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Article

Qualitative Modelling for Bridging Expert-Knowledge and the Social-Ecological Dynamics of an East African Savanna

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Abstract: Sub-Saharan social-ecological systems are undergoing changes in environmental conditions, including modifications in rainfall pattern and biodiversity loss. Consequences of such changes depend on complex causal chains which call for integrated management strategies whose efficiency could benefit from ecosystem dynamic modelling. However, ecosystem models often require lots of quantitative information for estimating parameters, which is often unavailable. Alternatively, qualitative modelling frameworks have proved useful for explaining ecosystem response to perturbations, while requiring fewer information and providing more general predictions. However, current qualitative methods have some shortcomings which may limit their utility for specific issues. In this paper, we propose the Ecological Discrete-Event Network (EDEN), an innovative qualitative dynamic modelling framework based on "if-then" rules which generates many alternative event sequences (trajectories). Based on expert knowledge, observations and literature, we use this framework to assess the effect of permanent changes in surface water and herbivores diversity on vegetation and socio-economic transitions in an East African savanna. Results show that water availability drives changes in vegetation and socio-economic transitions, while herbivore functional groups had highly contrasted effects depending on the group. This first use of EDEN in a savanna context is promising for bridging expert knowledge and ecosystem modelling.

Keywords: ecosystem dynamics; discrete-event model; qualitative modelling; boolean model; state-and-transition model

1. Introduction

African savannas provide many ecosystem services to human societies [1]. Their high primary production support livestock herding and smallholder farming [2], while their large mammals populations contribute to large-scale nutrient flows and tourism [3–5]. The dynamic nature of such systems has been widely acknowledged, with water availability being the primary driver of vegetation [1,6] (and thus wildlife, [7]), tourism [8], pastoralism and rain-fed agriculture. On the other hand, human activities locally retroact on wildlife and vegetation [9,10]. These feedbacks between social-ecological components thus call for an integrated ecosystem management. However, a sound management strategy requires efficient forecasting methods for assessing the possible

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consequences of changes in environmental conditions. Here, we introduce an innovative modelling framework for assessing the effect of water availability and herbivores diversity on vegetation and socio-economic dynamics of an East African savanna.

Dynamic models are key for predicting the consequences of changes in drivers, such as changes in rainfall regime [11] or the increase herbivore populations [12,13]. So far, many savanna models consider a few variables [e.g. 14] and may thus overlook some possible outcomes of such changes on complex interaction networks. In addition, most models are quantitative and thus require precise quantitative data which are often unavailable or highly costly to obtain [15–17]. This feature makes difficult for most dynamic models to take qualitative expert knowledge [18] or historical anecdotes [19] into account. Yet, a deep and abundant qualitative knowledge about social-ecological systems can be obtained from local people such as pastoral communities, land managers and farmers [20].

In contrast, qualitative modelling such as state-and-transition models [21], loop analysis [22], qualitative reasoning [23], Boolean Networks [24,25] or timed automata [26] enable using expert-knowledge and require less information for model conception. They have proven useful for assessing the effect of press perturbations on whole interaction networks [27], providing recommendations for rangeland management [28], modelling cerrado dynamics [29,30] or modelling the dynamics of fish communities in response to fisheries management [26]. As abstract as it may seem, qualitative modelling has many interesting features for modelling ecological systems. It enables building realistic models in data-poor situations [31,32] while assuring more general predictions. Indeed, its lower precision facilitates the integration of multiple and heterogeneous components and relations from various knowledge sources, while being less sensitive to parameter changes [33–35]. A qualitative perspective is also a convenient way to study long-term dynamics by abstracting away small quantitative variations [25]. It also generally facilitates the representation of system structure and dynamics, as exemplified by state-and-transition models which represent reversible and irreversible vegetation changes as intuitive box-and-arrow diagrams [28], or rule-based models generating complex dynamics from simple "if-then" rules [30]. This role of facilitation is especially useful for decision-makers which may seek robust and easily interpretable results for designing management actions.

However, most current qualitative modelling frameworks are constrained by several assumptions or methodological limitations which have been discussed [36]. Limitations, for instance, include (depending on the chosen method) determinism, assumptions about parameters values and the form of interactions, the inability to make predictions or the tendency to produce ambiguous (undeterminate) predictions [36]. These limitations thus call for an innovative modelling framework.

Discrete-event models [37] have shown their ability to provide understanding and recommendations for ecosystem management [26,38]. These models represent system components as discrete (and often Boolean) variables and dynamics (called transitions) are defined by logical functions or "if-then" rules. Their initial and most successful applications can be found in systems biology, where they are used to model e.g. cell differentiation [39] or response to cancer treatments [40]. In ecology, they have been used to model the assembly of plant-pollinator networks [41], their response to extinctions [42] and their invasibility [43], but also spatialized predator-prey dynamics [44] and ecosystem services assessment [45,46]. Importantly, they are able to qualitatively grasp key features of ecosystem behavior, such as the bistable behavior of budworm-forest dynamics [24] or bush encroachment in some Ethiopian savannas [47], without requiring precise parameterization. In addition, like most qualitative models, they provide a graphical and intuitive representation of social-ecological dynamics, thus improving communication of complex phenomena towards the non-scientific public such as stakeholders and students [48]. Finally, their co-evolution with computer science contributed to the development of efficient analysis tools which could be highly relevant for social-ecological applications [47].

In this study, we introduce the *Ecological Discrete-Event Network* (EDEN) modelling framework [49] for modelling the social-ecological dynamics of an East-African savanna. The EDEN framework relies on a qualitative discrete-event formalism deriving savanna dynamics from "if-then" rules represent social-ecological events (e.g. species extinctions, rainfall occurrences or livestock herds migrations). System dynamics are represented intuitively as a State-Transition Graph, which shares the same structure as the aforementioned State-and-Transition Models used for rangeland management [28]. In contrast with existing rule-based models of vegetation dynamics [50], an EDEN model computes all possible trajectories and can thus account for rare events and their far-reaching effects [51].

Based on field surveys in Northern Tanzania, on expert knowledge (from Istituto Oikos, Nelson Mandela African Institution of Science and Technology) and on scientific literature [e.g. 52–54], we built this qualitative model to study changes in vegetation and socio-economic dynamics in response to persistent changes in environmental conditions, namely surface water availability and herbivore diversity. More specifically, we assessed whether these changes in environmental conditions (Q1) induced irreversible ecosystem transitions, (Q2) modified the set of existing vegetation and socio-economic transitions (i.e. whether some transitions appeared or disappeared) and (Q3) why (i.e. which rules drove these changes). Although vegetation dynamics are influenced by spatial structure [55], the model presented here is spatially implicit, assuming that it still enables testing the following hypotheses.

We made the following hypotheses: (H1) permanently changing environmental conditions will induce an irreversible change (i.e. impossibility to reach back the initial savanna state); (H2) as water availability is known to modulate woody plant recruitment [56], low (resp. high) water availability is expected to induce (resp. prevent) drought-related tree mortality (i.e. woodland-savanna, savanna-grassland and woodland/savanna-bare soil). In addition, water scarcity is also expected to affect herbivores, including livestock and thus pastoralism. Finally, (H3) reducing herbivores diversity (either directly or through water deprivation) is expected to modify vegetation transitions, but also tourism, which would be deprived of attraction (i.e. socio-economic transitions).

2. Materials and Methods

2.1. Field surveys

Field surveys were conducted in 2018 in the Arusha region, Northern Tanzania. In this region, annual precipitation is bimodal, with a long and a short rainy season (from March to May and November to December, respectively). Mean annual precipitation is approximately 700 mm [57]. Two sites were surveyed, the Gelai plains and the Meru savanna, in order to get a broad view of northern-Tanzanian savannas. Vegetation was diverse, ranging from open grassland to wooded savannas. Gelai plains ($2°47'52.1''S$, $36°06'03.1''E$) are grassy plains located between the mount Kitumbeine and Lake Natron, mostly used for tourism and pastoralism. The Meru savanna is located north to the mount Meru volcano ($3°09'34.5''S, 36°46'53.2''E$). They consist of a mosaic of grasslands, savannas and woodlands, where agro-pastoral activities are practiced [58]. We did not find any fire scars on tree trunks nor charcoals attesting recent fire on any site. More information about the sites we surveyed is available in Appendix A. These surveys were a major source of information for building a big picture of East-African savannas, and were ultimately used for model conception.

