Fundamenta Informaticae XX (2018) 1–25
DOI 10.3233/FI-2012-0000
IOS Press

Petri Nets for modelling and analysing Trophic Networks

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Abstract. We consider trophic networks, a kind of networks used in ecology to represent feeding interactions (what-eats-what) in an ecosystem. Starting from the observation that trophic networks can be naturally modelled as Petri nets, we explore the possibility of using Petri nets for the analysis and simulation of trophic networks. We define and discuss different continuous Petri net models, whose level of accuracy depends on the information available for the modelled trophic network. The simplest Petri net model we construct just relies on the topology of the network. We also propose a technique for deriving a more refined model that embeds into the Petri net the known constraints on the transition rates that represent the knowledge on metabolism and diet of the species in the network. Finally, if the information of the biomass amounts for each species at steady state is available, we discuss a way of further refining the Petri net model in order to represent dynamic behaviour. We apply our Petri net technology to a case study of the Venice lagoon and analyse the results.

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1. Introduction

Ecosystems are very complex systems constituted by biotic communities (populations of different species), abiotic components of the environment (like air, water, soil), and interactions among these (living and non-living) elements. A branch of ecology deals with the study of feeding relationships within ecosystems and represents them as networks of interacting compartments called *trophic networks* or *food webs*, where each compartment represents a population of a given species or of a group of species with similar feeding behaviour. To study such networks, despite the common limited availability of experimental information, a static approach – the mass balance steady state approach, has been developed as an alternative to a dynamic description.

Complex networks of interacting entities are widely studied in computer science: computer networks, agent systems, and, in general, all concurrent and distributed systems fall into this category. Uncountably many formalisms and practical tools have been developed for the representation and analysis of interacting systems. This suggests the possibility of reusing modelling and analysis techniques from computer science for the study of trophic networks.

This idea is pursued in [23], where the authors advocate the use of process calculi for ecological modelling. Their claim is that the compositionality properties of process calculi can be fruitfully exploited for a modular representation of complex ecosystems. Moreover, process calculi provide individual-based modelling and stochastic extensions.

In this paper we explore the use of another widely used model of concurrency, namely Petri nets [25, 15], starting from the simple but crucial observation of a natural correspondence between methods and technologies used in the areas of Petri nets and trophic networks. Petri nets permit individual-based modelling, they explicitly represent parallelism and dependencies among entities, they offer stochastic and continuous extensions, and, as a major advantage, they enable a qualitative analysis of systems when kinetic information is not available. Many tools for system visualisation, analysis and simulation are also available (see *The Petri net World site* [29]).

A trophic network is usually represented as a directed graph where each node represents a compartment, aggregating similar species into groups with similar feeding behaviour, and each arc denotes an interaction (production, consumption, assimilation, predation, non-predatory mortality, respiration) between the source and target node, determining a flow of energy or biomass. When quantitative information is available, a quantity can be associated with each arc, representing the magnitude of biomass or energy flow or the relative strength of such a flow, as well as with each node, representing the magnitude of biomass or energy of the corresponding compartment.

The first basic observation is that the above representation naturally translates into a Petri net, that we call the *structural Petri net model*, where any species (or compartment) becomes a place and any flow between two compartments S_1 and S_2 in the network becomes a transition having the source S_1 as pre-condition and the target S_2 as post-condition. If there is no flow-related information available, all weights are set to one.

Thanks to its simplicity, the structural Petri net model enables standard structural analyses for Petri nets, like those based on T-invariants. The presence of T-invariants in a Petri net model of a trophic network is ecologically of interest as it can reveal the presence of steady states. The set of transitions involved in a T-invariant can be seen as a subsystem of the whole system, whose equilibrium is autonomously maintained. Indeed, interestingly enough, T-invariants have a natural correspondence with classical notions in the analysis of trophic networks, known as the Ulanowicz simple cycles and Ulanowicz straight-through flows [34, 35]. Both are used for decomposing a trophic network into smaller parts and to analyse recycling of matter.

The structural Petri net model of a trophic network can be refined, turning it into a *continuous Petri net model*. We introduce two approaches for associating constant rates to transitions, corresponding to two different assumptions on the system at steady state. The first approach assumes that *all* the subsystems, corresponding to minimal T-invariants, are active and perform at the same speed. The second one, more realistic from an ecological point of view, assumes that the steady state is determined by some subsystems that ensure that each flow is active, while minimising in some sense the system activity. This is a *maximal parsimony assumption,* capturing the intuition that the system stays active, but it minimises its effort. Our continuous models represent the system at steady state with the flows balanced at each compartment. This corresponds to the usual representation of a trophic network given by ecologists, that is a snapshot of the system at steady state, with the mass balance assumption. These Petri net models are only based on the topology of the system with transition rates inferred from T-invariants, relying on a technique similar to that used for Time Petri nets in [30]. Whenever additional information is available, either on the metabolism of the species or on their diet composition, we integrate it in the process of derivation of rates, by computing a sort of T-invariants "constrained" by this further information, so that the resulting models are ecologically plausible. This is done by expressing the constraints as linear inequalities, which are added to the system of equations used for the computation of the T-invariants. To the best of our knowledge this idea is original in the Petri net literature.

Whenever an estimation of the biomasses in compartments at steady state is available, we outline a technique for moving from a static representation to a dynamic Petri net model equipped with mass-dependent rates. Specifically, we propose to adopt for prey-predator flows as well as respiration and defecation flows a law inspired by the Lotka-Volterra models [24, 39], establishing a linear dependency of flows on the biomasses of the involved compartments. This allows us to perform dynamic simulation of transient behaviour and what-if analyses.

The presented techniques are applied, throughout the paper, to a case study consisting of a planktonic trophic network of the Venice lagoon, taken from [6], and the results are encouraging. The network provides a representation of the food items digested and assimilated by *R. philippinarum* (a marine bivalve mollusk), namely, green algae, cyanobacteria, diatoms, bacterioplankton, microzooplankton, and dead, dissolved, and/or particulate organic matter.

This paper builds on some preliminary work in [3], where we started the exploration of Petri nets to model and analyse trophic networks. Here, besides providing a more extensive and detailed presentation of the technique for inferring transition rates from T-invariants combined with available information on the trophic network, we propose a technique for deriving rates based on the maximal parsimony assumption and the whole approach for dynamic simulation and transient analysis.

The structure of the paper is as follows. In Section 2 trophic networks are introduced with a case study related to the Venice lagoon. In Section 3 the main concepts of Petri nets used to model trophic networks are briefly recalled. In Section 4 we show how to derive different continuous Petri net models for the representation and analysis of trophic networks when no quantitative information on the system is available. This is exemplified in the case study. In Section 5, by knowing the biomass amounts for each species at steady state, mass-dependent rates are derived for the flows and added to the Petri net model, thus permitting dynamic simulations. This is applied to the case study and some validation tests are discussed. Conclusions are given in Section 6.

2. Trophic Networks

An *ecosystem* is a community of living organisms, such as plants, animals and microbes, in conjunction with the nonliving components of their environment, such as air, water and bioavailable organic matter (detritus), which interact as a system. A *trophic network* (or *food web*) is a representation of feeding interactions in an ecosystem, where the components are connected by binary links (what-eats-what). Food webs permit to represent and analyse the trophic structure and functioning of an ecosystem. This knowledge can be used to identify key species and to detect anthropogenic impacts, such as the effects of pollution, physical disturbance and exploitation of resources.

Real trophic networks are very complex, hence models provide partial and abstract representations where, for instance, similar species are aggregated into groups with similar feeding behaviour. A model of a trophic network generally focuses on the flows of energy or biomass between nodes. Such flows are directional and encompass some relevant organism-level processes, such as *production, consumption, assimilation, predation, non-predatory mortality,* and *respiration*. Primary and secondary production, respectively, refer to the production of biomass by autotrophic and heterotrophic organisms. The latter one occurs through food consumption and subsequent assimilation.

An ecosystem is usually modelled as an open system, i.e. there are flows of material or energy between the system and the rest of the world. For this reason, when representing and analysing trophic networks, also the input and output flows are taken into account. Inputs can be *primary production, immigration* or *incoming of detrital matter* into the system, while outputs can be *emigration, harvesting by humans* and *exit of detrital matter* from the system. Some energy is dissipated into heat (*respiration*).

