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Discrete-event models for conservation assessment of integrated ecosystems

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24 Abstract

25 Ecosystems are complex and data-intensive systems, and the ecologists still struggle to understand
26 them in an integrated manner. Models that miss key dynamics can possibly lead to fallacious
27 conclusions about the ecosystem fate. To address these limits and encompass whole and realistic
28 ecosystems, we develop here a qualitative model with the help of discrete-event models. This model,
29 based on formal Petri nets, was able to integrate biotic, abiotic and human-related components (e.g.
30 grazing) along with their processes into the same interaction network. The model was also able to
31 grasp ecosystem development, as defined by sharp changes of the interaction network structure
32 itself. Furthermore, the model was possibilistic and thus rigorously computed all possible ecosystem
33 states reached after a specific (present-day) initial state. This innovative approach in ecology then
34 allows to rigorously and exhaustively identifying all possible ecosystem trajectories and to study their
35 impacts and outcomes. For the first time in a realistic ecosystem, we illustrated such discrete and
36 qualitative models in the case study of temporary marshes in the Mediterranean part of France, the
37 Camargue delta. The model demonstrated that when marshes are exposed to extensive grazing the
38 presence of marsh heritage species (i.e. with a conservation value) is facilitated by opening up the
39 vegetation through various trajectories. This supports the commonly used management practices of
40 extensive grazing to conserve certain protected habitats. The detailed analysis of the computed
41 ecosystem trajectories allows exploring a range of recommendations for management strategies.

42

43 Keywords: Integrated ecosystem; dynamical structure; qualitative models; Petri nets; heritage
44 species.

45

46 Introduction

47 Historically, ecosystems have been predominantly studied through a focus on species communities
48 embedded into the environment, thereby reducing the abiotic part to a simplified resource input or
49 as an external source of perturbations (e.g. Kéfi et al. 2016; Thébault and Fontaine 2010). Yet, abiotic
50 components are an intrinsic part of the biophysical and socio-economical entity that defines an
51 ecosystem, thus playing a key role in its dynamics through various feedbacks (Frontier et al. 2008;
52 Gaucherel 2018). Nowadays most ecologists are convinced that to integrate all abiotic, biotic and
53 even human components is required to improve our understanding of ecosystem functioning
54 (Gignoux et al. 2011; Marquet et al. 2014). How to proceed in realistic and complex ecosystems
55 made up of so many components and processes?

56 Ecosystem interactions are not only impacting the ecosystem dynamics (Cincotta et al. 2000;
57 Cumming et al. 2014; Ostrom 2009), they are also drastically transforming the ecosystem structure
58 (Gaucherel et al. 2017). Unfortunately, despite a common assumption that integration of abiotic,
59 biotic and human-related components is required to understand how ecosystem dynamics and
60 structure may be affected, attempts in this line are considerably outnumbered by studies dedicated
61 to simplified systems, to frozen structures or to single elements (but see Geijzendorffer et al. 2017;
62 Titeux et al. 2017). In addition, the integration of components (variables) of multiple natures also
63 enlarges the window of potential ecosystem transitions to an extent that is difficult to manage in a
64 computational and comprehensive manner. In this paper, we propose a conceptual and
65 methodological framework to develop a generic model of ecosystem *functioning* and *development*

66 (i.e. structural changes over the long term, Gaucherel et al. 2017) that can be used for prediction and
67 for conservation recommendation.

68

69 Modeled biotic interactions have been defined as trophic or non-trophic (Thébault and Fontaine
70 2010), parasitic or mutualistic (Campbell et al. 2011; Kéfi et al. 2016), competitive or facilitative
71 (Lefever and Lejeune 1997), and more rarely, a combination of several kinds simultaneously.
72 Recently, multiplexes have been proposed to represent several types of interactions between the
73 same species nodes within the same ecological network (Brose et al. 2006; Kéfi et al. 2016), thereby
74 improving the coverage of ecosystem functioning, yet still strongly simplifying the overall ecosystem.
75 Multiplexes are interesting models that intend to grasp a subset of processes that play a dominant
76 role in the overall system dynamics (fates) and, in particular, to study the effects of species
77 interactions on the system stability. Yet, nothing prevents to build a more complete interaction
78 network of the studied ecosystem for this purpose, what we propose to call the *ecosystem graph*.

79 Rather than limiting models to species interactions only? Interaction networks could also be used to
80 integrate abiotic, biotic and human components and related processes to study their combined
81 impacts on ecosystem functioning and structure (here defined as the shape or topology of the
82 interaction network). The model can then be used to study trajectories of the system, eventually
83 under different scenarios. This poses methodological challenges, with computations for a large
84 number of components and parameterisation of the model being a known hurdle (Frontier et al.
85 2008; Gaucherel et al. 2019; Ricklefs and Miller 2000).

86 To handle potentially huge and complex interaction networks, new kinds of models and
87 simplification methods are required. Here, we combine two different ways to simplify the study of
88 realistic ecosystem trajectories: first, we model qualitative interaction networks, as already explored
89 in systems biology (Blätke et al. 2011; Reisig 2013); secondly, we focus only on the structural changes
90 of this network (Gaucherel and Pommereau 2019; Gaucherel et al. 2017). Hence, we model the
91 topological changes of the interaction network (the ecosystem structure), instead of the dynamics
92 (fluxes and abundances) it carries. The objective of this study was to explore the diversity of
93 trajectories of an ecosystem when integrating numerous abiotic and biotic components. Depending
94 on the way the interaction network (the ecosystem graph) has been defined, structural changes best
95 represent long term dynamics as illustrated by the arrival of invasive species or pollutants, species
96 extinctions or human migrations.

97 Here, we illustrate the “ecosystem development” concept for a vulnerable ecosystem within the
98 European habitat Directive; the Mediterranean temporary marshes, located in the Camargue, South
99 of France (Beltrame et al. 2013; Grillas and Roché 1997). Their conservation poses several challenges
100 (Medail et al. 1998; Rhazi et al. 2006) and the need to understand their possible fate is urgent.
101 Temporary marshes are fragile ecosystems often subjected to grazing as part of the management
102 (Beltrame et al. 2013; Duncan 1992). The general current understanding being that grazing reduces
103 the cover of dominant species, which are often common species, thereby creating space for new or
104 rare species (Chambers and Prepas 1990; Gough and Grace 1998). However, this understood impact
105 of grazing on vegetation greatly depends on the intensity of the grazing (Noy-Meir et al. 1989;
106 Sternberg et al. 2000) and negative conservation impacts from grazing regimes are not uncommon
107 (Bouahim et al. 2010). An improved understanding of the impacts of extensive and intensive grazing

108 on these fragile ecosystems would allow managers to adjust the conservation plans (Beltrame et al.
109 2013; Duncan 1992). Yet, this paper is an illustration of an original approach, rather than a predictive
110 ready-to-use model for conservation decisions in wetlands.

111 To develop an integrated model of such marshes, we borrowed the formalism (mathematical
112 framework) from theoretical computer science precisely built to handle structural network changes:
113 a qualitative Petri net. Petri nets belong to the wide category of discrete-event models (Giavitto and
114 Michel 2003; Pommereau 2010). Such models have proven powerful when applied to biological
115 networks but, to our knowledge, are almost absent in ecology (but see Baldan et al. 2015; Gaucherel
116 and Pommereau 2019; Gaucherel et al. 2017). We demonstrate the ability of Petri nets to integrate
117 numerous abiotic and biotic components of a system and to handle its sharp topological changes
118 over the long term. For this purpose, we defined two contrasting scenarios of temporary marsh
119 systems: marsh dynamics without and with extensive grazing. We listed multiple extensive grazing
120 impacts (e.g. trampling, browsing or fertilizing effects) possibly observed on various marsh
121 vegetation types, and avoiding more intensive cattle actions. We then tested the hypothesis (H1)
122 that, in a holistic view of the system, grazed marshes would favour the presence of typical marsh
123 biodiversity (heritage species) in comparison to non-grazed marshes (Grillas and Roché 1997;
124 Mesléard and Perennou 1996). Additionally, we demonstrated that our qualitative model was able to
125 identify a diverse and comprehensive range of trajectories (also called the “development”, i.e. all
126 future states and structural changes) of the integrated ecosystem (H2), thus allowing for the
127 identification of a rich set of management recommendations (Beltrame et al. 2013). We finally
128 discussed the specificities, limits and originalities of this discrete, qualitative and possibilistic
129 modeling.

