THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Biologie des Populations et Écologie

École doctorale GAIA

Unité de recherche botAnique et Modélisation de l'Architecture des Plantes et des végétations

Modélisation qualitative à événements discrets des dynamiques d'écosystèmes

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Le 31 janvier 2022

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Résumé

Les écosystèmes se déploient dans le temps au rythme des événements successifs qui modifient leurs composants. Ces événements, qu'ils soient aléatoires ou non, sont les phénomènes par lesquels les écosystèmes s'assemblent et se désassemblent. Chaque séquence d'états – ou trajectoire – est une histoire possible de l'écosystème. Mais si ces événements, ou leur ordre, avait été différent, l'état futur aurait pu l'être également. Or, l'ordre des événements, du fait des limites de notre connaissance, est souvent incertain. Lorsque cette incertitude est grande, il est donc raisonnable de concevoir la dynamique de l'écosystème comme un ensemble de trajectoires possibles. Si l'ensemble des trajectoires possibles était connu, il pourrait notamment se révéler utile pour savoir si un état souhaitable est atteignable, et si oui, par quel(s) chemin(s). Dans cette thèse, nous proposons une approche de modélisation nommée EDEN (pour Ecological Discrete-Event Networks) permettant de répondre à cette question. Elle se présente sous la forme d'un formalisme dont les variables sont qualitatives et dont les valeurs sont modifiées par des règles "si-alors" représentant les événements de l'écosystème. Celles-ci sont tirées une à une, de façon non-déterministe et sans aucune probabilité. Cette approche non-déterministe et non-probabiliste a donc été qualifiée de possibiliste. Les dynamiques se présentent alors sous la forme d'un graphe états-transitions dont on peut vérifier l'existence de propriétés dynamiques (comme le fait qu'une espèce puisse persister). Dans un premier temps, une brève histoire de la modélisation en écologie des écosystèmes est présentée, avec une attention particulière aux approches de modélisation qualitatives, dont l'approche EDEN fait partie. Prenant appui sur les limites des approches existantes pour répondre à certaines questions, nous proposons l'approche EDEN et justifions la pertinence de ses propriétés par des exemples simples. Dans un second temps, l'approche EDEN est illustrée sur des écosystèmes semi-arides d'Afrique de l'Est et de l'Ouest dans le but de savoir si certains états d'intérêt sont atteignables (comme le maintien de la végétation en savane, ou de la fertilité dans un agroécosystème). Pour ce faire, nous présentons et utilisons des outils jusqu'ici peu utilisés en écologie, comme les summary graphs et les logiques temporelles. Pour un scénario donné, ces outils rendent possible de définir (1) les transitions possibles entre les états d'intérêt, (2) les conditions dans lesquelles elles peuvent advenir et (3) les événements responsables de ces transitions. En Afrique de l'Est, l'approche EDEN a permis de déterminer les effets à long terme sur la végétation et les activités humaines d'une réduction/accroissement de la disponibilité en eau de surface, indiquant une forte influence indirecte de cette dernière sur la végétation ligneuse. En Afrique de l'Ouest, en utilisant EDEN, il a été possible de déterminer les conditions permettant à de petits producteurs

du sud-ouest du Burkina Faso de développer un agropastoralisme persistant, ainsi que les événements nécessaires pour atteindre un tel état. Nous discutons enfin des apports de l'ensemble des modèles EDEN à divers champs de l'écologie, ainsi que des améliorations possibles et des ponts à dresser entre l'écologie, la biologie des systèmes et l'informatique théorique.

Abstract

Ecosystems unfold over time in response to successive events that modify their components. These events, whether random or not, are the phenomena by which ecosystems assemble and disassemble. Each sequence of states - or trajectory - is a possible history of the ecosystem. Yet, if these events, or their order, had been different, the future state could have been different. However, the order of events, due to the limits of our knowledge, is often uncertain. When this uncertainty is important, it is therefore reasonable to conceive the dynamics of the ecosystem as a set of possible trajectories. If the set of possible trajectories were known, it could be useful to know if a desirable state is attainable, and if so, by which path(s). In this thesis, we propose a modelling approach named EDEN (for Ecological Discrete-Event Networks) to answer this question. It is presented in the form of a formalism whose variables are qualitative and whose values are modified by "if-then" rules representing the events of the ecosystem. These rules are executed one by one, in a non-deterministic way and without any probability. This non-deterministic and non-probabilistic approach has therefore been called possibilistic. The dynamics are then presented in the form of a state-transition graph whose dynamic properties (such as the fact that a species can persist) can be verified. First, a brief history of dynamical modelling in ecosystem ecology is presented, with a particular focus on qualitative modelling approaches, to which EDEN belongs to. Based on the limitations of existing approaches to answer certain questions, we propose the EDEN approach and justify the relevance of its properties with simple examples. Then, the EDEN approach is illustrated on semi-arid ecosystems in East and West Africa in order to know if certain states of interest are reachable (such as the maintenance of vegetation in savanna, or soil fertility in an agroecosystem). To do this, we present and use tools that have not been used much in ecology until now, such as summary graphs and temporal logics. For a given scenario, these tools enable to define (1) the possible transitions between the states of interest, (2) the conditions under which they can occur and (3) the events responsible for these transitions. In East Africa, the EDEN approach was able to determine the long-term effects on vegetation and human activities of reduced/increased surface water availability, indicating a strong indirect influence of the latter on woody vegetation. In West Africa, using EDEN, it was possible to determine the conditions that allowed small-scale producers in southwestern Burkina Faso to develop persistent agropastoralism, as well as the events necessary to achieve such a state. Finally, we discuss the contributions of the EDEN set of models to various fields of ecology, as well as possible improvements and bridges to be built between ecology, systems biology and theoretical computer science.

Remerciements

Mes premiers mots iront naturellement à Cédric, que je remercie pour sa confiance et pour la liberté qu'il m'a laissée tout au long de ce travail. Ton esprit libre et tes idées subversives, en toute simplicité et sans provocation, ont été une grande source d'inspiration. Sans oublier toutes ces techniques merveilleuses pour que jamais l'oeuf ne se casse.

Je remercie également les membres du jury, Christine Largouët, Jacques Gignoux, Mélanie Blanchard, Alain Rapaport et Aurélien Naldi, pour leur intérêt porté à ce travail et pour avoir accepté de l'évaluer.

Merci aux collègues du projet SESASA, Mahamadou, Christine, Martin et Kofi qui m'ont accompagné, chacun à leur manière, dans ce plongeon professionnel si nouveau pour moi.

Marcel, Koné, Laetitia, Charles... La liste serait trop longues de toutes ces belles personnes qui m'ont si généreusement accueilli, là où nos perceptions de nos identité culturelle et même physique mutuelles se sont dissoutes dans la savane. Je te remercie tout particulièrement, Sabine, pour ton aide, le bissap au gingembre, ta bonne humeur, ton ouverture d'esprit et les rudiments de Mooré que tu as partagés avec moi (et que j'ai déjà oubliés, malheureusement).

Franck, merci pour ton écoute, tes mots simples, percutants et réconfortants pendant ces trois années. A bientôt autour d'un bon repas.

Un grand merci à toi Mao, tes conseils avisés, ton enthousiasme, tes démonstrations de taï-chi et ton esprit si vif.

Je remercie ces brillant.e.s scientifiques ayant mis leur esprit au service de la connaissance de la société. Tous ceux qui, depuis le début de mes études, mont fait ressentir tant de bonheur devant des idées clairement formulées. Merci également à tous ces enseignants qui se sont succédés depuis le collège jusqu'au Bac Pro, et qui m'ont encouragé à suivre le chemin de mon choix.

Boris, ta vie est un film américain perpétuel que je ne me lasse pas de regarder (d'écouter plutôt, promis je te stalk pas.). Tu es une personne pleine de relief et j'aime ça.

Je veux dire mon immense gratitude à Thierry Fourcaud et Thibaud Decaëns qui ont été exemplaires tout au long de ma thèse, et plus encore au moment où ma thèse, et mon moral, étaient au plus mal. Merci infiniment.

Impossible d'oublier tous (!) ces stagiaires et post-docs qui sont passés dans l'équipe durant ces quatre années, certains restant, d'autres repartant. Stolïan, Tam, Amandine, Olivia, Juliette, Santiago, Maxime, Mathieu. Cette thèse déjà très longue l'aurait été encore plus sans vous.

Parmi ces stagiaires, et heureusement pour moi (!), un Colin a oublié de repartir. Je suis heureux de ces trois années à avoir travaillé et rigolé avec toi. Ta constante bienveillance d'informaticien envers l'écologue naïf que je suis m'a ouvert un monde intellectuel dans lequel je n'aurais jamais cru me retrouver. Ton recul vis à vis de *tout ça* m'a vraiment permis de garder (un peu) les pieds sur terre. Sans toi, ce travail déjà modeste serait bien peu, voire ne serait pas. Que cette thèse ne soit qu'une étape dans notre relation.