Some knowledge on the species that are part of the studied ecosystem and on their feeding behaviour is a needed prerequisite for modelling a trophic network. First of all it is necessary to single out the living and non-living compartments to be represented. A *compartment* can represent a population of a given species or of some aggregation of species with comparable feeding habits. Depending on the size and the level of details of the model, the number of compartments can be a few tens or even a few hundreds. For each compartment it is necessary to determine which taxa are included in its diet, thus specifying the interactions among species or groups of species. This information determines the topology of the network, which already provides some relevant insights on the features of the ecosystem.

An ecosystem is traditionally represented as a directed graph where each node represents a compartment and each arc denotes an interaction between its source and target node. More precisely, an arc from node A to node B represents a flow of energy or biomass from A to B. When quantitative information is available, a quantity can be associated with each arc, representing the magnitude of biomass or energy flow or the relative occurrence of such a flow, and with each node, indicating the magnitude of biomass or energy of the corresponding compartment.

In order to move from a purely topological representation of a trophic network to a quantitative one, ecologists need quantitative data. Estimation of biomass in each compartment and knowledge of several rates (e.g. production rate, consumption rate, respiration rate, etc.), along with quantitative knowledge about diet composition of each living compartment, are required to quantify flows among compartments. Some information on primary production, specific consumption rates and diet compositions can be deduced from field and laboratory studies, but normally it is impossible to determine directly the magnitude of all flows. Therefore, for some of them it is necessary to estimate the magnitude by indirect means. The most common approach for estimating unknown flows consists in assuming that the inputs and outputs for each compartment are balanced. If a sufficiently long time period is considered, *mass balance* *in each node* of the network is a reasonable assumption because of the conservation of mass principle. Under the mass balance assumption, the system is represented as a steady state snapshot, with energy flows averaged over time.

The *trophic network reconstruction* is the problem to infer unspecified flows by solving the mass balance equations while satisfying some constraints among the flows, which represent known metabolic and diet properties of the species in the system. The problem is generally underdetermined and an infinite number of solutions comply with the data set, the known constraints and the mass balance assumption. Different techniques are used to choose a preferable solution. One technique is the *Inverse Model (IM)*, which has been firstly applied to trophic networks in [38] and has become quite common among ecologists. IM combines mass balance equations, data equations and constraints on the flows expressed as inequalities. It finds a unique solution based on some optimisation criteria, for example by minimising the sum of squared flows, which corresponds to a maximal parsimonious solution. The package LIM implements linear inverse models in R [27]. Ecopath [9], with its evolutions Ecopath-Ecosym-Ecospace [10, 11], is a popular freely available software package that supports representation of trophic networks and inference of unknown flows.

When a model of the trophic network has been defined, several analysis techniques developed in the last decades can be applied. Some of them are purely topological, i.e., based only on graph properties, for instance determining *food chain length*, *connectance* (i.e. the ratio between the number of actual food links and the number of possible links), and the *presence of cycles*. In a balanced model it is possible to study both qualitative and quantitative properties.

Static analyses of trophic networks are mostly based on linear algebra techniques, e.g. I-O modelling techniques for economics modified in order to be applicable to ecosystems [35]. With such techniques it is possible to study the *indirect effects* and the *trophic structure* [34, 35] of an ecosystem. Further properties concerning the status and the development of the global system, such as *stability* [22, 36], *ascendency* and *development capacity* [35] [1] are studied by using flow networks and information theory.

A crucial analysis focuses on the *degree of recycling* [2] in order to characterise the reuse of biomass or energy in a trophic network. Cycles are important features of an ecosystem because they augment its stability by acting as buffers for fluctuations in energy supply. Odum identified in [26] the amount of cycling as one of the criteria for "maturity" of an ecosystem. A quantitative description of cycling in ecosystems was defined by Finn [16] through an index expressing the fraction of flow that cycles relative to the total system flow. Finn's index has been extended and modified [18, 2] for better representing the amount of cycling in the system. On the other hand, Ulanowicz [34, 35] claims that both the topology of the pathways by which the medium is recycled and the amount are relevant in the recycling analysis. He proposes a two-step method to decompose the network into weighted cyclic and non-cyclic sub-networks: first all simple cycles in the network are identified, then cycled flows are removed from the network, obtaining straight-through flows. The removal of a cycled flow is based on the idea of subtracting the minimal flow in the cycle from all the arcs in the cycle. The proposed technique is actually more complex because different cycles (called nexus) can share an arc with the minimal flow.

Case study: the Venice lagoon planktonic network. We now introduce a trophic network that will serve as our running example along the paper. It is a planktonic trophic network of the Venice Lagoon,

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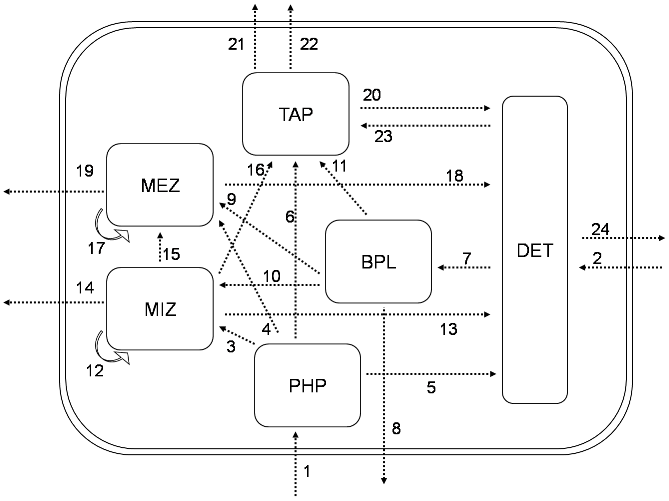
[1] Ascendency is a measure of total ecosystem development and growth, given by the average mutual information of the flow network scaled by the total throughput; development capacity is an upper boundary to ascendency.



Compartments
PHP = phytoplankton
BPL = bacterioplankton
MIZ = microzooplankton
MEZ = mesozooplankton
TAP = *Ruditapes philippinarum*
DET = organic detritus

No.	Flow	Description
1	CO_2→PHP	PHP net production
2	input→DET	DET import into the system
3	PHP→MIZ	MIZ consumption on PHP
4	PHP→MEZ	MEZ consumption on PHP
5	PHP→DET	PHP mortality
6	PHP→TAP	TAP consumption on PHP
7	DET→BPL	BPL consumption
8	BPL→CO_2	BPL respiration
9	BPL→MEZ	MEZ consumption on BPL
10	BPL→MIZ	MIZ consumption on BPL
11	BPL→TAP	TAP consumption on BPL
12	MIZ→MIZ	MIZ consumption on MIZ
13	MIZ→DET	MIZ defecation and mortality
14	MIZ→CO_2	MIZ respiration
15	MIZ→MEZ	MEZ consumption on MIZ
16	MIZ→TAP	TAP consumption on MIZ
17	MEZ→MEZ	MEZ consumption on MEZ
18	MEZ→DET	MEZ defecation and mortality
19	MEZ→CO_2	MEZ respiration
20	TAP→DET	TAP defecation and mortality
21	TAP→CO_2	TAP respiration
22	TAP→Harvesting	TAP harvesting (fishery)
23	DET→TAP	TAP consumption on DET
24	DET→Export	DET export outside the system

Figure 1. A trophic network $\mathcal{T}_V$ of the Venice Lagoon [6] (left, upper part), its compartments (left, lower part), and its flows (right).

taken from [6]. The network provides a representation of the food items digested and assimilated by *R. philippinarum* (a marine bivalve mollusk), namely, green algae, cyanobacteria, diatoms, bacterioplankton, microzooplankton, and dead, dissolved, and/or particulate organic matter. The topology of the trophic network is shown in Figure 1 (left). Numbers on arrows are flow identifiers. The flows are explicitly listed in Figure 1 (right). The table in Figure 1 (left) gives the correspondence between compartments and node names.

This trophic network has some peculiarities that are worth being pointed out:

- dissipation (respiration) of PHP is not considered because the flow from CO_2 to PHP (flow 1) models the *net* photosynthetic production, known from experimental data, i.e. the CO_2 needed for respiration has been already subtracted;

- effect of mineral nutrients limitation on productivity was not modelled explicitly, since photosynthetic production is known from experimental data;

- flow from BPL to DET (mortality of BPL) is not considered because experimental data suggest that it is negligible;

- flows from TAP, MEZ and MIZ to DET (flows 20, 18 and 13) include both natural mortality and production of faeces;

- flow from PHP to DET (flow 5) indicates only mortality, because PHP does not produce faeces;

- the case of MIZ and MEZ cannibalism is represented by arrows exiting and entering in the same compartment (flows 12 and 17).

