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Cedric Gaucherel, Stolian Fayolle, Raphael Savelli, Olivier Philippine, Franck Pommereau, Christine Dupuy

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Diagnosis of planktonic trophic network dynamics with sharp qualitative changes

ABSTRACT

Trophic interaction networks are notoriously difficult to understand and to diagnose (i.e., to identify contrasted network functioning regimes). Such ecological networks have many direct and indirect connections between species, and these connections are not static but often vary over time. These topological changes, as opposed to a dynamic on a static (frozen) network, can be triggered by natural forcings (e.g., seasons) and/or by human influences (e.g., nutrient or pollution inputs). Aquatic trophic networks are especially dynamic and versatile, thus suggesting new approaches for identifying network structures and functioning in a comprehensive manner.

In this study, a qualitative model was devised for this purpose. Applying discrete-event models from theoretical computer science, a mechanistic and qualitative model was developed that allowed computation of the exhaustive dynamics of a given trophic network and its environment. Once the model definition is assumed, it provides all possible trajectories of the network from a chosen initial state. In a rigorous and analytical approach, for the first time, we validated the model on one theoretical and two observed trajectories recorded at freshwater stations in the La Rochelle region (Western France). The model appears to be easy to build and intuitive, and it provides additional relevant trajectories to the expert community. We hope this formal approach will open a new avenue in identifying and predicting trophic (and non-trophic) ecological networks.

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

28

INTRODUCTION

29 Trophic networks (TNs) form the backbone of ecosystem functioning, as they simultaneously condition
30 food acquisition, prey and predator demography, individual and population behaviors, and phenotype
31 selection, among other consequences (Lindeman 1942, Johnson 2000, Majdi et al. 2018). Trophic processes
32 are responsible for most matter and energy fluxes within ecosystems, but the fates and properties of
33 ecosystems are hard to predict, mainly due to the lack of knowledge (Mouquet et al. 2015). Trophic processes
34 have been extensively studied in ecology, although mostly considered as frozen in time, i.e., with a fixed (or
35 static) topology and fixed signed interactions. This simplification may be due to a lack of long-term data as well
36 as to equation-based models dedicated to flux and abundance variations on a frozen network (e.g., Thébault
37 and Fontaine 2010, Kéfi et al. 2015). In this study, we provide an original framework to handle TNs with sharply
38 changing structures and to model their possible dynamics.

39
40 To date, TNs have been difficult to understand and handle, in other words, hard to *diagnose* between
41 contrasted functioning under changing environmental conditions. Any new functioning involves specific
42 ecosystem components and interactions, thus justifying why we have focused on qualitative functioning
43 *regimes* rather than quantitative component abundances and interaction intensities. In addition, TNs usually
44 gather a large number of populations or species in an even larger number of trophic interactions. Hence,
45 understanding trophic dynamics would require not only modeling a large and realistic number of components
46 but also being able to calibrate the weights (coefficients) of each component and each interaction involved
47 (Ings et al. 2009, Wallach et al. 2017, Majdi et al. 2018). For this reason, most trophic models to date have
48 focused on wide categories of populations, with functional categories, such as carnivores, herbivores, and/or
49 detritivores (e.g., Thébault and Fontaine 2010), and approximate their trophic parameters. Even powerful
50 models aimed at bypassing such limitations, such as qualitative models based on differential equation systems,
51 are limited in size (May 1973, Dambacher et al. 2003).

52
53 There is an even more pronounced limitation of trophic studies in ecology, as they mostly assume a frozen
54 network of interaction (Thébault and Fontaine 2010, Kéfi et al. 2016). Not only is it harder to handle a network
55 that changes in terms of topology (structure), but it is also not known how such a network may change over
56 time and, thus, how to model it. Indeed, as soon as the study covers several generations of some of the species
57 involved in the network, other species may invade and/or become extinct (Mooney and Hobbs 2001, Warren
58 et al. 2005). Hence, these events greatly modify the network structure and, in turn, the system dynamics.
59 Equation-based models are not well suited to handle dynamic systems *on* dynamic structures (sometimes
60 called DS², Giavitto and Michel 2003), whereas certain tools developed in theoretical computer science are
61 perfectly adapted to this task. In particular, discrete-event systems such as graph transformations or Petri nets
62 are able to handle sharply changing networks by formalizing the way components and interactions can appear
63 or disappear (König et al. 2018, Gaucherel and Pommereau 2019). While graph transformations directly
64 add/remove some nodes and edges, Petri nets only mimic such addition/removal by marking the
65 presence/absence of the handled nodes and edges with some tokens. In this study, we developed a Petri net
66 to model any interaction network topological change, and we illustrate its use on a realistic planktonic TN.

67
68 Planktonic TN models are usually composed of a fixed number of functional nodes that gather groups of
69 individuals sharing the same ecological function. Mass fluxes (usually in carbon or nitrogen) between nodes
70 are predefined according to trophic interactions. In a context of an emerging biological oceanography
71 discipline and considering the limited computing resources, the first planktonic TN (or food web) models simply
72 consisted of mass fluxes between nutrients, phytoplankton, and zooplankton nodes (Steele 1958, 1974). These
73 so-called NPZ models (NPZD, NPZDB, or even NPZF when detritus, bacteria, or fishes are comprised,
74 respectively) coupled to observed or simulated physical conditions have demonstrated their predictive ability
75 to capture bulk system properties (biomass and primary production) at both regional and global scales (Mitra
76 et al. 2007, Kriest et al. 2010, Oke et al. 2013, Hernández-Carrasco et al. 2014, Turner et al. 2014, Kumar and
77 Kumari 2015).

78 To better understand biogeochemical cycling (e.g., export fluxes, carbon sequestration, organic matter
79 recycling, microbial loop), planktonic TN should be delineated, and planktonic compartments in models could
80 thus be refined into Planktonic Functional Types (PFTs). Plankton groups are thus defined according to

81 common ecological functions (e.g., nitrogen fixers, calcifiers, and silicifiers), sizes (e.g., picophytoplankton,
82 nanophytoplankton, microphytoplankton), and/or key taxonomic groups (e.g., diatoms, flagellates) (Le Fouest
83 et al. 2013, Villaescusa et al. 2016, Kerimoglu et al. 2017, Petersen et al. 2017, Maar et al. 2018, Meddeb et al.
84 2019). However, refinements of planktonic TN models greatly complicate model formalization and
85 parametrization, as well as requiring more data, which increases uncertainties in terms of the model outcomes
86 and fluxes between defined groups (Anderson 2005).

