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Discrete-event models for conservation assessment of integrated ecosystems

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Abstract

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

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

Introduction

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

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

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

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

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

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

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

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

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

Materials and Methods

An integrated ecosystem Petri net

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

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

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

Petri nets and a simplistic Predator-prey model

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

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

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

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

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

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

Temporary marshes in Camargue

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

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

Methodology and scenarios

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

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

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

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

Results

State space and general analyses

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

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

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

Ecosystem development and scenarios

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

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

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

Discussion

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

Using discrete-event models to evaluate conservation decisions

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

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

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

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

Power and drawbacks of discrete-event models for ecosystem development

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

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

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

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

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

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

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Appendices

Appendix A: Temporary marsh functioning

Appendix B: Rules and constraints of the temporary marsh model

Appendix C: Protocol for the model definition

Appendix D: Formal definition of the marsh model

Table

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

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Figures

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

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

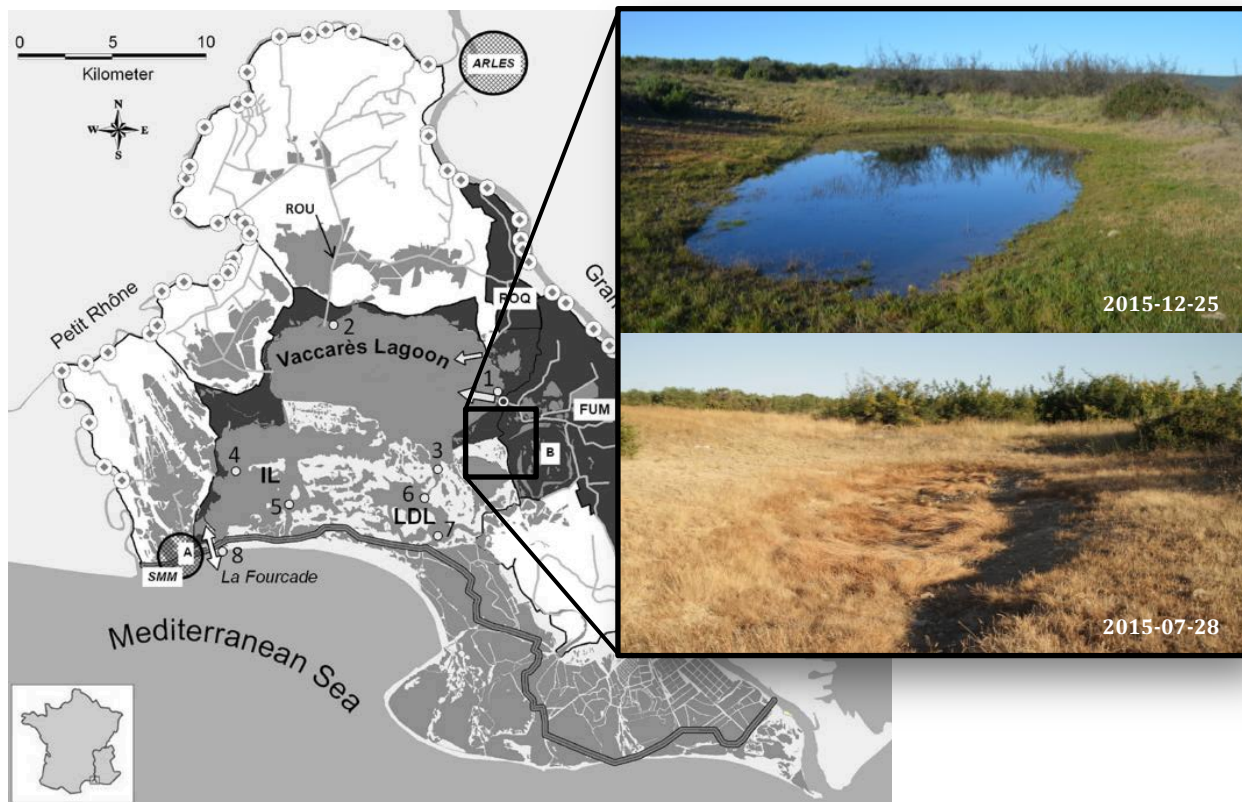
Figure 3. The merged state space of the NG (non-grazing) scenario (a), and its corresponding statistical analysis (PCA, b). The merged state space should be read from top to bottom, through the various trajectories connecting every structural stability (SCC, a, disks with identifiers) with various rules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

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

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a)



b)