3. Petri Nets

Petri nets are a well known formalism originally introduced in computer science for modelling discrete concurrent systems. Petri nets have a sound theory and many applications which are not limited to computer science (see, e.g., [25] and [15] for surveys). A large number of tools has been developed for analysing Petri nets (see *Petri Nets World* site [29]).

We denote a basic Petri net by $N = (P, T, W, M_0)$, where $P = \{p_1, \ldots, p_n\}$ is the set of places, $T = \{t_1, \ldots, t_m\}$ is the set of transitions, $W : \big((P \times T) \cup (T \times P)\big) \to \mathbb{N}$ is the weight function, and M_0 is the *initial marking* of the net, an n-dimensional integer vector assigning to each place its initial number of tokens.

We write t^- for denoting the *pre-condition* of a transition t, namely the n-dimensional vector $t^- = (i_1, \ldots, i_n)$, where $i_j = W(p_j, t)$ for $j \in \{1, \ldots, n\}$. Sometimes the same notation will be used to refer to the corresponding support, i.e., the set of places $\{p_j \mid i_j > 0\}$. The *post-condition* $t^+ = (o_1, \ldots, o_n)$ is defined dually.

The *incidence matrix* of a Petri net N, denoted by A_N, is the $n \times m$ matrix which has a row for each place and a column for each transition. The column associated with transition t is the vector $(t^+ - t^-)^T$, which represents the marking change due to the firing of t.

Depending on the available information, Petri nets may permit to represent and study a system qualitatively, based only on the graph structure, as well as quantitatively or dynamically. An interesting *structural analysis*, based on the incidence matrix, aims at determining the so-called *invariants* of the net. We focus here on T-invariants. Let N be a Petri net, with m transitions and n places, a *T-invariant* (transition invariant) of N is a multiset of transitions whose execution starting from a state will bring the system back to the same state, More explicitly, it is an m-dimensional vector whose components represent the number of times that each transition should fire to take the net from a state M back to M itself. T-invariants are solutions of the equation

$$A_N \cdot X = 0 \tag{1}$$

where $X = (x_1, \ldots, x_m)^T$ and $x_i \in \mathbb{N}$, for $i \in \{1, \ldots, m\}$. A T-invariant $X \neq 0$ indicates that the system can cycle via a state M enabling the cycle. As discussed in [19], T-invariants admit two possible interpretations. On the one hand, given an appropriate start marking enabling the transitions of a T-invariant, the components of the T-invariant itself represent a multiset of interactions (transitions) whose partially ordered execution reproduces the start marking. On the other hand, the components of a T-invariant may be interpreted as the relative rates of interactions (transitions) which occur permanently and concurrently in a steady state. Minimal T-invariants of a Petri net N, form a basis, $\mathcal{B}(N)$, for the set of semi-positive T-invariants (referred to as Hilbert basis [32], for integral spaces). Any T-invariant can be obtained as a linear combination, with positive rational coefficients, of elements of the basis. Uniqueness of the basis $\mathcal{B}(N)$ makes it a characteristic feature of the net N.

Two subclasses of Petri nets will be of special interest for the modelling of trophic networks [13]. A *state machine Petri net* is a Petri net where every arc has weight one and every transition has exactly one place in its pre- and post-condition. State machine Petri nets are conservative, namely the total number of tokens of the system remains invariant under the occurrence of transitions. A *free choice* Petri net [14] is characterised by the fact that for any place p, either p has at most one post-transition (i.e. no conflict) or it is the only pre-place of all its post-transitions. The class of state machine Petri nets is strictly included in the class of free choice Petri nets.

Petri nets supply an executable specification: in the case of basic Petri nets, we can play the *token game*, i.e., the non-deterministic firing of all enabled transitions. More sophisticated and realistic models and simulations can be obtained through extended Petri net models. The most interesting model class in our context are Continuous Petri nets. In *Continuous Petri nets* [19] the state is no longer discrete. Places contain non-negative real numbers, usually interpreted as the concentration of the species represented by the place. The instantaneous firing of a transition is carried out like a continuous flow. The firing rate expresses the "speed" of the transformation from input to output places. The rate functions associated with transitions may follow, under simplifying assumptions, known kinetic equations such as the mass action equation.

4. Petri Nets for Modelling and Analysing Trophic Networks

In this section we discuss how Petri nets can be used to model and analyse trophic networks. At first we assume to know only the species (or compartments) and their relations, which is the minimal knowledge generally available for a trophic network. Subsequently, we discuss how to include in the model the ecological knowledge possibly available for the metabolism of the species or their diet composition. As a running example, we consider the trophic network $\mathcal{T}_V$ of the Venice lagoon in Figure 1. We illustrate how to build corresponding Petri net models and discuss the applicability of some Petri net analysis techniques. We use the tools Snoopy [20], Charlie [21] and 4ti2 [1] for editing and analysing the Petri net models, and *glpsol* [17] for solving linear optimisation problems.

4.1. Structural modelling of trophic networks with Petri nets

Given a trophic network $\mathcal{T}$, a simple Petri net model can be immediately derived by replicating the topological structure of $\mathcal{T}$ in the Petri net. Recall that in the graph representation of $\mathcal{T}$ each species (or compartment) is a node and a relation between two species is a directed arc representing the flow of biomass or energy between the two species.

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 (relation) between two species S_1 and S_2 in $\mathcal{T}$ becomes a transition having S_1 as pre-condition and S_2 as post-condition;
- any outgoing flow from a species S_1 to the external environment (e.g., dissipation) in $\mathcal{T}$, becomes a transition with pre-condition S_1 and empty post-condition; similarly, 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 strength of flows, all weights (of existing arcs) are set to one. Transitions corresponding to interactions among species are referred to as *internal transitions*, while those corresponding to interactions with the environment are referred to as *interface transitions*.

Note that the structural Petri net model of a trophic network is a free choice Petri net, and its restriction to internal transitions is a state machine Petri net.

By applying the described construction to the running example $\mathcal{T}_V$ in Figure 1, we obtain a structural Petri net model which is depicted in Figure 2 (for the moment, please ignore the rates associated with transitions). The net includes six places (in yellow, in the coloured version) representing the six compartments (DET, PHP, BPL, MIZ, MEZ, TAP) of the trophic network, and as many transitions as there are flows of biomass. A transition representing a flow from compartment A to compartment B is named A_B. For instance, MIZ respiration, that produces CO_2 is denoted by MIZ_CO_2. In order to improve readability, in the coloured version, we use different colours for different classes of transitions. More specifically, respiration flows (producing CO_2) are represented by light blue transitions, defecation flows by brown transitions, mortality flows by purple transitions, input and export flows for DET as well as the harvesting flow for TAP by red transitions, and predation-prey flows by white transitions.

Note that there are two transitions in the Petri net model of Figure 2, which do not have a direct match in the trophic network $\mathcal{T}_V$ of Figure 1: the transition PHP_CO2 representing respiration of PHP and the transition BPL_DET representing BPL mortality. This is due to the fact that $\mathcal{T}_V$ was simplified by integrating the two flows PHP_CO2 and CO2_PHP (modelling CO_2 needed for photosynthesis), while BPL_DET was considered irrelevant and thus omitted.

4.2. Structural analysis of trophic networks modelled as Petri nets

Since the structural Petri net model adheres to the graph representation used by ecologists, it enables us to immediately reuse the usual analyses for trophic networks based on graph properties, which aim, for example, at determining food chains length and connectance.

In addition, standard structural analyses known for Petri nets can be used, like those based on T-invariants. The presence of T-invariants in a Petri net model of a trophic network is ecologically of interest as it can reveal the presence of steady states. The set of transitions involved in a T-invariant can be seen as a subsystem of the original system, whose equilibrium is autonomously maintained. According to the terminology in [19], we classify T-invariants into two groups:

- *internal T-invariants*, consisting of internal transitions only;
- *I/O T-invariants*, which include also interface transitions.