Camille, that escalated quickly. De "thésarde du labo toujours de bonne humeur", tu as pris une place démesurée dans ma vie ces derniers mois. Tu es un roc de bienveillance et de gentillesse. Me pointant en panique auprès de toi, tu as accepté de me porter à bout de bras sur les derniers (kilo)mètres. D'où que te vienne cette force, cette compassion, cette générosité... Je te remercie vraiment du fond du coeur.

Mes amis (presque) non-scientifiques, un écosystèmes peuplé d'êtres à mi-chemin entre des enfants et toutes sortes d'animaux aux pouvoirs magiques, navigant avec sérieux et insouciance dans le tumulte de leurs âmes. Vous êtes une source inépuisable de vie, dans ce qu'elle a de plus beau, de plus drôle et de plus triste : Déborah, Johanna, Thibault, Gaëtan, Margaux, Alex, Aman...

Je m'aplatis de gratitude et d'amour devant les sorciers qui m'ont accompagné pendant ces trois longues années et sans qui la folie était une issue certaine : Jon Hopkins, Cookies Slayer, Shpongle, Geck-O, Thys, Skee Mask, Nils Frahm, SHXCXCHCXSH, Boards of Canada, Aphex Twin... la liste est immense (et croissante !). L'inconnu que je suis et resterai à vos yeux vous remercie.

Papa, Maman, vous pourriez co-signer cette thèse. Vous êtes mes constructeurs. Des remerciements n'auraient aucun sens (merci de m'avoir fait exister ?), donc je vais en rester à : je vous aime de tout mon coeur et pour toujours.

Céline. J'aime ce que nous sommes et le chef d'oeuvre que, chaque jour un peu plus

nous devenons, chacun et ensemble.

Sommaire

Introduction

Un écosystème est constitué de composants vivants et non-vivants. Ces composants s'assemblent (coïncident) par des échanges de matière et d'énergie. L'assemblage des composants à un instant donné est appelé état de l'écosystème et le maintien d'un état est conditionné par le maintien de ces échanges [341, 129]. Le changement d'état d'un écosystème peut être décrit par les événements d'ajout ou de retrait des composants. Ces événements peuvent résulter de différentes causes comme des perturbations, des fluctuations de densité d'un composant, ou encore l'introduction ou le retrait de certains composants. Une question centrale émerge de cette conception : *comment se forme et se maintient un état donné ?* La notion d'état est répandue en écologie, avec toutefois des sens divers [119]. Dans cette thèse, j'aborderai cette question au sein des systèmes socio-écologiques (ou socio-écosystèmes), qui comprennent également les populations humaines et leurs activités (économiques, culturelles, politiques) [117]. Dans la suite du document, supposant l'influence des humains sur la majorité des écosystèmes, nous utiliserons les termes écosystème et socio-écosystème de façon interchangeable. Dans la mesure où les écosystèmes fournissent des services aux populations (humaines ou non) [79], différents états pourront être qualifiés de souhaitable ou non souhaitables du point de vue des objectifs visés. Chaque état résultant des précédents par une succession d'événements, un état souhaitable résulte donc d'une histoire d'événements passés. Le fait de s'intéresser à l'histoire de l'état (ou ensemble d'états) d'un écosystème complète les analyses habituelles de l'écologie comme la stabilité ou la diversité des composants [e.g. 213]. Dans cette thèse, je propose des concepts et formalismes pour répondre à ces questions écologiques.

Les mécanismes régissant la capacité des écosystèmes à se maintenir dans des conditions favorables aux populations humaines est l'objet d'intenses recherches [32]. Les questions et méthodes pour y répondre sont donc diverses. Certaines études ont par exemple étudié les modes de gestion permettant l'existence d'une agriculture durable [29]. D'autres ont montré l'influence des marchés mondiaux sur les changements de moyens de subsistance à l'échelle des foyers [220]. On peut enfin mentionner, sans prétendre à l'exhaustivité, les travaux sur les *socioecological traps*, i.e. des états socio-écologiques habituellement négatifs et renforcés par des boucles de rétroaction mettant en jeu les capitaux, cultures et activités humaines d'une part, le capital naturel d'autre part [194], y compris les maladies infectieuses [252]. La théorie de la viabilité, un cadre mathématique ambitieux, vient renforcer ces questions en étudiant comment les écosystèmes peuvent se maintenir dans un ensemble contraintes (comme la persistance d'une espèce ou d'un capital dans certaines limites [12, 294]). Ce cadre met explicitement l'accent sur les trajectoires du système étudié et les actions qui le ponctuent (voir [271] pour une revue de son utilisation en écologie). Dans la plupart de ces travaux, souvent accompagnés de modèles mathématiques et de simulations numériques, la question consiste à identifier un ensemble de paramètres permettant l'existence d'un équilibre souhaitable et d'éviter ceux non souhaitables.

Pour répondre à cette question sur un système observé, il faut donc collecter de nombreuses données et estimer avec fiabilité ces paramètres [173]. Or, ces données sont souvent peu disponibles (ou imprécises) et, par ailleurs, la question posée n'exige pas nécessairement d'en disposer. En effet, on peut, par exemple, poser la question de la possibilité d'atteindre un état de l'écosystème indépendamment de toute information quantitative. Cette question déplace le cadre de réflexion d'une nature quantitative vers une nature qualitative, misant sur l'importance de l'abstraction pour améliorer l'intelligibilité d'un résultat [170]. De plus, répondre à cette question peut s'avérer utile pour orienter de futures recherches quantitatives. Cependant, dans un écosystème, le nombre de composants en interaction et les événements qui en résultent font de cette question un véritable défi.

L'atteignabilité de l'état d'un écosystème

Le problème de l'atteignabilité consiste à déterminer si un état (ou ensemble d'états) cible peut être atteint depuis un état (ou ensemble d'états) initial [92]. Cette propriété n'a que rarement été étudiée en ces termes en écologie. On l'a toutefois vue émerger en écologie des communautés. Dans cette discipline qui s'intéresse à la façon dont les espèces vivantes s'assemblent et coexistent, certains se sont notamment demandé ce qui permet à un assemblage d'espèces (i.e. l'état d'une communauté) d'atteindre un nouvel assemblage [101, 199, 218, 381, 321, 380]. En effet, un assemblage peut, en perdant et/ou en gagnant des espèces, se transformer en un autre assemblage d'espèces. On dira alors que le deuxième assemblage est atteignable par le premier. Les écologues ont ainsi pu mettre en évidence le rôle déterminant de l'histoire du système écologique étudié [119]. Une histoire correspond ici à une séquence d'événements d'apparition et d'extinction d'espèces. L'histoire joue notamment un rôle lorsque plusieurs assemblages alternatifs (i.e. ne succédant pas l'un à l'autre, mais découlant de deux évolutions partiellement indépendantes) sont possibles [64]. Ainsi, lorsque deux assemblages alternatifs sont atteignables, l'ordre des événements joue un rôle déterminant dans le fait d'atteindre l'un des deux assemblages. On dira alors que cet état est contingent (il aurait pu ne pas être si le système avait pris un autre chemin possible). En écologie, cette contingence est notamment induite par des effets de priorité (*priority effects*, [64]). De tels effets ont été rapportés pour de nombreuses communautés terrestres et aquatiques [340] et est également à l'œuvre dans les écosystèmes. L'atteignabilité d'un état est également cruciale pour la gestion et la restauration des écosystèmes [342]. L'écologie des pâturages s'intéresse par exemple à l'atteignabilité et au maintien du pâturage dans un état productif capable d'alimenter durablement le bétail [384]. Il s'agit ainsi d'orienter l'écosystème vers un état souhaité tout en assurant l'alimentation du bétail tout au long de sa trajectoire [3]. Cependant, un écosystème, tout comme une communauté, peut présenter plusieurs états alternatifs. Cela a été montré pour les pâturages dont la quantité d'herbe peut rencontrer deux états alternatifs stables ("productif" et "dégradé") dans un intervalle de valeurs de densité du bétail [260]. En deçà de cet intervalle, le pâturage est productif, au-delà, il est dégradé par le surpâturage. Dans cet intervalle, la quantité d'herbe est dite "bistable" et c'est alors la quantité initiale d'herbe qui détermine le fait d'atteindre l'état "productif" ou "dégradé". L'état futur du système est donc sensible aux perturbations qui peuvent affecter la quantité d'herbe ou la densité du bétail. Un phénomène similaire pour les forêts boréales avait été discuté (mais non formalisé) par Holling dès 1973 [156]. Des questions plus complexes liées à l'atteignabilité de plusieurs états alternatifs ont émergé en gestion des pâturages et des parcs naturels [337]. Ces questions mettent en jeu de multiples événements de natures différentes (e.g. développement d'espèces, perturbations climatiques, surpâturage, formation des sols) pouvant faire basculer l'écosystème d'un état à l'autre [338]. Dès lors, si l'on souhaite comprendre pourquoi l'état d'un écosystème est atteignable ou non, il nous faut identifier les événements en jeu et leur(s) succession(s) menant jusqu'à cet état.