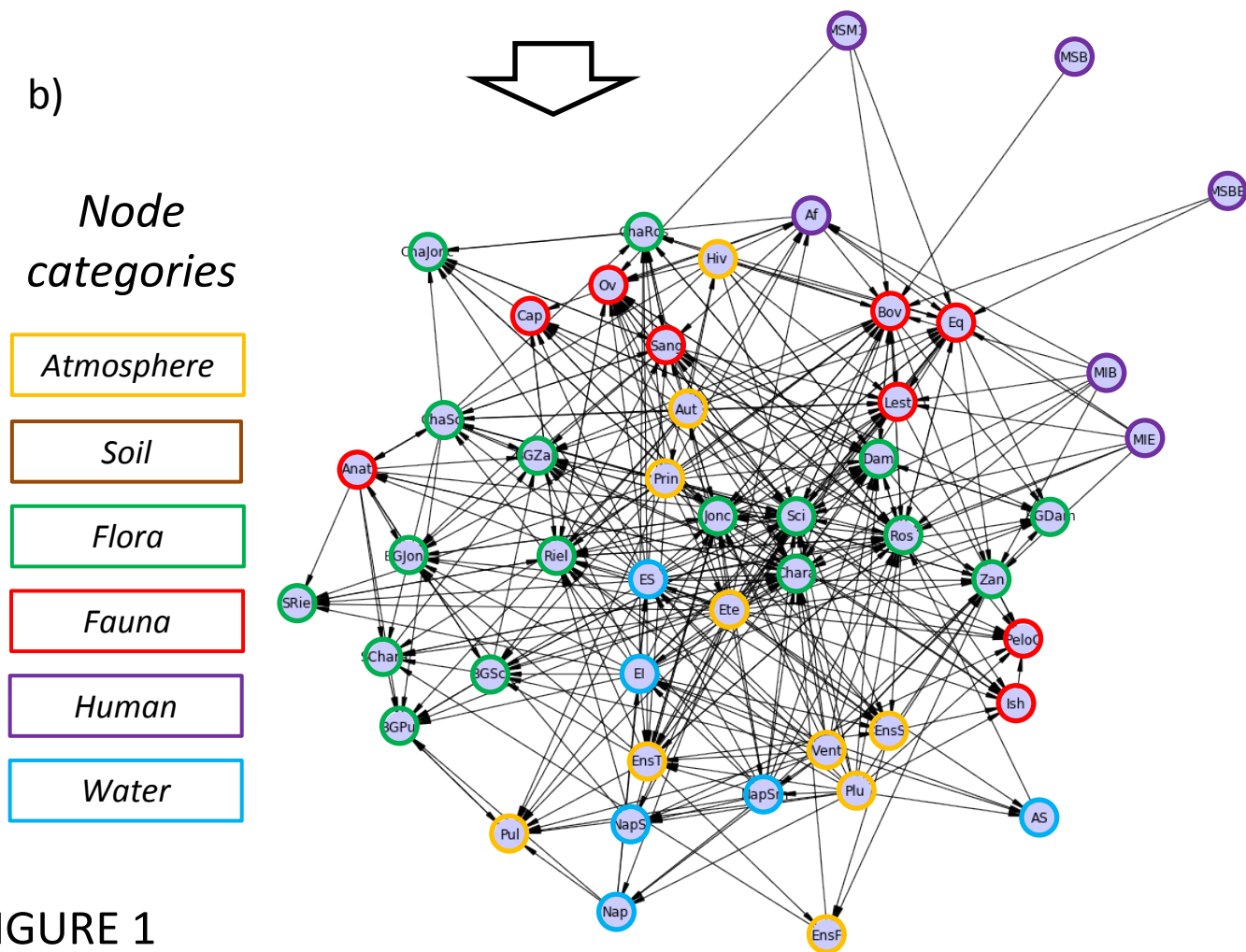


FIGURE 1

