Diagnosis of planktonic trophic network dynamics with sharp qualitative changes

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ABSTRACT

Trophic interaction networks are notoriously difficult to understand and to diagnose. Such ecological networks welcome numerous feedbacks between species and populations and are not frozen at all, as soon as we observe them over a long enough term. These topological changes may be triggered by natural forcings (e.g. seasons) and/or by human influences (e.g. nutrient or pollution inputs). Aquatic trophic networks are especially dynamics and versatile, thus supporting new approaches for diagnosing network dynamics in a comprehensive way.

In this study, we build a possibilistic model for this purpose. Borrowing discrete event models to theoretical computer sciences, we developed a mechanistic and qualitative model allowing computing exhaustive dynamics of a given trophic network. Once the model definition assumed, it provides all possible pathways of the trophic network from a chosen initial state. In a rigorous and analytical approach, we validated the model on one theoretical and two observed trajectories recorded at freshwater stations in La Rochelle region (Western France). The model appears easy to build and intuitive, and it provided other relevant pathways to the expert community. We hope such mathematical approach to open a new avenue in diagnosing and predicting trophic (and non-trophic) ecological networks.

Keywords: Interaction network; Freshwater ecosystem; Qualitative model; Discrete event model, Plankton

Introduction

Trophic networks (TNs) form the backbone of ecosystem functioning, as they simultaneously condition food acquisition, prey and predator demography, individual and population behaviours, and phenotype selection, among other consequences (Lindeman 1942, Johnson 2000, Majdi et al. 2018). Trophic processes are responsible for most matter and energy fluxes within ecosystems, but the fates and properties of ecosystems are hardly predictable mainly due to the lack of knowledges (Mouquet et al. 2015). Trophic processes have been well studied in ecology, although mainly considered as frozen in time, i.e. with a fixed topology and fixed signed relationships. This simplification may be due to lacking data over the long term and to equation-based models dedicated to flux and abundance variations on a frozen network (e.g. Thébault and Fontaine 2010, Kéfi et al. 2015). In this study, we provided an original framework to handle trophic networks with sharply changing structures.

So far, trophic networks are difficult to understand and to handle. First of all, they usually gather a large number of populations or species in an even larger number of trophic interactions. Hence, to understand trophic dynamics would require not only to model a large and realistic number of components, but also to be able to calibrate the weights (coefficients) of each component and each interaction involved (Ings et al. 2009, Wallach et al. 2017, Majdi et al. 2018). For this reason, most trophic models focus on wide categories of populations, with a functional approach, such as carnivores, herbivores and/or detritivores (e.g. Thébault and Fontaine 2010), and approximate their trophic parameters. Even powerful models intending to bypass such limitations, such as qualitative models based on differential equation systems are limited in size (May 1973, Dambacher et al. 2003).

There is a stronger limitation of trophic studies in ecology: they mostly assume a frozen network of interaction (Thébault and Fontaine 2010, Kéfi et al. 2016). Not only is it harder to handle a changing network, but we have no idea on how such a network may change (typologically) in time, and how to model it. Indeed, as soon as the study covers several generations of some of the species involved in the network, some other species may invade and/or go extinct (Mooney and Hobbs 2001, Warren et al. 2005). Hence, these events strongly modify the network structure and, in turn, the system dynamics. Equation-based models are not well adapted to handle dynamical systems on dynamical structures (sometimes called DS^2, Giavitto and Michel 2003), whereas some tools developed in theoretical computer sciences are perfectly adapted to this task. In particular, discrete-event systems such as graph transformations or Petri nets are able to handle sharply changing networks (König et al. 2018, Gaucherel and Pommereau 2019). In this study, we will provide a Petri net to model any trophic network change, and will illustrate it on a realistic planktonic trophic network.

Planktonic trophic network models are usually composed of fixed number of functional nodes that gather groups of individuals sharing the same ecological function. Mass fluxes (usually in carbon or nitrogen) between nodes are predefined according to trophic links. In a context of an emerging biological oceanography discipline and regarding the limited computing resources, first planktonic food-web models simply consisted in mass fluxes between nutrients, phytoplankton and zooplankton nodes (Steele 1958, 1974). These so-called NPZ models (NPZD, NPZDB or even NPZF when detritus, bacteria or fishes are comprised, respectively) coupled to observed or simulated physical conditions demonstrate their predictive ability to capture bulk system properties (biomass and primary production) at both regional and global scale (Mitra et al. 2007, Kriest et al. 2010, Oke et al. 2013, Hernández-Carrasco et al. 2014, Turner et al. 2014, Kumar and Kumari 2015).

However, in order to better understand biogeochemical cycling (e.g. export fluxes, carbon sequestration, organic matter recycling, microbial loop), planktonic food-web should be delineated and planktonic compartments in models could thus be refined into Planktonic Functional Types (PFTs). Plankton groups are thus defined according to common ecological functions (e.g. nitrogen fixers, calcifiers and silicifiers), sizes (e.g. picophytoplankton, nanophytoplankton, microphytoplankton) and/or key taxonomic groups (e.g. diatoms, flagellates) (Le Fouest et al. 2013, Villaescusa et al. 2016, Kerimoglu et al. 2017, Petersen et al. 2017, Maar et al. 2018, Meddeb et al. 2019). However, refinement of planktonic food-web models meets with model formulations, parametrization and lack of data, which increases uncertainties with model outcomes and fluxes between defined groups (Anderson 2005).

Facing gaps in ecological knowledge and lack of data, inverse modelling derives flows of energy within trophic networks from simple biomass estimates and rates measurements. Vézina and Platt (1988) were the

first to use it for inferring mass fluxes through a planktonic trophic network in the English Channel. Inverse modelling is therefore advantageous when dealing with underdetermined systems and results into a space of possible solutions that fulfil a set of linear equalities and inequalities. A unique solution is then selected from optimization or statistical methods. While vital rates and biomass can be easily measured for high trophic levels (e.g. fishes), their quantification for low trophic levels (e.g. bacteria, autotroph plankton) remains uncertain and questions the robustness of inverse modelling for planktonic compartments study (Vernet et al. 2017, Saint-Béat et al. 2018). Overall, biological constants (production, consumption, assimilation), biomass and ecological interactions are therefore not easy to measure in planktonic food-webs, resulting into an over-simplification of planktonic food-web models (Anderson 2005, Flynn 2006).