87
88 To address gaps in ecological knowledge and lacking data, inverse modeling is aimed at deriving flows of
89 energy within TNs from simple biomass estimates and rate measurements. Vézina and Platt (1988) were the
90 first to use this for inferring mass fluxes through a planktonic TN in the English Channel. Inverse modeling is,
91 therefore, advantageous when dealing with underdetermined systems and results in a space of possible
92 solutions that fulfill a set of linear equalities and inequalities. A preferred solution is then selected by
93 optimization or statistical methods. While vital rates and biomass can be readily measured for high trophic
94 levels (e.g., fishes), their quantification for low trophic levels (e.g., bacteria, autotrophic plankton) remains
95 uncertain and questions the robustness of inverse modeling for the study of planktonic compartments (Vernet
96 et al. 2017, Saint-Béat et al. 2018). Overall, biological constants (production, consumption, assimilation),
97 biomass, and ecological interactions are, therefore, not easy to measure in planktonic TNs, resulting in an
98 oversimplification of planktonic TN models (Anderson 2005, Flynn 2006). For all of these reasons, our main
99 objective in this study consisted of developing a model able to identify (diagnose) any qualitative functioning
100 regimes of the same TN under changing environmental conditions.

101
102 We here addressed the leading question: what are all the possible trajectories (pathways) of such an
103 aquatic TN? A trajectory is defined here as a sequence of TN states (regimes) and transitions in time, possibly
104 exhibiting bifurcations and not necessarily being quantitative. More specifically, we aimed to identify the
105 various qualitative regimes the system can reach between winter and summer environmental conditions. As a
106 second subquestion, we assessed whether a detailed model could exhibit new or counter-intuitive TN
107 trajectories. We assumed that the system may be qualified and thus exhibit a finite number of states,
108 computed and gathered into a Petri net *state space* (Pommereau 2010, Reisig 2013). A detailed and automatic
109 analysis of this state space then exhaustively provides the possible fates (e.g., stabilities, collapses, if any) of
110 the studied system. We chose to illustrate this original method with a well-studied plankton TN in wetlands,
111 namely freshwater marshes of the Charente Maritime region (Western France, Tortajada et al. 2011). Such a
112 system is well instrumented (measured) and will provide an expected theoretical trajectory of changing TN, as
113 well as two observed trajectories at different stations (Masclaux et al. 2014). The succession of planktonic TN
114 and the different regimes of the planktonic TN are well known according to the season (Masclaux et al. 2014).
115 We developed the corresponding Petri net of this system and then validated it, for the first time, on theoretical
116 and observed trajectories. We finally discuss the power and drawbacks of such discrete and qualitative models
117 for trophic ecology.

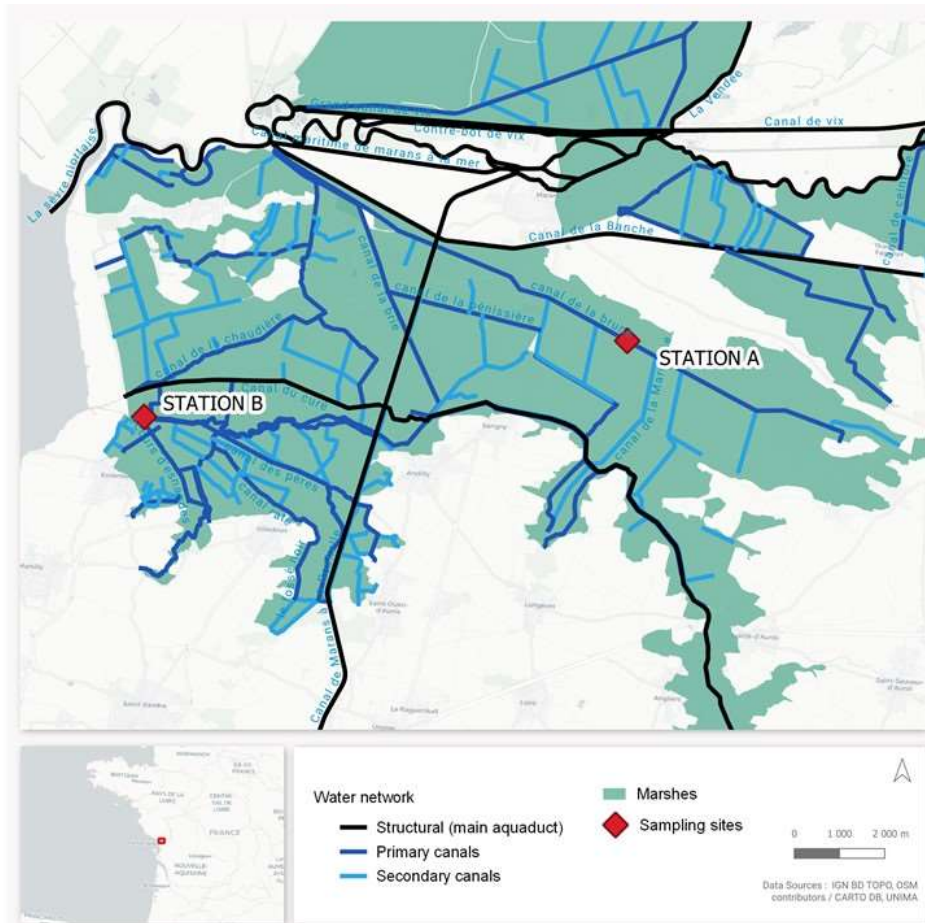
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MATERIALS AND METHODS

119 Aquatic trophic networks

120 The Charente-Maritime marshes of the French Atlantic coast (Fig. 1) are the second largest French wetland
121 zone (more than 1000 km²). The type of freshwater marshes is unreplenished drained marshes, which
122 constitute a significant artificial hydrographic network of channels and ditches. To mitigate and prevent drying
123 of the marshes, locks control the channels and ditches (for more details, see Masclaux et al. 2014). Samples of
124 the planktonic TN were recorded at two stations (stations A and B) on successive dates (eight weeks during
125 winter and spring 2012) to reconstruct the network trajectories and their environment over time (Masclaux et
126 al. 2014). All of the details have been presented in the publication by Masclaux et al. (2014). Briefly, the water
127 parameters studied were the temperature, nutrients (nitrates, etc.), the dissolved organic matter (*DOC*)
128 concentration, the biomass and production of bacteria, the biomass and primary production of phytoplankton
129 by size class (microphytoplankton for > 20 μm; nanophytoplankton for 3–20 μm; and picophytoplankton for <
130 3 μm), the bacterial biomass, the protozoa biomass, and the metazoan microzooplankton and
131 mesozooplankton biomasses. Different fluxes between preys and predators were measured: micro- and
132 mesozooplankton grazing rates on the three phytoplankton size classes, as well as mesozooplankton grazing

133 rates on protozoa (Masclaux et al. (2014). The TN regimes were determined with a hierarchical ascendancy
134 classification (HAC, Euclidean distance, and Ward method). The planktonic TN regime changed during the
135 winter to spring transition, from biological winters, followed by herbivorous TNs, to finally reach TNs qualified
136 as multivorous and distinguishing three levels of multivory (weakly multivorous, multivorous, and highly
137 multivorous) (Masclaux et al. 2014).