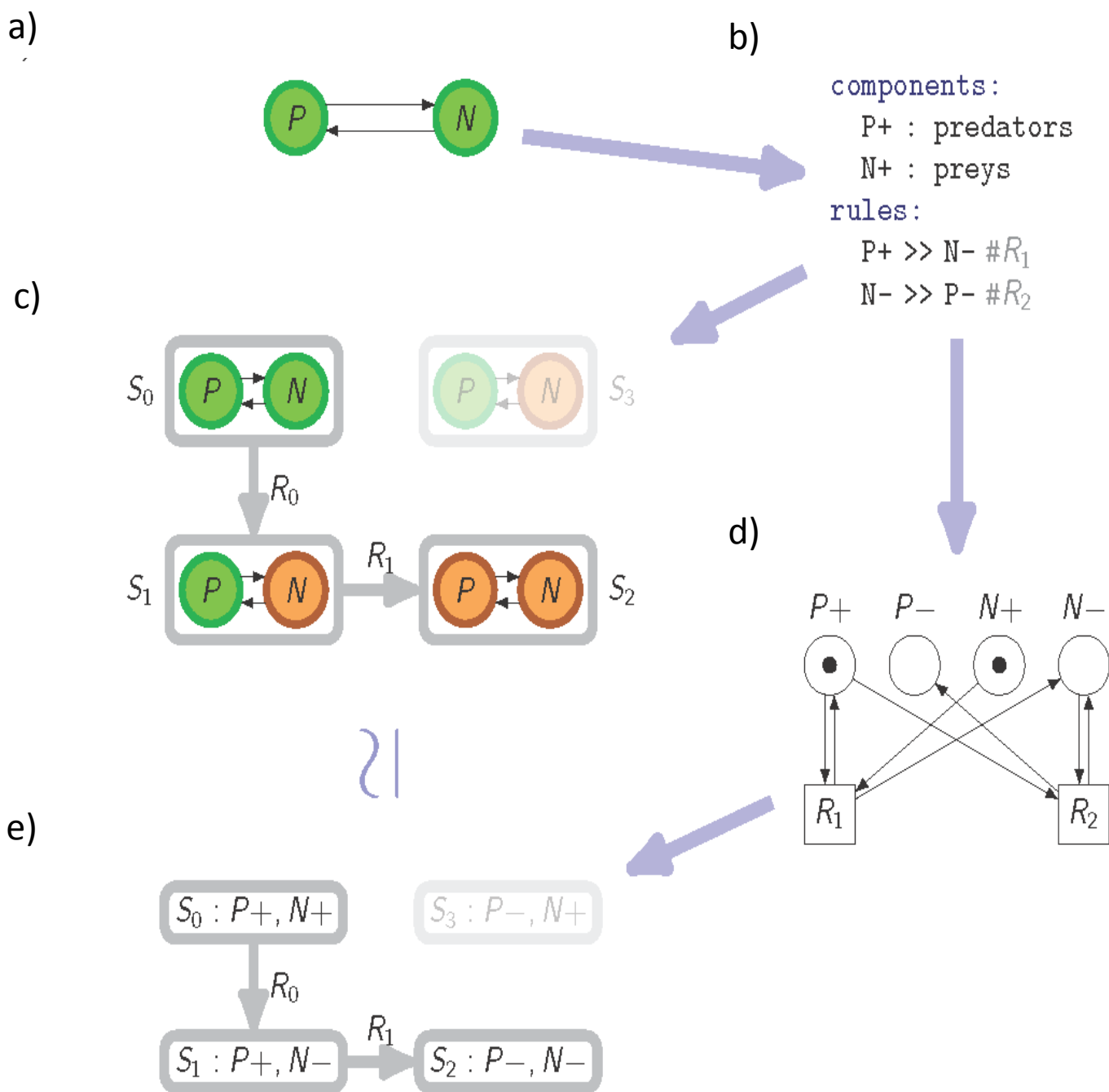


FIGURE 2