Choix de modélisation

Cette question peut être abordée par certaines méthodes traditionnelles de l'écologie comme l'expérimentation [e.g. 381] et la modélisation [e.g. 218]. Dans cette thèse, nous aborderons cette question sous l'angle de la modélisation en nous appuyant sur nos propres observations et sur des rapports d'observations et d'expériences.

L'état d'un écosystème peut être modélisé de différentes façons. Les composants d'un écosystème, représentés par les variables du modèle, sont distribués spatialement. L'état d'un modèle d'écosystème à un instant donné peut donc être représenté par la distribution spatiale de ses variables. Ces variables peuvent être représentés de façon discrète (modèles individu-centrés, [91] ou automates cellulaires [3]) ou continue (densité d'individus en chaque point de l'espace, e.g. [389]). A noter qu'au sein d'un espace explicitement représenté, les composants peuvent être représentés de façon abstraite par des groupes (d'éléments biotiques ou abiotiques) fonctionnellement homogènes (e.g. le groupe "arbres" dans l'écosystème "forêt"). Ces groupes, ou modules, peuvent alors être détaillés selon les objectifs de la modélisation (e.g. explicitation de certains groupes d'arbres, comme ceux à feuillage persistant ou décidu). Les relations entre ces variables agrégées représentent alors les couplages entre des modules fonctionnellement différents. Cette représentation agrégée des variables est notamment favorisée lorsque l'espace est représenté implicitement [241].

Le défi de cette représentation consiste à intégrer les effets dus à la distribution spatiale des variables, comme par exemple les refuges de prédation [325], sans en expliciter les mécanismes. Le choix dans la précision de la représentation de l'espace et des variables a d'importantes conséquences en termes de complexité et d'intelligibilité des modèles [366]. Or, on peut s'attendre à ce qu'un plus grand niveau de précision exige plus de données pour calibrer le modèle, ce qui reste un défi en écologie [173]. Pour des raisons d'intelligibilité et de limites des données disponibles, nous adopterons dans cette thèse une représentation spatialement implicite et agrégée des variables.

Objectifs généraux de la thèse

L'objectif central de la thèse est de proposer une approche de modélisation permettant de répondre à la question : "un état (ou ensemble d'états) d'un écosystème est-il atteignable, et pourquoi ?" Nous nommerons ici cette question, celle de l'atteignabilité, qu'il s'agisse d'un ou de plusieurs états de l'écosystème étudié. Ainsi, cette question implique une réponse descriptive des dynamiques du système étudié (l'état est-il atteignable ?) dont la réponse est oui ou non, et une réponse explicative (comment atteindre ledit état ?). Cette explication peut porter sur différents aspects qui seront détaillés selon les cas rencontrés. Elle pourra mettre l'accent sur (1) les événements (i.e. quels événements sont nécessaires pour atteindre cet état ?), (2) les raisons de ces événements (pourquoi ces événements adviennent-ils dans ces conditions ?) ou encore (3) les justifications du modèle (pourquoi ces événements ont-ils été choisis pour répondre à cette question ?). Chacune de ces réponses apporte une explication complémentaire à la question de l'atteignabilité. Dans cette thèse, nous nous intéresserons essentiellement aux évènements responsables de l'(in)atteignabilité.

L'approche EDEN

L'état d'un écosystème ne peut être dit "inatteignable" que si nous connaissons l'ensemble des états atteignables à partir de l'état initial choisit. Pour identifier cet ensemble, nous emploierons l'approche EDEN (pour *Ecological Discrete-Event Networks*) initialement développée par Cédric Gaucherel et Franck Pommereau [125, 285], et perfectionnée dans cette thèse et d'autres travaux de la même équipe de recherche.

Les méthodes employées au sein de l'approche EDEN pour calculer et analyser les dynamiques sont issues de l'informatique théorique [67, 286]. Le formalisme permettant de calculer les dynamiques de l'écosystème se caractérise par une représentation qualitative des composants par des variables discrètes booléennes (on/off) traduisant leurs présences et absences. Les valeurs de ces variables changent selon un ensemble fini de règles de type "si-alors" traduisant des événements socio-écologiques et leurs conditions d'occurrence. Les règles sont tirées une par une (i.e. de façon asynchrone), sans tenir compte de leur probabilité ni de leur durée, calculant ainsi un ensemble de trajectoires (i.e. des successions d'états) possibles du système modélisé. Nous qualifions de possibiliste cette approche consistant à étudier l'ensemble des trajectoires possibles, indépendamment de leurs probabilités respectives. Bien que ce terme se retrouve dans différents domaines, comme en métaphysique [206], en mathématiques [392] ou en sociologie [68, 69], notre utilisation se démarquera partiellement des conceptions existantes. Chaque fois qu'une règle est appliquée, le modèle calcule un nouvel état du système lié au précédent par une transition représentant l'évènement résultant de l'application de la règle. Une trajectoire correspond donc à une séquence d'états et de transitions. Un modèle de l'approche EDEN définit donc l'ensemble des états atteignables de l'écosystème à partir des règles et des états initiaux choisis. L'ensemble des états et transitions est représenté sous la forme d'un graphe états-transitions. Cet ensemble peut ensuite être exploré par des méthodes d'analyse adaptées aux graphes états-transitions pour évaluer et expliquer l'atteignabilité de certains états d'intérêt.

Bien que qualitative, la réponse à la question de l'atteignabilité remplit notre objectif et complète les méthodes quantitatives traditionnelles.

Si la question de l'atteignabilité peut être satisfaisante en écologie, il reste cependant à déterminer si l'approche EDEN permet effectivement d'y répondre. C'est pour cela que nous avons éprouvé cette approche de modélisation sur différents écosystèmes observés, ce que cette thèse souhaite illustrer.

Applications de l'approche EDEN à des socio-écosystèmes subsahariens

Nous avons appliqué l'approche EDEN à des écosystèmes tropicaux semi-arides d'Afrique subsaharienne, desquels nous souhaitions déterminer l'atteignabilité de certains états d'intérêt. Ces écosystèmes abritent des populations rurales dépendantes de l'agriculture et de l'élevage et qui, par conséquent, dépendent fortement de leur environnement local pour améliorer leurs conditions de vie [244]. En parallèle, ces populations sont croissantes et exercent sur leur environnement des pressions croissantes pouvant mettre à mal leur pérennité [42] ainsi que la biodiversité [272]. A ces pressions endogènes s'ajoutent des pressions exogènes telles que les changements climatiques et les instabilités politiques [351].

Ces questions sont au coeur du projet Européen SESASA (Leap-Agri call 2019-2022), impliquant quatre nations européennes et africaines et porté par Cédric Gaucherel (France), Christine Fürst (Allemagne), Benjamin Kofi Nyarko (Ghana) et Mahamadou Belem (Burkina Faso). L'objectif est de mettre à disposition des décideurs politiques des modèles capables de les assister dans leurs choix de gestion. C'est dans ce projet que s'inscrit mon travail de thèse.

En effet, le recours aux modèles peut être utile pour prendre en compte la complexité de ces systèmes et ainsi mieux comprendre comment ces sociétés peuvent persister, et dans quelles conditions elles peuvent maintenir ou améliorer leurs conditions de vie. Cette compréhension est une condition nécessaire à la mise en place d'actions de gestion efficaces et respectueuses des populations et de leur environnement.

Plan de la thèse

Cette thèse est composée de trois chapitres. Le premier offre un cadre historique et conceptuel à l'approche de cette thèse ; le second l'applique à des questions écologiques exploratoires sur un premier site ; et le troisième à des questions écologiques ciblées sur un second site.

Dans le premier chapitre, une brève histoire de la modélisation de la dynamique des écosystèmes est proposée. Nous discutons notamment des questions écologiques ayant mené au développement de chacune des approches de modélisation existantes, ainsi que de leurs contributions respectives. Une attention particulière est accordée aux approches qualitatives en soulignant l'unité de leurs justifications, bien qu'elles reposent sur des méthodes différentes. Les propriétés centrales de ces approches sont ensuite mises en évidence (déterminisme, stochasticité, valeurs et mise à jour des variables). Nous montrons que ces approches permettent difficilement de satisfaire simultanément quatre objectifs : (1) la capacité du modèle à capturer les dynamiques qualitatives de l'écosystème, (2) réduire au minimum les présupposés liés à la vitesse des processus (i.e. les valeurs des paramètres du modèle), (3) être explicatif (i.e. répondre à une question de type "pourquoi", [363]) et (4) être prédictif (i.e. être capable de présenter des états inobservés). Constatant les limites des méthodes existantes, l'approche EDEN est finalement proposée et les raisons pour lesquelles elle permet de satisfaire ces quatre objectifs sont détaillées. Nous soulignons enfin les similitudes existant historiquement entre la modélisation (notamment qualitative) des écosystèmes et l'approche EDEN.