To address these issues, we propose here to develop a qualitative and discrete model providing all possible trajectories (or pathways) of the trophic network under study, in order to keep a rigorous (mathematical) control on the model. This assumption allows the system to become finite and to exhibit a finite number of states, automatically computed into a so-called state space (Pommereau 2010, Reisig 2013). Then, a detailed and automatic analysis of this state space exhaustively provides the possible fates (e.g. trajectories, stabilities, collapses, if any) of the studied system. We chose to illustrate this original method on a well-studied plankton trophic network in wetlands, freshwater marshes of Charente Maritime region (Western France, Tortajada et al. 2011). Such a system is well instrumented and will provide an expected theoretical trajectory of changing trophic network, as well as two observed trajectories at different stations (Masclaux et al. 2014). The succession of planktonic trophic network and the different regimes of the planktonic trophic network are well known according to the season (Masclaux et al. 2014). We will develop the corresponding Petri net of this system and then validate it on theoretical and observed trajectories. We will finally discuss the power and drawbacks of such discrete and qualitative models for trophic ecology.

Methods

Aquatic trophic networks

The Charente-Maritime marshes of the French Atlantic coast (Fig. 1) are the second largest French wetland zone (over 100,000 hectares). The type of freshwater marshes is the unreplenished drained marshes which constitute a significant artificial hydrographic network of channels and ditches. To mitigate and prevent drying of marshes, locks control the channels and ditches (for more details, see Masclaux et al. 2014). The observed trajectories of the system were made with data recorded at two stations (stations A and B). The planktonic trophic network regime changed during the transition from winter to spring from biological winters, after that herbivorous trophic network to finally trophic networks qualified as multivorous distinguish three levels of multivory (weak multivorous, multivorous and strong multivorous) (for more details, see Masclaux et al. 2014).

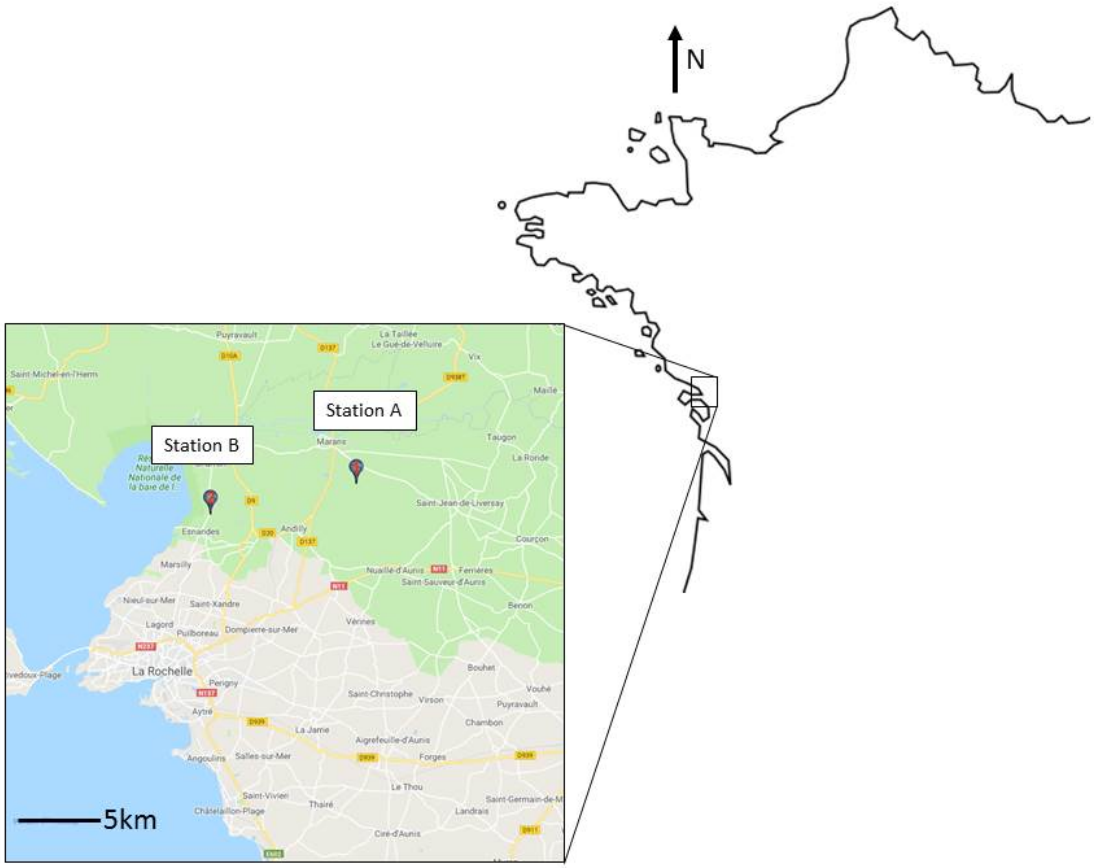

Figure 1

Figure 1 - Location of the study site and of the two sampled stations (A and B, inset) along the Atlantic coast of France.

In the model, the environmental conditions were summarized by a component envir, which corresponds to the conditions of temperature and light, a component nit corresponding to the presence or absence of nitrates, and renew corresponding to the possible renewal of water (i.e. flush) in the marshes depending on the rainfall and water usages (agriculture, breeding…). The main functional groups of plankton were: 1) phytoplankton by size class (microphytoplankton for > 20 µm: MicroP; nanophytoplankton for 3-20 µm: NanoP and picophytoplankton for < 3µm: PicoP), 2) different grazers as protozoa (Proto), metazoan microzooplankton (MicroZ) and mesozooplankton (MesoZ), and 3) bacteria, which uses dissolved organic matter (DOC) (Fig. 2). In more details, the planktonic trophic network and all the possible flux between components concerns grazing flux with some preferential predation, and potential competitions between organisms (Fig. 2). Protozoa graze on bacteria, PicoP and NanoP and are grazed by MicroZ and MesoZ. MicroZ graze on bacteria, PicoP, NanoP and Proto. MicroP is grazed principally by MesoZ, which used MicroZ, NanoP and Proto as preys. Three preferential fluxes are forcing the model: competition between bacteria and PicoP suggesting that each may survive and be detrimental for the second one, preferential grazing of MicroP by MesoZ and preferential grazing of NanoP by MicroZ. The ascendant arrows correspond to relation prey-predator, the descendant arrows are the matter in form of detritus (DOC compartment).