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2.2. *The EDEN modelling framework*

2.2.1. Variables

In the EDEN framework, variables represent any ecosystem component and are *Boolean* (i.e. can only take two values: "+" or "-"). A system *state* is a list of variables' valuation. For instance, a system composed of two variables (`v1` and `v2`) has its state described by its variables' values (e.g. {`v1+, v2-`}).

But what could justify the use of a Boolean abstraction in an ecological context? The answer lies in non-linear ecological phenomena, which appear ubiquitous in biology and ecology [17,59]. In such phenomena, a variable may exhibit a different response to a driver whether the driver is above or below a given threshold. Below the threshold, where the variable is not or slightly responding, the driver is considered "functionally inactive". Conversely, above the threshold, the driver is considered "functionally active" and may induce a qualitative change in variable response. As a simple ecological illustration, consider seed germination (the variable) triggered by soil moisture (the driver) [60]. Above a given (and often unknown [59]) threshold of soil moisture, a qualitative effect is observed on seed germination. In EDEN, we assume that such a threshold exists for each interaction represented in a model. In summary, by focusing on Boolean variables' activation and inactivation, we focus on the most abrupt changes in the ecosystem state and ignore quantitative variations that would exist below or above the threshold. Initially, the modeller defines a set of variables, their initial value and the set of "if-then" rules, as it has been done previously in other models [29,30,50]. The specific method applied here follows the work of [49].

2.2.2. "If-then" rules and their execution mode

The EDEN framework's formalism is based on *"if-then" rules*. Each rule is made of a *condition* part and a *realization* part (Table 1). A condition is a subset of active/inactive variables. When a state satisfies the condition of a rule, the rule is *enabled* and executed. When the rule is executed, its realization changes variables values. This process is symbolized by an arrow ($\rightarrow$ or $\gg$) (Table 1) [for formal details about rule execution, see 49]. The execution of a rule in a given state produces a *transition* resulting in a new system state (Fig. 1).

Such a rule-based formalism can be found in various ecological models, including cellular automata, agent-based models or fuzzy logic. When several rules are enabled in a given state, these models generally execute them simultaneously (i.e. synchronously) such that all variables values are updated at each time step. This may represent a strong assumption about ecological parameters as it implies that all variables always change at the same speed [61], which strongly affects the possible dynamics (which are thus deterministic if rules are non-stochastic), thus missing some event sequences (trajectories) and possibly creating spurious ones.

Alternatively, rules can be executed *asynchronously*: only one rule is executed at a time, which allows relaxing most assumptions about transitions durations. Therefore, a rule is executed every time its condition is satisfied in a given state and when several rules are enabled, each rule application opens an alternative trajectory. Note, however, that a rule may update several variables values synchronously (Table A2). Moreover, priority rules (called *constraints*) are also be used to model fast processes (discussed in Appendix B).

The asynchronous rule execution often generates many alternative system trajectories. In the EDEN framework, we do not consider the probability of each trajectory and adopt a *possibilistic* approach. Possibilism is based on the idea that rare (yet possible) events should also be considered in ecosystem dynamics, as they may have major consequences and would thus be highly relevant from a management viewpoint [62,63]. A possibilistic model is thus a non-deterministic, yet non-probabilistic, model.

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In summary, EDEN is a qualitative, asynchronous and possibilistic modelling framework.

Table 1. Rule set of the "Grasses-Trees-Cattle" toy-model. Variables are `Gr` (Grasses), `Tr` (Trees) and `Ct` (Cattle), which mostly consumes grasses.

N°	Condition		Realization	Interpretation
R1	`Gr+`	→	`Ct+`	Grasses attract cattle.
R2	`Gr+`	→	`Tr+`	Grasses promote tree growth.
R3	`Ct+, Gr+`	→	`Tr-`	Cattle control trees if there is enough grass.
R4	`Tr+`	→	`Gr-, Ct-`	Trees outcompete grasses and thus exclude cattle.
R5	`Tr-`	→	`Gr+`	Grasses reestablish if trees are cut.

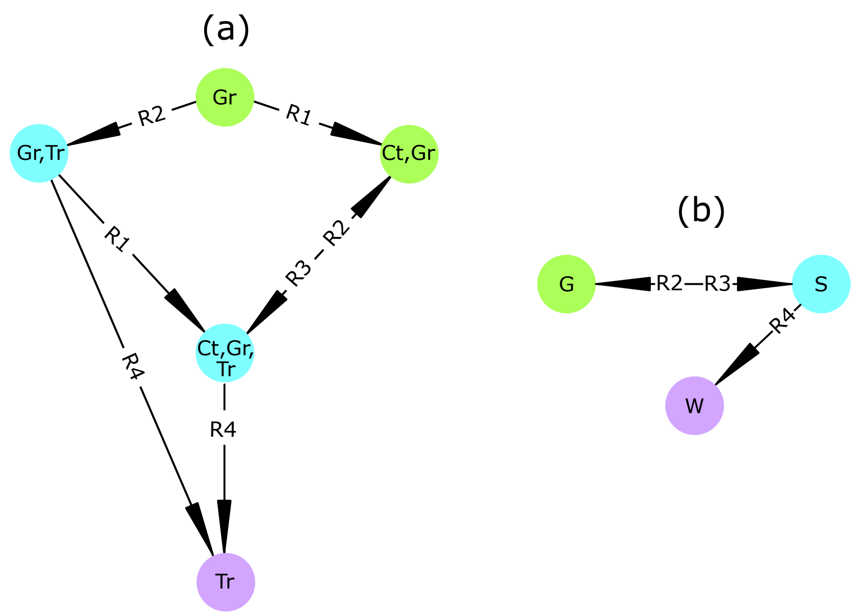

Figure 1. Transition graphs of the "Grasses-Trees-Livestock" toy-model (Table 1). (a) State-Transition Graph (STG) depicting every reachable states and transitions from the initial state. (b) Vegetation summary graph depicting transitions between vegetation types. This graph was made from (a) by merging nodes of the same color. In both graphs, node colors correspond to vegetation types, with green for grassland (G; defined as `Gr+, Tr-`), blue for savanna (S; `Gr+, Tr+`) and purple for woodland (W; `Gr-, Tr+`). Note that some rules may be defined and never be executed (e.g. R5).

2.2.3. The State-Transition Graph and its topological structures

The output of an EDEN model resulting from the successive rules executions is the *State-Transition Graph* (STG). The STG is a labeled directed graph whose nodes, edges and edge labels represent system states, transitions and the rule(s) driving the transition, respectively (Fig. 1a). A STG may include topological structures representing cyclic behaviors, transient states or stable states [49]. Here, we mostly focused on the concept of Strongly Connected Component (SCC), which represents a cyclic behavior. A SCC is a subset of states in which each state is reachable from any other state in this subset (Fig. 1a, e.g. states {`Ct,Gr`} and {`Ct,Gr,Tr`} form a SCC). Therefore, any ecosystem change within a SCC is reversible, either directly (as in Fig. 1a) or using a roundabout path. A SCC from which the system cannot exit is called an *attractor*. If an attractor is a single state, is is called a *stable state*.

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In Fig. 1a, the STG represents all reachable states from the initial state (topmost state). The oscillation between two states driven by rules R2 and R3 forms a Strongly Connected Component (SCC). Given the definition of our illustrative model (Table 1), this oscillation could be interpreted as a periodic control of woody plants by livestock. The bottom-most state has no successor and thus forms a stable state (i.e. a state which is impossible to exit). Details on STG computation have been discussed in another study [49].