Dans le deuxième chapitre, sont étudiés les rôles de l'eau de surface et des communautés d'herbivores dans les transitions de végétation et les transitions socio-économiques d'un écosystème semi-aride de Tanzanie (Afrique de l'Est). L'approche EDEN est ici employée pour représenter sous la forme de règles "si-alors" les événements de la dynamique (mise en place des cultures, croissance des arbres, changement de saison) sous la forme de règles "si-alors". Ce modèle décrit les transitions entre les quatre grands types de végétation (sol nu, prairie, savane et forêt) et entre huit profils socio-économiques combinant l'agriculture, le pastoralisme et le tourisme. Au travers de quatre scénarios disjoints simulant (1, 2) la présence/absence permanente de l'eau de surface et (3, 4) la disparition des herbivores consommant les plantes ligneuses ou non-ligneuses (respectivement appelés *browsers* et *grazers*). Nous décrivons les conséquences de ces scénarios sur la dynamique de la végétation et des activités humaines. Nos résultats montrent que le manque d'eau souterraine causé par le manque d'eau de surface induit une réduction du couvert ligneux. La disparition des *browsers*, qu'elle soit directe ou médiée par le manque d'eau de surface, prévient également les transitions entre plusieurs types de végétation. La dynamique du tourisme est également affectée dans ce scénario.

Dans le troisième chapitre, les transitions d'exploitations agricoles du sud-ouest du Burkina Faso (Afrique de l'Ouest) sont modélisées. En Afrique subsaharienne, les exploitations agricoles s'organisent en un faible nombres de types différents [98, 320]. Ces types diffèrent notamment par leurs capitaux disponibles [317] et les conditions de vie qui en découlent. Ces derniers critères peuvent changer dans le temps et faire ainsi transiter une exploitation d'un type à l'autre. En particulier, la question se pose de savoir dans quelles conditions et par quelles actions une petite exploitation peut changer de type et améliorer ses conditions de vie. A partir de cinq types d'exploitations prédéfinis, le modèle reproduit correctement les types observés, autant que les transitions entre eux. Il prédit également que la capacité pour une petite exploitation à devenir agropastorale (i.e. productions significatives d'animaux et de cultures de rente comme le coton) repose simultanément sur la protection du sol, le maintien d'une quantité suffisante de fourrage pour nourrir le bétail, ainsi que sur la production de fumure animale (pour amender les sols) et l'achat d'équipements pour l'épandre et travailler le sol. Le manuscrit termine sur une discussion générale, revenant sur l'objectif central énoncé, la question de l'atteignabilité et la capacité de l'approche EDEN à y répondre. L'approche EDEN se révèle effectivement capable de déterminer si un état est atteignable et, dans sa forme actuelle, apporte une première explication à cette atteignabilité. Je discute le fait qu'une telle approche, bien que qualitative, soit utile pour identifier les conditions menant à un état, et ainsi à mieux comprendre de tels systèmes complexes. J'y indique certaines voies d'amélioration de tels modèles écologiques, et les champs d'application possibles qui pourront bénéficier d'une telle approche.

Chapitre 1

On the history of ecosystem dynamic modelling : the rise and promises of qualitative models

Introduction

Ecosystem ecology emerges in the 1950-60's in the context of the growing popular and political awareness of radioactive pollution and land degradation [132]. New methodologies appeared during this period, for instance the use of radioactive tracers to study material flows. The 1950-60's also correspond to the computational turn [365], during which computer simulations and analysis of complex models became possible. Ecosystem models were introduced for simulation and systems analysis [278]. Most of them were quantitative and were mostly used for designing appropriate management policies [e.g. 260, 164]. However, these quantitative models require precise information on the shape and intensity (i.e. parameters) of ecological interactions, which are often costly to obtain, thus making calibration challenging [229]. Moreover, they are often unable to incorporate expert knowledge and direct observations, which are a great source of qualitative information in social-ecological systems [118]. Consequently, alternative avenues such as qualitative models [205] were soon investigated.

Qualitative ecological models emerged as a complementary approach to quantitative models [261], aiming to describe coarse-grained ecosystem dynamics. Qualitative models may be appropriate when quantitative information on parameters are insufficient or when the modelling objectives do not require a quantitative response. As qualitative model outputs are relatively independent from parameters values, their results are thus less precise yet more general [204]. Qualitative models accept broader inputs, thus they can make use of both expert and scientific knowledge, resulting in more robust outputs. Since the 1980's, several qualitative formalisms have been developped, such as loop analysis [205], qualitative reasoning models [46], fuzzy models [307] or discrete-event models [56, 125]. Qualitative models aim to address several issues, such as which quantitative information is required to disambiguate model predictions [81] or how a system can achieve qualitative stability [228].

Models are described both by their phenomena of interest and by their mathematical formalization, the choice of the latter often resulting from the former. For instance, nitrogen cycle is generally studied quantitatively and modelled by a biogeochemical model expressed as a set of differential equations. Alternatively, assessing the (qualitative) response sign (+, −, 0) of a resident species to an invasion can be achieved through qualitative methods such as loop analysis. Mathematical properties can be combined in a multitude of ways in order to design a model, resulting in different perspectives on system dynamics. The modelling process thus includes preliminarily choosing the best combination of properties for the desired objectives.

In section 1.1 of this article, we provide a non-exhaustive historical overview of dynamic ecosystem models, with an emphasis on qualitative models, and discuss their respective merits and limitations. Then, in section 1.2 we isolate the most salient model properties and discuss their relevance for (1) grasping (at least qualitative) system dynamics, while (2) keeping the model parsimonious, (3) explanatory and (4) predictive. In section 1.3, we propose the Ecological Discrete-Event Network (EDEN) approach for modelling ecosystem dynamics while meeting these objectives. Finally, we discuss the general relevance of qualitative modelling approaches for studying ecosystems.

1.1 Historical ecosystem dynamic modelling approaches

1.1.1 From physics to ecology

Formalizing nature consists in translating real world objects and phenomena into a mathematical shared and intelligible representation. The formalization of dynamic phenomena originated in the XVIIth century during the Scientific Revolution, initially through a realistic perspective and thus sought for the essence of physical phenomena (that is, for truth, as pointed by [167]). By the late XIXth century, the crisis in classical mechanics led most scholars to question the scientific realism [328]. An alternative formalizing strategy rapidly emerged, involving new mathematical objects called *models*. Abandoning realism and mathematical unity, models rely on the concept of analogy and seek for usefulness rather than truth [166]. Here we follow Minsky's definition, that is "to an observer B, an object A* is a model of an object A to the extent that B can use A* to answer questions that interest him about A" [235]. Note that this also includes non-formal models. Modelling spread out at the end of the XIXth century and brought major breakthroughs in life sciences in the early XXth century [52]. It is in this historical context that ecology started its formalization.

Ecological modelling originated from demography [105, 370, 15]. The first models (between the 1900-20's) described the continuous growth of single [215, 322] or interacting populations [216, 372]. The number of ecological modelling studies sharply increased in the following decades and diverse approaches emerged. Mathematical modelling extended to the ecosystem sub-discipline in the 1950's [e.g. 277] due to favorable scientific and technological contexts [132]. Without pretending to exhaustiveness, we extend previous review of model types [172] to include the most widely used qualitative modelling approaches. Focusing on spatially implicit dynamic models, we identified five major modelling approaches.

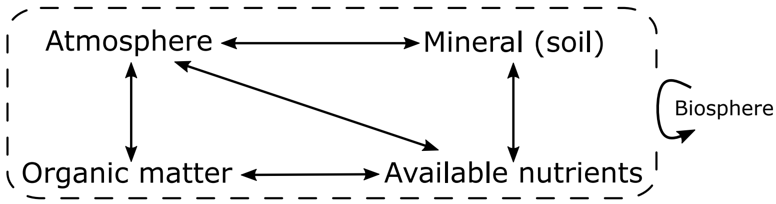
1.1.2 Compartment modelling

Ecosystem ecology as a science emerged in the 1950's, predominantly in the United States of America through the work of Eugene P. Odum [262] and close colleagues. Its main initial goal was to understand the propagation of radioactive material in ecosystems using early ideas and techniques from biogeochemistry [371, 299]. Tracing the radionuclides from their emission source to each compartment (e.g. plants, rivers or soil) revealed material flows in ecosystems [266]. These early studies were highly influenced by dynamic systems theory [373], a quantitative approach in which the ecosystem is conceived as a set of compartments linked together and with their environment through energy and material flows [263]. Generally, in these compartment models [50, 278], (1) variables represent compartments, (2) equations represent flows between compartments and (3) parameters determine the intensity of these flows [190]. In deterministic cases, quantitative phenomena are generally formalized using ordinary differential or difference equations [e.g. 37]. To account for uncertainty, stochastic parameters or events can be included [e.g. 43, 357, 44].