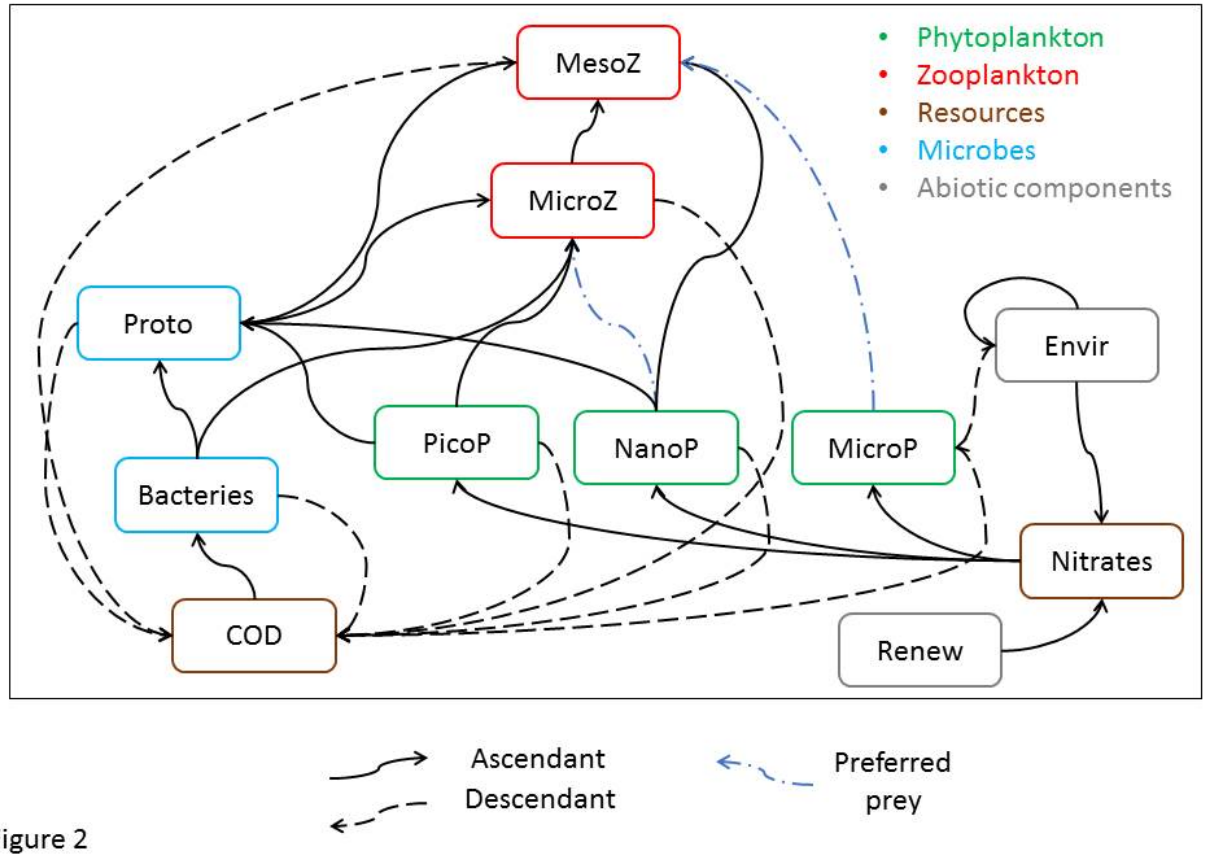

Figure 2

Figure 2 - The detailed interaction network used in this study. The trophic network components are displayed as nodes of various colors (red: zooplankton, green: phytoplankton, brown: resources, blue: microbes and grey: abiotic components). Predation interactions are displayed as plain (upward) and dashed (downward) edges, with preferred prey populations highlighted with doted-dashed blue edges.

Petri Nets and a simplistic Prey-Predator model

Any ecosystem Petri net is developed in three successive steps: i) an intuitive graph (i.e. a set of components and their related processes) is built to represent the studied ecosystem based on the leading question; ii) we transform this ecosystemic graph into a formal model based on a discrete-event Petri net and its associated rules; iii) each rule is finally normalized to make it simpler and unambiguous for allowing a rigorous handling of the network changes. Then, the Petri net is run (computed) to determine the whole range of ecosystem dynamics. However, the Petri net (steps i and ii) is hidden to the (ecologist) user and is automatically built (in Python language) once the ecosystem graph has been defined by ecologists. We first illustrate here the functioning of the model using a simplistic prey-predator system (Fig. 3a). Additional details on the principle and uses of Petri nets can be found in literature (Pommereau 2010, Reisig 2013, Gaucherel and Pommereau 2019).

Any ecosystem can be represented as a multi-digraph (i.e. a directed graph with parallel edges). In this graph, every material component of the ecosystem (e.g. abiotic: temperature; biotic: a population; anthropogenic: nitrate inputs) is represented by a node, with two Boolean states: “present” (the component is functionally present in the system, also denoted “+”) and “absent” (functionally absent of the system or “-”). In the prey-predator example, only two nodes are defined: the prey and the predator populations. Any state of the ecosystem is defined by the set of “+” and “-” nodes (Fig. 3b), and “±” in tables when they oscillate between successive states. The maximal number of possible system states is 2#nodes and grows exponentially with the node number. The state of a node depends on the nodes to which it is connected, while a connection between nodes is assumed as soon as one process explicitly connects the different components (Fig. 3b). The rules correspond to any physicochemical, bio-ecological and/or possibly socio-

economic processes (e.g. if the prey population is neglectable (-), the predator population becomes neglectable too), and thus represent all possible interactions between nodes composing the ecosystem studied. In the prey-predator system, two rules only are defined: R1, the predation itself: the predator eats the prey, and R2, the mortality: without prey, the predator dies (Fig. 3a and 3c). In the Petri net language, nodes are called places and rules are called transitions, both being connected through (oriented) arcs (Fig. 3b).