2.3. Model description

We modelled social-ecological dynamics of a tropical savanna. Spatial and temporal extensions were not precisely defined. However, as we focused on various socio-economic activities, the model is valid at a scale where each activity can exist (e.g. the village and its surroundings). Regarding the temporal dimension, the model described the seasonal rainfall variations. However, its upper-bound temporal limit is not known as transitions have no fixed duration.

Table 2. Variables and their initial value.

Acronym	Variable	Description	Initial value
`Rf`	Rainfall	Seasonal rainfall	+
`Sw`	Surface water	Any reservoir where mammals water.	+
`Gw`	Groundwater	Water below the grass root zone.	+
`Ca`	Carnivores	Grazers' or browsers' predators.	+
`Gz`	Grazers	Mammals feeding on grasses.	+
`El`	Elephants	Elephant population.	+
`Bw`	Browsers	Mammals feeding on woody plants.	+
`Ct`	Cattle	Cattle breeds.	+
`Go`	Goats	Goat breeds.	+
`Gr`	Grasses	Mostly Poaceae.	+
`Tr`	Trees	Woody plants.	+
`Cr`	Crops	Rainfed and irrigated crops.	+
`To`	Tourists	People attracted by wildlife and pastoral livelihoods.	+

The model included 13 biotic, abiotic and socio-economic variables (Table 2), 49 rules and 8 constraints representing system transitions (Table A2 and A1). This model was built based on observations, local knowledge, scientific literature and assumptions. Observations were obtained through field surveys while local knowledge was obtained through interviews of stakeholders (NGOs, biodiversity conservation scientists and farmers). The reviewed literature was about semi-arid vegetation and water dynamics, farming, the role of herbivory, pastoralism in East-Africa, human activities regulation and livestock-wildlife interactions. Some rules corresponded to assumptions about the relation between some variables. Disturbances (climatic, biological, ecological or anthropogenic) or management actions were represented as rules (i.e. considered intrinsic to the ecosystem). We did not include fire in the model, as surveyed sites did not exhibit any recent sign of fire (i.e. no fire scar or black ash on tree trunks, nor burned grass clumps). In addition, satellite products such as NASA's burned area product from the MODIS sensors clearly show that the region studied in northern Tanzania, and the region as a whole between Lake Victoria and the Indian Ocean is among the least burned areas in Africa despite the presence of vegetation. The chosen initial state (i.e. the initial valuation of variables, Table 2) was partly arbitrary and aimed to represent the Meru savanna.

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2.4. Scenarios

We first built a "reference scenario" to consider in one single model non-persistent ecosystem conditions (e.g. seasonal changes in water availability or herbivores populations). Then four other scenarios (two related to water availability, two related to herbivory) were developed. The *"dry period"* and *"wet period"* scenarios represented permanently insufficient and sufficient surface water reserves, respectively. This was done by adding a constraint maintaining the "surface water" variable inactive (`Sw-`) or active (`Sw+`), respectively (Table A1). The *"no grazers"* and *"no browsers"* scenarios represented the permanent absence of grazers and browsers, respectively. This was done by adding a constraint maintaining inactive either grazers (`Ct-, Gz-`) or browsers (`Go-, Bw-, El-`), respectively (Table A1).

2.5. State-Transition Graphs analyses

First, to answer question Q1, we characterized the global properties of the STG for each scenario. The main property of interest is the reversibility (i.e. whether a path exists from any state to the initial state). In our case, STG reversibility is interpreted as the ability of the system to recover from any transition (perturbations or any other transition). If the STG is not reversible, this means that some transitions induce changes that cannot be reversed. In this case, the system ends up into one or several attractors (a SCC or a stable state). If an attractor is sufficiently small, it can be isolated to characterize its internal trajectories in detail. When the STG is not reversible, it can be represented using a Hierarchical Transition Graph [HTG, 64]. The HTG is a graph whose nodes are SCCs, transient sets of states and stable states, and transitions represent irreversible changes (as, by definition, reversible changes are included in SCCs) (Fig. A3). In this study, HTGs only included SCCs.

Often, STGs are reversible (and thus cannot be simplified by a HTG) and are too large to be analyzed by hand (Fig. A1). Therefore, to answer question Q2, we focused on specific aspects of the dynamics, i.e. vegetation and socio-economic states and transitions that were relevant to our model questions. For that purpose, we defined two partitions [65], namely vegetation types (based on grasses and trees) and socio-economic profiles (based on agriculture, pastoralism and tourism) (Table 3). In order to compare vegetation and socio-economic transitions between the reference and the other scenarios, we used such partitions to draw *summary graphs* [see 65, for detailed procedure] (Fig. 1b). A summary graph results from the merging of states belonging to the same group in order to summarize transitions (e.g. vegetation transitions) between groups of interest (e.g. vegetation types) (Fig. 1b). Summary graphs of vegetation types and socio-economic activities were called *vegetation summary graph* and *socio-economic summary graph*, respectively. Differences between the summary graphs of the various scenarios were then explained (Q3) by the analysis of the rule set.

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Table 3. Vegetation and socio-economic partitions. Each partition consists of several groups which are defined by state properties (i.e. the values of specific variables). Symbols $\wedge$ and $\vee$ correspond to the logical AND and OR, respectively. Agriculture (A) = `Cr+`, Pastoralism (P) = (`Ct+` $\vee$ `Go+`) and Tourism (T) = `To+`. Groups within a partition are mutually exclusive.

Partitions	Groups	State properties
Vegetation types	Bare soil (B)	`Tr-` $\wedge$ `Gr-`
	Grassland (G)	`Tr-` $\wedge$ `Gr+`
	Savanna (S)	`Tr+` $\wedge$ `Gr+`
	Woodland (W)	`Tr+` $\wedge$ `Gr-`
Socio-economic profiles	APT	`Cr+` $\wedge$ (`Ct+` $\vee$ `Go+`) $\wedge$ `To+`
	AP	`Cr+` $\wedge$ (`Ct+` $\vee$ `Go+`) $\wedge$ `To-`
	AT	`Cr+` $\wedge$ (`Ct-` $\vee$ `Go-`) $\wedge$ `To+`
	AP	`Cr+` $\wedge$ (`Ct+` $\vee$ `Go+`) $\wedge$ `To-`
	PT	`Cr-` $\wedge$ (`Ct+` $\vee$ `Go+`) $\wedge$ `To+`
	A	`Cr+` $\wedge$ (`Ct-` $\vee$ `Go-`) $\wedge$ `To-`
	P	`Cr-` $\wedge$ (`Ct+` $\vee$ `Go+`) $\wedge$ `To-`
	T	`Cr-` $\wedge$ (`Ct-` $\vee$ `Go-`) $\wedge$ `To+`
	$\emptyset$	`Cr-` $\wedge$ (`Ct-` $\vee$ `Go-`) $\wedge$ `To-`

3. Results

3.1. General observations

Scenarios had highly contrasted STGs (Table A3). All scenarios displayed as much or less transitions in their summary graph than that of the reference scenario. Only the "dry period" scenario had an irreversible STG. Its attractor was small (three states) and was thus characterized in detail (Fig. A4). Vegetation (Fig. 2) and socio-economic (Fig. 4) summary graphs highlighted specific aspects of ecosystem dynamics.

3.1.1. Vegetation transitions

In all scenarios, the initial state had a savanna vegetation (Table 3). In the reference model, bare soil and grasslands were both reachable from any other vegetation type (Fig. A2). Once reached, bare soil could only be colonized by grasses before trees to invade. Vegetation transitions were driven by herbivory and water availability. Rules responsible for these vegetation transitions in Fig. 2 can be visualized in Fig. A2 and are detailed in Table A2.

In the "dry period" scenario, the vegetation summary graph indicated that the lack of surface water did not modify vegetation transitions. However, the HTG showed that the system experienced sequences of irreversible transitions (Fig. 3a) towards a regime of seasonal grassland (Fig. A4). Once that regime was reached, woody plants were unable to colonize due to the lack of groundwater (R33).