Compartment models were at the core of systems ecology, which was the meeting between ecosystem ecology and simulation models. Systems ecology was strongly underpinned by a holistic philosophy [247, 274]. Following Clements' ideas from the early XXth century [70], it emphasizes the irreducible complexity and self-regulating nature of ecosystems and emerging from their internal relations [106, 281]. Drawing upon emerging simulation techniques, systems ecologists proposed the "total-system modelling" approach which aimed to include "abiotic, producer, consumer, decomposer and nutrient subsystems [in order to] assure that the modeling effort plays the integrative role delegated to it" [165]. This approach was central to the Biome studies investigating the response of biomass to changes in external conditions [279]. Today, this integrative approach is still highly promoted in ecosystem modelling, although with different formalisms such as individual-based models [e.g. 291, 145]. These models allowed to predict the nutrient-productivity relationships in macrophytes populations [115] or the impact of habitat fragmentation on larger animals [19]. However, as pointed by **(author?)** [173], technical limitations greatly limit data collection and thus the estimation of precise parameter values which are required for making reliable predictions. Additionally, while parameters generally remain constant during simulations, real systems actually display variable parameter values (which **(author?)** [173]

calls for structural dynamics).

(a)



(b)

$$\frac{dx_k}{dt} = \underbrace{\sum_{i=1}^{n} f_{ki} - \sum_{j=1}^{n} f_{jk}}_{\text{Intra-ecosystem exchanges with } x_k} + \underbrace{E_{ke} - E_{ek}}_{\text{Environmental exchanges with } x_k}$$

FIGURE 1 – **Compartment model of a terrestrial ecosystem a** : Ecosystem compartments linked through matter and energy fluxes represented by arrows. Each compartment may be split into several sub-compartments (e.g. organic matter can be split into living and dead organic matter). The dotted box represent ecosystem boundaries, through which the ecosystem is also linked to the whole biosphere through biotic and abiotic processes. Adapted from [209]. **b** : A system of ordinary differential equations (ODEs) of n variables $(x_k)_{k \leq n}$ for $k \in \{1, ..., n\}$ and $n^2 + 2n$ parameters. With f_{ki} and f_{jk} describing incoming (from i to k) and outgoing (from k to j) fluxes within the ecosystem, respectively, and E_{ke} and E_{ek} describing incoming and outgoing environmental exchanges, respectively [114].

One way to cope with such structural dynamics is the application of thermodynamic principles to ecology [255]. This holistic approach was developed in the 1950-80's and proposed general predictions about the ecosystem development [120, 264]. This directional development is driven by goal functions (or orientors) which tend to be maximized or minimized over time [280]. These include emergy (i.e. content of solar energy equivalent in matter [265]) or exergy (i.e. system's deviation from thermodynamic equilibrium [174]). Self-organization processes such as ecosystem development have been explained by goal functions maximization [264]. The first thermodynamic principles in ecology were proposed in the 1920's [217] and most of their theoretical foundations come from the thermodynamics of open systems (i.e. systems exchanging matter and energy with their environment) far from equilibrium [255, 288]. While these ideas have undergone numerous developments and unification since the 1970s [107], they remain poorly used for applied issues [6].

1.1.3 Qualitative modelling approaches

Qualitative models rely on the abstraction of quantitative phenomena by focusing on qualitative changes in system state or in the sign of variables' derivative. This abstraction generally aim to account for the lack of precise measurements. In contrast with quantitative models, they do not necessarily rely on numeric inputs and mostly use relational (e.g. >,< or =), set (e.g. inclusion or exclusion) or logical (and, or, not) operations. Despite their recent rise with the computational turn in ecological modelling, their history goes back to the late XIXth century, with the work of Lorenzo Camerano.

1.1.3.1 Camerano's "reaction networks"

Lorenzo Camerano is an Italian entomologist of the XIXth century, mostly known for his seminal representation of an ecological community as an interaction network [72]. However the dynamic model provided alongside this network has been overlooked, although it is probably one of the first dynamic trophic model in the history of ecology [54]. This qualitative model of trophic cascades consists of variables representing species (or functional groups) and interactions between these variables (noted by an arrow $\rightarrow$). For example, if a species A feeds upon a species B and B feeds upon C, we have :

$$A \rightarrow B = B- \text{ and } C+$$

Where = states for the result of the interaction and – (resp. +) for a negative (resp. non-negative) effect. The decrease in B is instantaneously associated to an increase in C (i.e. its resource).

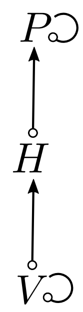
This model is qualitative because it focuses on abundance increase or decrease without quantifying it. Ecological interactions are split into separate rules, which probably makes this model the first rule-based model in ecology. Since any cause is followed by its immediate and non-random effects, this model is deterministic (i.e., the future is fully predictable given an initial condition). This is further confirmed by the figures depicting non-branching trajectories and the main text ("a reaction which [. . .] bring[s] about certain determinate changes"). Camerano informally generalizes cascading effects using a deterministic mechanical analogy based on the sound vibrations. Unfortunately, the work of Camerano was quickly forgotten. It was rediscovered one century later [72] and had no known impact on ecology. However it highlights the early need by some naturalists for qualitative models as a theory-building tool.

1.1.3.2 Loop analysis

Almost one century after Camerano's model, **(author?)** [205] proposed a qualitative analysis of ecological interaction graphs (Fig.2a), called loop analysis. It aims to predict the consequences of press perturbations [28] in an ecological system. Levins proposed loop analysis mainly as complementary to total-system models [261], the latter promoting precision and realism at the cost of generality [204]. This technique emerged in economy in the 1920s [386], but have been considerably extended to address ecological issues [81, 82].

Loop analysis is applied on signed directed graphs (digraphs). In these graphs, nodes represent ecosystem components (generally species) and edges represent interactions. Additionally, edges are directed and have a positive (symbolized by $\rightarrow$) or negative (symbolized by —∘) sign representing the effect of interactions. These graphs are built from the community matrix (representing the constant interaction signs) derived from the Jacobian matrix of a system of differential equations near equilibrium (Fig.2b). Loop analysis assesses how the effects of an external press perturbation (affecting growth rates positively or negatively) are mediated through an ecological network. In particular, it aims to predict whether a change in the growth rate of a variable has a positive (+), negative (−) or neutral effect (0) on the equilibrium abundance of each variable [175] (Fig. 2c). More detail on calculations ca be found in [290]. Loop analysis relies on a particular epistemology seeking to deduce rigorous predictions in spite of few information on parameter values and functional forms [176]. The resulting predictions are thus robust to quantitative variations in parameters values.

(a)



(b)

	V	H	P
V	-	-	0
H	+	0	-
P	-	+	-

(c)

	V	H	P
V	+	+	+
H	-	+	+
P	+	-	+

FIGURE 2 – **Loop analysis of a signed digraph**. **(a)** : A signed directed graph (digraph) representing the interactions of the Vegetation-Hare-Predator interaction network. Reciprocal interactions are merged into a single bidirectional edge. **(b)** : Community matrix whose elements are the sign of the corresponding pairwise interaction represented in (a). **(c)** : Effect of an increased growth rate of each variable on others variables. Adapted from [83] and [226].

A well-known property of signed digraphs is ambiguity (i.e. the indeterminate response of a variable to a press perturbation), which can only be resolved by considering the parameters quantitative values. This property helps ecologists by pinpointing the additional data required to disambiguate the model predictions [176, 258]. Ambiguity can be circumvented by keeping network structure constant and randomly drawing interaction parameters and running each resulting quantitative model independently. This so-called ensemble ecosystem modelling procedure generates a set of ecosystem models whose outputs are then filtered and analyzed [40].

Using loop analysis, [270] identified keystone species in marine ecosystems and [269] proposed management actions to preserve kelp populations. However, the fact that the applicability loop analysis is limited to the local neighborhood of a point equilibrium has at least two consequences. First, the system has to have a reachable equilibrium, which is not guaranteed. Second, the sign of interactions can only be constant, thus restricting the analysis to linear and monotonic interactions [176], although non-monotonic effects are known to play an important role in ecosystem dynamics and stability [393].