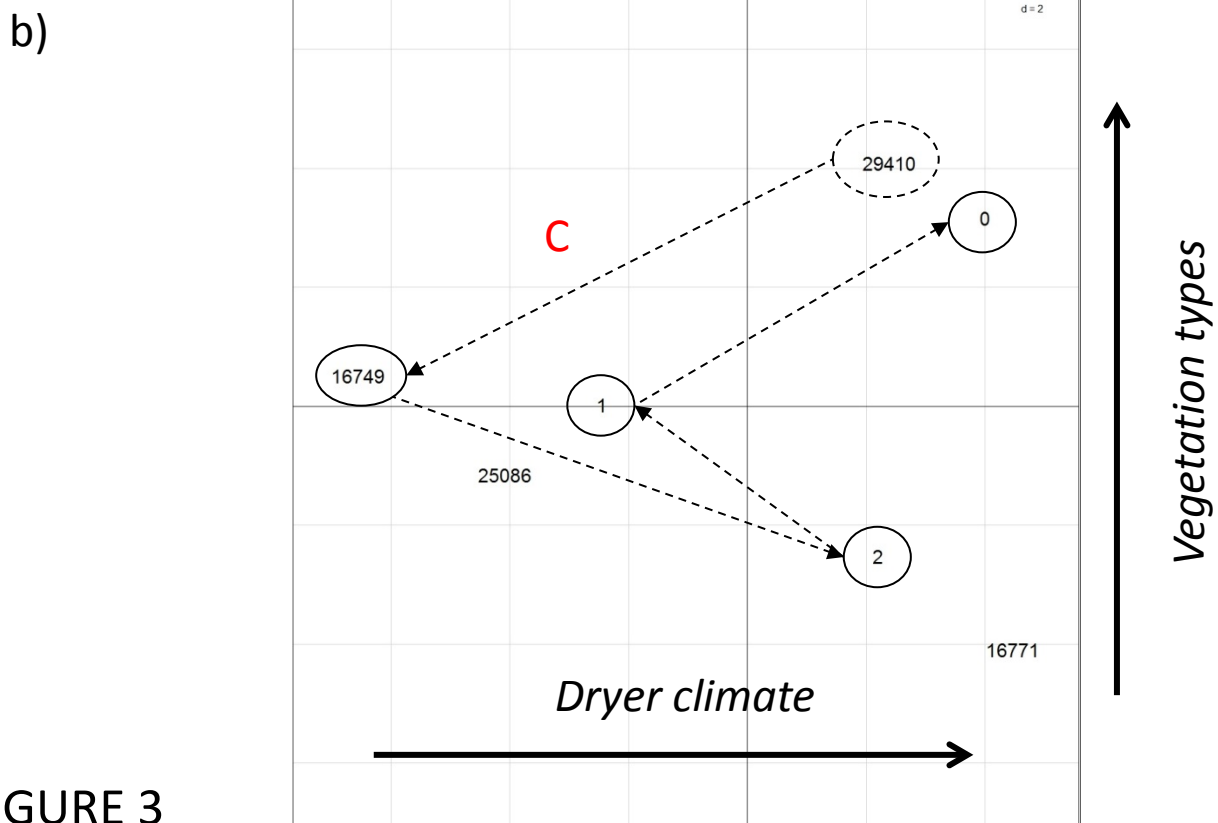
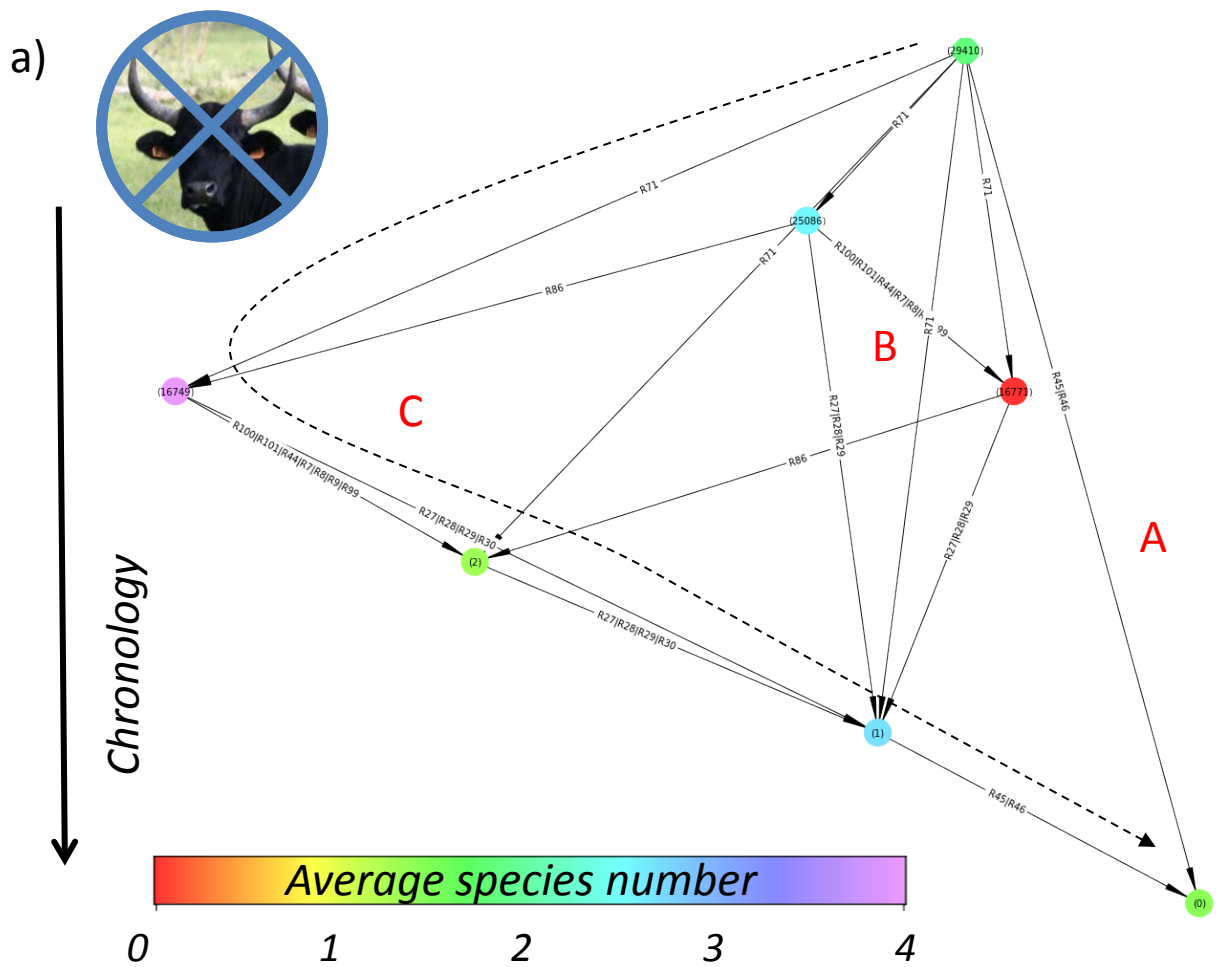