130

131 [Materials and Methods](#)

132 [An integrated ecosystem Petri net](#)

133 To test our central hypothesis, we used the heritage species community as a proxy of ecosystem
134 structure changes. To analyse the impacts of grazing on a subset of species uniquely linked to the
135 temporary marshes in Camargue (Fig. 1a), we successively modelled: i) the hydrology of a temporary
136 marsh, ii) requirements of domestic animals, and iii) characteristics of species of the temporary
137 marsh ecosystems with conservation value. We represent the ecosystem by its interaction network
138 and with an *ecosystem graph* made of material components, the nodes, connected through their
139 related (immaterial) processes, the edges. For each set of processes, we identified the components
140 of interest based on literature and expert knowledge (Table 1), namely: surface water for temporary
141 marshes, bovines and equines for domestic mammals and species of conservation value listed by the
142 Tour du Valat (Grillas et al. 2004; Mesléard and Perennou 1996). The definition and integration of
143 these components and their processes were populated using literature and interviews with experts
144 at the Tour du Valat research institute (Appendix B, Tables S1 and S2, with references therein).

145 This resulted into a qualitative model consisting in 46 components with 105 interactions *stricto sensu*
146 and 57 interaction *constraints*, standing for mandatory processes (Fig. 1b and Appendix C). To gain
147 objectivity, all modelled components within the ecosystem should be connected to other
148 components (i.e. at least one process impacts it, and at least one process depends on it). We call
149 such connected nodes *characterized* components, and follow a protocol to avoid mistakes and misses

150 during the model definition (Gaucherel and Pommereau 2019). In the temporary marsh model, the
151 components best described are those associated with the central question addressed (*i.e.* concerning
152 species grazed by domestic animals and related species of temporary marshes, Appendix B, Tables S1
153 and S2). Finally, the remaining semi-characterized components were fixed if they had an impact on
154 the defined ecosystem but were not influenced by it (e.g. components relative to the atmosphere
155 and to grazing). The resulting model handles Boolean components (*i.e.* being functionally present or
156 absent, not to be confused with Boolean functions) and qualitative processes (being executed or
157 not), to ultimately explore all possible ecosystem developments in the future from an initial
158 ecosystem composition called the *initial state* (Gaucherel and Pommereau 2019; Gaucherel et al.
159 2017). Such an approach is called a possibilistic model, as it explores all possible outcomes from a
160 specific state, and strongly differs from models traditionally used in ecology (see discussion).

161

162 [Petri nets and a simplistic Predator-prey model](#)

163 Before showing the realistic models, we illustrated here the functioning of the model using a
164 simplistic predator-prey system (Fig. 2). Additional details on the principle and uses of Petri nets can
165 be found in literature (Gaucherel and Pommereau 2019; Pommereau 2010; Reisig 2013) and in
166 Appendix D. The ecosystem Petri net itself is developed in three successive steps: a) an intuitive
167 graph (*i.e.* a set of components and their related processes called the ecosystem graph) is built to
168 represent the studied ecosystem based on the leading question; b) we then transformed this
169 ecosystem graph into a formal model based on Boolean components and changing rules. The
170 components have an initial value that define the initial state, and every new state of the system
171 corresponds to different values and to a different topology of the ecosystem graph; c) applying these
172 rules on the initial state allowed computing new states, causally linked, on which the processes may
173 be repeated until no new state can be computed; this progressively yields *the state space* of the
174 ecosystem; d) to avoid building the state space by ourselves, we translated the rules into a Petri net
175 with SNAKES, a dedicated software tool (Pommereau 2015); e) the state space of the Petri net is
176 always strictly equivalent to the state space we would have obtained at step (c). It is worth noting
177 that steps (d) and (e) are usually hidden to the users who directly get the state space (c) obtained
178 from the computed state space (e).

179 Any ecosystem can be represented as a multi-digraph (*i.e.* a directed graph with parallel edges). In
180 this graph, every material component of the ecosystem (e.g. abiotic: precipitation; biotic: species;
181 human-related: domestic cattle) is represented by a *node*, with two Boolean states: “present” (the
182 component is functionally present in the system, also denoted “+” or On) and “absent” (functionally
183 absent of the system or “-” or Off). In the simplistic example predator-prey system only two nodes
184 are defined: the prey N and the predator P populations. Any *state of the system* is defined by the set
185 of “+” and “-” nodes (Fig. 2b). The maximal number of possible system states is $2^{\text{\#nodes}}$ and grows
186 exponentially with the number of nodes. The *rules* correspond to any physicochemical, bio-ecological
187 and/or possibly socio-economic processes (e.g. if there is (almost) no prey there is (almost) no more
188 predator), and thus represent all possible interactions between nodes composing the ecosystem
189 studied. The word “almost” specifies that an absent node does not necessarily mean that the
190 corresponding population has no more individual; it only means that the number of individuals of
191 this population is too low (or below a defined threshold) for having functional effects on the other
192 nodes. Such definition fit with the boundary limits of any metapopulation dynamics. In the predator-

193 prey system, two rules only are defined: R1, the predation itself: the predator eats the prey, and R2,
194 the mortality: without prey, the predator dies (Fig. 2b and 2c), then easily translated into a Petri net
195 (Fig. 2d).

196

197 A separate rule describes the *condition* and a *realization* parts as: “rule’s name: condition >>
198 realization” (see Appendix D for formal definitions). For a rule to be applied the state of the node
199 must satisfy its application condition. In this case, the application of the rule modifies the state of the
200 nodes as stipulated in its realization part. The firing of a rule, including testing its condition, is always
201 atomic (i.e. no other rule can interfere during the firing). In the predator-prey system, the rules are
202 written as $R1: P+, N+ \gg N-$ and $R2: N-, P+ \gg P-$ (Fig 2b). Since the rules modify node states, they
203 change the overall system state aggregating all node states. Therefore, the entire system shifts from
204 one state to another one through the discrete successive application of rules (Fig. 2c). The repeated
205 execution of the rules progressively produces the *state space*, which provides the set of all system
206 states reachable by the rules defined (Fig. 2c), often showing bifurcations; this can be equivalently
207 and more conveniently obtained through the Petri net computation. As a corollary, the system states
208 are connected to each other in the state space by transitions coming from some of these rules. The
209 size of this state space is usually much smaller than the number of possible system states, because
210 the computation starts from a specific initial condition and because rules have specific application
211 conditions. We develop some tools to automatically segment large state spaces into *merged*
212 (simplified or aggregated) state spaces (Appendix D).

213 Firing a rule independently to some others often leads to unrealistic trajectories (e.g. removing water
214 without removing fishes in it). Therefore, we defined particular rules, called *constraints*, preventing
215 the model from reaching such unrealistic (ecological) trajectories. Constraints have a condition and a
216 realisation part, just as rules *stricto sensu* do, and model mandatory events given the system state.
217 The sole difference between rules and constraints is that constraints have priority on rules *stricto*
218 *sensu*. In the predator-prey system, the system state $S_1 = (N-, P+)$ showing predators without prey
219 may be considered as unrealistic; so, the rule R2 may be transformed into a constraint ($C1: N-, P+ \gg$
220 $P-$). From a given state, the model first computes all trajectories opened up by the defined
221 constraints and then only, when all the system states obtained are realistic (i.e. no more enabled
222 constraint), the enabled rules are fired (Fig. 2c).

223 In brief, the discrete-event model proposed here is qualitative, mechanistic (processes are explicit),
224 deterministic (no stochasticity yet with several deterministic outcomes) and asynchronous (all rules
225 are applied as soon as possible, no rule conflict) (Gaucherel and Pommereau 2019; Reisig 2013). To
226 use deterministic rules also allows considering the extreme cases (with probability equals to 0 and 1)
227 to simplify the study into a discrete-event scheme, and to avoid the difficult (if not impossible)
228 quantification of transition probabilities. Our model is handling time qualitatively and with discrete
229 steps, meaning that any new step is the result of at least one qualitative change in the system. The
230 model is rigorously respecting precedence between states which corresponds to causality in most
231 cases (as the cause precedes its effects). This directly yields state spaces that are often, yet not
232 always, oriented.

233

234 Temporary marshes in Camargue

235 Temporary Mediterranean marshes are defined as small shallow depressions (<10 ha and less than
236 2m depth) fed by precipitation in autumn or spring (Fig. 1a). These ecosystems are characterized by a
237 natural alternation of flooding and drying out phases providing a niche for many aquatic (Appendix
238 A), amphibian and terrestrial species (Grillas et al. 2004). Temporary marsh allows the development
239 of an adapted flora rich in aquatic (e.g. *Zannichellia sp.*) and amphibious (e.g. *Damasonium*
240 *polyspermum*) species, thus totally dependent on water dynamics (Grillas and Roché 1997). Similarly,
241 the temporary marsh fauna usually show a two-phase life cycle (Grillas et al. 2004), such as for
242 remarkable amphibian species (e.g. *Pelobates culripes*) and dragonflies (e.g. *Lestes macrostigma*),
243 while ichthyofauna are absent (Grillas and Roché 1997). Moreover, the abundance of plant and
244 animal resources in these marshes make them a feeding habitat for many birds (e.g. *Anas crecca*), as
245 well as for wild (e.g. boars *Sus scrofa*) and domestic mammals (e.g. cattle).