1.1.3.3 Qualitative reasoning

Qualitative reasoning emerged in the 1970's and is an area of Artificial Intelligence designed to model qualitatively the continuous behavior of a system. It emerged in the 1970's as a means to model physical systems based on qualitative information about system interactions and variables. Predictions about system dynamics are thus possible even when information is scarce or non-numerical. Qualitative reasoning has been used in ecology since the 1990's [138], and since the 2000's for ecosystem issues [305]. Contrary to loop analysis, these models are generally associated to a simulation engine, QSIM [192] and Garp3 [45] being the most used in ecology. QSIM simulates a system of Qualitative Differential Equations (i.e. qualitative abstractions of Ordinary Differential Equations (ODEs)). Garp3, on the other hand, aims to represent expert-knowledge by building model fragments and assembling them to compute the whole system dynamics. Like signed digraphs used in loop analysis, these models are based on a set of qualitative variables, whose interactions are signed, unweighted and non-probabilistic. Each variable is described by its magnitude (e.g. zero, low, normal, maximum) and its direction (i.e. increasing, stable or decreasing). As in loop analysis, ambiguity (i.e. indeterminacy of change) may occur. Every ambiguous situation leads to alternative trajectories, one for each possible resolution of the ambiguity. The resulting dynamics are thus non-deterministic.

Qualitative reasoning has been used to model Brazilian savanna (cerrado) dynamics [305], avian communities' changes in response to farming practices [133] and the impact of Palaeozoic land plants evolution on the carbon cycle [177]. [192] proved that QSIM guarantees that each simulated trajectory will be observed in the corresponding ODE. However, the main limitation to qualitative simulations is that they may produce spurious behaviors, that is trajectories predicted by the qualitative model but not predicted by any corresponding ODE.

1.1.3.4 Fuzzy approach

Although ecologists often deal with continuous variables, their descriptions are mostly qualitative [303] and thus they think and speak using discrete categories. However, these discrete categories are often vaguely defined (e.g. "low", "high"), and thus display fuzzy boundaries. The fuzzy approach (derived from the fuzzy set theory, [391]) is designed to account for such linguistic uncertainty. Discrete fuzzy sets are defined either based on a partition of continuous observations (e.g. a temperature data set partitioned into the "cold" and "warm") or linguistic expert formulations. In contrast with Boolean logic in which elements either belong to a set or not, fuzzy logic assigns a probability of membership (between 0 and 1) of an element to a fuzzy set. For instance, a temperature of 35°C in a boreal forest is unequivocally (i.e. with probability equal to 1) "hot", while 25°C is "hot" with probability 0.7 and "warm" with probability 0.3. Such a fuzzy approach can be used in a dynamic model based on if-then rules, where the "if" and "then" are fuzzy sets [5]. It can also be combined with signed digraph, thus augmenting loop analysis with semi-quantitative predictions [293]. As a result, model outputs are thus fuzzy sets that can later be transformed into a crisp and unambiguous output. Applications of the fuzzy approach in ecosystem dynamic models remain scarce, although authors repeatedly pointed their potential for incorporating expert-knowledge and enhancing communication with stakeholders [5].

1.1.3.5 Models based on states and transitions

Since the early days of ecology, dynamics have been represented as sequences of discrete states and transitions, such as the vegetation succession diagrams (e.g. [70, 144, 355]). These diagrams are conceptual models representing temporal changes in vegetation composition as a directed graph [211]. These changes in vegetation state are generally considered reversible but can also include irreversible transitions (e.g. [144] showing that bad management induces "more or less permanent deterioration of the soil", inducing irreversible vegetation transitions). These diagrams have largely been used for illustrating the Clementsian succession theory, which states that vegetation, if left undisturbed for a sufficiently long time, develops predictably through vegetation phases towards a fixed state called climax [70]. These concepts were the basis for rangeland management from the 1910's to the 1990's [309, 308, 103]. However, some rangeland ecologists were questioning traditional ideas about vegetation succession, asserting that rangelands can undergo irreversible transitions preventing the return to a climax vegetation, thus contradicting the Clementsian theory. In this context, [384] developed a new non-formal modelling approach called States-and-Transitions Models (STMs) to account for (i) the existence of multiple pathways between vegetation states, (ii) irreversible transitions in rangeland states and (iii) to gather expert knowledge and as a tool for decision-aid [338].

Like succession diagrams, STMs are directed graphs whose nodes and edges represent ecosystem states and transitions respectively (Fig. 3), which are both derived from direct observations. They are generally used as dynamic databases for rangeland management, not based on time but on events. Note that similar graphs representing states and transitions have anecdotally been used in the 70's under the term "behavior graph" [278] or "replacement sequence" [256] where, in the latter, transitions have specific time durations. While succession diagrams and STMs are not formal models, several authors have proposed to use Markov Chains for modelling vegetation succession [375, 158] and rangeland dynamics [313].

Central STMs concepts have been well defined by [338] : (1) A state is "a recognizable,

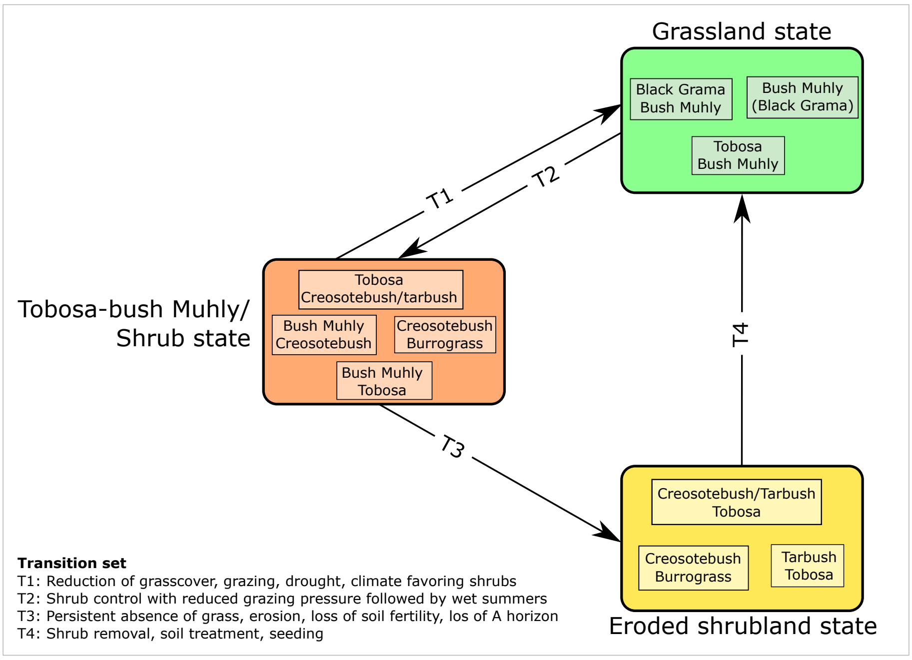


FIGURE 3 – **State-and-Transition Model**. Boxes inside each state correspond to community phases linked through community shifts. While community pathways may not be explicitly represented (as is the case here), community phases within one state should always be mutually reachable. Additionally, a shift between two community phases is generally considered bidirectional. Transitions (arrows) are considered irreversible unless substantial management efforts are engaged. Adapted from [362].

resistant and resilient complex of two components, the soil base and the vegetation structure" ; (2) A transition is "a trajectory of system change away from the current stable state that is triggered by natural events, management actions, or both" ; (3) Reversible transitions occur within states, which may consist in several community phases (e.g. reversible changes in plant species composition) ; (4) Irreversible transitions (at least on in time scales relevant to management) occur between states.

As in Qualitative Reasoning models, any state in a STM may have several outgoing non-probabilistic transitions, i.e. they represent all possible states and transitions. They are generally built upon observations and thus cannot predict novel ecosystem structures [49, 153]. This limitation led scientists to combine them with mathematical tools such as Dynamic Bayesian Networks [254] or Markov Chains [313].

Each modelling approach emphasizes new aspects of a system and thus widens the range of questions that can be addressed. Each of them simultaneously impose methodological and practical limitations. On the one hand, methodological limitations overdetermine both the systems or phenomena that can be modeled. They originate from the methodology or the mathematical tools employed to model the system. For instance, STMs cannot be used to predict unobserved transitions or loop analysis cannot be applied to non-equilibrium systems. On the other hand, practical limitations generally stem from the relationships between the data and the model (e.g. limiting data availability). For instance, insufficient data may impede quantitative and robust parameterization of compartment models. The choice of model properties can contribute to circumvent some practical limitations. For instance, stochasticity or qualitative variables are a privileged way to cope with the lack of data. Models can thus be viewed as assemblages of properties specifically designed to address particular questions. Therefore, understanding the limitations of each model property would strongly help modelers in their choice between alternative methods (or help them to design new ones) to better tackle their ecological questions.

1.2 Ecosystem models' properties and their limitations

Dynamic ecosystem models seek to predict and/or explain ecosystem trajectories, either by reproducing some of their internal interactions and external influences (process-based approach, as in most compartmental models), or by reproducing parts of the observed phenomena (phenomenological approach, as in States-and-Transitions Models). Depending on their objectives, these models improve our understanding and/or bring solutions to applied issues. These objectives are generally reflected in their mathematical properties. For instance, loop analysis aims to assess the direction of change of a equilibrium population size to a press perturbation, and thus only focuses on the sign of interactions. Therefore, the formalism and properties used to design a model often result (at least partly) from a motivated choice.