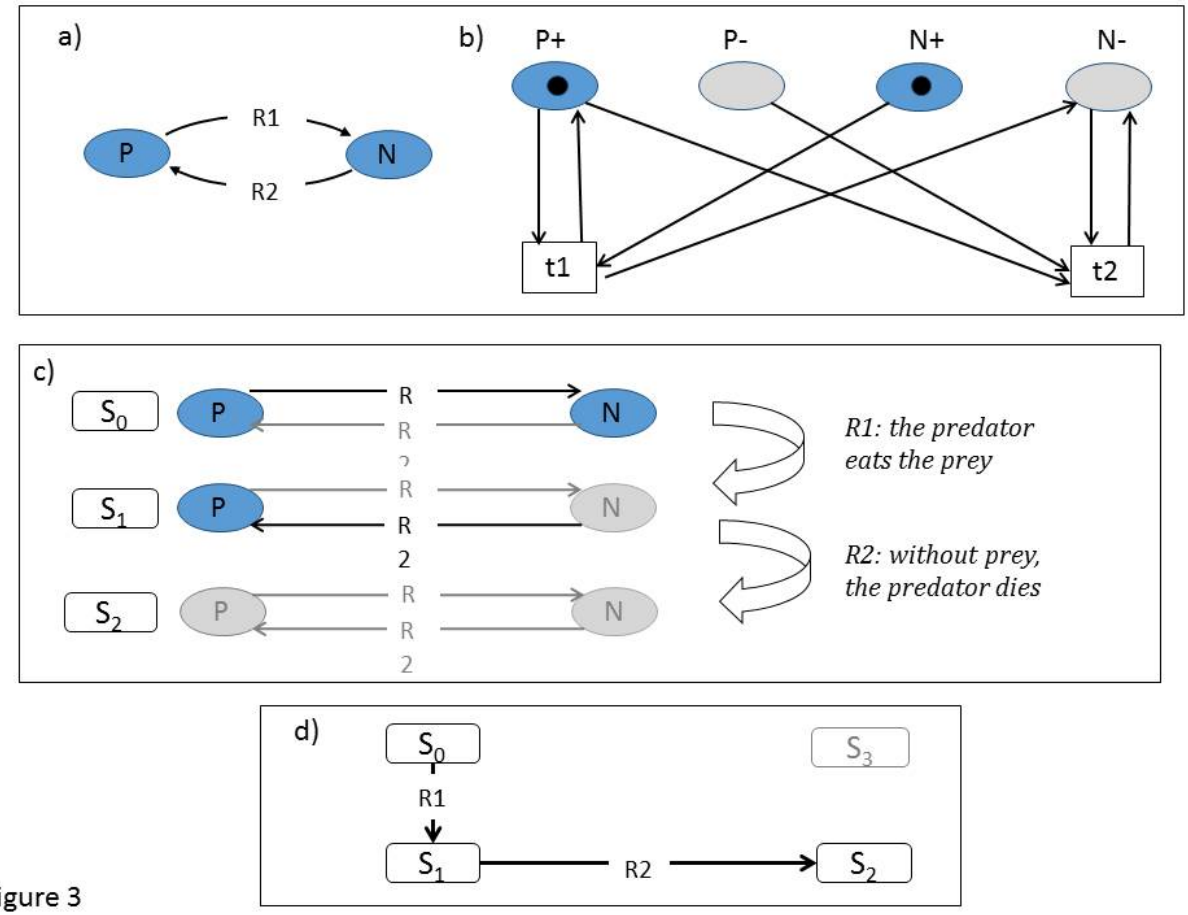

Figure 3

Figure 3 - Illustration of a simplistic prey-predator system (a), with its associated Petri net (b), its qualitative dynamics (c), and the marking graph also called state space (d). The system is made up of two components, the prey (N) and predator (P) populations, and two interactions connecting them (rules R1 and R2), as seen on the automaton (a). The corresponding Petri net is made up of four places (P+, P-, N+, N-) and two transitions R1 and R2, where unlabeled and unweighted arcs (b). Starting with the presence of both populations, it is possible to list all system states encountered (c), and to connect them with the rules (absent nodes and inactivated rules are displayed in grey). The net is depicted in the initial state (c), and the successive states may be deduced from the token circulation seen in the dynamics (b). The marking graph of the Petri net (d) is depicted with each state number (S0, S1, S2) referring to the dynamics described above (b). Notice that a specific state of the system (S3) may not be reached from this initial condition and with these rules (d).

A separate rule describes the condition and a realization parts as: “transition’s name: condition >> realization”. For a rule to be applied, the state of the node must satisfy its application condition; the rule is then said “enabled”. If so, the application of the rule modifies the state of the nodes as stipulated in its realization part; the rule is fired. In the prey-predator system, the rules are written as R1: P+, N+ >> N- and R2: N-, P+ >> P-. Since the rules modify node states, they change the overall system state (i.e. the state of the system aggregate all node states). Therefore, the entire system shifts from one state to another one through the successive application of rules (Fig. 3c). The computation of the defined Petri net produces the state space, which provides the set of all system states reachable by the rules defined (Fig. 3d). As a corollary, the

system states are connected to each other by some of these rules in the state space too. The size of this state space is usually much smaller than the number of possible system states, because the computation starts from a specific initial condition and because rules have specific application conditions. We develop some tools to automatically divide large state spaces into merged (simplified) state spaces.

Firing a rule independently to some others often leads to unrealistic trajectories (e.g. removing water without removing fishes in it). Therefore, we defined new objects called constraints, preventing the model from simulating such unrealistic (socio-ecological) trajectories. Constraints have a condition and a realisation part, just as rules stricto sensu do, and model inevitable (mandatory) events given the system state. The sole difference between rules and constraints is that constraints have priority on rules stricto sensu. In the prey-predator system, the system state S1 = (N-, P+) is unrealistic; so, the rule R2 has to be transformed into a constraint (C1: N-, P+ >> P-). From a given state, the model first simulates all trajectories opened up by the defined constraints and then only, when all the system states obtained are realistic (i.e. there is no longer any enabled constraint), the enabled rules are fired (Fig. 3d). In brief, the discrete model proposed here is qualitative, mechanistic (processes are explicit), non-deterministic (no stochasticity yet several possible outcomes from each state) and asynchronous (all rules are applied as soon as possible, no rule conflict) (Reisig 2013, Gaucherel and Pommereau 2019).

Methodology and trajectories

The theoretical plankton trophic network modeled here combines nine different nodes, associated to the dominant functional groups possibly present in the channel freshwater marshes, and two additional nodes featuring environmental conditions (Table 1, Fig. 2). To link them, we defined 34 processes and seven constraints encompassing at least four trophic levels (Table 2, Fig. 2). A theoretical trajectory (T1) has been defined and two observed trajectories (T2-3) recorded the studied system at two distant stations (Table 3). As a validation stage, we intend not only to detect these successive states in the modeled state space, but also to detect them in the correct succession orders. The model always starts in winter conditions or with a flush in summer conditions, with the node Renew present only, which brings back some source of inorganic nitrogen in the system (Table 1). We tested two variants of the model: i) the full model and, ii) the same model yet without return in winter conditions (R3, called the “seasonal model”), thus getting the model stuck in summer conditions. For each model, we will compute the state space and the merged state space, and check whether trajectories T1 to T3 are correctly recovered.