In the "wet period" scenario, drought no longer drove of vegetation transitions. Transitions from woodland or savanna to bare soil were impossible as water was always sufficient (thus C9 cannot be executed) and tree mortality was only due to browsing (R29 to R31).

The "no grazers" scenario (i.e. without cattle and wild grazers) had the same vegetation summary graph as the reference scenario. Indeed, the only rule in the reference scenario involving grazers and affecting vegetation was rule R14 (which diminishes grass cover). As reduction in grass cover could be induced by drought-related rules (R6,R13), the transitions were maintained, although not necessarily by the same drivers.

Finally, when browsers (i.e. goats, mesobrowsers and elephants) were absent, tree mortality was only induced by drought (R13), which makes savanna and woodland shift into bare soil. Transitions from savanna or woodland to grassland were impossible.

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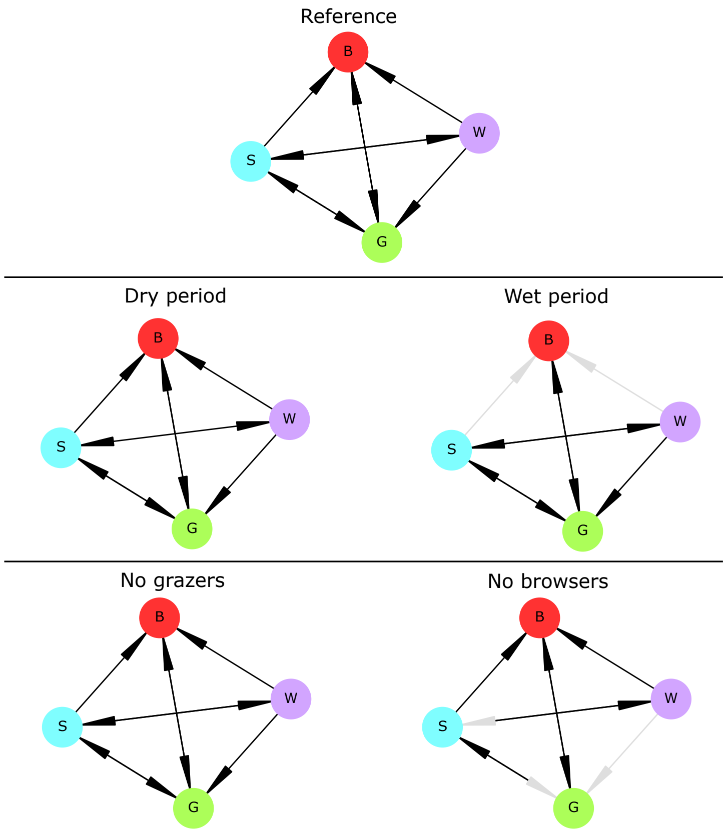

Figure 2. Vegetation transitions for each scenario Vegetation summary graphs for (a) the reference scenario, (b) the "dry period", (c) the "wet period", (d) "no grazers" and (e) "no browsers". Node labels indicate vegetation types as defined in section 2.5. Node colors are arbitrary and correspond to vegetation types. Grayed out edges are absent from the graph and are used to highlight the differences between the references and other scenarios. Grayed out arrow tips indicate that the transition was bidirectional and is now unidirectional.

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Likewise, the transition from woodland to savanna which resulted from the competitive advantage of grasses over trees in presence browsers was no longer possible.

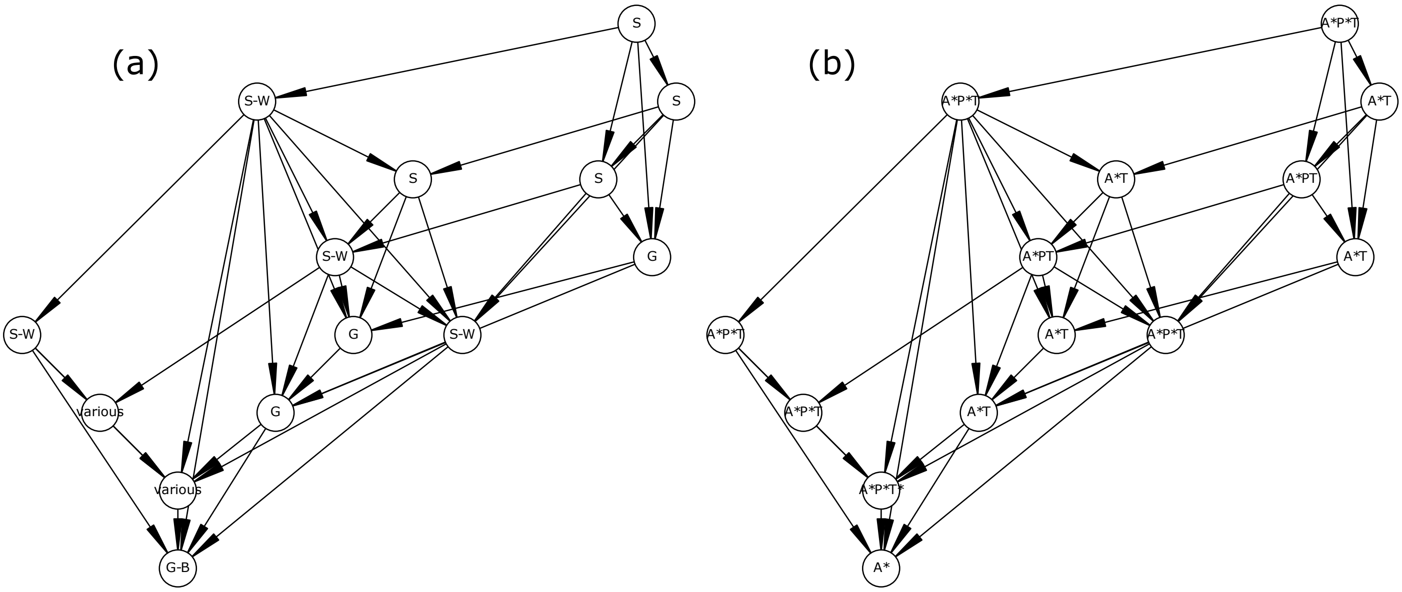

Figure 3. HTG of the "dry period" scenario. The same HTG is represented with a focus on either vegetation (a) and socio-economic (b) dynamics. Graph nodes are SCCs and each transition is, by definition, irreversible. Therefore, dynamics within each node display some form of oscillation. In (a), node labels correspond to a stable vegetation type (e.g. "S") or an oscillation between two (e.g. "G-B") or more ("various") types. In (b), node labels correspond to human activities which can be stable (e.g. T in "A*T") or oscillating (e.g. A*).

3.1.2. Socio-economic transitions

In all scenarios, the initial state had a mixed economy including agriculture, pastoralism and tourism (APT).

In the reference model, the absence of activities (red node, Fig. 4) was directly reachable by any socio-economic profile (i.e. all activities can be lost simultaneously). Moreover, only one activity could be gained at a time. When pastoralism and tourism co-occurred, tourism alone could not be lost (i.e. transitions APT $\rightarrow$ AP and PT $\rightarrow$ P were impossible).

In the "dry period" scenario, transitions were not modified. However, as for vegetation, further analyses were required. The HTG showed that pastoralism could be lost and never recover (Fig. 3b). This irreversible transition was due to the drying up of groundwater (R13), which prevented its use for livestock watering (R37 and R39). Other rules activating livestock (R36 and R38) were *de facto* impossible as surface water is always inactive in this scenario. The absence of pastoralism and wildlife then made tourism impossible (C1, Table A1). The system ended up in an attractor in which the only human activity being seasonal agriculture (Fig. A4).

In the "wet period" scenario, the transitions APT $\rightarrow \emptyset$, AP $\rightarrow \emptyset$ and AT $\rightarrow \emptyset$ were impossible. Indeed, these transitions were driven by rules R13 (which is now impossible as `Sw+` is constant) and R6 (which was able to induce these three transitions through constraints C6 to C8 when `Sw` was inactive, which is never the case in this scenario).