We now briefly expose our objectives :

1. grasping the qualitative dynamics of the system,
2. making as few assumptions as possible about interactions (parameters or functional form),
3. being explanatory in the most general sense, i.e. answering to why-questions [363] and
4. being predictive, i.e. forecasting the future state of a system before the system reaches it [25].

Based on these objectives, we will discuss the benefits and limitations of general model properties. Therefore, this should not be seen as a critique *per se* of each property, but only with respect to the aforementioned objectives.

1.2.1 Quantitative or qualitative variables ?

Quantitative or semi-quantitative models such a compartmental models generally involve differential/difference equations. They provide precise and unambiguous predictions that can (in principle) be readily measured [82]. One strategy is to “sacrifice generality” [175] and greatly detail interactions in the model. However, information about processes is often partial and thus ecological parameters estimations remain limited [229, 82]. This issue is generally addressed by a strategy of simplification by reducing model size (i.e. the number of variables and parameters) in order to reduce the number of required measurements (the “sacrificing realism” strategy [175]).

Yet, reducing the model size is only one of the possible simplifications. An alternative strategy to the previously mentioned ones is to simplify the variables’ behavior through a *qualitative approach*. Instead of focusing on their precise quantitative values, the emphasis can be put on crisp (e.g. qualitative reasoning) or overlapping (e.g. fuzzy models) intervals or on their sign of variation (as in Camerano model or loop analysis).

Moreover, much ecological knowledge is qualitative [303] and is held by ecosystem stakeholders [102]. Taking into account this qualitative information makes model building easier and provides general results [204]. Also, some ecological questions do not necessarily require quantitative information, such as the identification of keystone species [270].

Therefore, objectives (1) and (2) lead us to opt for the qualitative approach. Note however, that the predictive power of some qualitative models (such as loop analysis) generally decreases as the number of variables increases due to higher indeterminacy in model responses [81], this will be addressed in section 1.3.1.

1.2.2 How changes occur over time : the variables update mode

In most dynamic models, the changes of variables values at a time t depend on the system state at time $t-1$. Hence, at each time step, all possible changes are executed simultaneously, i.e. all variables are updated *synchronously*. Such a synchronous update mode is appropriate in quantitative models but becomes problematic when variables values represent intervals such as “low”, “medium”, “high”. This implicitly assumes that all qualitative changes (e.g. shifts from “low” to “medium”) are equally fast, which is a strong assumption for social, biological and ecological processes. As these major changes happen at regular time steps, it is all as if a “global clock” were driving the behavior of each ecosystem component.

On the contrary, it has been argued that ecosystems are distributed [106]. That is to say that each ecosystem component does not respond in a synchronized way with others but rather responds at its own speed. This implies that responses to a given stimulus may be delayed between components due to their mutual independence or to different reactivity. Synchronous qualitative dynamic models may fail to predict the qualitative behavior of a system (see section 1.3.4), even though the model accurately represents interactions between variables (thus increasing the risk of false negatives). Therefore, in line with objective (2), section 1.3.3 will demonstrate the inadequacy of the synchronous update mode in a case study and will propose using an non-synchronous alternative.

1.2.3 Deterministic or not deterministic ?

Determinism is a property commonly found in historical ecological models [301, 372]. In a deterministic model, initial conditions and model structure are sufficient to predict the (unique possible) future. However, as knowledge about the system is often limited, including a certain amount of noise likely better reflects our ignorance and the intrinsic variability in interaction intensities. For instance, dispersion of individuals cannot be precisely predicted and is thus represented as single stochastic events or as a fixed dispersion rate representing the mean number of individuals leaving the system. Such stochastic events may have tremendous consequences on system dynamics and induce, e.g. priority effects [119] and alternative stable states [332, 381]. Stochastic disturbances may also lead an ecosystem towards alternative thermodynamic trajectories [255]. Although determinism can be relevant for specific issues, objective (2) requires to explicitly incorporate uncertainty as random parameters, as a set of probabilistic transitions (e.g. Markov Chains) or implicitly accounting for it (as in States-and-Transition Models).

1.2.4 Uncertainty as stochasticity

Ecological dynamics are influenced by events (e.g. birth, storm, predation, or dispersal) which can usually not be precisely identified and represented. In this case, a stochastic model can be convenient to account for such events. Stochastic models represent system dynamics as a set of probabilistic trajectories (sequences of discrete transitions). In particular, they can be used to predict the probability for a system to reach a given state after a given time or to take a given trajectory. Stochastic models compute the temporal evolution of a system based on its (past or current) state and the probability for a system to shift from one state to the other (called transition probability). This is typically what Markov Chains do. Considering probabilistic changes is undeniably more parsimonious approach and requires less information than a precise deterministic description. However, estimating transition probabilities [21] remains costly and more adapted to well-studied systems. Additionally, transition probabilities may also change over time, which requires even more information about the system. Therefore, when measurements are scarce, setting probabilities represents an assumption which can be avoided, thus not satisfying objective (2). Consequently, in section 1.3.4, we will propose an alternative approach based on a non-probabilistic non-determinism called *possibilism*.

1.2.5 Predictive capacity

Ecosystem dynamics be represented through formal and non-formal models. Non-formal dynamic models such as succession diagrams [70], replacement sequences [256] or states-and-transitions models [384] are well suited for ordering qualitative knowledge about the dynamics of a specific system. They are intuitive, which makes them practical e.g. for decision support [49]. They represent all possible states and transitions according to observations, thus they provide an exhaustive visualization of system dynamics, while explicitly representing ecological events. However, as these models are limited to observed ecosystem states, they are not predictive [sensu 25]. Moreover, their size is constrained by the fact that they are usually hand made and visually interpreted. Although they provide a valuable representation of available knowledge about system dynamics, their inability to infer ecosystem states with no historical analogue limits their applicability in a context of changing environment due for example to climate forcing or anthropogenic disturbances. As a consequence, they do not satisfy objective (4) and we will thus opt for a formal approach.

1.2.6 From the limitations of properties to the selection of a formalism

All the aforementioned properties may assembled in various ways (Fig. 4). Modelling formalisms are thus composite objects which inherit the limitations of their constituents. As each specific assemblage is designed to address specific questions, we can now discuss the relevance of existing formalisms regarding our four objectives.

1. The ability to grasp the qualitative dynamics does not discard any formalism, as both quantitative and qualitative models can provide insights about the qualitative dynamics. However, loop analysis is restrained to equilibrium systems, which can hardly be known a priori and may be inappropriate for non-equilibrium systems.
2. As we aim to make as few assumptions as possible about parameters, we will discard quantitative formalisms for they impose strong constraints on data requirement (e.g. fixed or variable interaction coefficients, knowledge of functional forms) for building models. Estimating transition probabilities for Markov models also require sufficient amounts of data which are not always available.
3. All formalisms can provide some form of explanation. However, some ecosystem models may act as black-boxes and thus prevent a detailed and meaningful analysis. In contrast, models like states-and-transitions models can enable tracking causal pathways leading to a particular outcome.
4. Predictive capacity refers to the ability to forecast the future state of a system to some specific level of accuracy using a computational or mathematical model [25].

In this regard, non-formal models such as states-and-transitions models are not predictive as they rely only on observed states and transitions between them and do not infer unobserved states.

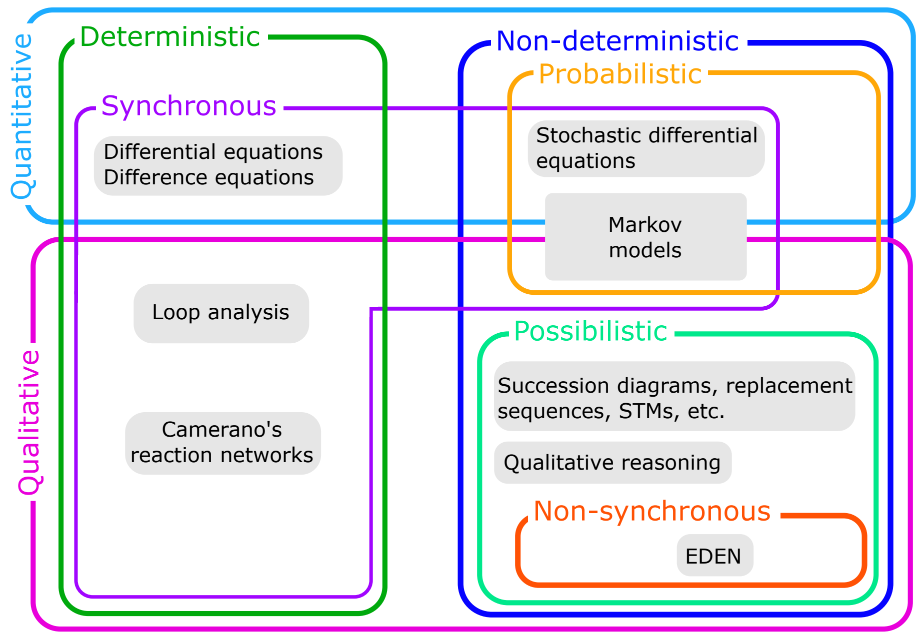


FIGURE 4 – **Assemblages of properties of ecosystem dynamic models**. Note that fuzzy set theory is not considered here as it can be used in various dynamic modelling approach but is not one of them.