Table 1 - The model components and their associated nodes in the TN interaction network, with their abbreviations, and descriptions. Whether these ecological components are present (+) or absent (-) in the initial state is also displayed.

Acronym	In initial state	Description
Bact	-	Bacteria
PicoP	-	Picophytoplankton
NanoP	-	Nanophytoplankton
MicrP	-	Microphytoplankton
Proto	-	Protozoa
MicrZ	-	Microzooplankton (metazoa)
MesoZ	-	Mesozooplankton
DOC	-	Dissolved organic matter
Nit	-	Nitrates, linked to seasons or flush
Envir	-	Environmental and climate conditions
Renew	+	Water and Nitrate inputs (rain or humans)

Table 2 - Trajectories of the theoretical expert elicitation and observed at stations A and B. For each trajectory, theoretical and observed regimes are listed in columns and present (+)/absent (-) components of the trophic network are listed in lines. The corresponding regimes displayed in Fig. 5a-c are listed in the last line of each trajectory, with a single index A1 to A3 and B1 to B4 for successive regimes.

THEORY	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6
Bact	-	-	-	+	+	+
PicoP	-	-	-	+	+	+
NanoP	-	+	+	+	-	-
MicrP	-	+	+	-	-	-
Proto	-	-	-	+	+	-
MicrZ	-	-	+	+	+	-
MesoZ	-	-	+	+	-	-
Nit	+	+	+	-	-	-
DOC	-	-	+	+	+	+
Envir	-	+	+	+	+	+
Renew	+	+	-	-	-	-
Regimes (Fig. 5)	Biological winter	Low herbivorous TN	Herbivorous TN	Multivorous / Strong multivorous TN	Microbial TN	Microbial loop

Results

State spaces

The full model provides a state space made up of 765 states gathered into a unique dynamical structure (a so-called structural stability, Fig. 1a Suppl.). This structure was interpreted as a stable and highly resilient dynamics as, by definition, any state in this stability may be reach by any other state belonging to it. Yet, when rule zero (R0, seasonal oscillation) is deactivated, the model gets stuck into a high number (12, plus two basins) of successive structural stabilities of various sizes (Fig. 1b Suppl.). When oriented downward in time (following causality), the whole system inexorably converges toward a small terminal stability (four states) in which the system appears in a biological winter (i.e. few living species, in green, Fig. 1b Suppl.). Some of the reached stabilities exhibit a large number of states and may keep the system into such specific stabilities during indefinite time (Fig. 1b Suppl.). We call such structural stabilities TN "regimes", i.e. a set of interconnected states displaying a coherent TN behaviour.

Table 3 - Rules and constraints used in both full and seasonal models, with their formal expression (first column) and descriptions (second column). Only the rule N°0 (in italic) is discarded in the seasonal version of the model.

CONSTRAINTS	Descriptions
DOC- >> Bact-	C1 Without organic matter (DOC), Bacteria disappear
Nit- >> NanoP-, MicrP-, DOC+	C2 Without Nitrates, all kinds of phytoplankton except Pico disappear (and produce organic matter)
Bact+, PicoP-, NanoP- >> Proto-, DOC+	C3 Without all its preys (but Bacteria), Protozoa disappear (and produce organic matter)
Bact-, Proto-, PicoP-, NanoP- >> MicrZ-, DOC+	C4 Without all its preys (but Bacteria), Microzooplankton disappear (and produces organic matter)
Proto-, MicrZ-, NanoP-, MicrP- >> MesoZ-, DOC+	C5 Without all its preys, Mesozooplankton disappear (and produces organic matter)
Envir- >> PicoP-, NanoP-, MicrP-	C6 In winter, all Phytoplankton disappear (and do not produce organic matter)
PicoP+, NanoP+, MicrP+ >> Nit-	C7 With all Phytoplankton (present), Nitrates disappear

RULES

Envir+ >> Envir-, Renew+	*R0 After summer (and spring) comes winter*
Envir- >> Envir+	R1 After winter comes summer (and spring), with a bloom
Envir+, Renew+ >> Nit+, Renew-	R2 Nitrate input is due to water flush from human management or rainfall
Envir-, Renew+ >> Nit+, DOC-, Bact-, Proto-, PicoP-, NanoP-, MicrP-, MicrZ-, MesoZ-	R3 In winter, the Reset of the system is due to water flush from rainfall (but there is a Nitrate inputs)
Envir-, Renew+ >> Renew-	R4 In winter, we stop the flush after its action (reset)
DOC+ >> Bact+	R5 Bacteria use organic matter, without removing it
Bact+, DOC+ >> DOC-	R6 Bacteria use organic matter and remove it
Envir+, Nit+ >> MicrP+, NanoP+	R7 Microphytoplankton and Nanophytoplankton use Nitrates in summer, without removing them
Envir+, Nit+ >> PicoP+	R8 Picophytoplankton use Nitrates, without removing them
Bact+ >> Proto+	R9 Protozoa graze on Bacteria, without removing them
Bact+, Proto+ >> Bact-, DOC+	R10 Protozoa graze on Bacteria, which disappear and produce organic matter
PicoP+ >> Proto+	R11 Protozoa graze on Picophytoplankton, without removing it
PicoP+, Proto+ >> PicoP-, DOC+	R12 Protozoa graze on Picophytoplankton, which disappears and produce organic matter
NanoP+ >> Proto+	R13 Protozoa graze on Nanophytoplankton, without removing it
NanoP+, Proto+ >> NanoP-, DOC+	R14 Protozoa graze on Nanophytoplankton, which disappears and produce organic matter
MicrP+ >> MesoZ+	R15 Mesozooplankton graze on Microphytoplankton (its PREFERED prey), without removing it
MicrP+, MesoZ+ >> MicrP-, DOC+	R16 Mesozooplankton graze on Microphytoplankton, which disappears and produces organic matter
MicrP-, NanoP+ >> MesoZ+	R17 Mesozooplankton graze on Nanophytoplankton, without removing it
MicrP-, NanoP+, MesoZ+ >> NanoP-, DOC+	R18 Mesozooplankton graze on Nanophytoplankton (secondary preferential prey), which disappears and produces organic matter
MicrP-, Proto+ >> MesoZ+	R19 Mesozooplankton graze on Protozoa, without removing them
MicrP-, Proto+, MesoZ+ >> Proto-, DOC+	R20 Mesozooplankton graze on Protozoa, which disappears and produces organic matter
NanoP+ >> MicrZ+	R21 Microzooplankton graze on Nanophytoplankton (its PREFERED prey), without removing it
NanoP+, MicrZ+ >> NanoP-, DOC+	R22 Microzooplankton graze on Nanophytoplankton, which disappear and produce organic matter
NanoP-, PicoP+ >> MicrZ+	R23 Microzooplankton graze on Picophytoplankton (secondary preferential prey), without removing it
NanoP-, PicoP+, MicrZ+ >> PicoP-, DOC+	R24 Microzooplankton graze on Picophytoplankton, which disappear and produce organic matter
NanoP-, Proto+ >> MicrZ+	R25 Microzooplankton graze on Protozoa, without removing them
NanoP-, Proto+, MicrZ+ >> Proto-, DOC+	R26 Microzooplankton graze on Protozoa, which disappear and produce organic matter