138 **Figure 1**

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

141 The model was built with several categories of variables (Fig. 2): Phytoplankton, Zooplankton, Resources,
142 Microbes, and Abiotic components characterizing the environment. The main functional groups were: 1)
143 phytoplankton by size class (microphytoplankton for $> 20 \mu\text{m}$: *MicroP*; nanophytoplankton for $3\text{--}20 \mu\text{m}$:
144 *NanoP*; and picophytoplankton for $< 3 \mu\text{m}$: *PicoP*) all in green (Fig. 2); 2) metazoan microzooplankton (*MicroZ*)
145 and mesozooplankton (*MesoZ*) in red; 3) resources as nitrates (*Nit*) and Dissolved Organic Matter (*DOC*) in
146 brown; 4) microbes such as bacteria (*Bact*) and protozoa (*Proto*) in blue; and 5) abiotic variables in grey with
147 the component *envir*, which corresponds to the temperature and light conditions and *renew* which
148 corresponds to the possible renewal of water (i.e., flush) in the marshes depending on the rainfall and water
149 usages (agriculture, breeding, etc.). In more detail, the planktonic TN and all the possible fluxes (interactions)
150 between components concern grazing fluxes with some preferential predation, and potential competitions
151 between organisms (Fig. 2). Protozoa graze on bacteria, *PicoP* and *NanoP*, and are grazed by *MicroZ* and *MesoZ*.
152 *MicroZ* graze on bacteria, *PicoP*, *NanoP*, and *Proto*. *MicroP* is grazed mainly by *MesoZ*, which used *MicroZ*,
153 *NanoP*, and *Proto* as preys. Two preferential interactions force the model: i) competition between bacteria
154 and *PicoP*, suggesting that each may survive and be detrimental to the second one, and ii) preferential grazing
155 of *MicroP* by *MesoZ* and preferential grazing of *NanoP* by *MicroZ*. In brief, plain upward edges correspond to
156 prey-predator interactions, while dashed downward edges are the resulting detritus (toward the *DOC*
157 variable).

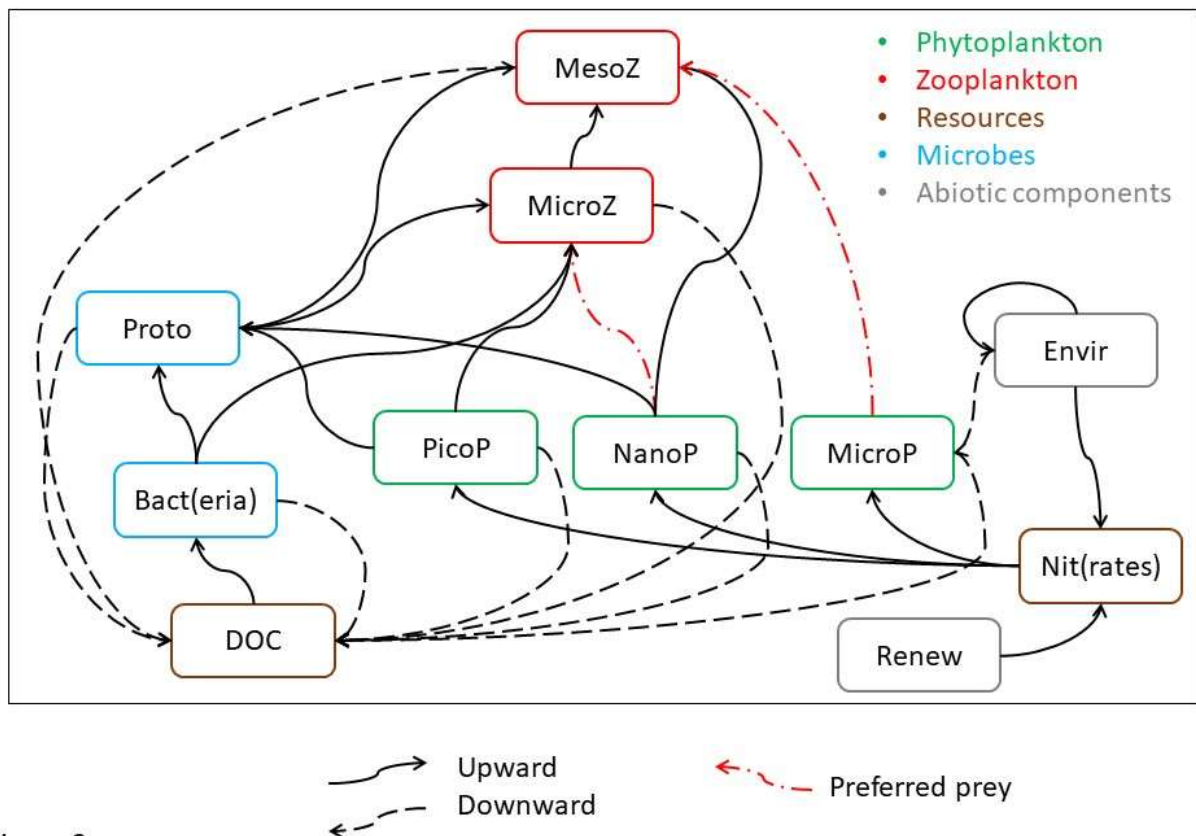


Figure 2

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Figure 2 - The detailed interaction network used in this study. The trophic and non-trophic components are displayed as nodes with various colors (Phytoplankton: green, Zooplankton: red, Resources: brown, Microbes: blue, and Abiotic components characterizing the environment: grey). Predation interactions are displayed as plain (upward for trophic) and dashed (downward for degradation) edges, with preferred prey populations highlighted with red dotted-dashed edges.

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Petri Nets and a simplistic Prey-Predator model