In the "no grazers" scenario, the socio-economic summary graph was not modified.

However, in the "no browsers" scenario, AT and T were unreachable because, in this scenario, tourism T cannot exist without pastoralism P. Indeed, tourism could persist as long as `Ct`, `Gz` or `Ca` were active (see constraint C1, Table A1). However, `Gz` necessarily became active simultaneously to `Ct` (R39) and became inactive before or at the same time as `Ct` (see Table A2 for rules (in)activating `Ct` and `Gz`). Therefore, when `Ct` became inactive, this implied that `Gz` already were, which instantaneously made `Ca` (C5) (and thus `To`) inactive.

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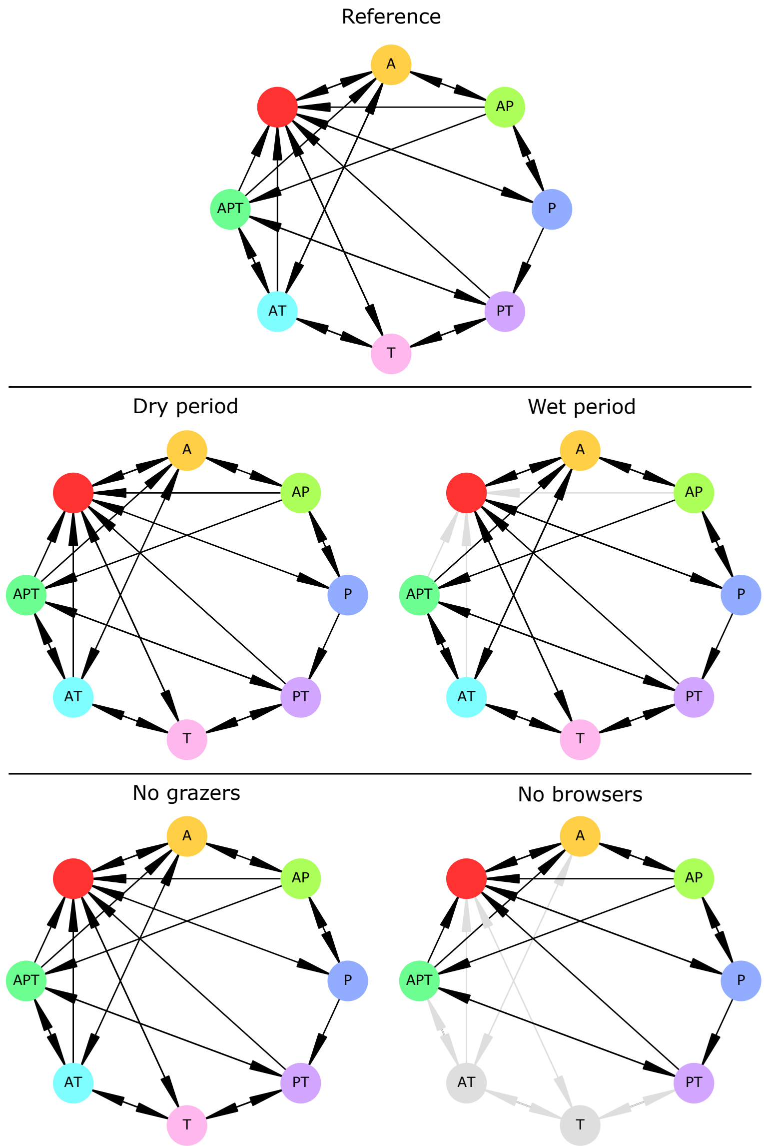

Figure 4. Socio-economic transitions for each scenario. Socio-economic summary graphs for (a) the reference scenario, (b) the "dry period", (c) the "wet period", (d) "no grazers" and (e) "no browsers". Node labels indicate socio-economic profiles as defined in section 2.5. Non-gray node colors are arbitrary and correspond to socio-economic profiles. Grayed out nodes and edges are absent from the graph and are used to highlight the differences between the references and other scenarios. Grayed out arrow tips indicate that the transition was bidirectional and is now unidirectional.

4. Discussion

In this paper, we applied the Ecological Discrete-Event Network (EDEN) modelling framework to an East-African savanna ecosystem. We aimed to understand and explain how vegetation and socio-economic transitions are affected by changes in water availability and herbivores diversity. Model conception was based on (i) direct field observations from two northern-Tanzanian savannas, (ii) expert knowledge and (Iii) literature about savannas across Africa [5,66–69]. For each of the five scenarios, the model computed State-Transition Graphs (STGs) representing all possible ecosystem trajectories given its predefined "if-then" rules. These STGs were then summarized to focus on vegetation and socio-economic aspects of the dynamics.

The reversibility of the STGs in all scenarios except the "dry period" suggests that the ecosystem is able to recover its initial state under most permanent changes. Only the "dry period" scenario displayed irreversible dynamics as the initial vegetation type (i.e. tree-grass coexistence) and socio-economic profile (a mix of agriculture, pastoralism and tourism) could not be maintained. This invalidates hypothesis H1 which stated that any permanent change of the reference scenario would induce an irreversible ecosystem change.

This result points to a need to clearly define reversibility and should be cautiously interpreted for at least two reasons. First, a reversible STG is defined by the existence of *at least one path* from any reachable state towards the initial state, which does not preclude the existence of *potentially infinite* trajectories (i.e. SCCs) inside it. For instance, in Fig. 1a, the ecosystem may remain inside the SCC (an infinite trajectory) without never reaching the attractor. Therefore, STG reversibility should not be equated with resilience [70], but rather to a potential resilience. Second, our model is possibilistic and may thus includes highly unlikely transitions. Therefore, using such models for management recommendations may require assessing the sensitivity of STG reversibility to rare events.

4.1. Vegetation dynamics

Vegetation transitions are a major issue for rangeland ecology as current increase in woody cover (i.e. generally composed of unpalatable plant species) threatens human activities such as pastoralism and especially cattle production [71]. Based on two plant types (grasses and trees), we defined four vegetation types, namely bare soil, grassland, savanna and woodland.

In the reference scenario, all transitions establishing one plant type at a time were realized and all vegetation types were able to shift to bare soil. Predicted transitions were realistic as most have already been reported or hypothesized [56,72].

When subjected to a persistent lack of surface water ("dry period" scenario), the savanna vegetation (i.e. the initial vegetation type) underwent an irreversible shift towards a seasonal grassland in which woody plants could not establish (Fig. A4). This transition was mediated by groundwater reserves, which requires the infiltration of surface water for being recharged (rule R11). The drying up of groundwater then affects woody plants which are assumed to rely on this resource (R32). Such drought-induced transitions have long been suggested [56,73]. Conversely, when water was non-limiting ("wet period" scenario), drought-induced transitions were not possible anymore, and thus transitions from savanna or woodland to bare soil were impossible. These two results do not invalidate hypothesis H2 and confirm the role of water availability in vegetation dynamics.

When herbivory was removed from the ecosystem ("no grazers" and "no browsers" scenarios), drought preserved most vegetation transitions. This was especially true for grazers whose extinction had no effect on vegetation transitions (Fig. 2). This was not in agreement with current knowledge as grazing is known to favor trees over grasses [74]. Indeed, the only rule relating grazing mammals (here, livestock) and grasses was R14, i.e. overgrazing. This rule could be rewritten to better represent the effect of livestock

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(and grazing mammals in general) on the increase in woody cover. On the other hand, browsers were necessary to three transitions (Woodland → Grassland, Woodland → Savanna and Savanna → Grassland) as those disappeared when browsers were removed from the system. Therefore, hypothesis H3 is invalidated and should be reassessed after model adjustments.

These results highlight the role of surface water (indirectly, through the watering of herbivores) and groundwater (directly, through its use by woody plants) as drivers of vegetation change [56,73,75–77]. Browsers contributed to reduction in woody cover, which confirms current knowledge [78]. Fire and soil nutrients, which are not considered here, are well-known drivers of vegetation dynamics [73] and could easily be included in later model versions. Besides, vegetation summary graphs (Fig. 2) share many similarities with State-and-Transition Models [21] which have been extensively used to represent rangeland or savanna dynamics ([28,72]). The vegetation part of the model can be improved by adding more components to it (e.g. shrubs, bushes or different life stages for trees) or accounting for other plant-water-herbivore interactions. Such an improvement could involve experts from this domain and/or new field surveys.