Given a trophic network $\mathcal{T}$, consider the set of semi-positive T-invariants of the structural Petri net model $N_s(\mathcal{T})$ and the corresponding invariant basis $\mathcal{B}(N_s(\mathcal{T}))$, consisting of the minimal T-invariants. Then the following holds.

Remark 4.1. *Minimal T-invariants in $N_s(\mathcal{T})$ are set of transitions corresponding to either simple cycles or acyclic paths connecting two interface transitions.*

In fact, recall that in the Petri net model $N_s(\mathcal{T})$ of a trophic network $\mathcal{T}$ all transitions have at most one place in their pre- and post-set. This immediately implies that set of transitions corresponding to simple cycles or acyclic paths connecting two interface transitions are minimal T-invariants.

In order to see that also the converse holds, let I be a minimal T-invariant and take the corresponding set of transitions $T_I = \{t \mid I(t) > 0\}$.

Inv no.	Transitions
1	MEZ_MEZ
2	MIZ_MIZ
3	DET_TAP; TAP_DET
4	DET_BPL; BPL_DET
5	DET_BPL; BPL_MEZ; MEZ_DET
6	DET_BPL; BPL_MIZ; MIZ_DET
7	DET_BPL; BPL_TAP; TAP_DET
8	DET_BPL; BPL_MIZ; MIZ_MEZ; MEZ_DET
9	DET_BPL; BPL_MIZ; MIZ_TAP; TAP_DET

Table 1. Internal minimal T-invariants of the structural Petri net model of $\mathcal{T}_V$.

- If the subnet corresponding to T_I includes a cycle, then the cycle must be simple and it must coincide with I due to minimality of I.
- If, instead, the net corresponding to T_I is acylic, take any transition $t_0 \in T_I$ such that $t^+ \cap {t_0}^- = \emptyset$ for all $t \in T_I$ (which exists by acyclicity and finiteness of T_I). Since no transition in T_I generates tokens in ${t_0}^-$ and I is an invariant, t_0 must be an interface (input) transition with ${t_0}^- = \emptyset$. Now, either ${t_0}^+ = \emptyset$, i.e., t_0 is also an interface output transition or, since I is an invariant, there is at least one transition t_1 in T_I consuming the tokens produced by t_0, i.e., such that ${t_0}^+ \cap {t_1}^- \neq \emptyset$. Now, again, either ${t_1}^+ = \emptyset$, i.e., t_1 is an interface (output) transition or there must be $t_2 \in T_I$ such that ${t_1}^+ \cap {t_2}^- \neq \emptyset$, and so on. Since T_I is acylic, the construction terminates producing an acyclic path in T_I of the kind $t_0, t_1, \ldots, t_n$ where t_0 and t_n are interface transitions. This is an invariant and by minimality of I, it must coincide with I itself.

Observe that, in particular, for any minimal T-invariant $I = (x_1, \ldots, x_m)$ we have $x_i \leq 1$ for all $i \in \{1, \ldots, m\}$, namely each transition occurs at most once and the invariant is a set rather than a proper multiset.

Summing up:

- *Minimal internal invariants are simple cycles*, involving only internal transitions.
- *Minimal I/O invariants are acyclic paths*, connecting two interface transitions.

In both cases we have a clear correspondence with well-known concepts in trophic networks as presented, e.g., in [35]. The internal minimal T-invariants are Ulanowicz simple cycles, which are associated with the internal recycling of matter. The minimal I/O T-invariants are Ulanowicz straight-through flows, which represent the way in which energy and matter are provided by the environment, used by the network and then (partially) released back to the environment. Such correspondences are at the structural level, for Ulanowicz analyses the quantities of flows are needed.

In our case study, the structural Petri net model has an invariant basis consisting of 69 minimal T-invariants, nine are internal and sixty are I/O invariants. The internal T-invariants are shown in Table 1. The first two invariants describe the self-predation (cannibalism) of MEZ and MIZ. All the other T-invariants “traverse” the DET place, pointing out that, in this network, Detritus is the way for recycling matter. The I/O invariants start from the source transitions CO2_PHP and input_DET and end in the sink transitions PHP_CO2, BPL_CO2, MIZ_CO2, MEZ_CO2, TAP_CO2, and TAP_harvesting. They model trophic chains allowing for respiration of the various compartments and for input and output of matter.

4.3. Deriving continuous Petri net models from structural information

In this section we show how to refine the structural Petri net model of a trophic network, turning it into a continuous Petri net model with constant rates derived by T-invariants. We propose two distinct constructions, based on different assumptions on the behaviour of the system at steady state, and we discuss them with respect to our case study.

4.3.1. Deriving continuous Petri net models with constant rates

We start with deriving continuous Petri net models from structural information, i.e., relying only on the network topology in a way similar to what has been done in [30] for Time Petri nets. We obtain a representation of the trophic network which closely resembles the one usually adopted by ecologists, where the system is at a steady state and the input and output flows in all the compartments are balanced (mass balance assumption). The choice of considering continuous Petri nets is motivated by the fact that flows of biomass are appropiately modelled by continuous flows. Additionally, moving from ordinary to continuous Petri nets has some computational advantages, since we avoid the need of dealing with integer (in)equations, making our technique more scalable. In particular, hereafter, whenever we refer to the set $\mathcal{B}(N)$ of the minimal T-invariants of a Petri net N, we actually mean a basis of the solution space of $A_N \cdot X = 0$, $X \geq 0$ in the rationals, as provided by the tool `qsolve` of 4ti2 [1].

In the proposed continuous Petri net models, each transition of the structural model $N_s(\mathcal{T})$ is associated with a constant rate. Rates are computed by assuming that the system is at a steady state resulting from a specific linear combination of a suitable set of minimal T-invariants. In the combination chosen, the invariants with non-zero coefficients correspond to the minimal subsystems which are assumed to be active. Different combinations will produce models with different transition rates. Before providing the details, a couple of observations are in order.

Remark 4.2. In a structural Petri net model of a trophic network, $N_s(\mathcal{T})$, any place has at least one incoming and one outgoing transition, otherwise the place would unnaturally correspond to a compartment with monotonically increasing or decreasing content. Under this assumption, $N_s(\mathcal{T})$ *is covered by T-invariants*, namely each transition in the Petri net belongs to at least one minimal T-invariant. In fact, $N_s(\mathcal{T})$ is a state machine if we exclude interface transitions, hence for any transition, by following all the predecessors and successors, we will go back to the transition itself (internal T-invariant) or to an interface transition on both sides (I/O T-invariant).

Remark 4.3. *A derived continuous Petri net model of a trophic network satisfies the mass balance assumption.* In fact, all continuous models use as underlying net the structural model $N_s(\mathcal{T})$, where all arcs are 1-weighted. As a consequence, rates and flows per time unit coincide in such continuous models, and using this fact, it is immediate to see that for all compartments the sum of incoming and outgoing flows coincide, i.e., the mass balance assumption is satisfied. In fact, recall that due to the special shape of $N_s(\mathcal{T})$, minimal T-invariants are simple cycles or paths. This implies that for any place p and for any invariant I_i that "crosses" place p, it happens that p is in the pre-set of exactly one transition in I_i and in the post-set of exactly one transition in I_i, meaning that the flow through p via I_i is balanced. Therefore, the input and output flows coincide for any place of the network.

We propose two different approaches for inducing rates keeping the model in a steady state. They correspond to two different assumptions: either assuming that all minimal subsystems are uniformly active or assuming that only a set of subsystems covering all flows in the system are "minimally" active.

Uniform activation of all minimal subsystems. Our first approach for associating rates with the transitions assumes a sort of "uniform" activation of all the subsystems corresponding to minimal T-invariants, namely it assumes that each subsystem

1. is active and
2. performs all its transitions once per time unit.