NanoP-, Bact+ >> MicrZ+	R27 Microzooplankton graze on Bacteria, without removing them
NanoP-, Bact+, MicrZ+ >> Bact-, DOC+	R28 Microzooplankton graze on Bacteria, which disappear and produce organic matter
MicrZ+ >> MesoZ+	R29 Mesozooplankton graze on Microzooplankton, without removing it
MicrZ+, MesoZ+ >> MicrZ-, DOC+	R30 Mesozooplankton graze on Microzooplankton, which disappears and produces organic matter

Four regimes were revealed by the model (Fig. 4 and Table 1 Suppl.): S0) biological winter regimes, without planktonic bloom, with oscillations of both zooplankton feeding on bacteria and organic matter; S1) a regime in which all components are present because the environment is favourable to the development of organisms with many fluctuations of them; S2) a multivorous TN regime with a mix of preys and various predators such as protozoa and both zooplankton (MicrZ and MesoZ), and finally, S3) a regime centred on protozoa and mesozooplankton with a few preys but the oscillation of Bacteria (Fig. 4a, Table 1 Suppl.). The trajectories passing through different regimes were diverse and depend on the rules fired from the initial state (Fig. 4b): either the TN system shifts between various types of S0 regimes, or it crosses successively regimes S0 to S1, S2, S3 (with possible ways back) and then back to S0.

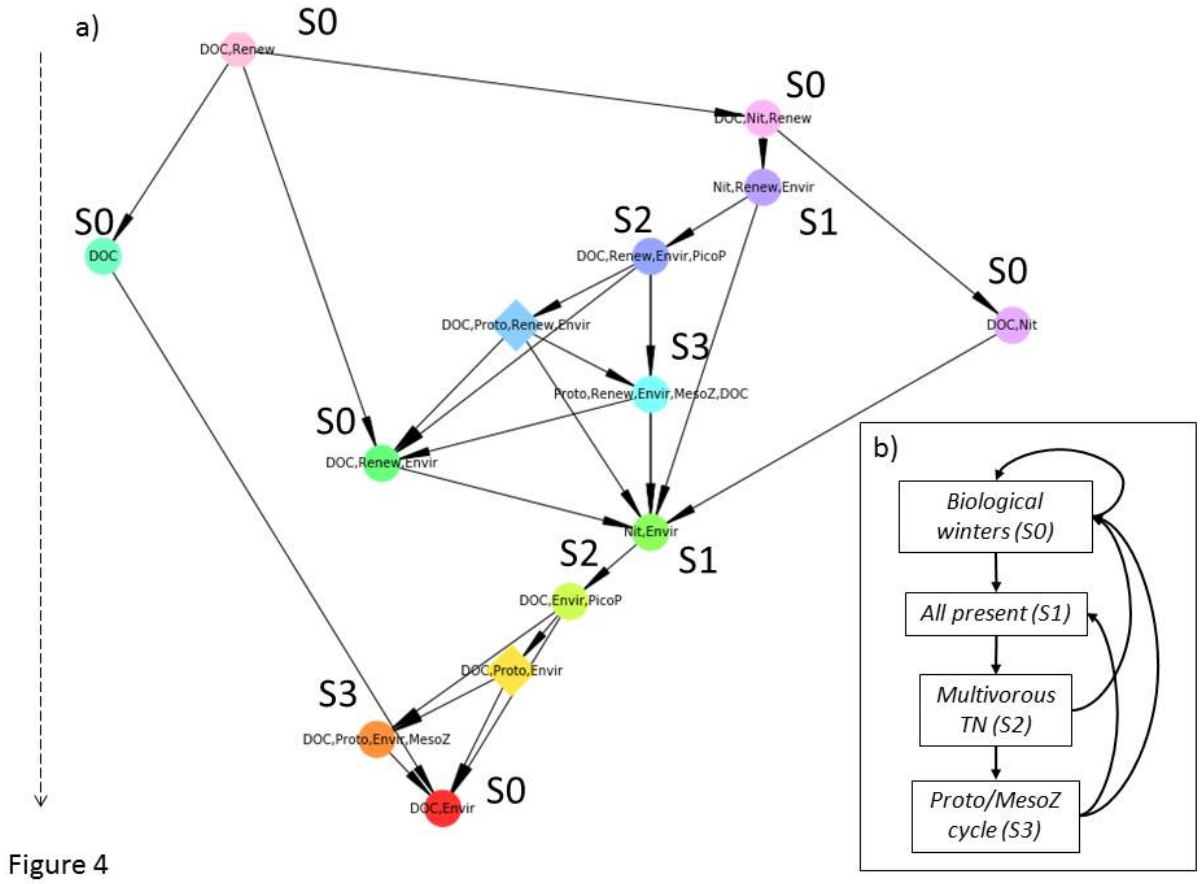

Figure 4

Figure 4 - The merged state spaces of the seasonal model (a, as in Fig. 1a Suppl.), on which each node corresponds to a structural stability (i.e. a set of TN states), and each edge corresponds to specific transitions between two successive stabilities. Here, structural stabilities are labeled with system components that are systematically present (+) in their associated states. This figure helps identifying

the various regimes (b, Table 1 Suppl.) reached by the trophic network system along to the (downward) trajectories computed.

Model validation

All states of the theoretical trajectory are correctly recovered by the model and, as the model exhibited a single stability, the system is certain to successively reach all these states (although we do not know by which complex trajectories, Fig. 4a, Table 1 Suppl.). This observation definitely validates the model. The theoretical planktonic TN trajectory (Table 2 and Fig. 5a) started by an immature regime, here named a biological winter. They then evolved toward low herbivorous TN, herbivorous TN and variable multivorous TN (from weak to strong multivorous regimes, with protozoa, microzooplankton or mesozooplankton, respectively), and microbial TN regime, and to finally reach a microbial loop regime. When water in the marshes is renewed (Renew+), the TN returned to an immature regime, as may the herbivorous and biological winter regimes too. All these TN regimes are recovered by the model (Fig. 5a), yet with slightly different stabilities. Note that this modeled trajectory is crossing many other intermediate states (Fig. 5a) not found in the observations of (Masclaux et al. 2014). When the seasonal oscillation (rule R0) is deactivated, the theoretical trajectory is predicted too (colored states, Fig. 5a), yet in a reverse order for the last two states (blue states at the bottom): the fourth multivorous regime may directly reach the last depleted one.

