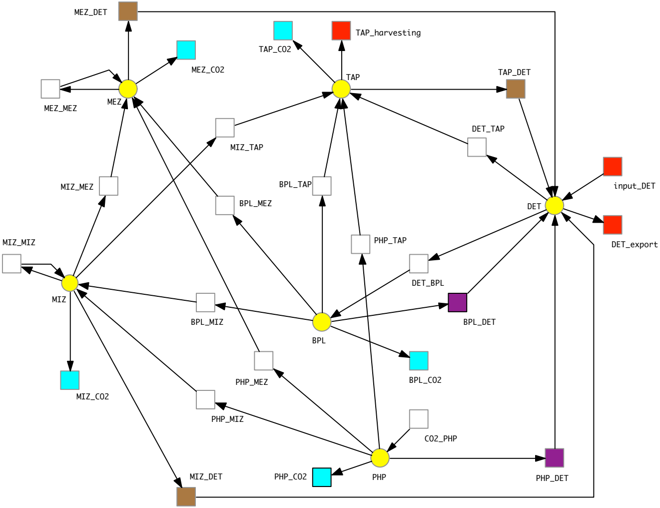
Modelling trophic networks as Petri nets

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



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

In order to associate rates with the transitions, we assume that each subsystem corresponding to a minimal T-invariant

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

Continuous Petri net model of a trophic network

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

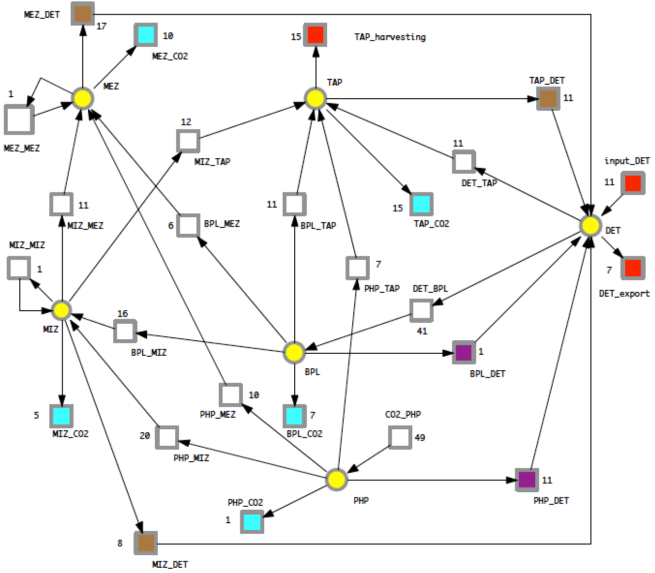
- considering the structural model $N_s(\mathcal{T})$ as underlying Petri net
- associating to each transition t a constant rate given by:

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

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

The continuous Petri net of the Venice Lagoon



Ecological validation of the 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 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

Improving the continuous model

Use additional ecological knowledge to make the continuous model closer to real trophic networks

Two directions:

- Drop the assumption that all the subsystems perform their path exactly once in one time unit and "speedup" some subsystems according with the indications of the additional knowledge
- Embedding the additional knowledge in the system by imposing some constraints

Speeding up subsystems

Consider a gereric linear combination of minimal T-invariants:

$$\sum_{I_i \in \mathcal{B}(N_c(\mathcal{T}))} k_i I_i \ , \qquad k_i \in \mathbb{R}.$$

- In the simple continuous Petri net model all k_i are set to one.

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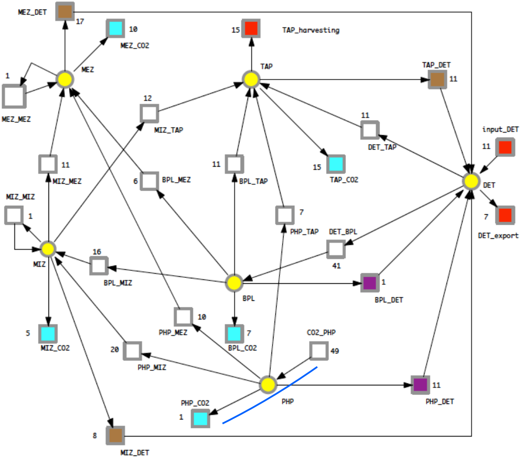
- In the simple continuous Petri net model all k_i are set to one.

We refine the simple continuous model by allowing constants k_i to be set to values possibly greater than one

The rate associated with each transition is generalised to:

$$rate(t) = \sum_{I_i \in \mathcal{B}(N_s(\mathcal{T})),\ t \in I_i} k_i .$$

Speeding up the Venice Lagoon model



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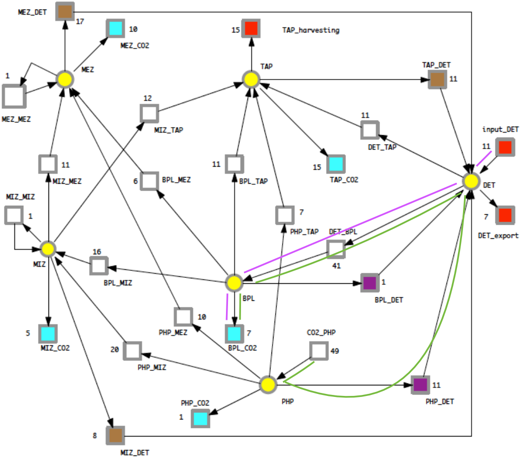
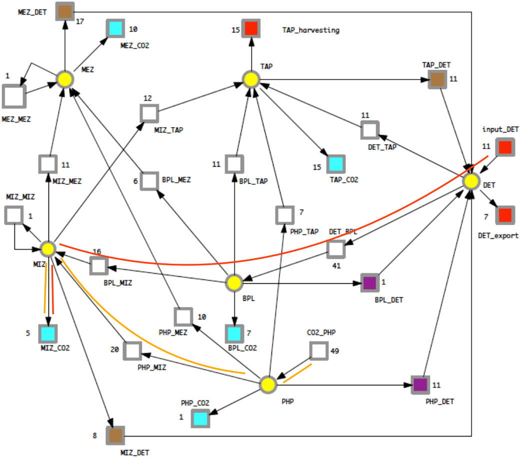


Speeding up the Venice Lagoon model



Including constraints in the simple 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 the simple 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 associated with a constant rate:

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

For the Venice Lagoon continuous model we obtain a constrained Hilbert basis with 349 minimal T-invariants

$\Rightarrow$ this approach might have scalability problems

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 refined into a continuous model
  - system at steady state with all fluxes balanced
- two further refinements of the continuous model:
  - fine tuning of the speed of the minimal T-invariants
  - ecological knowledge embedded into the calculation of the Hilbert basis.

Conclusions and future work

The proposed Petri net models are still simplicistic but:

- the continuous model of the Venice Lagoon realistically reproduces some main ecological processes
- the model can be fruitfully used for an early stage validation of the trophic network under study

Future work: making the continuous model more realistic and dynamic

- adding biomass information to compartments
- using rates dependent on biomasses (e.g. mass action law)