More formally, consider the structural Petri net model $N_s(\mathcal{T})$ of a trophic network $\mathcal{T}$ as described in Section 4.1 and its invariant basis $\mathcal{B}(N_s(\mathcal{T}))$. The assumptions 1 and 2 above can be implemented by letting the rate of a transition t depend on the number of minimal invariants in which t occurs. Then, for the trophic network $\mathcal{T}$, we define the *uniform continuous Petri net model* $N_c(\mathcal{T})$ as the continuous Petri net obtained from the structural model $N_s(\mathcal{T})$ by associating to each transition t a constant rate given by:

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

With such rates, all the transitions in all the invariants in $N_c(\mathcal{T})$ are performed once per time unit and the system is in a steady state. This is similar to what has been done in [30] for Time Petri nets. In an ecosystem, the assumption that all the subsystems are equally active and perform all their transitions exactly once per time unit is somehow simplistic and unrealistic, even if it could be acceptable when any further information on the behaviour of the system is missing. When additional information is available, it can be exploited for selecting a suitable subset of minimal invariants out of $\mathcal{B}(N_s(\mathcal{T}))$ to be active or for the attribution of different speeds to the selected subsystems. We will see in Subsection 4.4 that this can be automated in some situations.

Minimal activation of subsystems. From an ecological point of view, rather than assuming that all subsystems are active, it can be sensible to suppose that the steady state is determined by some subsystems, a subset of $\mathcal{B}(N_s(\mathcal{T}))$, that covers the net, i.e., that ensures that all the flows of the system are active, while minimising their sum. This is a maximal parsimony assumption somehow capturing the intuition that the system stays "fully active", but it minimises the overall effort.

In order to implement this maximal parsimony assumption we consider a linear optimisation problem

$$\begin{array}{ll} \text{minimise} & \Sigma_{i=1}^{m} x_i \\ \text{subject to} & A_N \cdot X = 0 \\ \text{and} & X \geq 1 \end{array} \tag{2}$$

where $X = (x_1, \ldots, x_m)^T$. Given a solution $K = (k_1, \ldots, k_m)$, a *minimal continuous Petri net model* $N_c^m(\mathcal{T})$ is the continuous Petri net obtained from the structural model $N_s(\mathcal{T})$ by associating to each transition t_i a constant rate k_i, for $i \in \{1, \ldots, m\}$.

Clearly, the solution of the linear optimisation above can be expressed as a linear combination of a subset of elements of the basis $\mathcal{B}(N_s(\mathcal{T}))$ that can be determined a posteriori. If $K = (k_1, \ldots, k_m)$ is the solution from (2) and $\mathcal{B}(N_s(\mathcal{T})) = \{I_1, \ldots, I_n\}$, consider the matrix I, having $I_1, \ldots, I_n$ as rows, and solve the system

$$\begin{aligned} Y \cdot I &= K \\ Y &\geq 0 \end{aligned} \tag{3}$$

with $Y = (y_1, \ldots, y_n)$. The active invariants (subsystems) are those that contribute positively to the solution K, i.e., the invariants I_j such that $y_j > 0$.

In both the continuous models $N_c(\mathcal{T})$ and $N_c^m(\mathcal{T})$, the system is represented in a steady state, with the flows of biomass balanced in all compartments as noticed in Remark 4.3. This corresponds closely to the ecologists' representation of a trophic network as a snapshot of the system at steady state. The continuous Petri net models $N_c(\mathcal{T})$ and $N_c^m(\mathcal{T})$, despite the fact that they build on some further assumptions on the system behaviour, are still based only on the topology of $\mathcal{T}$. When additional knowledge on the trophic network is available, it can be integrated in the model, as we will show in the next section. Note that so far biomasses do not play a role in the definition of the rates, hence rates represent just relations among flows. This fact and the choice of constant rates make the models rather unrealistic. This issue will be discussed in Section 5.

4.3.2. Applying the continuous modelling idea to the case study

We apply the approach outlined above to our case study and evaluate the corresponding continuous Petri net models with respect to some ecological knowledge extracted from the literature.

The *uniform continuous Petri net model* $N_c(\mathcal{T})$, resulting from the first technique, has the structural model given in Figure 2 as underlying Petri net, and a constant rate is associated with each transition. As stated in Remark 4.3, all places are balanced. We validate the model by considering some basic ecological processes and checking their plausibility from an ecological point of view. For each compartment we compute the throughput, namely the total amount of flow per unit of time, in order to measure the degree of activity of the compartment. Moreover, we compute food consumption (the total amount of ingested food per time unit), food assimilation (the amount of ingested food minus amount of faeces per time unit), respiration and mortality as percentages of the consumption. Table 2 shows the throughputs, the assimilation and respiration values as resulting from the model compared with those found in the literature.

The values derived from the uniform continuous model are quite interesting. Considering the throughput, the various compartments are ordered as follows:

DET>PHP>BPL=TAP>MIZ>MEZ.

We may distinguish two main groups: lower trophic level compartments (DET, PHP and BPL), having higher throughput, and higher trophic level compartments (TAP, MIZ and MEZ), having lower throughput. This is coherent with the general knowledge on metabolic and growth rates of the two different groups of compartments under consideration.

Assimilation of the top compartment TAP is just over the maximum indicated in the literature, while assimilation requirements for MEZ and MIZ are perfectly met. However, MEZ assimilation is close to

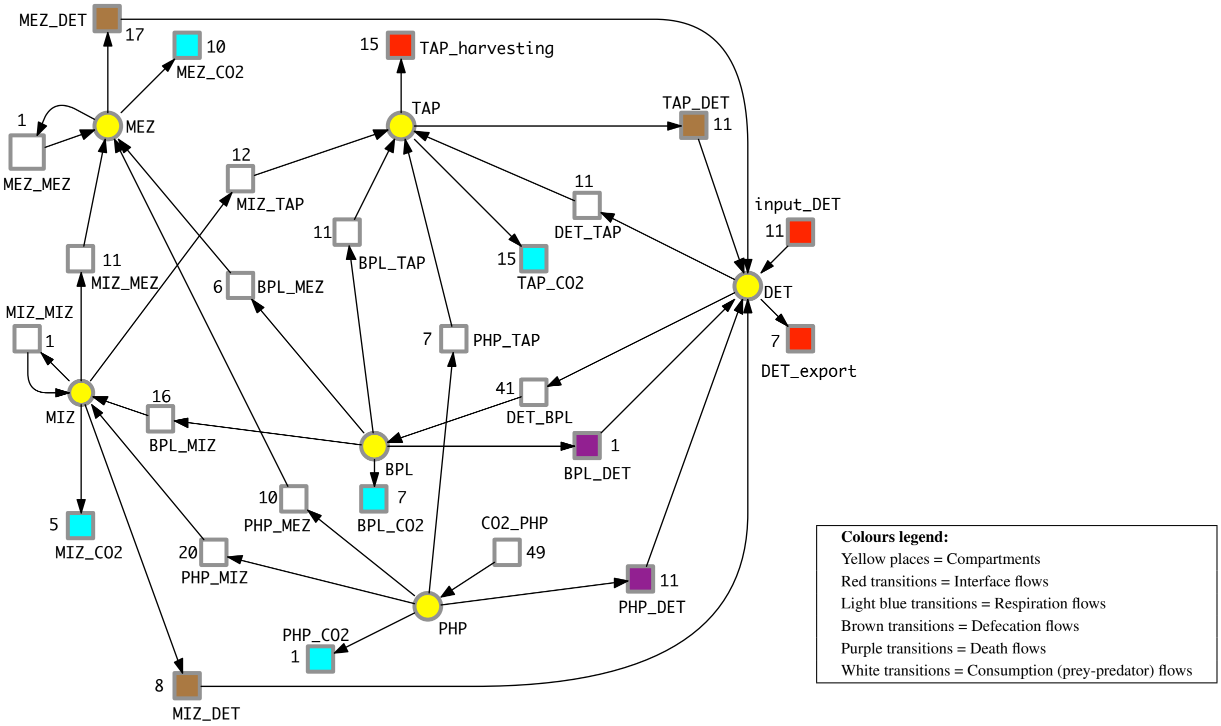


Figure 2. Continuous Petri net model for the case study

the lower bound of the indicated range. This is due to the fact that MEZ is a top level compartment in the network and no predators are modelled for it. This is a quite unrealistic assumption: in natural systems MEZ are actually preyed by other species, like fishes. By adding an external predation for MEZ, we found that its assimilation becomes close to TAP and MIZ assimilation values.

Concerning respiration, TAP and MEZ satisfy the constraints found in the literature, while MIZ and BPL are slightly below the literature value. Respiration of PHP is instead far below the lower bound of the indicated range. The low respiration flows for MIZ, BPL and PHP is caused by the fact that there are only a few I/O minimal invariants involving these compartments. This is a misbehaviour of the uniform continuous model.