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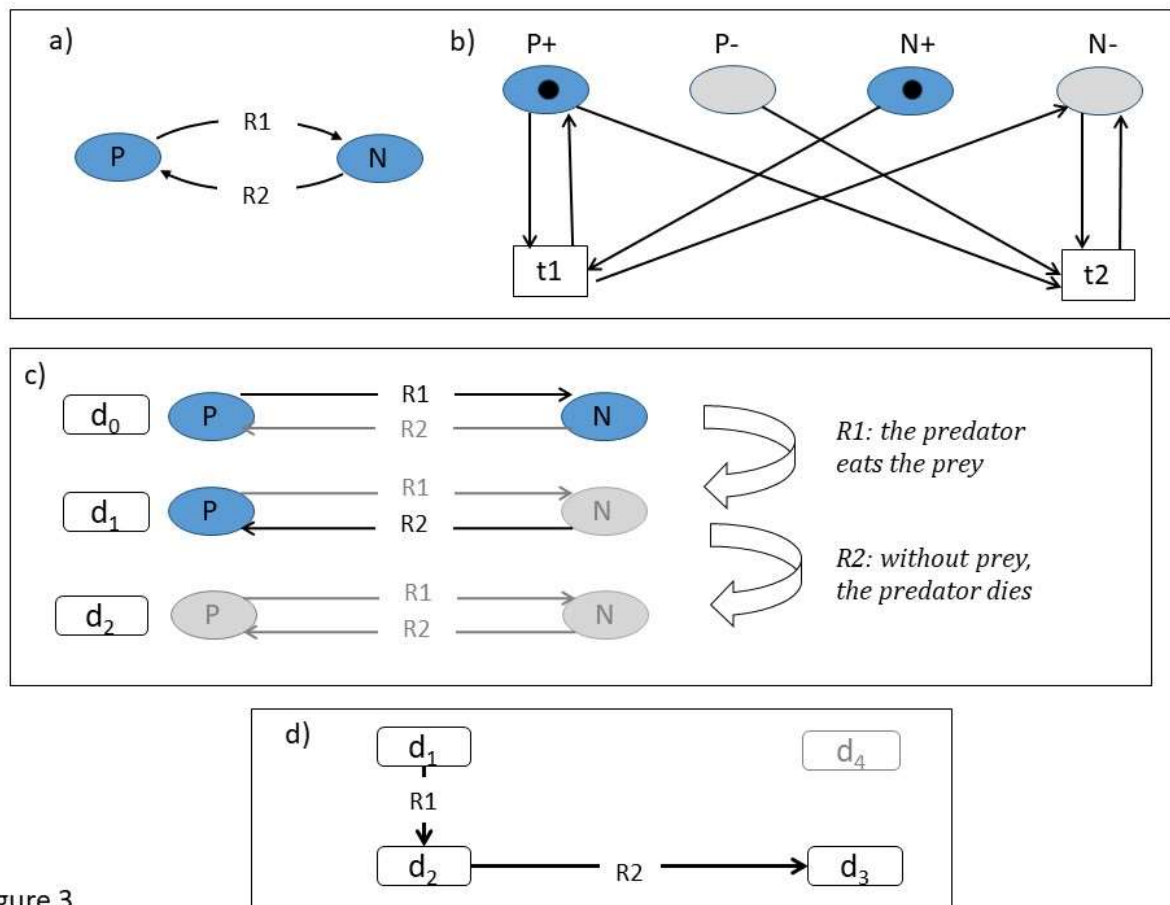
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We first summarize the successive steps required to build any ecosystem Petri net and we then illustrate these steps with a toy model. Our generic approach to model ecosystems has been called the EDEN (Ecological Discrete-Event Network) modeling framework and is specifically applied here to an aquatic trophic TN. Any ecosystem Petri net is developed in three successive steps (Fig. 3): i) an intuitive graph (i.e., a set of nodes and edges) is built to represent the studied ecosystem with its components and their related processes, focusing on the leading question addressed by the model (Fig. 3a); ii) this ecosystemic graph, now called the *interaction network*, is then transformed into a formal model based on a discrete-event Petri net and its associated rules (as explained in the next paragraph, Fig. 3b); iii) the Petri net is run (computed, Fig. 3c) and analyzed (Fig. 3d) to determine the entire range of the ecosystem dynamics. However, the Petri net (steps i and ii) is hidden from the (ecologist) user and is automatically built (in Python language, see Suppl. Mat.) once the ecosystem components and processes have been chosen by the ecologists. Additional technical details regarding the principle and use of Petri nets, in particular the way they are computed, can be found in the literature (Pommereau 2010, Reisig 2013, Gaucherel and Pommereau 2019).

We here illustrate the basic functioning of the model using a simplistic prey-predator system (Fig. 3). Any ecosystem network can be represented as 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 (or variable), with two Boolean states: “present” (the component is functionally present in the system, or above a chosen threshold, also denoted “+”) and “absent” (functionally absent from

184 the system, or below the same threshold, denoted “-”). In the prey-predator toy model, only two nodes are
 185 defined: the prey and the predator populations. Any state of the ecosystem is defined by the set of “+” and “-”
 186 nodes (Fig. 3b), and “±” in the tables of this paper, when they may oscillate between successive states. The
 187 state of a node depends on the nodes to which it is connected, while a connection between nodes is assumed
 188 as soon as one process explicitly connects the different components (Figs. 3a-b). The rules correspond to any
 189 physicochemical and/or bio-ecological processes (e.g., if the prey population is below a chosen threshold (-),
 190 the predator population also ends up below its associated threshold), and thus represent all possible
 191 interactions between the components comprising the studied ecosystem. In the prey-predator system, only
 192 two rules are defined: R1, the predation itself: the predator eats the prey, and R2, the mortality: without prey,
 193 the predator dies (Figs. 3a and c). In the Petri net language, nodes are called places, and rules are called
 194 transitions, both being connected through oriented arcs (Fig. 3b).



195 **Figure 3**

196 **Figure 3** - Illustration of a simplistic prey-predator system (a), with its associated Petri net (b), its
 197 qualitative dynamics (c), and the computed marking graph, also called state space (d). The system
 198 comprises two components, the prey (N) and predator (P) populations, and two interactions connecting
 199 them (rules R1 and R2, (a)). The corresponding Petri net comprises four places (P+, P-, N+, and N-) and
 200 two transitions, R1 and R2, linked by unlabeled and unweighted arcs (b). Starting with the presence of
 201 both populations, it is possible to list all system states encountered {d₁, d₂, and d₃} (c), and to connect
 202 them with the rules (absent nodes and inactivated rules are displayed in grey). The net is depicted in the
 203 initial state (c), and the successive states can be deduced from the token (black dot in (a)) movements
 204 between places (b). The marking graph of the Petri net (d) is depicted with each state number {d₀, d₁, and
 205 d₂} referring to the dynamics described above (b). It should be noted that a specific state of the system
 206 {d₄} may not be reached from this initial condition and with these rules (d).

207 **Discrete and qualitative dynamics**

208 Any rule of such discrete-event models combines the left-hand *condition* and right-hand *realization* as:
 209 “transition’s name: condition >> realization”. For a rule to be applied, the state of the node (variable) must

210 satisfy its application condition; the rule is then designated as *enabled*. If so, the application of the rule modifies
211 the state of the node as stipulated in its realization part; the rule is then *fired* (i.e., executed or applied). In the
212 prey-predator system (Fig. 3), the rules are written as R1: P+, N+ >> N- and R2: N-, and P+ >> P-. Since the rules
213 modify node states, they change the overall system state (i.e., the state of the system aggregates all node
214 states). Therefore, the entire system shifts from one state to another through the successive applications of
215 the enabled rules (Fig. 3c). Computation of the defined Petri net produces the *state space*, which provides the
216 set of all system states reachable by the rules defined (Fig. 3d). As a corollary, the system states are also
217 connected to each other by some of these rules in the state space. The size of this state space is usually much
218 smaller than the number of possible system states (2^n , where n is the number of components or
219 nodes/variables), because the computation starts from a specific initial condition and because the rules have
220 specific application conditions. Following the computer science community, we developed certain tools to
221 automatically divide large state spaces into *merged* (simplified) state spaces, as explained in the next
222 subsection.