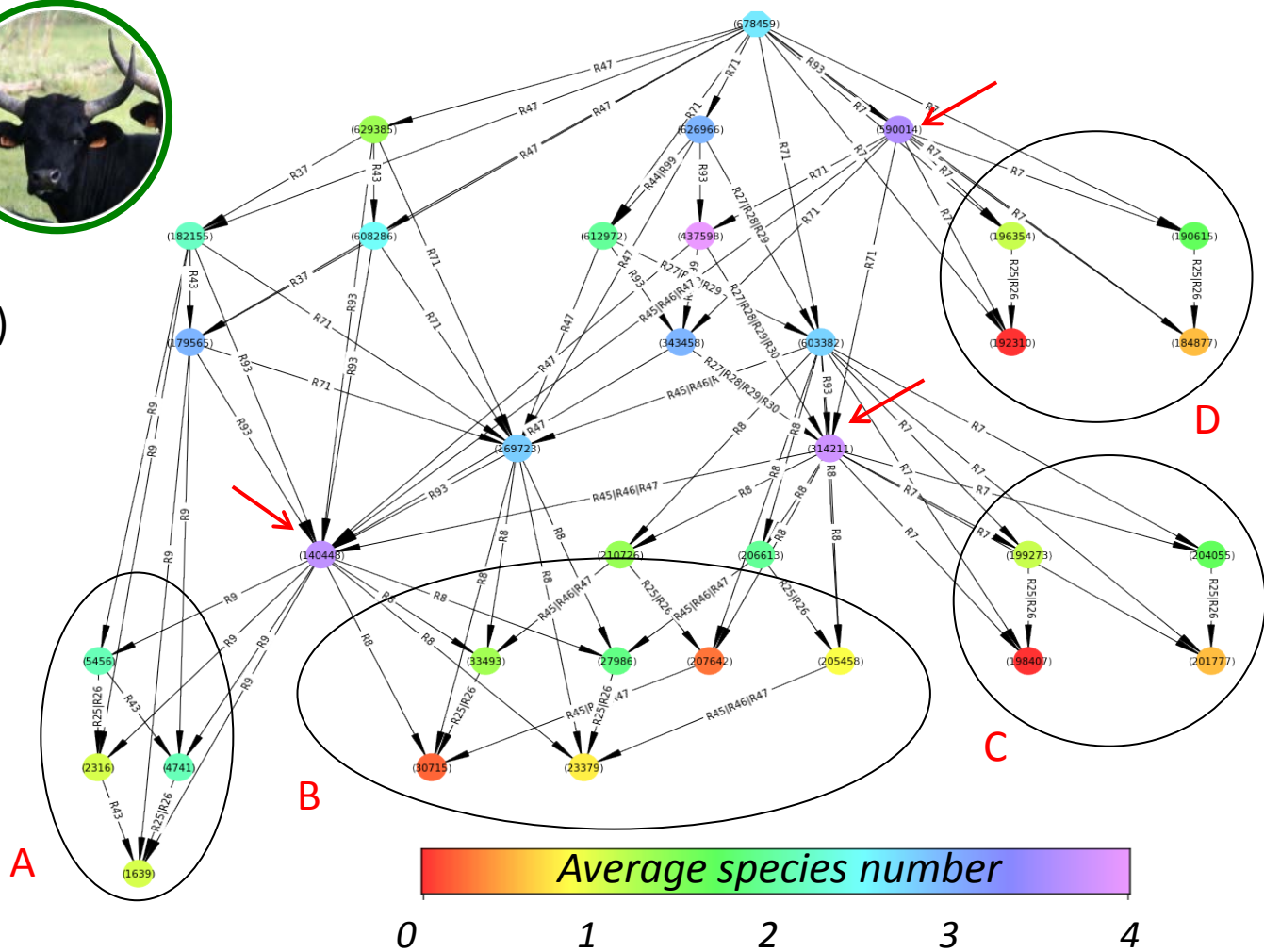