Mortality of BPL is negligible, which is in accordance with experimental data (see discussion in Section 2). Mortality of PHP is instead quite high: this is probably due to the fact that some PHP grazers, like fishes usually living in lagoon systems, are not modelled.

On the whole, the uniform continuous Petri net model realistically reproduces the main processes of the trophic network considered in the case study. Even if it based only on the network topology, it allows for deriving some quantitative information on trophic network flows, which is coherent with results of experimental measures taken in natural ecosystems. Moreover, the quantitative validation shows that the model is somehow incomplete, indicating that two further predation flows, one for MEZ and one for PHP, should be represented in the model.

We now focus on the *minimal continuous Petri net model* $N_c^m(\mathcal{T}_V)$ of the case study. The underlying Petri net is still $N_s(\mathcal{T}_V)$, but the transition rates are now computed according to (2), and this determines a

Compartment	throughput	Literature values	Model values
TAP	41	[33] Respiration $\geq$ 20% [33] 37% $\leq$ Assimilation $\leq$ 70%	Respiration = 36% Assimilation = 73% Defecation and Mortality = 27%
MEZ	28	[37] Respiration $\geq$ 20% [28, 12] 40% $\leq$ Assimilation $\leq$ 80%	Respiration = 37% Assimilation = 39% Defecation and Mortality = 61%
MIZ	37	[37] Respiration $\geq$ 20% [28, 12] 40% $\leq$ Assimilation $\leq$ 80%	Respiration = 14% Assimilation = 78% Defecation and Mortality = 22%
BPL	41	[31, 8] Respiration $\geq$ 20% Assimilation = Consumption	Respiration = 17% Assimilation = Consumption Mortality = 2,4%
PHP	49	[40, 4] 10% $\leq$ Respiration $\leq$ 30% Assimilation = Consumption	Respiration = 2% Assimilation = Consumption Mortality = 22%
DET	58	not relevant	not relevant

Table 2. Literature values and measured values for the *uniform continuous Petri net model* of the case study.

modification of the corresponding ecological processes. Table 3 shows the throughputs, the assimilation and respiration values as obtained from the model compared to those found in the literature.

Considering the throughput, the various compartments are ordered as follows:

$$\text{DET}=\text{PHP}>\text{BPL}=\text{MIZ}>\text{MEZ}=\text{TAP}$$

and, again, we notice a higher activity on the lower level organisms and a lower activity on the higher level ones. By considering the literature values and the measured values, we observe that the model satisfies all the constraints, including those regarding respiration of MIZ, BPL and PHP. The throughput values for the second model are much smaller than in the first one, but the absolute values of the flows and throughput are not relevant in our models. In fact, our models do not use any quantitative information on flows or biomasses, hence only the ratio between the flows is represented, not their absolute values.

4.4. Enforcing ecological constraints

In the previous section we introduced two techniques for obtaining a continuous Petri net model of a trophic network by relying on structural information. Generally some additional information on the trophic network is available, such as the metabolism of the species or their diet composition. Examples of such knowledge for our case study are the constraints reported in the columns "Literature Values" of Tables 2 and 3. In this section we propose a way to "embed" into a continuous Petri net model the information possibly available on the metabolism of the species or their diet. Such information can be expressed as constraints on the rates of the corresponding transitions. This produces a model which automatically satisfies such constraints and which is hence closer to the actual trophic network.

4.4.1. Deriving constrained continuous models

We work under the simplifying assumption that the flow constraints imposed on the model are linear. This restriction is not severe since it is generally satisfied by the constraints on metabolic flows and on

Compartment	throughput	Literature values	Model values
TAP	4	[33] Respiration $\geq 20\%$ [33] $37\% \leq$ Assimilation $\leq 70\%$	Respiration = 25% Assimilation = 50% Defecation and Mortality = 50%
MEZ	4	[37] Respiration $\geq 20\%$ [28, 12] $40\% \leq$ Assimilation $\leq 80\%$	Respiration = 50% Assimilation = 75% Defecation and Mortality = 25%
MIZ	5	[37] Respiration $\geq 20\%$ [28, 12] $40\% \leq$ Assimilation $\leq 80\%$	Respiration = 20% Assimilation = 80% Defecation and Mortality = 20%
BPL	5	[31, 8] Respiration $\geq 20\%$ Assimilation = Consumption	Respiration = 20% Assimilation = Consumption Mortality = 20%
PHP	7	[40, 4] $10\% \leq$ Respiration $\leq 30\%$ Assimilation = Consumption	Respiration = 14% Assimilation = Consumption Mortality = 14%
DET	7	not relevant	not relevant

Table 3. Literature values and measured values for the *minimal continuous Petri net model* of the case study.

the diet partitions. An example of such constraints for our case study are the metabolic constraints taken from the literature shown in Table 2.

We define a continuous Petri net model which structurally coincides with $N_s(\mathcal{T})$ and whose transition rates satisfy a set of linear inequalities. As in the previous continuous models, the transition rates correspond to the "speed" k_i of each T-invariant, but now we are interested only in T-invariants that satisfy the constraints.

In order to determine these invariants we compute the solutions of a system of inequalities

$$\begin{array}{lcl} A_N \cdot X & = & 0 \\ C \cdot X & \geq & 0 \\ X \geq 0 & & \end{array} \tag{4}$$

where A_N is the incidence matrix of $N_s(\mathcal{T})$ and $C \cdot X \geq 0$ are the linear constraints. Also in this setting we can consider a basis for the solution space, referred to as the *constrained invariant basis* $\mathcal{B}_C(N_s(\mathcal{T}))$, so that any solution of (4) will be a linear combination of elements in $\mathcal{B}_C(N_s(\mathcal{T}))$.

Continuous Petri net models for the trophic network $\mathcal{T}$ satisfying the constraints C are defined exactly as in the previous subsection. In both cases, the underlying Petri net is $N_s(\mathcal{T})$.

The *uniform constrained continuous Petri net model* $N_c(\mathcal{T}, C)$ is defined by associating each transition t with a constant rate:

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

In this way, each transition in each constrained invariant I_i in $\mathcal{B}_C(N_s(\mathcal{T}))$ can be performed once in one time unit.

Alternatively, we can consider the *minimal constrained Petri net model* $N_c^m(\mathcal{T}, C)$, which associates with each transition a constant rate corresponding to minimising $\Sigma_{i=1}^m x_i$ in the system (4). This ensures that all the flows in the system are active, they satisfy the constraints, and the system as a whole satisfies a maximal parsimony assumption.

4.4.2. Applying the constrained modelling idea to the case study

When applied to our case study, the constrained approach produces a linear system of equalities and inequalities, where the inequalities express the literature knowledge summarised in Table 2. In this case, the constrained invariant basis contains 993 elements. We construct the uniform constrained model and the minimal constrained model, both endowed with constant rates automatically satisfying the given ecological constraints.

Despite the fact that they incorporate some additional knowledge on the system, the constrained continuous models are still unsatisfactory as they provide a static view of the trophic network. In fact, the use of constant transition rates does not allow for a sensible dynamic simulation and analysis of the system. Moreover, in all the continuous models proposed so far, the amounts of biomass of the compartments in the steady state do not play any role and our rates represent just relations between flows. In the next section we address these issues and illustrate how to extend the models and overcome these limitations.

5. A continuous PN model with mass-dependent rates

In this section we do one step forward, showing how to obtain a more realistic dynamic model, when estimations of the amount of biomass in the compartments at steady state are available. What we derive now are continuous Petri net models with mass-dependent rates associated to transitions, that can be used to perform dynamic simulation and what-if analyses.

The first step for building a dynamic model consists in choosing a suitable kinetic law for modelling prey-predator flows as well as respiration and defecation flows. In analogy with Lotka-Volterra models [24, 39], a prey-predator flow should depend on the biomass of both the prey and the predator, while the respiration or defecation flow of a given compartment should depend only on the biomass of the compartment itself.

In chemistry, the law of *mass action* defines the rate of a chemical reaction as proportional to the product of the masses of reactants. Analogously, the law of mass action can be used to define the process rate, prey-predator, respiration or defecation, as proportional to the biomasses of the interacting compartments. Hence we choose the mass action law to associate the following rate expression to a prey-predator flow

$$rate_1 = k_1 \cdot M_{prey} \cdot M_{predator} \tag{5}$$

while for a respiration or defecation flow of a compartment C the rate expression is the following

$$rate_2 = k_2 \cdot M_C \tag{6}$$

where M_{prey}, $M_{predator}$ and M_C are the amounts of biomass associated to compartments, and k_1 and k_2 are suitable constants. This makes the system sensitive to any variation of the biomass or of the constants.