223
224 Firing a rule independently of some others often leads to unrealistic trajectories (e.g., flushing water
225 without removing the plankton in it). Therefore, we defined *constraints*, which prevent the model from
226 simulating such unrealistic trajectories. Constraints have a condition and a realization part, just as rules *stricto*
227 *sensu* do, and the model inevitable (mandatory) transitions given the system state. The sole difference
228 between rules and constraints is that constraints have priority over *stricto sensu* rules. In the prey-predator
229 system, the system state $d_1 = \{N-, P+\}$ is unrealistic; so, the rule R2 has to be transformed into a constraint C1:
230 N-, P+ >> P-. From a given state, the model first simulates all trajectories opened up by the defined constraints,
231 and then, when all the system states obtained are realistic (i.e., there is no longer any enabled constraint),
232 only the enabled rules are fired (Fig. 3d). It should be noted that the modeled system can remain an indefinite
233 time in any of the computed states, as no rule forces it to leave the qualitative state (i.e., the system can
234 experience quantitative dynamics, yet without sharp qualitative changes). In brief, the discrete model
235 proposed here is qualitative, mechanistic (the processes are explicit), non-deterministic (no stochasticity yet
236 several possible outcomes from each state), and asynchronous (i.e., all rules are applied as soon as possible,
237 no rule conflict) (Reisig 2013, Gaucherel and Pommereau 2019). The EDEN models are also causal and
238 chronological yet non-temporized, i.e., transitions and time steps are not quantified (and not probabilized).
239

240 **TN trajectories and validation methodology**

241 The theoretical plankton TN modeled here combines nine different components, associated with the
242 dominant functional groups that may be present in the channel freshwater marshes, and two additional
243 components featuring environmental conditions (Table 1, Fig. 2). To connect them, we defined 34 processes
244 and seven constraints encompassing at least four trophic levels (Tables 2-3, Fig. 2). To validate the TN model,
245 one theoretical trajectory was defined and two observed trajectories were recorded at two distant stations
246 (Supplementary Materials, Tables SM1-2). For the model to be validated, we expect not only to detect these
247 successive states (e.g., {S0, S1, S2, S3}) in the modeled state space but also to detect them in the correct
248 succession order. To determine whether the model was able to recover the expected trophic regimes, we
249 tested two variants of the model: i) the full model intending to encompass the TN functioning, and ii) a similar
250 model (called *seasonal*) yet without a return to winter conditions (R0, Table 2), thus resulting in the model
251 being stuck in summer conditions. The model starts in winter conditions or with a flush in summer conditions,
252 with only the node *Renew* present, which returns a source of inorganic nitrogen to the system (Table 1).
253

254 For the full and seasonal models, we computed the state space and the *merged* state space, and we
255 checked whether the observed trajectories were correctly recovered. A merged state space is a simplified state
256 space gathering the sets of mutually reachable states of the modeled system, a topological structure called a
257 *structural stability*, into the same nodes. This type of structure is interpreted as a stable regime as, by
258 definition, any state in this stability can be reached by any other state belonging to it. Other stabilities can be
259 identified automatically, such as *terminal stabilities*, from which the system can no longer exit, *basins* gathering
260 states that have the same following states, and *deadlocks*, which are single states from which the system can
261 no longer exit. Merged state spaces are much more compact than full state spaces, and summarized
262 trajectories are readily revealed.

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Table 1 - The plankton TN components and their associated modeled variables, with their abbreviations and descriptions. Whether these ecological components are present (+) or absent (-) in the initial state is also indicated (second column).

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)

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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 rows. The corresponding regimes displayed in Figs. 5a-c are listed in the last row 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/Highly multivorous TN	Microbial TN	Microbial loop

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RESULTS

State spaces and computed dynamics

274 The full model provides a state space comprising 765 states gathered into a single dynamic structure (a so-called structural stability, Fig. SM1a). The seasonal model becomes stuck in a high number (12, plus two basins) of successive structural stabilities of various sizes (Figs. 4 and SM1b). When oriented downward in time; i.e., following causality and chronology, the whole system inevitably converges toward a small terminal stability (made up of four states) in which the system is in a biological winter (i.e., few living species, in green, Fig. SM1b). Some of the stabilities that are reached exhibit a large number of states and may keep the system into such specific stabilities for an indefinite time (in purple, Figs. 4 and SM1b). In brief, the seasonal model displays

281

282 the same state space as the full model, but with a possible return to the initial biological winter regime, thus
 283 connecting the bottom states (in red, Fig. 4a) to the top states (in pink, Fig. 4a). This is why we observed a
 284 single cycling stability in the full model state space (Fig. SM1a).

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

CONSTRAINTS

DOC- >> Bact-

Nit- >> NanoP-, MicrP-, DOC+

Bact+, PicoP-, NanoP- >> Proto-, DOC+

Bact-, Proto-, PicoP-, NanoP- >> MicrZ-,
DOC+

Proto-, MicrZ-, NanoP-, MicrP- >>
MesoZ-, DOC+

Envir- >> PicoP-, NanoP-, MicrP-
PicoP+, NanoP+, MicrP+ >> Nit-

Descriptions

C1 Without organic matter (DOC), Bacteria disappear

C2 Without Nitrates, all types of phytoplankton except
Pico disappear (and produce organic matter)

C3 Without all its preys (but Bacteria), Protozoa disappear
(and produce organic matter)

C4 Without all its preys (but Bacteria), Microzooplankton
disappear (and produces organic matter)

C5 Without all its preys, Mesozooplankton disappear (and
produces organic matter)

C6 In winter, all Phytoplankton disappear (and do not
produce organic matter)

C7 With all Phytoplankton (present), Nitrates disappear

RULES

Envir+ >> Envir-, Renew+

Envir- >> Envir+

Envir+, Renew+ >> Nit+, Renew-

Envir-, Renew+ >> Nit+, DOC-, Bact-,
Proto-, PicoP-, NanoP-, MicrP-, MicrZ-,
MesoZ-

Envir-, Renew+ >> Renew-

DOC+ >> Bact+

Bact+, DOC+ >> DOC-

Envir+, Nit+ >> MicrP+, NanoP+

Envir+, Nit+ >> PicoP+

Bact+ >> Proto+

Bact+, Proto+ >> Bact-, DOC+

PicoP+ >> Proto+

PicoP+, Proto+ >> PicoP-, DOC+

NanoP+ >> Proto+

NanoP+, Proto+ >> NanoP-, DOC+

MicrP+ >> MesoZ+

R0 After summer (and spring) comes winter

R1 After winter comes summer (and spring), with a bloom
R2 Nitrate input is due to water flush from human
management or rainfall