The data of stations A and B, and associated to observed trajectories were correctly recovered too. At station A, three regimes succeed along time, from A1 to A3 (Table 2 Suppl., Fig. 5b). The TN started by biological winter during four weeks with presence of nitrates and organic matter, but did not reach favourable conditions for biological development. Then, the favourable conditions at week 5 allowed the development of phytoplankton (micro- and pico-plankton), and thus their zooplankton predators with bacteria. This situation was typical of situations between herbivorous and multivorous TNs. Then, a multivorous regime of TN settled until the week 8. At station B, the observed succession displayed four regimes, from B1 to B4 (Table 2 Suppl., Fig. 5c). The TN started by biological winter during three weeks and favourable conditions arrived at week 4 which allowed a presence of multivorous TN ("weak multivorous TN" according to (Masclaux et al. 2014)) and at week 5 an herbivorous TN. Then, a multivorous regime of TN settled from week 6 to week 8.

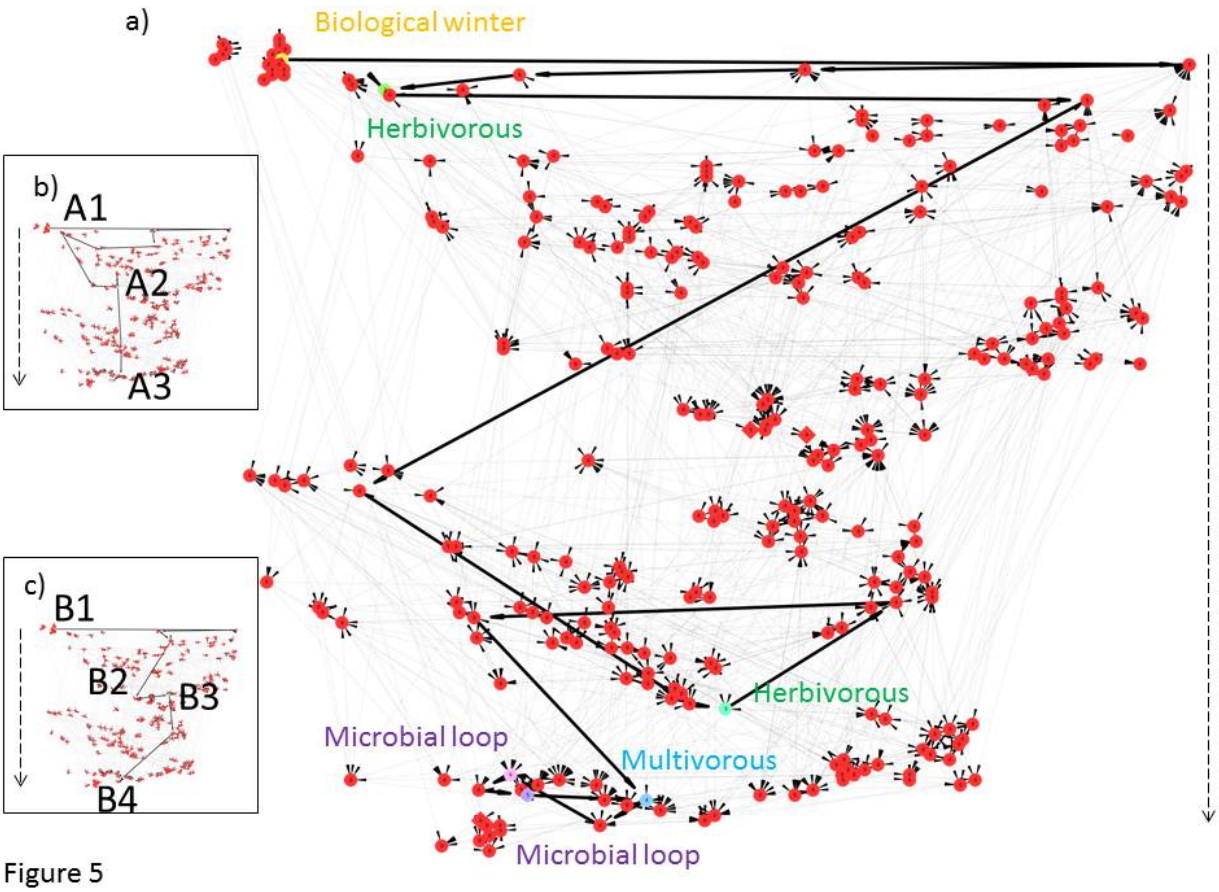

Figure 5 - The full (not merged) seasonal state space highlighting the three trajectories used in this study (Table 2), namely the theoretical (a), station A (b) and station B (c) ones (Table 2 Suppl.). Here, each node corresponds to a trophic network state, connected to each other by downward transitions. The specific states building the three trajectories are highlighted by node colors other than red and identifiers corresponding to their numbers (last lines of trajectories in Table 2) and by bold edges.

Discussion

The discrete event and qualitative model of trophic network (TN) presented here is computed almost instantaneously (< 0.01s) and provided, once the model is defined and assumed, all possible trajectories of this system (Fig. 4). Such approaches are called possibilistic (i.e. non-deterministic and non-probabilistic) and appear relevant for most ecological studies. To our knowledge, it is the first attempt to model exhaustively a detailed (11 components, Table 1) trophic network (but see Baldan et al. 2015, Gaucherel and Pommereau 2019), and to accurately validate its qualitative dynamics.

Complex dynamics of aquatic trophic networks

In the Charente-Maritime trophic system, we discovered that this trophic system may have followed other trajectories than the one identified by experts in the theoretical model and the ones observed (Fig. 5). First, the station B proves that DOC may be present in winter, thus with the trophic network fluctuating in intermediary states before reaching the usual trajectory observed in Masclaux et al. (2014). Indeed, DOC in winter could be an allochthonous input from terrestrial environment (Del Gorgio and Davis 2003). After winter (i.e. when Renew+ and Envir+ were present, Table 1), all the modeled trajectories and all the TN regimes appeared at reach. The TN may come back to immature system states due to the nitrate inputs (Nit+, with R2) and to anthropogenic activities (Tortajada et al. 2011). This situation happens when the water renewal is important and no planktonic biomass accumulation is possible (David et al. 2020). Also, rainfall could happen and favour nitrate leaching (R3), then pushing back the planktonic trophic network to immature system states. The model confirmed the key role of organic matter (DOC), as the system trajectories differed when organic matter was present or absent at the beginning of winter.