Then we proceed as follows in order to determine the constants k_1 and k_2 in the mass-dependent flow rate expressions. We take a continuous model of the trophic network produced by a construction proposed in Section 4.4. In such a model, a rate value is associated to each transition t at steady state.

Instead of considering this rate as a constant, i.e., state-independent, as we did before, we now assume that it is regulated by the mass action law, namely it is defined by (5) or (6) depending on the kind of flow it represents. In this way we can infer the constants k_1 and k_2 by exploiting the knowledge of the biomasses of the involved compartments (M_{prey}, $M_{predator}$ or M_C).

5.1. Application to the case study

In this section we apply the method described above to the *minimal constrained continuous model*, as proposed in Section 4.4.2, which seems to be the most realistic one. We associate the law of mass action to the rates of internal transitions. Concerning the boundary flows, the model is simplified by assuming a constant flow of the detritus both incoming and outgoing from the lagoon and a constant harvesting of clams. To be more specific, *input_DET*, *DET_export* and *TAP_harvesting*, have the same constant rates as in the original minimal constrained continuous model. These boundary flows will be then perturbed in the analysis.

In order to validate the dynamic representation of the system, we set up some test cases, corresponding to realistic hypotheses based on the available scientific knowledge on the Venice lagoon. The test cases consist in varying some relevant flows selected from those described in [7, 5].

The first flow we consider is the harvesting of the clam *R. philippinarum* (TAP), an important economic activity in the territory of the Venice lagoon. Its sustainable management is needed in order to limit the environmental impacts generated by this type of fishing on other traditional fishing practices, on bottom habitat conservation (for example on areas vegetated with submerged rooted plants), and on lagoon morphological structures (shallow water areas, intertidal flats). Therefore, testing the possibility to simulate changes of the flow *TAP_harvesting* is important from a management point of view. Changes of plus/minus 30% in the values of *TAP_harvesting* (flow number 15) were considered.

A second interesting flow is concerned with the organic matter (DET) that represents a relevant source of food for clams (TAP). DET is generated by the food web itself (from mortality and faeces), but it can also be imported from the surrounding areas of the lagoon (flow *input_DET*). In the real system this import depends on several environmental factors like current regime, sediment resuspension due to winds and/or boats traffic and algae growth. The possibility of simulating changes of the flow *input_DET* is important in order to understand the degree of dependence of clam production (TAP) in a given area on the larger lagoon environment. Changes of plus/minus 30% in the values of *input_DET* (flow number 11) were considered.

According to the processes described above, four dynamic simulations were generated:

- **Test case 1**: $TAP\_harvesting = TAP\_harvesting\_(staticmodel) * (1 + 0.3)$
- **Test case 2**: $TAP\_harvesting = TAP\_harvesting\_(staticmodel) * (1 - 0.3)$
- **Test case 3**: $input\_DET = input\_DET\_(staticmodel) * (1 + 0.3)$
- **Test case 4**: $input\_DET = input\_DET\_(staticmodel) * (1 - 0.3)$

We discuss now the results of these tests. Please note that the time unit is not defined in the system. Hence in the following discussion we can only focus on the dynamic behaviour of the system (the way compartments evolve and interact), but no comments can be given about the absolute timing of the observed processes.

- **Test case 1**: Figure 3 shows the system behaviour on the short-term (upper picture) and long-term period (lower picture). Due to the increase of the $TAP\_harvesting$ flow, the biomass of TAP decreases very rapidly until it reaches 0 (disappearance of the compartment). The disappearance of TAP favours MEZ (feeding on the same sources) that shows an increasing trend. BPL and MIZ also increase, being the feeding pressure from TAP decreased and eventually cancelled. It is interesting to note that on the long run, the system shows an oscillatory dynamics, characterised by the predator-prey relationships between MEZ and MIZ−BPL−PHP. In this test case, the system demonstrates its ability to reproduce a realistic scenario: under unsustainable fishing pressure clams disappear and a dramatic change in the ecosystem structure occurs, leading on the long-term to a new, different, dynamic equilibrium.

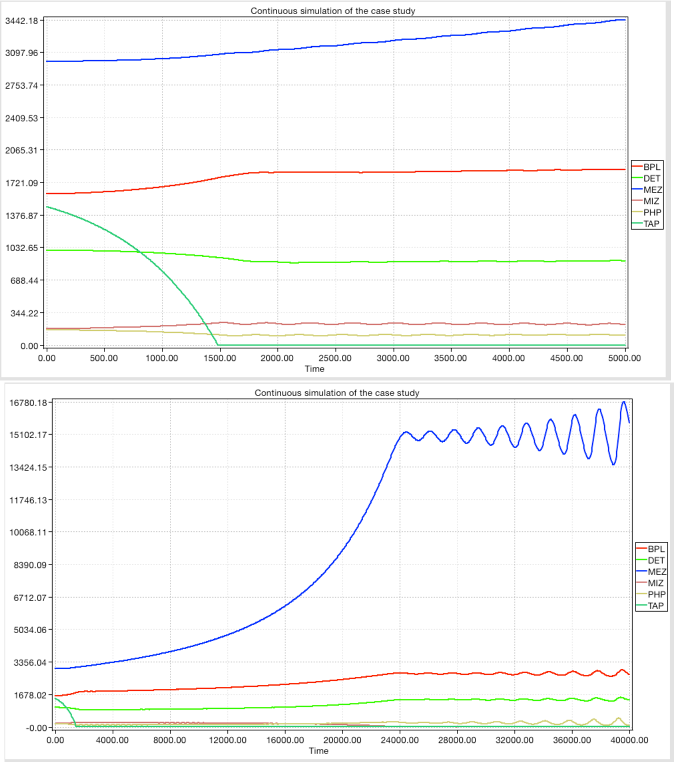


Figure 3. Test case 1: short-term run (upper picture) and long-term run (lower picture)

- **Test case 2**: The results for this test case are shown in Figure 4 for both the short-term and the long-term period. Notice that, due to the decrease of $TAP\_harvesting$, the biomass of TAP increases rapidly. As a consequence, MEZ is outcompeted and its biomass sharply decreases. The increase of TAP determines an increased feeding pressure on BPL and a consequent decline of its biomass. On the long run (Figure 4, lower picture), the system shows an oscillatory dynamics, different from the one before, characterised in this case by the predator-prey relationships between TAP and its sources of food PHP and DET. Also in this test case, the system demonstrates its ability to reproduce a realistic scenario: fishing pressure acts as an important control factor for TAP biomass and for the equilibrium of the ecosystem. When changing the fishing pressure, dramatic changes in the ecosystems occur. Sensitivity of the food web model to the values of this flow is notably very high.

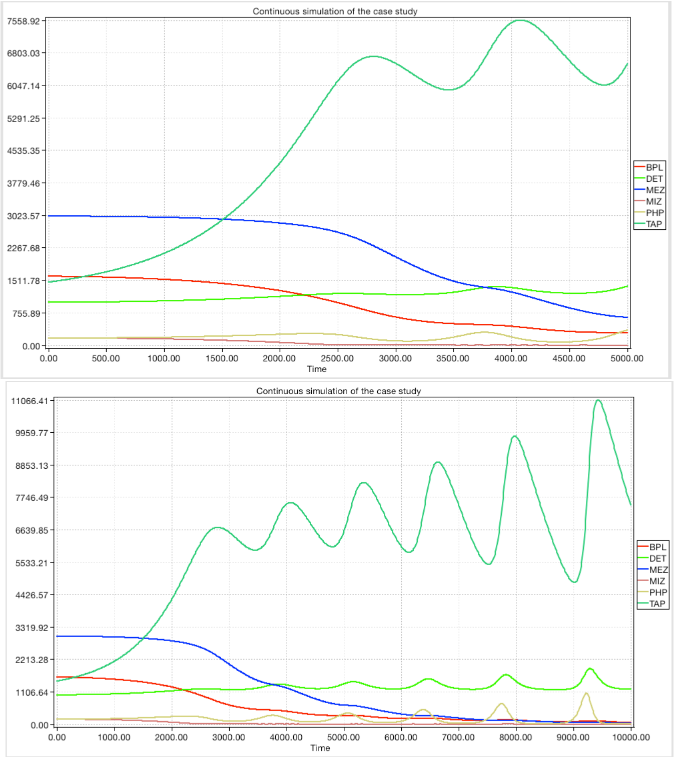


Figure 4. Test case 2: short-term run (upper picture) and long-term run (lower picture)

- **Test case 3**: As can be noticed in the upper picture shown in Figure 5, the increased input of DET determines some increase of DET biomass in the system, but most of the additional input is utilised by TAP which exhibits a rapid increase. Consequently - and similarly to the Test case 2 results - MEZ is outcompeted and BPL is overexploited by TAP. As it can be noted from the long-term results (Figure 5, lower picture) the system shows again an oscillatory dynamics, very similar to the Test case 2 results, characterised again by the predator-prey relationships between TAP and its source of food PHP and DET. Also external food sources like $input\_DET$ can act as important control factors for TAP biomass and for the equilibrium of the ecosystem. Their changes can induce dramatic changes in the ecosystems. Sensitivity of the food web model to the values of this flow is also very high.