R3 In winter, the Reset of the system is due to water flush
from rainfall (but there is a Nitrate input)

R4 In winter, we stop the flush after its action (reset)

R5 Bacteria use organic matter, without removing it

R6 Bacteria use organic matter and remove it

R7 Microphytoplankton and Nanophytoplankton use
Nitrates in summer, without removing them

R8 Picophytoplankton use Nitrates, without removing
them

R9 Protozoa graze on Bacteria, without removing them

R10 Protozoa graze on Bacteria, which disappear and
produce organic matter

R11 Protozoa graze on Picophytoplankton, without
removing it

R12 Protozoa graze on Picophytoplankton, which
disappears and produce organic matter

R13 Protozoa graze on Nanophytoplankton, without
removing it

R14 Protozoa graze on Nanophytoplankton, which
disappears and produce organic matter

R15 Mesozooplankton graze on Microphytoplankton (its
PREFERRED 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 PREFERRED 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

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289 Four TN regimes were revealed by the full and seasonal models (Fig. 4a and Table SM1): the S0 biological
290 winter regime, without planktonic bloom, with oscillations of both zooplankton feeding on bacteria and
291 organic matter; the S1 regime, in which all components are present because the environment is favorable to
292 the development of organisms with many fluctuations of them; the S2 multivorous regime, with a mix of preys
293 and various predators such as protozoa and both zooplankton (MicrZ and MesoZ), and finally, the S3 regime,
294 centered on protozoa and mesozooplankton with a few preys but oscillation of Bacteria (Fig. 4a and Table
295 SM1). The trajectories passing through different regimes were diverse and depended on the rules fired from
296 the initial state (Fig. 4b): either the TN system shifts between various types of S0 regimes, or it successively
297 crosses regimes S0 to S1, S2, and S3 (with possible ways back) and then back to S0.

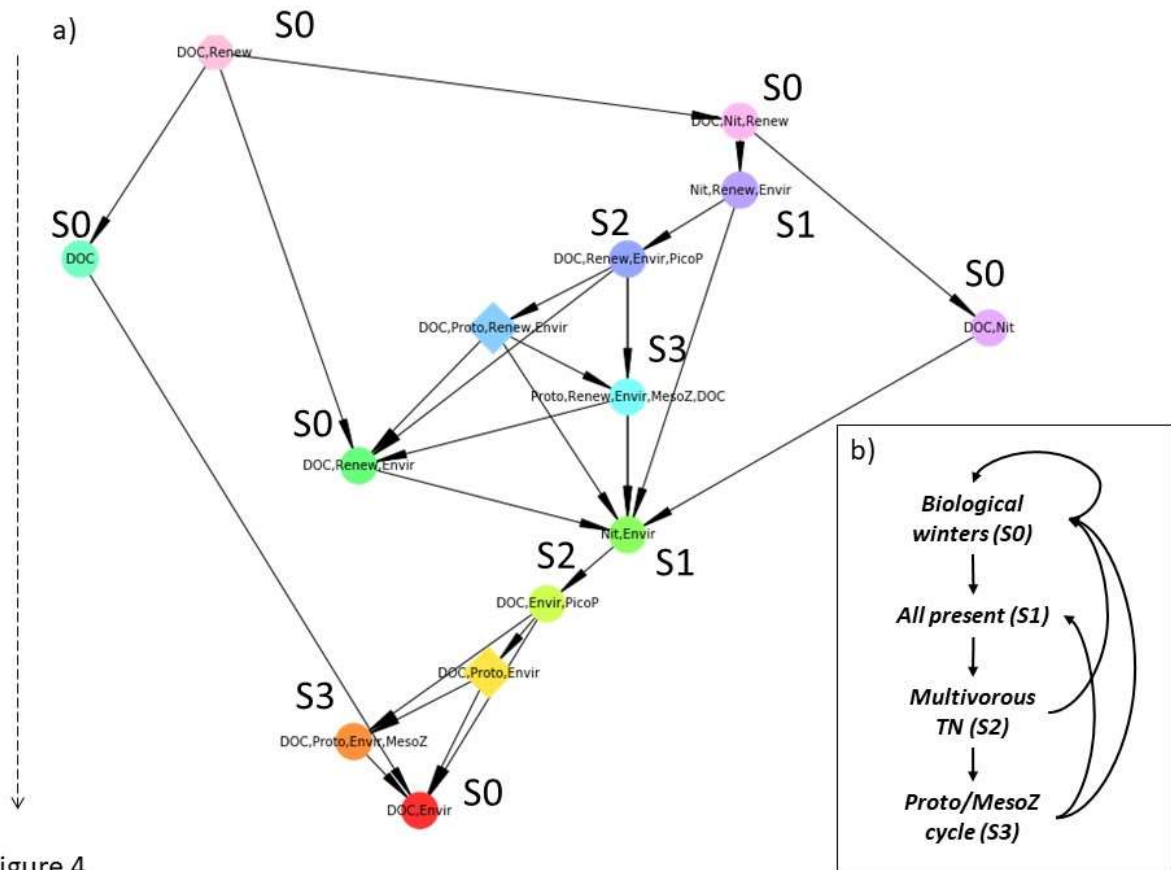


Figure 4

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Figure 4 - The merged state space of the seasonal model (a, as in Fig. SM1a), in which each node corresponds to a structural stability (i.e., a set of mutually reachable states), and each edge corresponds to irreversible transitions between successive stabilities. Here, structural stabilities are labeled with system components that are systematically present (+) in their associated states (see Fig. SM2). To see components that are systematically absent in stabilities). This figure helps identify the various regimes (b, and Table SM1) reached by the TN system along to the (downward) trajectories computed.