FIGURE 3



a)



b)

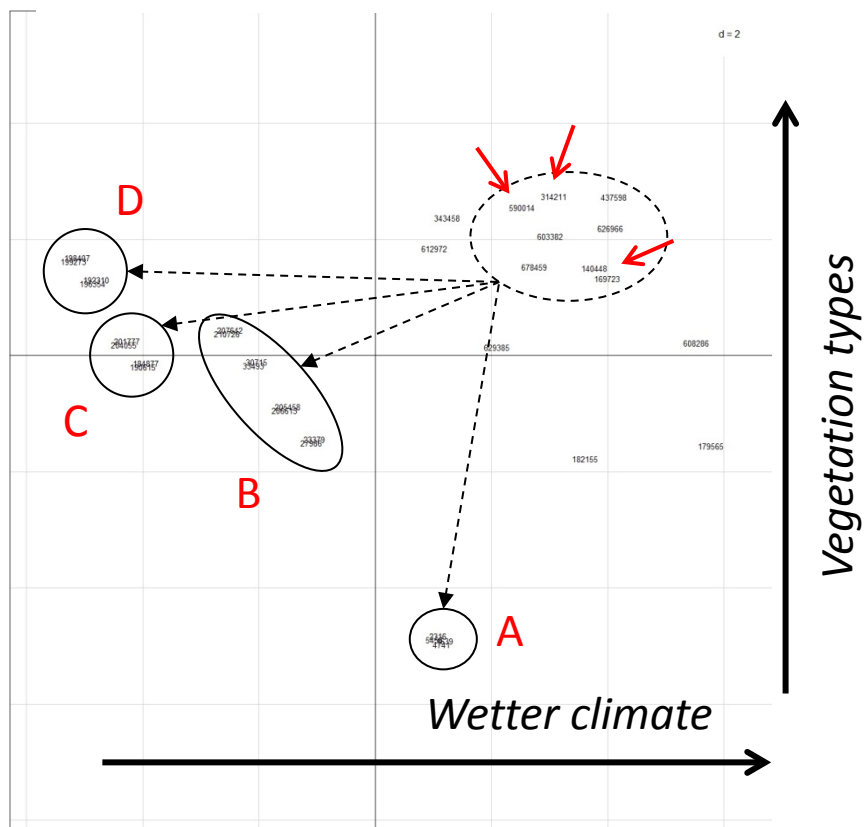
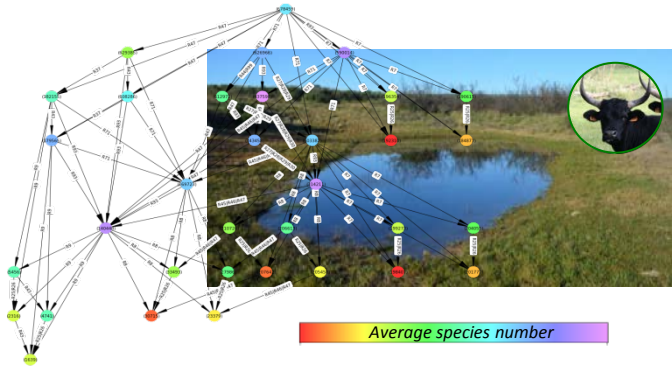


FIGURE 4

Chronology



Average species number