246 Domestic cattle (e.g. equines and bovines) graze marshes during their terrestrial phase and/or their
247 drying out phase (Appendix A). The act of grazing entails various disturbances such as trampling,
248 browsing or fertilizing inputs (Mésleard and Perennou 1996). In the Tour du Valat domain, in the
249 Camargue delta, temporary (non-brackish) marshes account for 250 ha. Within the model, we do not
250 consider any other major disturbance than the extensive grazing by domestic animals, excluding
251 thereby the potential impact of invasive species and assuming no connection with permanent water
252 bodies (Duncan 1992; Grillas and Roché 1997; Mésleard and Perennou 1996). This point explains why
253 our present model, although realistic, is not yet ready-to-use for conservation management. We
254 developed a spatially implicit model (although it is possible to take into account for spatial units in
255 the ecosystemic graph, Gaucherel et al. 2012). Also, we considered relatively short term processes,
256 namely, intra- and inter-annual changes cumulated over less than five-year duration (e.g. vegetation
257 growth and boar herbivory), but explored the cumulative long term changes of the ecosystem (e.g.
258 vegetation succession, long drought and species extinction). Indeed, every process could be modeled
259 in theory; while in practice, we prevent combining processes with incommensurable time durations
260 to avoid difficult interpretations of state spaces coupling rapid and slow changes.

261

262 Methodology and scenarios

263 The impact of grazing on the marsh species was studied by comparing two contrasting scenarios,
264 namely no grazing (noted NG) and seasonal bovine grazing (SBG). The latter scenario corresponded
265 to extensive bovine grazing during spring and summer, and to the absence of bovine in winter and
266 fall (seasons during which bovines graze more productive lands, Duncan 1992; Grillas and Roché
267 1997). For an easier comparison, each scenario was simulated on the basis of the same sets of nodes
268 and rules; only their initial states differed. This allowed some rules to be enabled in one scenario but
269 not in the other one, thus corresponding to contrasted *development* for the same ecosystem, i.e.
270 contrasted NG and SBG sequences of states and specific state spaces. Since both scenarios were
271 based on the same nodes and rules, a subset of system states will be in common (except for the
272 modified node in the initial state). We first plotted the histograms of presence/absence counts of the
273 marsh species (ranging from zero to a maximum of seven species with conservation value) in each
274 state space to quantitatively visualise the differences between both scenarios.

275 Both (NG and SBG) initial states considered a temporary marsh to contain water in spring, with a
276 *Phragmites australis* population. The initial state of the SBG scenario had two more present nodes:

277 “Bovine” and “Seasonal bovine grazing”, fixed and semi-characterized nodes. This initial state
278 allowed four constraints to be enabled at each season shift (Appendix B, Tables S1 and S2). As each
279 state space was explicitly computed (i.e. all states are known and described), we may compute the
280 present and absent nodes in each state and look for states satisfying specific criteria (Appendix D). In
281 addition, we developed specific tool to *merge* both (NG and SBG) *full* state spaces (Appendix D) and
282 to automatically compute the *strongly connected components* (SCCs) of state spaces, defined as
283 structural stabilities gathering interconnected ecosystem states. All stabilities (containing many
284 ecosystem states) of the final merged state space were analyzed in terms of vegetation types and
285 average number of marsh species with conservation value. In such analyses, we plotted both NG and
286 SBG merged spaces colored by averaged species numbers and by their downward (causal) locations
287 relatively to the initial state. Finally, we performed two principal component analyses (PCAs) on the
288 two merged state spaces to analyze details in the dominant (merged) trajectories followed by the
289 ecosystem.

290 In the modelling approach presented here, every *material* component involved in the long term
291 changes of the ecosystem was represented as a node, while every (immaterial) process is
292 represented as an oriented edge between two or often more nodes. Such an informational
293 conception of ecosystems is based on a theoretical view still under test (Gaucherel et al. 2019), and
294 out of the scope of this paper. The focus here is that the Petri net engine allowed to mathematically
295 formalize the topological changes of the integrated interaction network also called the ecosystem
296 graph (Gaucherel et al. 2017). By this way, in a first step, every ecological process (e.g. predation,
297 parasitism, mutualism and competition) has a formal and qualitative definition whose consequences
298 in the interaction changes can be rigorously assessed, and merged with others (Fig. 2). Every
299 topological change of the ecosystem graph does not need to be quantified, but each topological
300 change will have a concrete effect on the system dynamics in the state space. In a second step, this
301 approach allows identifying all possible trajectories of the studied systems (Gaucherel and
302 Pommereau 2019), by handling the node and edge changes (the topology) of the ecosystem graph.
303 As the state space of the system has been demonstrated as equivalent to the defined Petri net
304 (Gaucherel and Pommereau 2019), it becomes possible to explore all reachable trajectories of the
305 ecosystem, and then to identify sustainable or potentially unwanted trajectories. The model provides
306 results that resemble those of differential equations, while equations focus on singular, statistically
307 most probable trajectories only (Dambacher et al. 2003; Thébault and Fontaine 2010). These
308 discrete-event and qualitative models strongly differ to others used in ecology by many properties
309 discussed below.

310

311 Results

312 State space and general analyses

313 The initial states for NG and SBG scenarios led to two different state spaces showing 1.6 and $1.54 \cdot 10^6$
314 states, respectively (Appendix C, Fig. S2). Both state spaces have $1.19 \cdot 10^6$ states in common,
315 hereafter called the reference set. By removing this reference set, we identified exclusive states for
316 the scenario without grazing (NG $\rightarrow 4.04 \cdot 10^5$ states) and with seasonal bovine grazing (SBG $\rightarrow 3.53$
317 $\cdot 10^5$ states). Considering the number of species with conservation value in these two set of states, the
318 SBG set is associated to a significant increase in heritage species (p-val $< 2^{-16}$, Fig. S2). Moreover, the

319 NG shows a more exclusive dynamics, as 58.59 % of the state successors of any NG state are also in
320 this NG set (6 % only for SBG).

321 Ecologically, the NG set suggests a marsh dynamics more frequently undergoing a strong drying out:
322 the exclusive NG states encompass less surface water (SW, Table 1), a saturated soil (Ssoil), more
323 brackish and saline soil (Brsoil, Sasoil) and long drought (Dr). All these nodes appeared significantly
324 more in the NG set than in the reference set ($p\text{-val} < 2^{-16}$), but the lack of grazing is not responsible
325 for this correlation and the marsh drying out. The SBG set is characterized by more spring states
326 during which grazing is taking place, but this frequency does not impact the number of species with
327 conservation value. In addition, the SBG scenario shows a significant decrease of helophytes (*Scirpus*
328 *maritimus*, *Juncus sp.* and *Phragmites australis*) compared to NG scenario, and a significant increase
329 of the light on the site. The merged state spaces of NG and SBG scenarios (Fig. 3a and 4a) highlight
330 the causal (chronological) trajectories of the ecosystem (by following downward the ecosystem
331 structural stabilities SCCs, Fig. 3a and 4a dashed arrows).

332

333 Ecosystem development and scenarios

334 The merged state spaces of NG and SBG scenarios highlighted the trajectories of the ecosystem in
335 terms of average species numbers in structural stabilities (colors in Fig. 3a and 4a). In terms of
336 conservation needs, cold (blue and green) stabilities should and may be preferred. The principal
337 component analysis (PCA) performed on structural stability profiles (each gathering many ecosystem
338 state compositions) does not provide a straightforward biological interpretation for the number of
339 heritage species (Fig. 3b and 4b): no univocal relationship is found between species number and
340 marsh properties, thus showing that any conclusion about heritage species is an emergent and
341 unpredicted behaviour of the ecosystem. The NG scenario produced a merge state space made up of
342 seven structural stabilities, gradually and irreversibly shifting toward a terminal stability with
343 herbivory (id. 0, Fig. 3a). The NG variance distribution of the PCA decreased sharply (with 48.8+22.2
344 % on the two main PCs), with PC1 closely related to climate and seasonal variations (left/negative
345 hand side with wetter and hotter ecosystem states, Fig. 3b) with the main abiotic components. The
346 PC2 is mainly related to the marsh vegetation and helophyte types, between rushes on negative
347 values and scirpae (*scirpus maritimus*) on positive values of this axis, highlighting the main biotic
348 components irrespective the abiotic (seasons) ones. When locating the structural stabilities (with id.
349 in Fig. 3) in the PC1/PC2 plane, the chronological trajectories of the ecosystem (Fig. 3, dashed arrows)
350 shift from the relatively dry and scirpae-type vegetation to relatively wet and richer ecosystem
351 states, and reversely then (Fig. 3-C).