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Model validation

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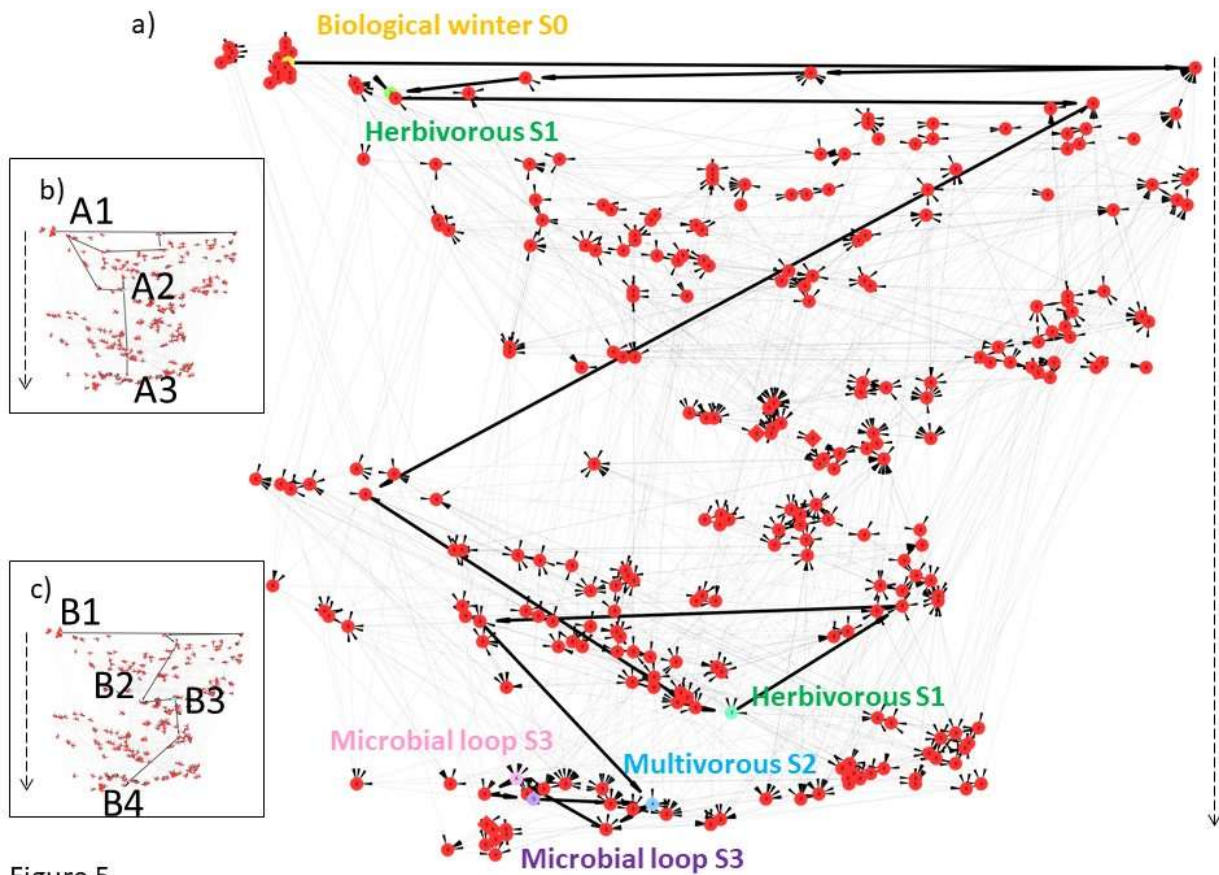
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All states of the theoretical trajectory were correctly predicted by the model and, as the model exhibited a single stability, the system is certain to successively reach all these states (although we do not know by which complicated trajectories, Fig. 4a, Table SM1). This observation definitely validates the model. The theoretical planktonic TN trajectory (Table 2 and Fig. 5a) started by an (immature) regime found during the biological winter. It then evolved toward low herbivorous TN, herbivorous TN, and variable multivorous TN (from weak to highly multivorous regimes, with protozoa, microzooplankton, or mesozooplankton, respectively), and a microbial TN regime, to finally reach a microbial loop regime. When the water in the marshes was renewed (*Renew+*), the TN returned to the biological winter regime, as can the herbivorous regimes as well. All these TN regimes were recovered by the model (Fig. 5a), yet with slightly different stabilities. Figure 5 is not meant to demonstrate this validation stage (already achieved by identification of the successive trajectory states), rather than *showing* that all predicted states (colored nodes) were correctly recovered in the computed state space, and indeed connected through successive transitions (bold edges). Note that this modeled trajectory crossed many other intermediate states (Fig. 5a) not found in the observations of (Masclaux et al. 2014). In the seasonal model (rule R0 deactivated), the theoretical trajectory was also predicted (colored states, Fig. 5a), yet with the last two states (blue states at the bottom) in the reverse order, as the fourth multivorous regime can directly reach the last depleted one.

The data recorders at stations A and B, and associated with observed trajectories, were also correctly recovered. At station A, three regimes succeeded over time, from A1 to A3 (Table SM2, and Fig. 5b). The TN

325 started with biological winter for four weeks with the presence of nitrates and organic matter, but it did not
326 reach favorable conditions for biological development. Then, the favorable conditions at week five allowed the
327 development of phytoplankton (micro- and pico-plankton), and thus their zooplankton predators with
328 bacteria. This situation was typical of situations between herbivorous and multivorous TNs. A multivorous
329 regime of TN then took hold until week eight. At station B, the observed succession displayed four regimes,
330 from B1 to B4 (Table SM2 and Fig. 5c). The TN started with biological winter for three weeks and favorable
331 conditions occurring at week four, which allowed the presence of multivorous TN ("weak multivorous TN"
332 according to (Masclaux et al. 2014)) and at week five an herbivorous TN. Then, a multivorous regime of TN
333 took hold from week six to week eight.



334 Figure 5

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

340

DISCUSSION

341 The discrete-event and qualitative model of trophic networks (TN) presented here can be computed
342 instantaneously (< 0.01 s) and provided, once the model was defined and assumed, all possible trajectories
343 of this system (Fig. 4). To our knowledge, this is the first attempt to exhaustively model a detailed TN (11
344 components, Table 1) and to accurately validate its qualitative dynamics.

345 **Complex dynamics of aquatic trophic networks**

346 In the Charente-Maritime trophic system, we discovered that this TN may have followed other
347 trajectories than the one identified by experts in the theoretical model and in the ones observed (Fig. 5
348 and Supplementary Materials tables). First, station B showed that *DOC* may be present in winter, thus with
349 the TN fluctuating in intermediary states before reaching the usual trajectory observed in Masclaux et al.
350 (2014). Indeed, *DOC* in winter could be an allochthonous input from the terrestrial environment (Del Gorgio
351 and Davis 2003). After winter (i.e., when *Renew+* and *Envir+* were present, Table 1), all the modeled
352 trajectories and all the TN regimes appeared at reach. The TN can return to biological winter system states
353 due to the nitrate inputs (*Nit+*, with R2) and to anthropogenic activities (Tortajada et al. 2011). This
354 situation occurs when the water renewal is substantial and no planktonic biomass accumulation is possible
355 (David et al. 2020). Moreover, rainfall could occur and favor nitrate leaching (R3), thus pushing back the
356 planktonic TN to biological winter system states. The model confirmed the key role of organic matter (*DOC*),
357 as the system trajectories differed depending on whether or not organic matter was present at the
358 beginning of winter.