4.2. Socio-economic dynamics

Socio-economic transitions describe the loss and development of new economic activities. Here, we focused on three activities, namely agriculture, pastoralism and tourism, which substantially contribute to East-African economies. However, agriculture and pastoralism are affected by changes rainfall frequency and intensity [79,80]. In our model, on one hand, water scarcity ("dry period scenario") and subsequent lack of forage constrained livestock production and pushed the system into a regime of purely rainfed agriculture (Fig. A4). For the same reasons, wildlife populations declined, thus making tourism disappear. This latter prediction corroborates other findings [81]. On the other hand, increasing water availability ("wet period" scenario) did not prevent any socio-economic profile (Fig. 4). Rather, drought-induced transitions (here, general disruption of all human activities) disappeared. These results thus do not invalidate hypothesis H2.

The extinction of grazers and browsers had contrasting effects. The absence of grazers neither modified the set of reachable socio-economic profiles nor transitions compared to the reference scenario. On the contrary, the absence of browsers made tourism necessarily associated to pastoralism. We insist on the fact that this does not mean that they depended on each other. This is due to the fact that (1) cattle necessarily enter the system simultaneously to wild grazers when forage and water are available in rainy season and (2) that cattle either leave the system simultaneously (through the lack of forage (C6), water scarcity (C9, C10) or diseases (R48)) or after (through cattle predation by carnivores (R19)) wild grazers. As in this scenario carnivores only rely on cattle and wild grazers (browsers are absent), once these preys have gone extinct, carnivores quickly go extinct, which deprives tourism of attraction. Herbivores diversity (species richness, abundance and phylogenetic diversity) has been showed to be positively related to the number of tourists [82]. Although this relationship is likely to be driven by the interest for biodiversity *per se*, our results also suggest that herbivores diversity may play a role in maintaining tourism by sustaining predator populations. As for vegetation transitions, hypothesis H3 is partly invalidated as grazers did not affect socio-economic transitions, while browsers absence affected the dynamics.

Our results point to a link between herbivores diversity and socio-economic changes. Although this relationship may be explored in more detail (through another model), our model already suggest mechanisms relating these two aspects of the social-ecological system. This highlights the need, at least in some specific systems, to consider ecological and anthropogenic aspect integratively for designing management interventions.

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4.3. The scope and verification of EDEN models

This study showed how the EDEN modelling framework can make use of qualitative information, which is often the most abundant (and sometimes the only) knowledge source. Despite its qualitative nature, it can be used to derive predictions and explanations about specific social-ecological issues.

Here, questions were related to (1) the reachability of specific states from the initial state (e.g. "is woodland reachable from initial state under dry conditions?") and (2) the existence of some transitions under various environmental conditions (e.g. "is the woodland-grassland transition possible under wet conditions?"). Such questions, or propositions, can be verified or refuted (e.g. "this state is not reachable" or "this transitions is impossible"). In addition, results can be "causally" explained, as studying model rules enables to identify which rule sequences (ecological events) are disrupted or forced by changes in environmental conditions. This form of event-based explanations may thus be promising for providing a coarse-grained mechanistic understanding of ecosystem trajectories. However, this by-hand explanation (by the visual examination of rules) is prone to errors and may require automated tools to be made more rigorous. Beside the comparison of model trajectories with observations, validation/refutation can be extended to the driving events behind them (approximated by model rules), i.e. assessing whether predicted trajectories are consistent with observed states *and* events. Model verification can also be improved by the use of model-checking techniques [83] which enable the automatic exploration of large ecological State-Transition Graphs [47]. Experts and managers may play a key role in this validation/refutation process and help designing and improving models, especially through State-and-Transition Models [21]. In return, researchers can provide modelling tools to derive predictions from this abundant expert knowledge. Ultimately, this interaction between ecosystem management and modelling may be used to improve management interventions.

5. Conclusion

In this study, we propose the EDEN modelling framework as a tool for computing trajectories of an ecosystem from a qualitative knowledge base in the form of "if-then" rules. This qualitative and possibilistic model aims to predict and explain ecosystem trajectories by the interplay between multiple socio-economic and ecological events.

Here, we chose to apply this framework for modelling the socio-economic and ecological aspects of an East African savanna. We focused on vegetation and socio-economic transitions and showed that a reduction in surface water may lead to a disruption of human activities and biodiversity which is mediated by groundwater reserves and herbivores. Removing grazers or browsers herbivores had contrasting effects and highlighted the potential role of drought in controlling woody cover by itself.

This study is a first step and the EDEN framework is still evolving. It has the potential to bridge, on one hand, expert-knowledge, e.g. derived from rangeland managers who design State-and-Transition Models, and, on the other hand, modelling through an intuitive event-based approach which can be used for assessing long-term impacts of management actions on biodiversity and livelihoods.

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Abbreviations

The following abbreviations are used in this manuscript:

EDEN	Ecological Discrete-Event Network
STG	State-Transition Graph
SCC	Strongly Connected Component
HTG	Hierarchical Transition Graph

Appendix A. Study area description

Gelai plains are located in the East African Rift, south of Lake Natron, and are part of the Tarangire-Manyara ecosystem [84] and the Maasailand. These grass-dominated plains have volcanic ash-derived alkaline soils. Indeed, their proximity with the Ol Doinyo Lengai stratovolcano, with its natrocarbonatite lava and ashes, strongly influences soil pH. Woody vegetation is confined to adjacent reliefs [85] and vegetation changes are mainly driven by water availability and herbivory [54,86]. Mean annual precipitation strongly varies seasonally and inter-annually [57]. This high variability constrains primary, but also secondary production since the Gelai plains are important calving grounds for wildebeest populations [84]. The Gelai plains also provide resources for Maasai pastoralists and their cattle, goat and sheep herds. Agriculture is practiced but confined to village surroundings and wetter areas [57]. Lake Natron, mount Kitumbeine and Ol Doinyo Lengai are also important touristic sites, adding another economic value to this ecosystem. On the other hand, Northern-Meru savannas are more densely populated. The different ethnics have contrasting economic activities, with characterized by the respective roles of agriculture and pastoralism during the year [58]. Villages and local authorities (called land managers in the model) manage human activities by allowing water resources use, preventing overgrazing and allowing tourism. Their decisions also affect pathogen exchanges, vaccination, pest management and/or spatial and temporal grazing regulations. NGOs, such as Oikos, play a major role in improving livelihoods, promoting local development and sustainable practices. The area exchanges many goods and services with the Arusha city, south of the mount Meru.

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Appendix B. Model rules

Rules represent events, i.e. changes in system state. When an event occurs from a state, it produces a transition which generates a new state. In the EDEN framework, transition durations are not considered. Some events are considered too fast to be explicitly considered and are thus represented as constraints. For instance, if a pond dries up, we expect fishes living in it to die (almost) simultaneously. Therefore, we neglect the time interval between the event "the pond dries up" and the event "fishes die" by qualifying the latter event as a constraint. Constraints have priority over rules and thus, no rule can be executed as long as a constraint is satisfied. Hence, the state "the pond is dry and fishes are alive" satisfies a constraint and prevents other rules executions. Thereafter, we remove all states satisfying a constraint because they are considered too fast (or too transient) and irrelevant for our questions.

Therefore, qualifying an event as a "regular" rule or a constraint is partly arbitrary and depends on the scientific question. For the aforementioned reasons, states satisfying a constraint are considered transient, and may be removed prior to analysis (as we did here). Note, however, that transient states may be considered in order to keep all states while recognizing that some events must have priority over others.