From the initial state of the TN, the trajectories could be passing through slightly different biological winter regimes (Fig. 4a-b) with oscillations of organic matter, bacteria, micro- and meso-zooplankton. Similarly, Masclaux et al. (2014) found two types of Biological winters, mainly depending on the presence or absence of bacteria, and on some preys and predators combinations. The model correctly recovered different states of biological winters. The regime of multivorous TN was well recovered by the model too (Masclaux et al. 2014). The multivorous TN is known to be highly stable (Legendre and Rassoulzadegan 1995). However, the microbial loop, which has a transient nature (Legendre and Rassoulzadegan 1995) did not appeared as a structural stability in the model either.

The regime gathering protozoa and mesozooplankton (Proto/MesoZ cycles) characterized by the presence of predators with a few preys but the oscillation of bacteria was not found in the observations (Masclaux et al. 2014). The modeled trajectory is crossing many intermediate states (Fig. 5a-c) not sampled in the field. The field sampling frequency or the structural characteristics of the sampled wetlands likely did not allow capturing all the possible states of TN: this reveals the ability of the model for exploring many other possible states of the planktonic TNs and other trajectories of TN. In particular, the predicted Proto/MesoZ regime has not yet been identified at the Charente Maritime sites, but work in progress at other Atlantic arc territories has identified related TNs (ROBIN, pers. Comm.). Finally, bacteria were frequently present in the ecosystem, and occupied a large place in the model (Table 1 Suppl., Table 2, Table 2 Suppl.). Bacteria seemed to frequently oscillate (Fig. 4a), although not visible in the merged state space. The model confirmed that bacteria are frequently grazed by their grazers, as small protists are (Pernthaler 2005, Šimek et al. 2013). Indeed, we know the strong control of bacteria by the protozoa in freshwater ecosystems.

Power and drawbacks of discrete event models

An increasing number of trophic network models are being developed today (Thébault and Fontaine 2010, Kéfi et al. 2016). But they still have three main limitations: a limited size and complexity and a frozen network with frozen interactions. In this study, we proposed an original model family (called the EDEN framework (Gaucherel and Pommereau 2019, Cosme et al. 2022)) to bypass these limitations. It is based on a discrete-event system well-known by computer scientists and more recently by biologists (Thomas and Kaufman 2001, Reisig 2013). The price to pay by using our qualitative model is that no more quantitative and detailed dynamics is available; but in turn, no difficult parameterization is required.

Consequently, such approach is fully complementary to already existing models in (trophic) ecology. Here, we provide for the first time to our knowledge a discrete and qualitative model of TN to bypass such limitations. By the way, in the continuity to previous theoretical attempts (May 1973, Dambacher et al. 2003), we open here new avenue for using such original models in (ecosystem) ecology. The foundations of this proposition, yet out of the scope here, are based on a theoretical ground assuming that ecosystems are informational systems made up of material components and immaterial processes (Gaucherel 2019) represented in the interaction network.

Such a model is intuitive, easy to build, tractable and rigorous (i.e. no trajectories have been forgotten or added according to the mathematical engine). In addition, it does not require any detailed and quantitative calibration, as no parameter is required. The central assumption of this approach is that it is possible to summarize ecological processes into qualitative rules, possibly interpreted as long term and discrete events. Other studies show that this approach is not limited to trophic processes and may be applied to a high diversity of social-ecosystems (Gaucherel and Pommereau 2019, Mao et al. 2021). In this study, we were lucky enough to collate several theoretical and observed trajectories on which to validate the model, thus confirming it is conform and accurate (Fig. 5). Another quality of this type of models is to be heuristic, to force scientists questioning the knowledge they have on the studied system and to collate it into a single coherent framework.

As perspectives, it appears at hand to model many TN stressors such as pollution, cleaning, drought, invasive species and/or climate changes (Mooney and Hobbs 2001, Mouquet et al. 2015). Any complexification of the studied social-ecosystem is also possible, in theory, as the model is still far from reaching its limits in terms of components, processes and of their nature diversity. It may then be used in a more applied way, exploring other scenarios by changing initial conditions. Coupling this model with other components describing the mechanisms behind these stressors would provide a relevant territorialized model to anticipate trends in a context of global warming and coastline change. In a near future, it would be relevant not only to improve the model realism, but also to develop analysing tools (Mao et al. 2021, Cosme et al. 2022). Indeed, with more components and processes, the computed state space may become increasingly huge and difficult to interpret (Reisig 2013). A way to proceed would be to develop methods based on model checking already in use in computer sciences (Burch et al. 1992). Another relevant line to explore is to complexify our discrete and qualitative approach by using quantitative and multivalued scheme, so that we will bridge the gap with more traditional (e.g. equation-based or individual-based) models (Vézina and Platt 1988, Kéfi et al. 2016).

In brief, by modeling trophic networks with an original framework, we recovered observed and theoretical trajectories. With such possibilistic models, we understood its dynamics and predicted new states and new TN regimes that may be observed in the field. We illustrated them on a specific and well instrumented freshwater TN. Such models provide an intuitive and robust approach to diagnose any trophic (and non-trophic) network by computing all possible trajectories it may reach from a chosen initial state. The known processes at play in the system help identifying all possible dynamics and thus studying the contingency of such complex (social-eco-)systems. To connect such biotic dynamics to human related components would reveal even more insightful understanding of complex ecosystems.

Appendices

Additional Tables and Figures (Appendix 1)

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Data, scripts, code, and supplementary information availability

Data are available in this article (Tables and Figures) (*citation of the data* Gaucherel et al, 2023);

Scripts and code are available online: DOI:10.1111/2041-210X.13242 of the webpage hosting the data https://github.com/fpom/ecco (*citation of the scripts and code* Pommereau et al., 2022);

Supplementary information is available online: XXXXDOI of the webpage hosting the data https://doi.org/10.5802/fake3.doi (*citation of the scripts and code* Gaucherel et al, 2023);

[The references of the datasets, scripts and codes should also be present in the reference list and cited in the text.]

Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article. *[C. Gaucherel is a recommender PCI ecology]*

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