352 The SBG scenario produced a much more complex merge state space made up of 34 structural
353 stabilities, gradually and irreversibly shifting toward four terminal stability groups (id. 1639 group A,
354 30715, 23379, 207642 and 205458 group B, 198407 and 201777 group C, and 192310 and 184877
355 group D, Fig. 4a, ellipses). Terminal stabilities show dominant monospecific vegetations: A bulrush
356 beds (*Scirpus maritimus*), B rush beds (*Juncus sp.*) and C/D reed beds (*Phragmites australis*). For
357 example, if the conservation managers want to promote reed beds with more patrimonial species,
358 they should follow processes leading to stabilities n° 204055 (Fig. 4a-C) and 190615 (D). The SBG
359 variance of the PCA decreased sharply too (41.5+17.8 % on the two main PCs), with the same
360 interpretation than for NG scenario, yet with PC1 reversed (wetter climate for positive vales). Most
361 ecosystem trajectories under NG scenario are projected in the upper and early part of the SBG

362 scenario merged space (not shown), thus confirming that bovines are later on reducing the marsh
363 salinity, opening up the lower strata of vegetation and thus providing longer trajectories (i.e. with
364 more discrete steps) with more monospecific vegetation types (the stability groups, Fig. 4). When
365 locating these stabilities in the PC1/PC2 plane (Fig. 4b), the ecosystem basically shifts from rich and
366 wet (spring) states on average (red arrows) to a drier ecosystem with various vegetation types
367 (stability groups). Yet, in terms of number of species with conservation value (Fig. 4a, colors), the
368 terminal stability groups are not systematically the poorest states. Optimal trajectories may be
369 selected on this basis, in particular those reaching some decisive and richer stabilities (id. 590014,
370 314211 and 140448, Fig. 4b, arrows). The ecosystem may stay indefinitely in such stabilities, but if it
371 leaves them, it irreversibly shifts toward some more specific and less diversified groups (ellipses
372 around groups). Indeed, with this vertically oriented state space, the model demonstrates that the
373 ecosystem may not recover previous states after reaching the terminal stability groups (Fig. 4a).

374

375 Discussion

376 This study is a step towards a more integrated understanding of any complex ecosystem as a whole,
377 simultaneously to a long term developmental trajectory analysis. With the conceptual framework
378 proposed here (Gaucherel et al. 2019), it avoids excluding a priori any ecosystem component and
379 process type. The simplified interaction network representation, here called the *ecosystem graph*,
380 combined to a topological handling of it, allows reaching this genericity in ecosystem integration and
381 exhaustive dynamics. The size and complexity of the model remains manageable mainly due to its
382 fully qualitative conception, thus providing a rigorous formalization of the *ecosystem development*
383 (Gaucherel et al. 2017). Similar models have been developed in computer science and in systems
384 biology, for example on molecular signalling networks (Blätke et al. 2011) but, to our knowledge,
385 they have never been applied in ecology. Other qualitative models are used in ecological studies, yet
386 focusing on small and rather unrealistic interaction networks (Dambacher et al. 2003; Gaucherel and
387 Pommereau 2019). The exhaustive trajectories computed by our models, in particular the long-term
388 effects on marshes of extensive bovine grazing, would be almost impossible to obtain through long-
389 term experiments or by more traditional modeling method (e.g. equation-based models or
390 individual-based models).

391

392 Using discrete-event models to evaluate conservation decisions

393 In this paper, we illustrated the understanding of a realistic and integrated ecosystem in the case
394 study of temporary Mediterranean marshes (in Camargue) with a discrete-event model based on
395 Petri nets. Temporary marshes are protected habitats located in a wetland landscape and hosting
396 several heritage species (Beltrame et al. 2013; Grillas and Roché 1997). Temporary Mediterranean
397 marshes are recognised as a vulnerable habitat in the European Habitat Directive and, as such, form
398 the direct object of conservation management plans. One of the means that is often included in
399 conservation management plans to maintain this habitat includes extensive grazing, but this
400 management entails challenges that require a balancing of economic and ecological costs (Cote and
401 Nightingale 2012; Cumming et al. 2014) and should be argued. Comparing the results from scenarios
402 without and with extensive grazing confirmed and even “demonstrated” the hypothesis that
403 extensively grazed marshes tend on average to host more species with conservation value (H1, Fig

404 4a-5a). This observation is in good agreement with the literature (Bouahim et al. 2010; Noy-Meir et
405 al. 1989; Sternberg et al. 2000). Our innovative approach also confirmed that the increase or
406 decrease of marsh species richness is not systematic, suggesting that it is not unequivocally related
407 to abiotic (hydro-climate) and anthropic (grazing) influences (Fig. 3a-4a, colored states). Basically, the
408 model suggested that bovines by their trampling and grazing tend to reduce the salinity of the marsh
409 and then open up the vegetation toward lower strata of the vegetation. On longer term,
410 monospecific vegetation types are more likely to occur (either with rushes, scirpae or reeds, Fig. 4b).

411 To validate the system development (chronological trajectories) implies a kind of expert *qualitative*
412 *validation* of the model. Computer specialists apply two separate ways for validating such discrete-
413 event and qualitative models (Reisig 2013): either the model is deemed *correct* (i.e. some modeled
414 trajectories, at least, are observed or logical), or the model is deemed *complete* (all trajectories
415 modeled are known/observed). Here, we assumed a list of isolated and atomic processes, to finally
416 compute and confirm a known holistic behaviour of the studied ecosystem. While each process
417 included in the marsh model was validated independently either by literature or experts (Appendix B,
418 Table S1-S2), their numerous feedbacks and the integrated response of the ecosystem as a whole
419 was not preconceived (hypothesis H2, Fig. 3b-4b dashed arrows). In particular, we defined the model
420 according to some (often negative, e.g. eating, trampling) impacts of grazing isolated processes, not
421 to any hypothesized (positive) impacts of grazing on heritage species: the benefit for conservation is
422 an emergent result of the model.

423 We focused on a set of species specifically linked to temporary Mediterranean marshes (Appendix C,
424 Table S3), and the model showed an increase in the number of such species under extensive bovine
425 grazing. This observation is in good agreement with what experts know about temporary marshes
426 (Beltrame et al. 2013; Grillas and Roché 1997; Rhazi et al. 2006). The modeled trajectories under
427 various grazing pressures were a qualitative validation (correctness, H2) of the model able to recover
428 them. This literature suggests that species number of temporary marshes would decrease under no
429 or under intense grazing regimes (Duncan 1992; Grillas et al. 2004), due to differential negative
430 impacts of cattle on vegetation. In this study, we focused on extensive bovine grazing, although other
431 impacts on the ecosystem could have been integrated (e.g. invasive species). This explains why this
432 paper is a realistic illustration of this original approach, rather than a predictive model directly usable
433 in making conservation decisions. This paper is the first to show that our conceptual framework and
434 methodological tool, initially developed on simplistic ecosystems (Gaucherel et al. 2019), is also
435 capable to recover empirical behaviours for complex and realistic ecosystems. Given that it embeds
436 multiple direct and indirect transitions simultaneously, this model provides a valuable help for
437 management to identify sustainable scenarios (Beltrame et al. 2013; Mesléard and Perennou 1996).
438 In addition, such a discrete and qualitative model appears quite powerful in the context of a few or
439 lacking data and knowledge on studied socio-ecosystems, as it requires a simplified and intuitive
440 assessment on processes at play in the ecosystem. Both of these perspectives appear at hand.

441

442 [Power and drawbacks of discrete-event models for ecosystem development](#)

443 An increasing number of integrated ecosystem models are being developed today (e.g. Gaucherel
444 and Pommereau 2019; Ings et al. 2009; Kéfi et al. 2016). Yet, the realistic integration of biotic, abiotic
445 and human-related components remains scarce and is hardly improving. In addition, although the
446 number of ecosystem models increases (Dambacher et al. 2003; Lafond et al. 2017; Thébault and

447 Fontaine 2010), they usually focus on relatively short term fluxes supported by frozen network
448 structures and rarely on alternative developmental (structural) trajectories. Tools to handle the
449 ecosystem integration with a rigorous (formalized) framework are still lacking. In this paper, we
450 developed a discrete-event, qualitative and non-stochastic model, based on Petri nets (Pommereau
451 2010; Reisig 2013), to analyse system properties and long term changes of any ecosystem. These
452 kinds of models can potentially be extended into quantitative, spatially explicit and multi-temporal
453 schemes to allow more realistic and applied analyses.