359

360 From the initial state of the TN, the trajectories could pass through slightly different biological winter
361 regimes (Figs. 4a-b) with oscillations in organic matter, bacteria, and micro- and mesozooplankton.
362 Similarly, Masclaux et al. (2014) found two types of Biological winter regimes, mainly depending on the
363 presence or absence of bacteria, and on some prey and predator combinations. The model correctly
364 recovered different states of biological winters. The regime of multivorous TN was also well recovered by
365 the model (Masclaux et al. 2014). The multivorous TN is known to be highly stable (Legendre and
366 Rassoulzadegan 1995). However, the microbial loop, which has a transient nature (Legendre and
367 Rassoulzadegan 1995) did not appear as a structural stability in the model either.

368

369 The regime gathering protozoa and mesozooplankton (*Proto/MesoZ* cycles) characterized by the
370 presence of predators with a few preys but oscillation of bacteria was not found in the observations
371 (Masclaux et al. 2014). The modeled trajectory crossed many intermediate states (Figs. 5a-c) not sampled
372 in the field. The field sampling frequency or the structural characteristics of the sampled wetlands likely
373 did not allow capture of all the possible states of TN: this reveals the ability of the model to explore many
374 other possible states of the planktonic TNs and other trajectories of TN. In particular, the predicted
375 *Proto/MesoZ* regime has not yet been identified at the Charente Maritime sites, but work in progress at
376 other Atlantic arc territories has identified related TNs (F.-X. Robin, pers. comm.). Finally, bacteria were
377 frequently present in the ecosystem, and they occupied a prominent place in the model (Table SM1–2,
378 Table 2). Bacteria appeared to oscillate frequently (Fig. 4a), although this was not visible in the merged
379 state space (i.e., bacteria frequently appear and disappear within structural stabilities). The model
380 confirmed that bacteria are frequently grazed by their grazers, as are small protists (Pernthaler 2005, Šimek
381 et al. 2013). Indeed, the high level of control of bacteria by the protozoa in freshwater ecosystems is already
382 known.

383 **Power and drawbacks of discrete-event models**

384 An increasing number of TN models have been developed (Mitra et al. 2007, Kriest et al. 2010, Thébault
385 and Fontaine 2010, Turner et al. 2014, Kéfi et al. 2016, Hansen and Visser 2016, Kloosterman et al. 2016).
386 But they still suffer from three main limitations: limited size and complexity, and a frozen (static) network
387 with frozen (i.e., topology) interactions. In this study, we proposed a novel model family (called the EDEN
388 framework (Gaucherel and Pommereau 2019, Cosme et al. 2022)) to bypass these limitations. Our model
389 is based on a discrete-event system, well-known to computer scientists and more recently also some

390 molecular biologists (Thomas and Kaufman 2001, Reisig 2013). The price to pay for using our qualitative
391 model is that no quantitative and detailed dynamics are available; but in turn, no difficult parameterization
392 and construction are required. Consequently, such an approach is fully complementary to already existing
393 models in (trophic) ecology. Here, to the best of our knowledge, we provide for the first time a discrete
394 and qualitative model of TN to bypass such limitations. Of note, in continuity with previous theoretical
395 attempts (May 1973, Dambacher et al. 2003), we here open a new avenue for the use of such novel
396 qualitative models in (ecosystem and trophic) ecology. The foundations of this proposition, yet beyond the
397 present scope, are based on a theoretical consideration that assumes that ecosystems are informational
398 systems comprised of material components and immaterial processes (Gaucherel 2019) summarized into
399 their interaction networks.

400
401 Such a model is intuitive, easy to build, tractable, and rigorous (i.e., no trajectories have been forgotten
402 or added according to the mathematical Petri net engine). In addition, we claim that it does not require
403 any detailed or quantitative calibration, as no parameter is required. The central assumption of this
404 approach is that it is possible to summarize ecological processes into qualitative rules, possibly interpreted
405 as long-term and discrete events. Other studies have shown that this approach is not limited to trophic
406 processes and can be applied to a high diversity of social-ecosystems (Gaucherel and Pommereau 2019,
407 Mao et al. 2021). In this study, we were fortunate enough to collate several theoretical and observed
408 trajectories with which to validate the model, thus confirming that it is conform and accurate (Fig. 5).
409 Another quality of this type of model is to be heuristic, to force scientists questioning the knowledge they
410 have regarding the studied system and to collate it into a single coherent framework.

411
412 As perspectives, it appears suitable to model many TN stressors such as pollution, cleaning, drought,
413 invasive species, and/or climate changes (Mooney and Hobbs 2001, Mouquet et al. 2015). Any
414 complexification of the studied social-ecosystem is also possible, in theory, as the model is still far from
415 reaching its limits in terms of components, processes, and their nature diversity. It may then be used in a
416 more applied manner, for exploration of other scenarios by changing the initial conditions. Coupling this
417 model with other components describing the mechanisms behind these stressors would provide a relevant
418 territorialized model to anticipate trends in a context of global warming and coastline changes. In the near
419 future, it would be relevant not only to improve the model's realism but also to develop analysis tools
420 already used in similar studies focusing on social-ecological systems (Mao et al. 2021, Cosme et al. 2022).
421 Additionally, it would be relevant to complexify our discrete and qualitative approach by using quantitative
422 and multivalued schemes, to bridge the gap with more traditional (e.g., equation-based or individual-
423 based) models (Vézina and Platt 1988, Kéfi et al. 2016).

424
425 In brief, by modeling trophic networks with a novel (EDEN) framework, we recovered theoretical as
426 well as observed trajectories. With such qualitative models, the dynamics and predicted new states and
427 new trophic network functioning regimes that may be observed in the field can be better understood. We
428 illustrated these with a specific and well-documented freshwater trophic network. Such models provide an
429 intuitive and robust approach to diagnosing any trophic (and non-trophic) network by computing all
430 possible trajectories it can reach from a given chosen initial state. The known processes at play in the
431 system help identify all of the possible dynamics and thus counter-intuitive trajectories of such complex
432 (social-eco-)systems. Connecting such biotic dynamics to human-related activities can be expected to
433 provide additional insightful understanding of trophic systems.

434

435 **APPENDICES**

436 Additional Tables and Figures (Appendix 1)

437 **ACKNOWLEDGMENTS**

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439

DATA SCRIPTS CODE AND SUPPLEMENTARY MATERIAL AVAILABILITY

440 Data are available in this article (Tables and Figures) (*citation of the data* Gaucherel et al, 2023);
441 Scripts and code are available online: DOI:10.1111/2041-210X.13242 of the webpage hosting the data
442 <https://github.com/fpom/ecco> (*citation of the scripts and code* Pommereau et al., 2022);
443 Supplementary information is available online: XXXXDOI of the webpage hosting the data
444 <https://doi.org/10.5802/fake3.doi> (*citation of the scripts and code* Gaucherel et al, 2023);
445 [The references of the datasets, scripts and codes should also be present in the reference list and cited
446 in the text.]

447

CONFLICT OF INTEREST DISCLOSURE

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

450

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453

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