Table A1. Model constraints. Ecologically similar constraints share the same interpretation. Note the slight differences (in condition) between the various groups of plants and animals with respect to their resource requirements (food or water). Model scenarios correspond to versions of the reference scenarios in which some constraints have been added to represent a "press perturbation", i.e. maintaining the value of some variables constant. Within a scenario (e.g. "No grazers") all corresponding constraints are activated (i.e. C11 and C12).

N°	Condition	Realization	Interpretation	References
C1	`Ct-, Bw-, Ca-, El-, Go-, Gz-`	`To-`	Without any attraction, tourism disappears.	CS
C2	`Gr-, Tr-`	`El-`	Without food resources, wildlife and livestock die or migrate.	CS
C3	`Gr-`	`Ct-, Gz-`		CS
C4	`Tr-`	`Bw-, Go-`		CS
C5	`Ct-, Bw-, Go-, Gz-`	`Ca-`		CS
C6	`Gw-, Rf-, Sw-`	`Ct-, Bw-, Ca-, El-, Go-, Gz-`	Without water resources, wildlife, livestock and plants (including crops) die or migrate.	CS
C7	`Rf-, Sw-`	`Ct-, Ca-, Gz-`		CS
C8	`Gw-, Rf-`	`Cr-, Gr-, Tr-`		A
C9	`Sw+`	`Sw-`	**"Dry period" scenario**	
C10	`Sw-`	`Sw+`	**"Wet period" scenario**	
C11	`Ct+`	`Ct-`	**"No grazers" scenario**	
C12	`Gz+`	`Gz-`		
C13	`Bw+`	`Bw-`	**"No browsers" scenario**	
C14	`Go+`	`Go-`		
C15	`El+`	`El-`		

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Table A2. Model rules. Rules with similar descriptions are grouped within the same multirow. A: Assumption, FO: field observation or report from experts.

N°	Condition	Realization	Interpretation	References
R1	Bw-, El-, Go-, Rf-, Tr+	Rf+, Sw+	Rainy season switch. If (1) at least one browsers group exert a pressure on woody plants or (2) trees are rare, then grass can grow.	[67]
R2	Bw+, Rf-, Tr+	Gr+, Rf+, Sw+		[67]
R3	El+, Rf-, Tr+	Gr+, Rf+, Sw+		[67]
R4	Go+, Rf-, Tr+	Gr+, Rf+, Sw+		[67]
R5	Rf-, Tr-	Gr+, Rf+, Sw+		[67], FO
R6	Rf+	Rf-	Dry season	A
R7	Bw+, Rf+, Tr+	Gr+	Grass growth	FO
R8	El+, Rf+, Tr+	Gr+		FO
R9	Go+, Rf+, Tr+	Gr+		FO
R10	Rf+, Tr-	Gr+		
R11	Rf+, Sw+	Gw+	In rainy season, aquifers may fill up, while in dry season, surface and groundwater may sequentially dry up.	[87]
R12	Rf-	Sw-		[87]
R13	Rf-, Sw-	Gw-		[87]
R14	Ct+, Rf-	Gr-	In dry season, non-managed livestock may overgraze the area.	[88]
R15	Gz+	Ca+	Wild herbivores (preys) may increase carnivore populations.	A
R16	Bw+	Ca+		A
R17	Ca+	Gz-	Carnivores may strongly affect wild herbivores populations.	A
R18	Ca+	Bw-		A
R19	Bw-, Ca+, Gz-	Ct-	Without managers support to protect livestock, carnivores may attack livestock if wildlife populations are low.	[89]
R20	Bw-, Ca+, Gz-	Go-		[89]
R21	Rf-, Sw-	Bw-, El-, Go-	Low water availability may lead browser and generalist herbivores to leave the area.	[90,91]
R22	Ct+	Gz-	Herbivores may outcompte one another.	A
R23	El+, Gr-	Go-		A
R24	Go+, Gr-	El-		A
R25	Go+	Bw-		A
R26	Bw+	Go-		A
R27	El+	Bw-		A
R28	Gr+, Gw+, Rf+, Tr+	Gr-	Trees outcompete grasses at high water availability.	[66]
R29	Go+	Gr+, Tr-	All browsers may strongly affect woody plants cover and favor grasses.	[92]
R30	El+	Gr+, Tr-		[92–94]
R31	Bw+	Gr+, Tr-		[92,95,96]
R32	Bw-, El-, Go-, Gr+, Gw+, Rf+	Tr+	In rainy season, the absence of browsers may promote tree recruitment.	[66]
R33	Gr+, Gw+, Rf-, Tr+	Gr-	In dry season, trees maintain a higher productivity than grasses due to their deeper root system.	[67]
R34	Rf+	Cr+	In rainy season, rainfall and surface water enable rainfed farming as well as animals watering. In dry season, groundwater pumping enable irrigated agriculture and watering livestock.	[97,98]
R35	Gw+, Rf-	Cr+		[99]
R36	Gw+, Sw-, Tr+	Go+		[100]
R37	Sw+, Tr+	Bw+, El+, Go+		FO
R38	Gw+, Sw-, Gr+	Ct+		[100]
R39	Sw+, Gr+	Ct+, El+, Gz+		FO
R40	El+	Cr-	Elephants may destroy crop fields.	FO and [5]
R41	Gz+	To+	Wildlife and tourism monitoring may allow for tourism development.	FO
R42	El+	To+		FO
R43	Bw+	To+		FO
R44	Ca+	To+		FO
R45	Ct+	To+		FO
R46	Go+	To+		FO
R47	Bw+, Go+, Rf+, Sw+	Bw-, Go-	Browsers may die from diseases.	[101]
R48	Ct+, Gz+, Rf+, Sw+	Ct-, Gz-	Grazers may die from diseases.	[101]
R49	Rf+	Cr-	In rainy season, pest may destroy crops.	[102]

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Appendix C. Model scenarios

As mentioned in Table A1, scenarios result from the application of constraints. These constraints are disabled in the reference scenario and each specific set of constraint is enabled for each scenario.

These constraints make some states impossible, and thus prevent some rules executions. This explains the observed differences between STGs and vegetation or socio-economic transitions.

Table A3. General properties each scenario's STG. STG size: number of states; Reversibility: each reachable state from the initial state can reach back the initial state; Attractors: "itself" if the whole STG is reversible or indicates the number of attractors (i.e. either stable states or inescapable SCCs).

Scenario	STG size	Reversible	Attractors
Reference	482	Yes	itself
Dry period	163	No	1
Wet period	390	Yes	itself
No grazers	302	Yes	itself
No browsers	106	Yes	itself

Appendix C.1. Reference

The STG of reference scenario has 482 states (Fig. A1) and is reversible (i.e. forms a unique SCC). Its complexity prevents any analysis by hand, thus justifying the use of summary graphs to simplify its dynamics (Fig. 2 and 4).

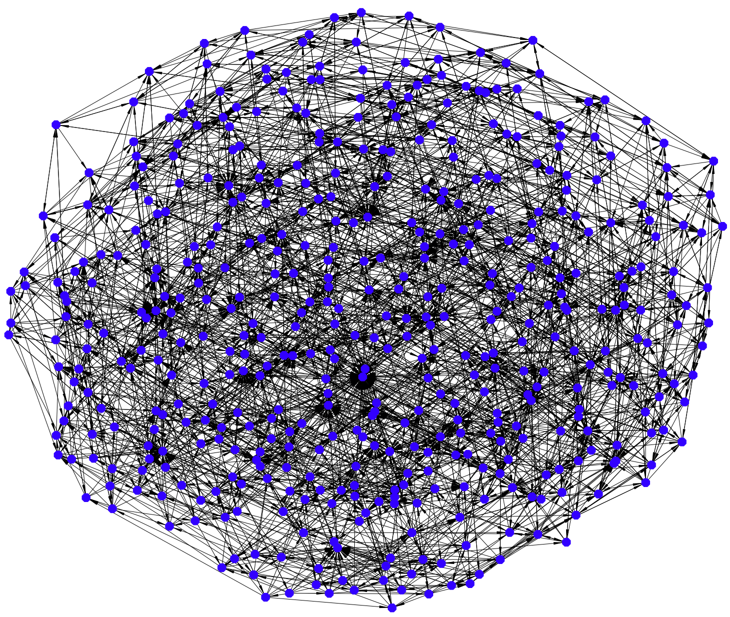

Figure A1. STG of the reference scenario. Graph nodes and edges represent ecosystem states and transitions, respectively. This STG consists of 482 states and 2640 transitions. Nodes color is arbitrary.