454 Such models provide at least four original properties that we would like to synthesize here and to
455 rapidly compare to existing models in ecology. i) The real strength of such Petri net models is to
456 exhaustively explore all possible trajectories; they are called possibilistic and asynchronous, because
457 each process effect on the ecosystem is computed independently (Fig. 3, 4). Differential equations
458 and statistical models, for example, change involved variables according to the same time step (Ings
459 et al. 2009; Thébault and Fontaine 2010). For this reason, discrete-event models are highly different
460 and complementary to usual models, most of them being probabilistic in spirit (e.g. equation-based,
461 individual-based and statistical models, Ginot et al. 2002; Kéfi et al. 2016). ii) In addition, Petri nets
462 have much less constraints on the modeled processes, as they allow processes that are not
463 mathematical functions (i.e. with a single output, Appendix B) as do equation-based models and
464 Boolean networks (Gaucherel et al. 2017; Thomas 1973). This advantage also avoids conflicting
465 processes. iii) To focus on qualitative (and structural) changes of the system that is, on topological
466 changes of the whole interaction network and ecosystem graph, is equivalent to exploring the
467 system changes over a long time period (Gaucherel and Pommereau 2019; Gaucherel et al. 2017). It
468 allows integrating a large number of ecosystem components (Fig. 1b), whereas even qualitative
469 models based on equations remain limited to approximately 12 variables for rigorously analyzing
470 system dynamics (Dambacher et al. 2003). iv) By the way, the qualitative and discrete natures of our
471 models allow a rigorous and analytical analysis of the studied ecosystem, as we have demonstrated
472 that exactly all states, not more not less, are computed in the state space (Gaucherel and
473 Pommereau 2019; Giavitto and Michel 2003). This ultimate advantage is found in other traditional
474 models too, such as equation-based models, but never combined to the other (i - iii) properties listed
475 here.

476 Yet, discrete-event modeling in ecology is still in its infancy and shows a number of limitations. As in
477 every modelling task, the model definition remains partly subjective and dependent on the network
478 definition (Blätke et al. 2011; Gaucherel and Pommereau 2019). In ongoing works, we are testing
479 strict protocols for model building and analyses, for instance based in the characterization of nodes
480 (Appendix C). Also, the model outcomes may vary depending on individual components and
481 processes, and we need to develop sensitivity tests to quantify the impacts of this variability on the
482 ecosystem emergent behaviours. Also, the PCA statistics used here help interpreting the computed
483 state space, but are not yet a reliable analyzing tool for such possibilistic spaces. Finally, the
484 calibration and validation (correctness) stages remain real challenges for such complex, integrated
485 and possibilistic models. On the one hand, developing a qualitative rather than a quantitative model
486 significantly reduces the amount of data (variables and parameters) that need to be collected: the
487 model provides an intuitive abstraction and remains simple, even for complex ecosystems. On the
488 other hand, the major cost and disadvantage of this simplicity is that the model remains blind to any
489 quantitative and probabilistic dynamics: we have no information about the intensity, probability and
490 duration of each trajectory computed here. To get some insights about variable variations and timing

491 information would require either to transform such discrete-event models into a more quantitative
492 one (which is feasible, Blätke et al. 2011; Reisig 2013) or to come back to traditional (e.g. equation-
493 based, individual-based or statistical models Ginot et al. 2002; Thébault and Fontaine 2010) models.

494 In brief, the proposed discrete-event model intentionally avoids rapid and quantitative processes (i.e.
495 related to ecosystem functioning), and focuses on long term and structural (developmental) changes
496 in the ecosystem behaviour. The modelling approach proposed here let us hope to grasp all relevant
497 interactions underlying the changes at the ecosystem level, whatever the ecological or even human-
498 related interactions. According to the question addressed, discrete-event models such as these Petri
499 nets can identify the components and processes responsible for specific responses of any integrated,
500 large and realistic ecosystem.

501

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508

509 References

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- 511 Baldan, P., M. Bocci, D. Brigolin, N. Cocco, and M. Simeoni. 2015, Petri nets for modelling and
512 analysing trophic networks. M. Heiner, and A. K. Wagler, eds. BioPPN 2015, a satellite event
513 of PETRI NETS 2015 1373.
- 514 Beltrame, C., E. Cohen-Shacham, M. Trouillet, and F. Guillet. 2013. Exploring the links between local
515 management and conservation applying the ecosystem services concept: conservation and
516 tourism service in Camargue, France. *International Journal of Biodiversity Science, Ecosystem
517 Services & Management* 9:166-177.
- 518 Blätke, M. A., M. Heiner, and W. Marwan. 2011, Tutorial. Petri Nets in Systems Biology. Magdeburg,
519 Germany, Otto-von-Guericke University
- 520 Bouahim, S., L. Rhazi, B. Amami, N. Sahib, M. Rhazi, A. Waterkeyn, A. Zouahri et al. 2010. Impact of
521 Grazing on the Species Richness of Plant Communities in Mediterranean Temporary Pools
522 (Western Morocco). *Comptes Rendus Biologies* 333:670-679.
- 523 Brose, U., R. J. Williams, and N. D. Martinez. 2006. Allometric scaling enhances stability in complex
524 food webs. *Ecology Letters* 9:1228-1236.
- 525 Campbell, C., S. Yang, R. Albert, and K. Sheab. 2011. A network model for plant-pollinator community
526 assembly. *Proceedings of the National Academy of Sciences (PNAS)* 108:197-202.
- 527 Chambers, P. A., and E. E. Prepas. 1990. Competition and coexistence in submerged aquatic plant
528 communities: the effects of species interaction versus abiotic factors. *Fresh. Biol.* 23:541-550.
- 529 Cincotta, R. P., J. Wisniewski, and R. Engelman. 2000. Human population in the biodiversity hotspots.
530 *Nature* 404:990-992.
- 531 Cote, M., and A. J. Nightingale. 2012. Resilience thinking meets social theory : Situating social change
532 in socio-ecological systems (SES) research. *Progress in Human Geography* 36:475-489.

533 Cumming, G. S., A. Buerkert, E. M. Hoffmann, E. Schlecht, S. v. Cramon-Taubadel, and T. Tschardtke.
534 2014. Implications of agricultural transitions and urbanization for ecosystem services. *Nature*
535 515 50-57.

536 Dambacher, J. M., H.-K. Luh, H. W. Li, and P. A. Rossignol. 2003. Qualitative Stability and Ambiguity in
537 Model Ecosystems. *The American Naturalist* 161:876–888.

538 Duncan, P. 1992. Equids in Grazing Systems, Pages 195-204 *Horses and Grasses. The Nutritional*
539 *Ecology of Equids and Their Impact on the Camargue*, Springer.

540 Frontier, S. P.-V., D., A. Lepêtre, D. Davoult, and C. Luczak. 2008, *Ecosystèmes. Structure,*
541 *Fonctionnement, Evolution: Sciences SUP. Paris, Dunod.*

542 Gaucherel, C. 2018. Physical concepts and ecosystem ecology: a revival? *Journal of Ecosystem and*
543 *Ecography* 8:DOI: 10.4172/2157-7625.1000259.

544 Gaucherel, C., F. Boudon, T. Houet, M. Castets, and C. Godin. 2012. Understanding Patchy Landscape
545 Dynamics: Towards a Landscape Language. *PLoS One* 7:e46064.

546 Gaucherel, C., P. H. Gouyon, and J. L. Dessalles. 2019, *Information, the hidden side of life:*
547 *Information systems, web and pervasive computing series. London, UK, ISTE, Wiley.*

548 Gaucherel, C., and F. Pommereau. 2019. Using discrete systems to exhaustively characterize the
549 dynamics of an integrated ecosystem. *Methods in Ecology and Evolution* 00:1–13.

550 Gaucherel, C., H. Théro, A. Puisseux, and V. Bonhomme. 2017. Understand ecosystem regime shifts by
551 modelling ecosystem development using Boolean networks. *Ecological Complexity* 31:104-
552 114.

553 Geijzendorffer, I., E. Cohen-Shacham, A. F. Cord, W. Cramer, C. Guerra, and B. Martín-López. 2017.
554 Ecosystem services in global sustainability policies. *Environmental Science & Policy* 74:40-48.

555 Giavitto, J. L., and O. Michel. 2003. Modeling the topological organization of cellular processes.
556 *Biosystems* 70:149-163.

557 Gignoux, J., I. D. Davies, S. R. Flint, and J.-D. Zucker. 2011. The ecosystem in practice : interest and
558 problems of an old definition for constructing ecological models. *Ecosystems* 14 1039-1054.

559 Ginot, V., C. Le Page, and S. Souissi. 2002. A multi-agents architecture to enhance end-user individual
560 based modelling. *Ecological Modelling* 157:23-41.

561 Gough, L., and J. B. Grace. 1998. Herbivore effects on plant species density at varying productivity
562 levels. *Ecology* 79:1586-1594.

563 Grillas, P., P. Gauthier, N. Yavercovski, and C. Perennou. 2004. *Mediterranean Temporary Pools. Arles*
564 *(France), Station Biologique de la Tour du Valat.*

565 Grillas, P., and J. Roché. 1997, *Vegetation of temporary marshes. Ecology and management:*
566 *Conservation of Mediterranean wetlands. Arles (France), Station Biologique de la Tour du*
567 *Valat. ed.*

568 Ings, T. C., J. M. Montoya, J. Bascompte, N. Blüthgen, L. Brown, C. F. Dormann, F. Edwards et al. 2009.
569 Ecological networks – beyond food webs. *Journal of Animal Ecology* 78:253–269.