- **Test case 4**: The reduced input of DET to the system determines, as shown in the upper picture of Figure 6, a sharp decrease of TAP and ultimately the disappearance of this compartment. The other compartments look quite constant in value on the short-term, with some tendencies in growth for BPL and MIZ. Long-term results (Figure 6, lower picture) point out again an oscillatory dynamics, similar to the Test case 1 results, characterised by the predator-prey relationships between MEZ and its source of food BPL$-$DET$-$PHP. Given the overall lower amount of biomass available for

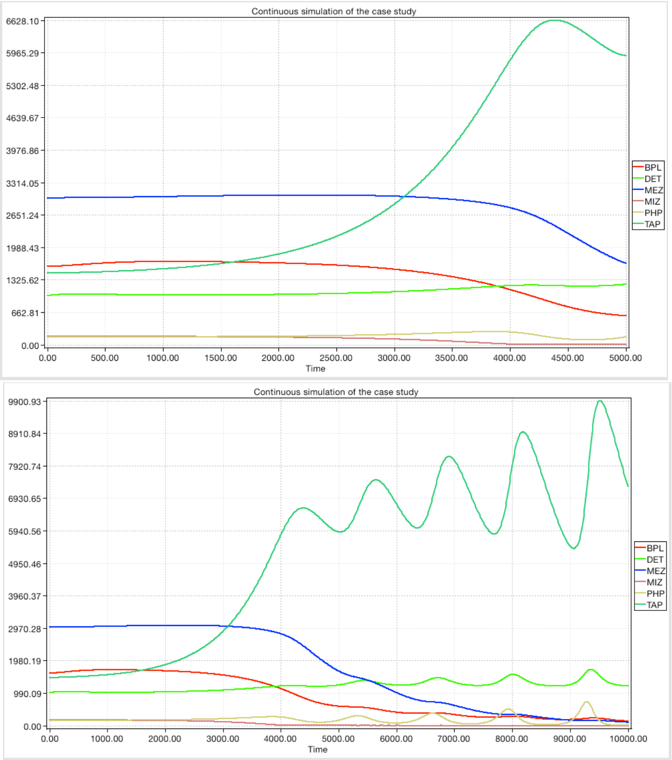


Figure 5. Test case 3: short-term run (upper picture) and long-term run (lower picture)

the system, oscillations look smaller in value than in Test case 1. $Input\_DET$ is confirmed to be an important control factor for TAP biomass, and the sensitivity of the food web model on its values is confirmed to be very high.

From these test cases we can conclude that the dynamic behaviour of the modelled system appropriately responds to changes of the external conditions. Simulation results are reasonable from a general ecologic point of view and in agreement with expectations based on the knowledge available for real ecosystems similar to the Venice lagoon.

6. Conclusions

In this paper we explored the use of Petri nets for representing and analysing trophic networks. Ecologists usually represent trophic networks as networks of flows of energy or biomass between species or compartments. By averaging over a reasonable period of time, the ecosystem is represented as a steady state snapshot where the input and output flows in each species/compartment are balanced. Quantitative information on such networks is generally difficult to estimate, and they are partially computed by some inference technique. In order to represent and analyse a trophic network, we proposed several techniques for building Petri net models based on the available data. In order to evaluate our proposal, we applied such models to a case study, a simplified view of the ecosystem of the Venice lagoon.

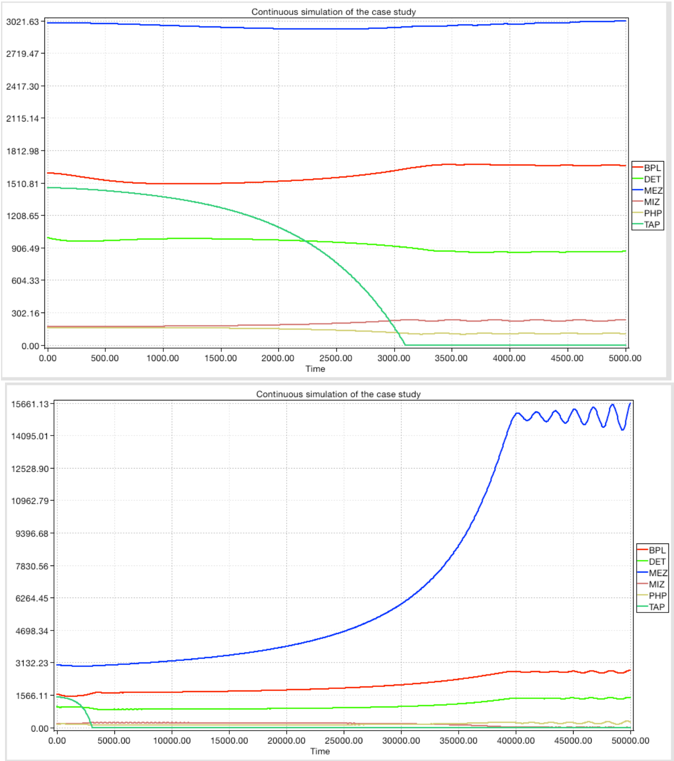


Figure 6. Test case 4: short-term run (upper picture) and long-term run (lower picture)

We showed how the structural information on a trophic network naturally translates into a structural Petri net model which allows for recovering classical trophic networks concepts and structural analyses.

By exploiting the set of minimal T-invariants, we refined the structural Petri net model into continuous Petri net models that closely resembles the representation of the trophic network usually adopted by ecologists, where the system is at a steady state and the input and output flows are balanced in all the compartments. We defined several continuous models based on different assumptions: either by assuming a uniform execution of all the minimal subsystems (the minimal T-invariants), or by assuming a global minimisation of the flows in the system, which are however all active.

Despite the fact that such continuous Petri net models are rather simplistic (in particular, they have constant rates, independent of the masses), the analyses of such models applied to the case study of the Venice lagoon showed that they realistically reproduce the main ecological processes. Furthermore, they showed that the continuous Petri net models can be fruitfully used for an early stage validation of the trophic network under study.

Next, we outlined a technique for refining the continuous Petri net models by “embedding” some possibly available ecological knowledge on the metabolism of the species and on their diet composition. This knowledge, typically expressed as linear inequalities, intervenes the computation of T-invariants that in turn influences the transition rates.

We further proposed a refinement of the constrained continuous Petri net models for deriving more realistic models capable of representing the dynamic behaviour of the systems. The refinement relies on the availability of biomass estimates for all compartments at a steady state, that is used to derive dynamic rates for flows governed by the mass action law. Introducing flow rates dependent on biomasses in the continuous Petri net model allows for dynamic simulations and what-if analyses.

We defined such a dynamic model for the case study of the Venice lagoon and analysed the evolution of the system behaviour by applying perturbations to flows relevant for the ecosystem, like harvesting of clams and incoming detritus. Although the time scale cannot be easily fixed and thus the temporal system evolution cannot be properly validated, the results of the simulations are encouraging since the modelled behaviour is reasonable from an ecological point of view and in agreement with expectations based on the available knowledge.

We plan to perform further experiments by modelling different and possibly larger trophic networks. This could help us for better validating our approach as well as indicating further extensions.

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