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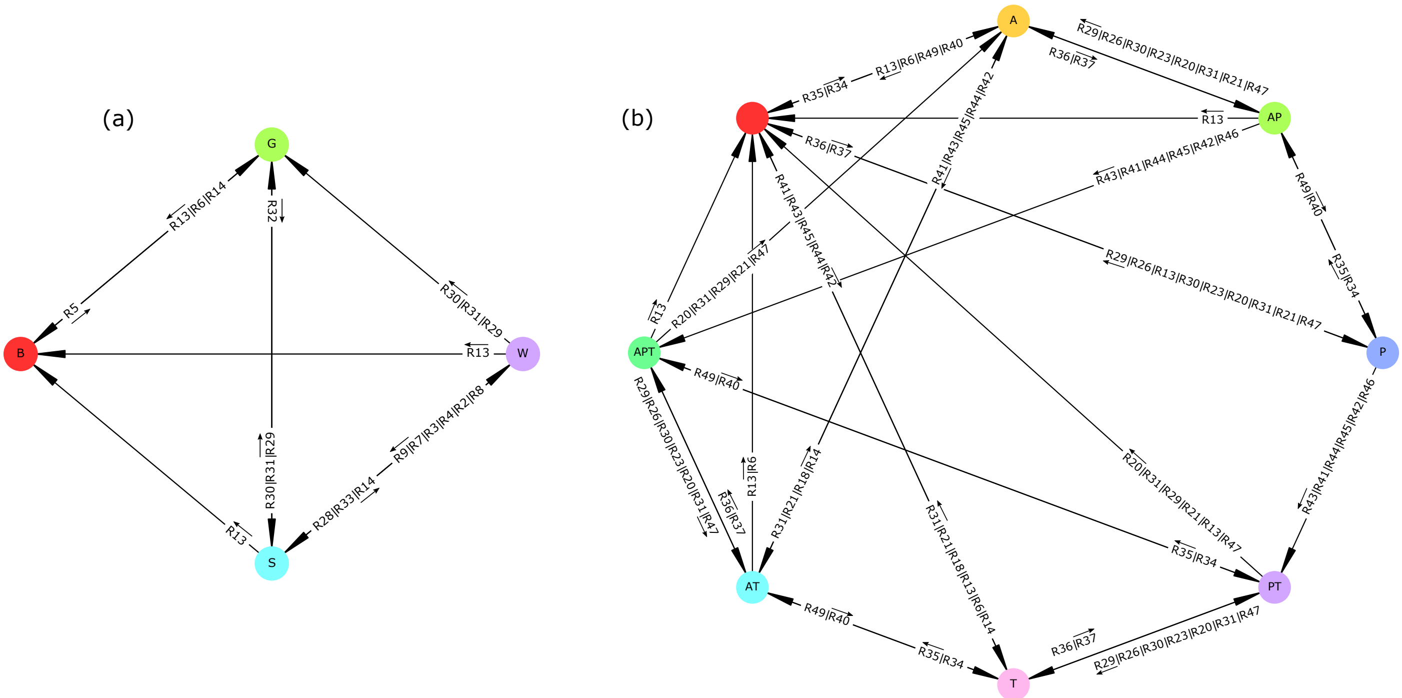

Figure A2. Vegetation and socio-economic summary graphs of the reference scenario. Summary graphs (a) and (b) are the same as Fig. 2 and 4, respectively, and indicate the rules involved in each transition. Small arrows associated to each transition labels (rules) indicate to which transition are associated the considered group of rules.

Appendix C.2. "Dry period" scenario

Appendix C.2.1. The Hierarchical Transition Graph

The "dry period" scenario is the only scenario exhibiting an irreversible STG. Trajectories converge towards a small (three states) SCC attractor. One convenient way to represent such a graph is to draw its Hierarchical Transition Graph [HTG, for formal definitions, see 64]. A HTG merges as single nodes SCCs (depicted as round nodes), basins of attraction (i.e. sets of states necessarily ending up in a stable state, generally depicted as squares) and basins (i.e. states not belonging to a SCC nor a basin of attraction and leading to the same SCCs or stable states, depicted as lozenges). Is is an acyclic graph focusing only irreversible aspects of the system dynamics (Fig. A3).

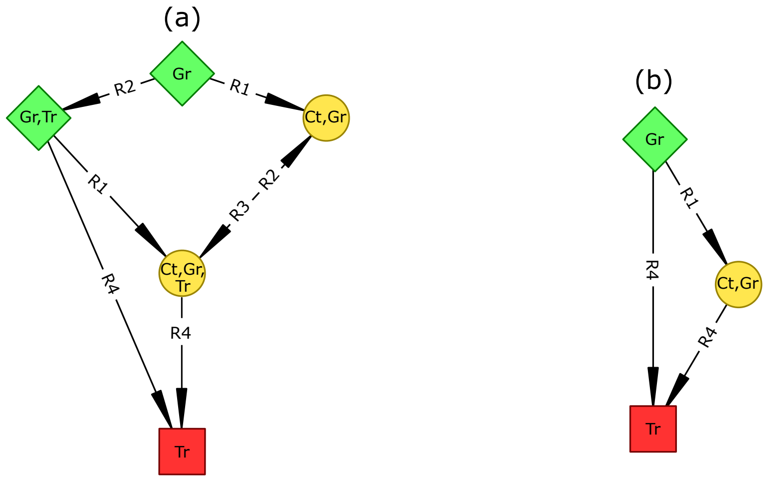

Figure A3. Comparison between the STG and HTG of the "Grasses-Trees-Cattle" toy-model. (a): This STG is the same as Fig. 1a and rules are those from Table 1. In (b), green lozenges nodes belong to a basin, yellow round nodes belong to a SCC and the red square node to a stable state (i.e. a basin of attraction of one state). (b): The HTG resulting from the merging of corresponding nodes in (a) into a single node. Hence the green lozenge and yellow round nodes include two states each and their "internal" transitions (e.g. the R2-R3 oscillation) are "hidden" within them. In both graphs, node labels correspond to variables that are always active. For instance, `Tr` oscillates in the yellow SCC in (a) and is thus not mentioned in the corresponding yellow node in (b).

Appendix C.2.2. The attractor

The "dry period" attractor is not a stable state and is not cyclic. Some authors have proposed to call it *complex attractor* (i.e. involving intertwined cycles [103]). Indeed, while the whole attractor is a cycle, it also comprises two small cycles (R5-R6 and R34-R49) (see Table A2 for rules details). Ecologically, this attractor represents an ecosystem regime in which periodic rainfall drives a seasonal grassland and enables a rainfed agriculture. This is further confirmed by the fact that when the rainy season stops (R6), grass and crops disappear until the next rains (R5). One fundamental issue here is the existence of an infinite rainy season driven by the loop R35-R50. Resolving this issue is beyond the scope of this paper, but one possible solution is to force, during model analysis, to only consider trajectories in which rainy season is necessarily followed by dry season, and reciprocally (i.e. to apply a fairness constraint on seasonality).

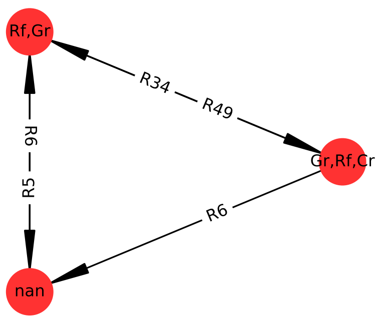

Figure A4. STG of the attractor of the "dry period" scenario. Graph nodes and edges represent ecosystem states and transitions, respectively. Node color is arbitrary.

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