570 Kéfi, S., V. Miele, E. Wieters, S. Navarrete, and E. Berlow. 2016. How Structured Is the Entangled
571 Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to
572 Increased Persistence and Resilience. *PLoS Biology* 14:e1002527.

573 Lafond, V., T. Cordonnier, M. Zhun, and B. Courbaud. 2017. Trade-offs and synergies between
574 ecosystem services in unevenaged mountain forests: evidences using Pareto fronts.
575 *European Journal of Forest Research*:10.1007/s10342-10016-11022-10343.

576 Lefever, R., and O. Lejeune. 1997. On the origin of tiger bush. *Bulletin of Mathematical Biology*
577 59:263–294.

578 Marquet, P. A., A. P. Allen, J. H. Brown, J. A. Dunne, B. J. Enquist, J. F. Gillooly, P. A. Gowaty et al.
579 2014. On Theory in Ecology. *BioScience* 64:701–710.

580 Medail, F., H. Michaud, J. Molina, G. Paradis, and R. Loisel. 1998. Conservation de la flore et de la
581 végétation des mares temporaires dulcaquicoles et oligotrophes de France méditerranéenne.
582 *Ecol. Medit.* 24:119–134.

583 Mesléard, F., and C. Perennou. 1996, Aquatic emergent vegetation. Ecology and management:
584 Conservation of Mediterranean wetlands. Arles (France), Station Biologique de la Tour du
585 Valat. ed.
586 Noy-Meir, M. Gutman, and Y. Kaplan. 1989. Responses of Mediterranean grassland plants to grazing
587 and protection. *J. Ecol.* 77:290-310.
588 Ostrom, E. 2009. A general framework for analyzing sustainability of social-ecological systems.
589 *Science* 325:419-422.
590 Pommereau, F. 2010. Algebras of coloured Petri nets. Lambert Academic Publishing (LAP).
591 Pommereau, F. 2015, SNAKES. A flexible high-level Petri nets library Proceedings of PETRI NETS'15.
592 LNCS 9115.
593 Reisig, W. 2013, Understanding Petri Nets. Berlin, Heidelberg, Springer Berlin Heidelberg.
594 Rhazi, L., M. Rhazi, P. Grillas, and D. El Khyari. 2006. Richness and structure of plant communities in
595 temporary pools from western Morocco: influence of human activities. *Hydrobiologia*
596 570:197-203.
597 Ricklefs, R. E., and G. L. Miller. 2000, *Ecology*. New York, USA, Freeman (4th edition).
598 Sternberg, M., M. Gutman, A. Perevolotsky, E. D. Ungar, and J. Kigrl. 2000. Vegetation response to
599 grazing management in a Mediterranean herbaceous community: a functional group
600 approach. *J. App. Ecol.* 37:224-237.
601 Thébault, E., and C. Fontaine. 2010. Stability of Ecological Communities and the Architecture of
602 Mutualistic and Trophic Networks. *Science* 329:853 -856.
603 Thomas, R. 1973. Boolean formalization of genetic control circuits. *Journal of Theoretical Biology*
604 42:563-585.
605 Titeux, N., K. Henle, J. B. Mihoub, A. Regos, I. R. Geijzendorffer, W. Cramer, P. H. Verburg et al. 2017.
606 Global scenarios for biodiversity need to better integrate climate and land use change.
607 *Diversity and Distributions* 23:1231-1234.

608

609

610 [Appendices](#)

611 [Appendix A: Temporary marsh functioning](#)

612 [Appendix B: Rules and constraints of the temporary marsh model](#)

613 [Appendix C: Protocol for the model definition](#)

614 [Appendix D: Formal definition of the marsh model](#)

615

616 Table

617

618 Table 1. The 46 components used in the temporary marsh model, with names and abbreviations.
 619 Whether these ecological components are useful for the ecosystem functioning (in plain) or of
 620 interest (in italic) for the addressed question is displayed, while species with conservation value are
 621 in bold. Components present in the initial states of both NG and SBG scenarios have an asterisk,
 622 while only the two components “Bovines” and “Seasonal bovine grazing” are added in the SBG
 623 scenario initial state.

ABBREVIATIONS	NAMES AND DEFINITIONS
Spring *	Spring
Sum	Summer
Fall	Fall
Win	Winter
Rain	Rain
Wind *	Wind
Tsun *	Total sunlight
Bsun *	Sunlight on bank
Ssun *	Sunlight on surface water
PeloC	<i>Pelobates cultripes</i>
Lest	<i>Lestes macrostigma</i>
Ish	<i>Isnhura pumilio</i>
Sus	Sus scrofa
Anat	<i>Anatidae</i>
Zan	<i>Zannichellia sp.</i>
SZan	Zannichellia seeds
Chara	<i>Characeae (Chara sp. and Tolypella sp.)</i>
SChara	Characeae spores
Phra *	Phragmites australis
SOPhra *	Phragmites australis storage organ
Sci	Scirpus maritimus
SOSci	Scirpus maritimus storage organ
SSci	Scirpus sp. seeds
Junc	Juncus sp.

SJunc	Juncus sp. seeds
SOJunc	Juncus sp. storage organ
Riel	<i>Riella helicophylla</i>
SRiel	Riella helicophylla spores
Dam	<i>Damasonium sp.</i>
SDam	Damaosnium sp. seeds
Fod	Fodder
Bov	<i>Bovines</i>
Eq	<i>Equines</i>
Cap	<i>Caprines</i>
Ov	<i>Ovines</i>
IBG	<i>Intensive bovine grazing</i>
IEG	<i>Intensive equine grazing</i>
SBG	<i>Seasonal bovine grazing</i>
SBEG	<i>Seasonal equine and bovine grazing</i>
SMG	<i>Seasonal equine, bovine and ovine grazing</i>
Phr *	Fresh phreatic water
Ssoil *	Saturated soil
SW *	<i>Surface water</i>
Brsoil	Brackish soil
Sasoil	Salty soil
Dr	Long drought

624

625

626 Figures

627

628 Figure 1. Map of the Camargue delta (a), with photographs of a temporary marsh at two different
629 seasons, and the ecosystem graph (b) defining the temporary marsh model. The Camargue is located
630 between the Mediterranean sea and the city of Arles (a), south of France, and hosts numerous
631 temporary marshes (a, insert © Flavie Barreda) alternatively drying and filling up during the year. We
632 modeled such marshes with 46 components (nodes, here with French names, b) connected through
633 105 interactions *stricto sensu* and 57 interaction constraints (b) standing for ecosystem processes
634 (Appendix B, Tables S5 and S6).

635

636 Figure 2. Illustration of a simplistic predator-prey system (a, b), with its qualitative dynamics (c), its
637 associated Petri net (d), and its computed state space (e). The system is made up of two components,
638 the prey (N) and predator (P) populations, and two interactions connecting them (rules R1 and R2),
639 as seen on the automaton (a). The corresponding Petri net is made of four places (P+, P-, N+, N-) and
640 two transitions R1 and R2, where unlabeled arcs have weight 1 (d). Starting with the presence of
641 both populations, it is possible to list all system states encountered (c), and to connect them with the
642 rules (the absent state is displayed in grey). The net is depicted in the initial state (c), and the
643 successive states may be deduced from the token (dots) circulation seen in the dynamics (b). The
644 state space (e) computed by the Petri net (d) is depicted with each state number (S_0, S_1, S_2) referring
645 and equivalent to the dynamics described above (c). Notice that a specific state of the system (S_3)
646 may not be reached from this initial condition and with these rules (c and d).

647

648 Figure 3. The merged state space of the NG (non-grazing) scenario (a), and its corresponding
649 statistical analysis (PCA, b). The merged state space should be read from top to bottom, through the
650 various trajectories connecting every structural stability (SCC, a, disks with identifiers) with various
651 rules (on edges). The stabilities are gathered (a, ellipses) according to their locations in the PC1/PC2
652 plan (b), and each stability is colored according to its average species number with conservation
653 values. Various trajectories may be identified in the state space: A herbivory (by boars *Sus scrofa*), B
654 development of lower strata (e.g. *juncus sp.*), and C persistent drought. The statistical analysis (b) is
655 easily interpreted according to the projections of the ecosystem components (Table 1) involved in
656 each stability, and allows reconstructing the ecosystem trajectories (a, vertical paths) in terms of
657 ecosystem composition (b, dashed arrows). For example, the trajectory combining drought (C) with
658 herbivory (A) is displayed in the PCA plane (a and b, dashed arrows).

659

660 Figure 4. The merged state space of the SBG (seasonal bovine grazing) scenario (a), and its
661 corresponding statistical analysis (PCA, b). The merged state space should be read from top to
662 bottom, through the various trajectories connecting every structural stability (SCC, a, disks with
663 identifiers) with various rules (on edges). The stabilities are gathered (a, ellipses) according to their
664 locations in the PC1/PC2 plan (b), and each stability is colored according to its average species
665 number with conservation values. The terminal stabilities (a, groups in capital letters) at the bottom
666 of the state space are characterized by their dominant monospecific vegetations: A bulrush beds
667 (*scirpus maritimus*), B rush beds (*juncus sp.*), and C/D reed beds (*Phragmites australis*). The statistical

668 analysis (b) is easily interpreted according to the projections of the ecosystem components (Table 1)
669 involved in each stability, and allows reconstructing the ecosystem trajectories (a, vertical paths) in
670 terms of ecosystem composition (b, dashed arrows). For example, red arrows (a and b) are pointing
671 three stabilities playing the role of bifurcations in the trajectories before the marsh drying out and
672 appearance of monospecific vegetations.

673

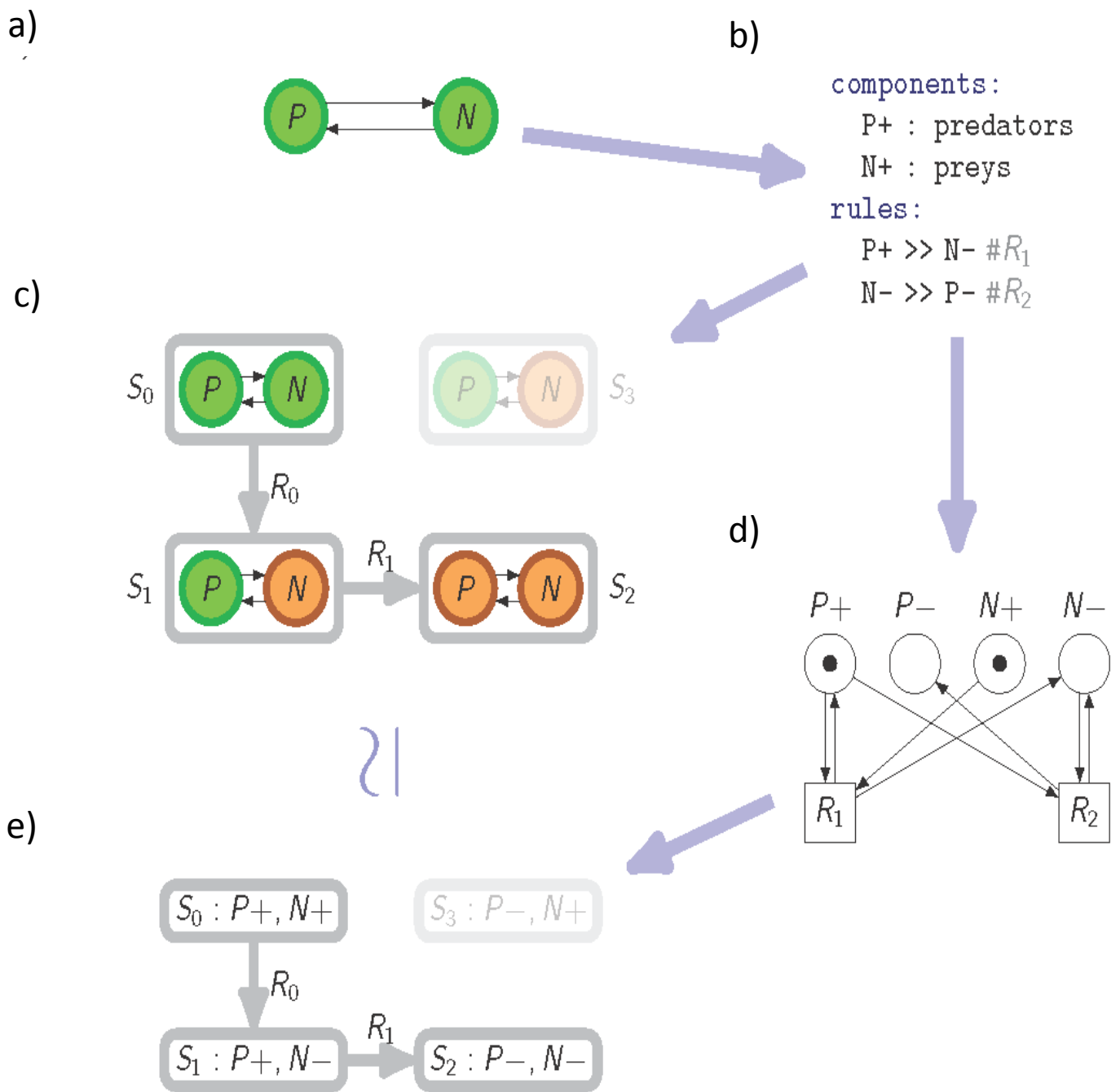


FIGURE 2

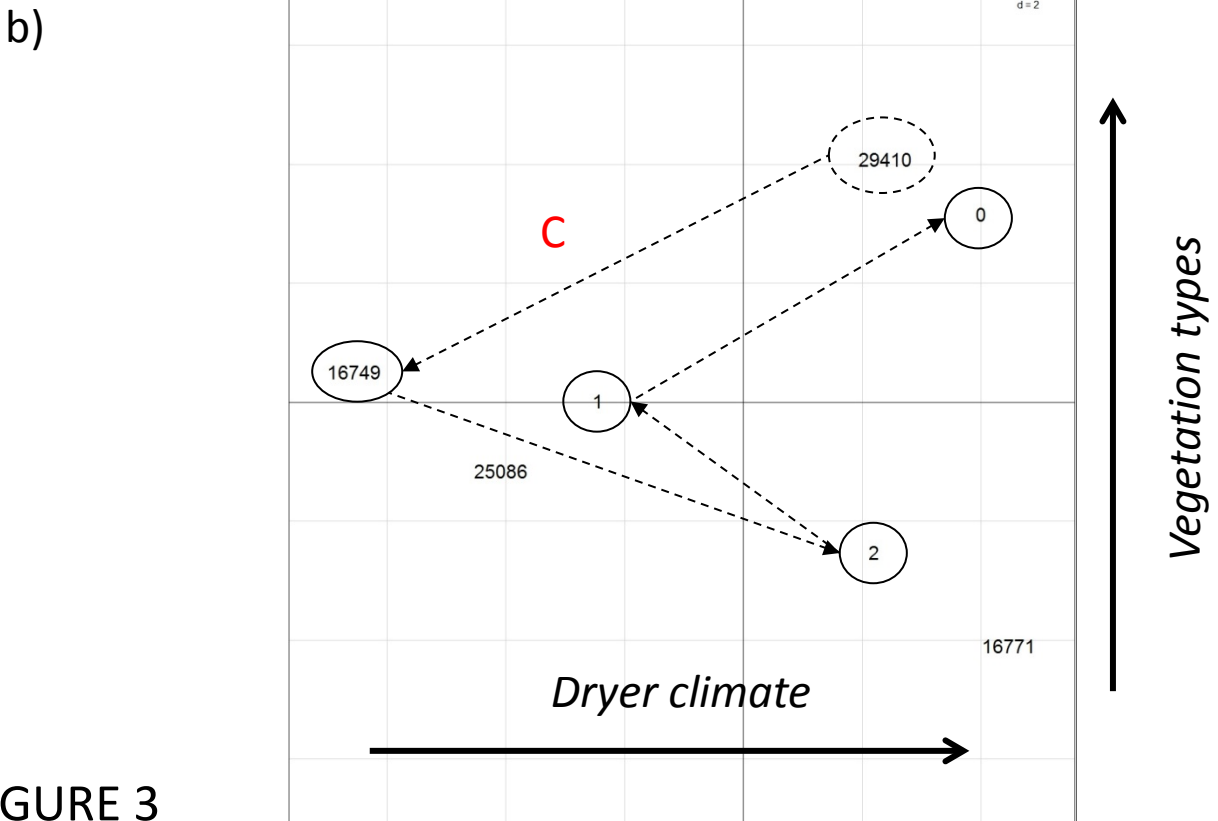
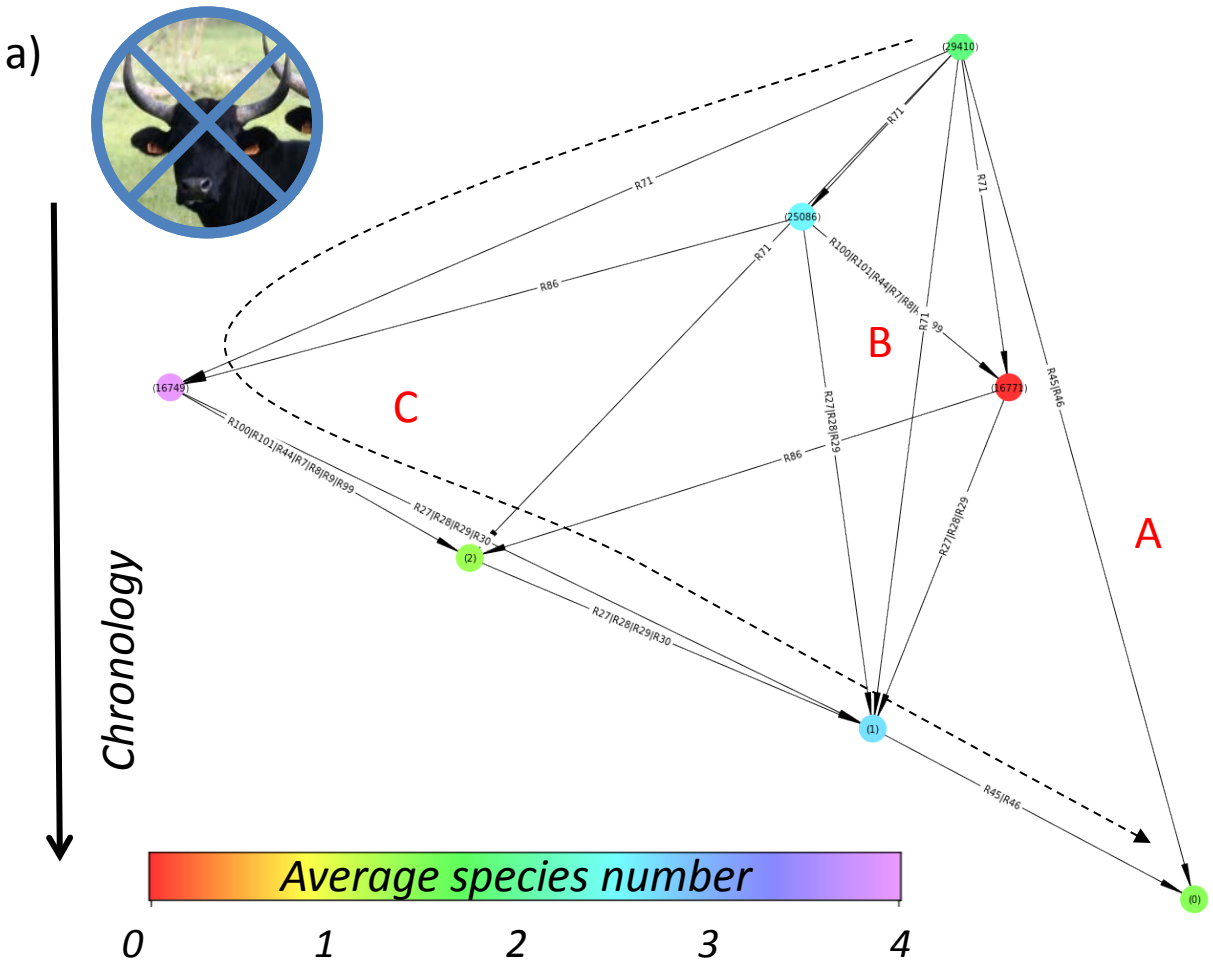
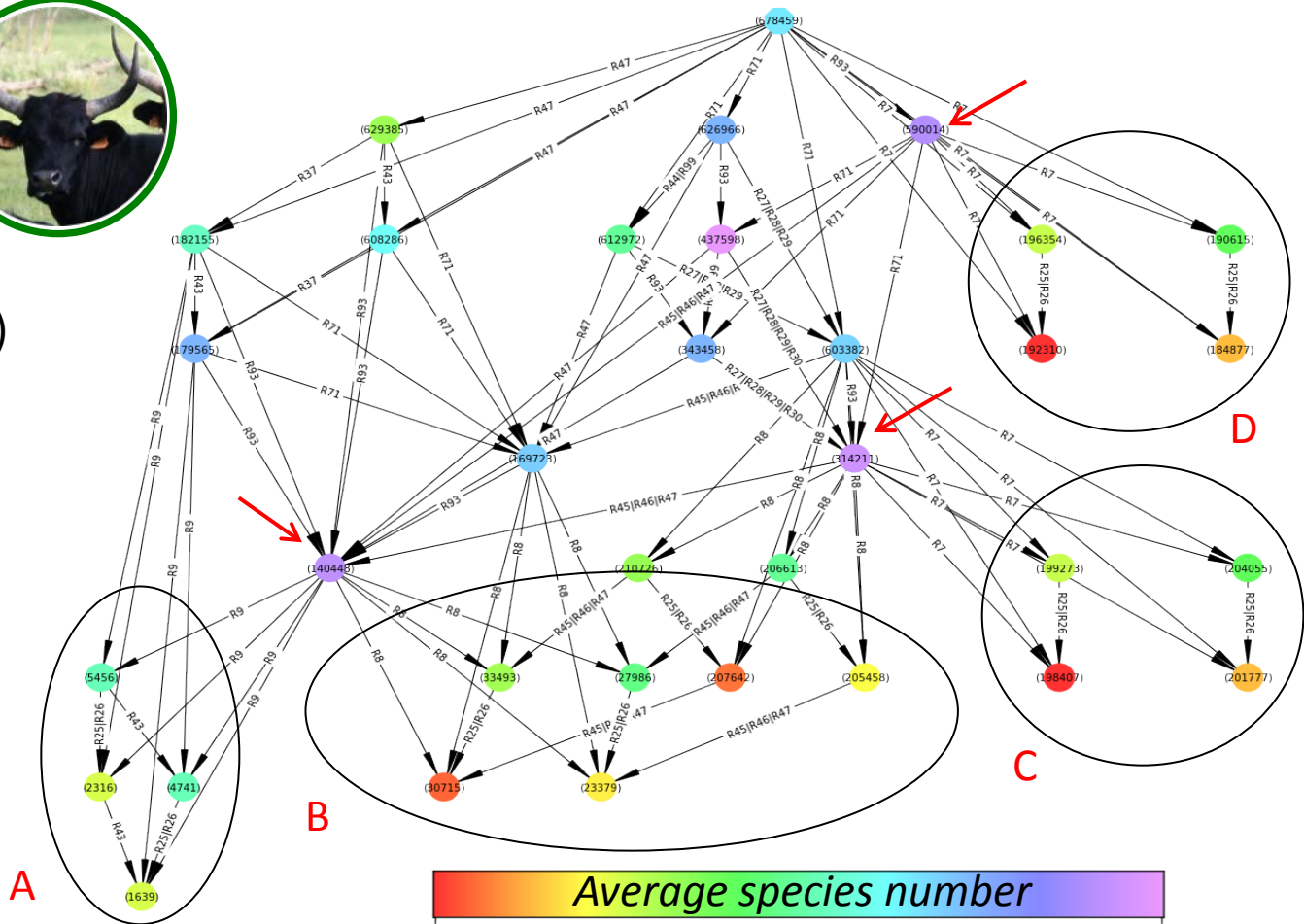


FIGURE 3



a)



b)

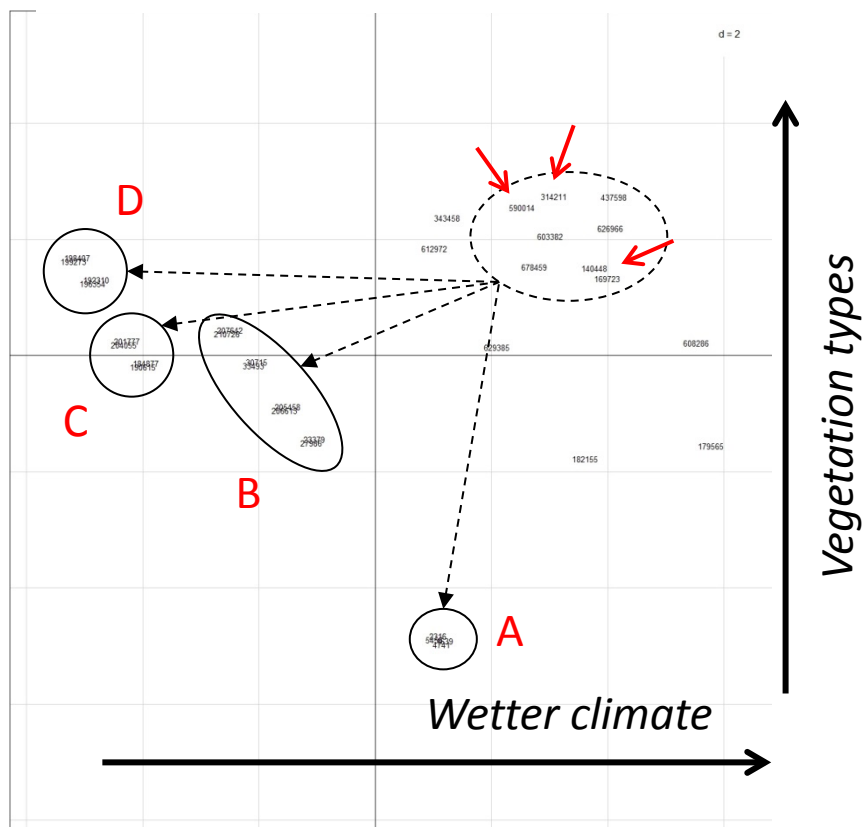


FIGURE 4

Chronology