Building on a vast literature and a long tradition in systems biology starting with [347] and [179], the aforementioned limitations of current formalisms led us to develop an innovative dynamic modelling approach in ecology called *Ecological Discrete-Event Networks* (EDEN).

1.3 The Ecological Discrete Event Networks (EDEN) modelling approach

Before discussing the major properties of the EDEN approach in detail, we first illustrate them through a simple community model of species extinctions (or community disassembly) induced by trophic and competitive interactions (Fig. 5). It is derived from experiments on protist communities [381]. While ecological interactions (Fig. 5a) are the driver of change, the model focuses on *qualitative changes* induced by these interactions (in accordance with objective (1)). Here, *events* are the qualitative changes of interest. These events are species extinctions and are summarized as a set of if-then *rules* (Fig. 5b). Starting from the $\{APT\}$ state, the *asynchronous* execution (i.e. one by one) of these rules results in a several alternative trajectories. Due to stochasticity, population sizes or interaction strength, these trajectories may have different probabilities of occurrence. However, the EDEN approach is *possibilistic* (i.e. non-probabilistic non-determinism), and thus aims to account for all possible alternative trajectories, irrespective of their probabilities or duration. We will show that these three model properties (event-based, asynchronous and possibilistic approach) contribute to satisfy objective (2). Computed dynamics are represented as a *State-Transition Graph* (STG) representing cascading extinction events (Fig. 5c). In this STG, nodes and edges represent states and transitions, respectively. The model predicts (objective (4)) three alternative trajectories with distinct extinctions sequences, thus providing a historical explanation (objective (3)) for the two distinct stable states $\{T\}$ and $\{\emptyset\}$. One such explanation is : "the extinction of P is a necessary but not sufficient condition for $\{T\}$ to persist". These results will be discussed in more details in section 1.3.3.

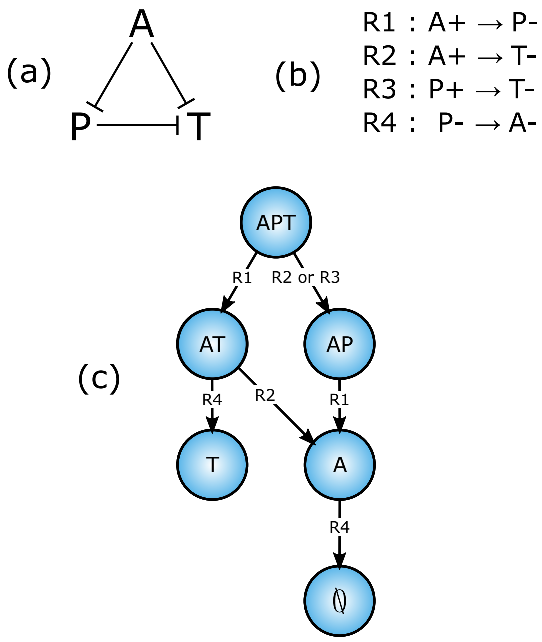


FIGURE 5 – **Discrete-event model of community disassembly**. **(a)** : Interaction graph of three protist species : *Amoeba proteus* (A), *Paramecium caudatum* (P) and *Tetrahymena pyriformis* (T), edges represent directed negative interactions. **(b)** : Rule set describing species extinctions and their conditions. These extinctions result from the following interactions : A eats and depends on P, A eats T and P competes (unidirectionally) with T. **(c)** : The State-Transition Graph resulting from all possible rules executions from the initial state $\{APT\}$. State (nodes) labels indicate which species are present, while transition (edges) labels indicate which rules can be executed for each transition. Note that one transition can result from several alternative rule executions (as in the transition from $\{APT\}$ to $\{AP\}$).

1.3.1 A qualitative perspective on ecological components

Ecosystems are continuously reshaped under the influence of internal and external factors. These changes do not manifest as jumps, but rather as more or less abrupt continuous variations. However, we already pointed that modelling such continuous phenomena often requires difficult parameter estimation, which is generally out of reach given technical and financial limitations. Biologists faced the same issue when they first aimed to model the dynamics of regulatory networks. They circumvented this limitation by abstracting gene expression to a switch-like behavior in which genes are either expressed (ON, 1) or not (OFF, 0) [339]. This marked the beginning of logical formalisms in biology, the most famous one being Boolean Networks [179]. Although this "logical caricature" [161] may seem excessively simple, it proved surprisingly insightful in theoretical [e.g. 179] and applied cases [38]. In particular, this appeared to closely match the nonlinear nature of gene expression [348]. These simplified, yet qualitatively valid and robust models enabled studying larger regulatory networks exhaustively without resorting to numerical simulations. However, the use of logical models did not percolate in ecology. To our knowledge, the first attempt was a Boolean predator-prey model proposed by Jean Richelle in 1979 [298]. He showed that the Boolean model displays the same cyclical behavior than the continuous model, while a slightly refined model displays the same stable states and cyclic attractor. More recently, the qualitative approach was adopted through the use of timed automata for studying land use changes [195], coral reefs dynamics [319]. These early attempts are promising for designing relevant abstractions of more complex quantitative models, yet with much lower data requirements. The qualitative approach in EDEN bets on the decades-long use of qualitative models in systems biology and we expect it to provide valid and insightful approximations of the continuous behavior of ecological systems (objective (1)).

1.3.2 Discrete events as the basic unit of qualitative change

The EDEN modelling approach is not time-driven (i.e. no global clock drives the model) but event-driven, and thus belongs to discrete-event models [61]. In such models, changes happen at possibly irregular time intervals. A transition occurs when a variable crosses a threshold and thus becomes functional or non-functional. The functionality of a variable corresponds to its ability to cause or prevent qualitative changes in other variables (Fig. 5a). To illustrate this phenomenon, we will use a well-known example of nonlinear response : seed germination rate in response to a soil moisture threshold [e.g. 152]. This threshold delineates the range of values above which the variable (soil moisture) becomes functional (induces seed germination). Hence, the emergence of seedlings resulting from seed germination is a discrete event, also called a *transition*. While the EDEN approach can also include multiple thresholds (multivalued framework, Fig. 5b), we will mostly focus on the Boolean framework where only one threshold is considered for the sake of simplicity. In the Boolean representation, when moisture is above (+) (resp. below, (−)) this "functionality threshold", it is said to be "present" (resp. "absent"). The transition from low to high germination rate is represented as a if-then rule expressing the following sentence : "*If* soil moisture is high enough (M^+), *then* seedlings may develop (S^+)", in which the word "enough" indicates the moisture threshold below which germination cannot occur (here, the base water potential ; [113]), and the word "may" indicates that the transition may not occur, even if soil moisture is sufficiently high (e.g. if the soil is below the base temperature ; [113]). Formally, the system dynamics can be formalized with the rules :

$$M^+ \to S^+$$

$$M^- \to S^-$$

Note that Fig. 6 implies that if soil moisture is insufficient, the reverse transition may occur. A rule consists of a left-hand side (called condition, here M^+) and a right-hand side (called realization, here S^+), with an arrow between them (noted $\to$) representing the event (here, germination). Note that the condition as well as the realization of a rule can include one (as in our example) or several variables. Due to their high simplicity, such Boolean rules can be easily derived from any knowledge source (e.g. experts, observations or experimental data), while providing a highly general, yet realistic description of the transition considered. In the EDEN approach, we assume that such a functionality threshold exists for any interaction, such that the Boolean abstraction is always valid (i.e. captures the qualitative properties of the phenomenon of interest, [298]). The threshold value is unknown a priori (Fig. 6a). This is an advantage as it allows building a model with a highly limited knowledge about the system under study. Indeed, ecological thresholds values are costly to measure and are often highly variable in time and space, thus hampering any threshold estimation for most ecological interactions [248, 80].

However, variables are not equally sensitive to a given input. Consider now two plant species (with their respective seedlings S_1 and S_2) with specific soil moisture requirements for germination. If one seeks a more detailed representation, we can substitute the Boolean model for a multivalued one. In this case, we use four different rules associated to three different soil moisture thresholds (0, 1 and 2) (Fig. 6b) :

$$M \geq 1 \to S_1^+$$

$$M \geq 2 \to S_2^+$$

$$M < 1 \to S_1^-$$

$$M < 2 \to S_2^-$$

In the Boolean framework, as we ignore quantitative differences, if S_1 (i.e. the species with the lowest moisture requirement) can germinate, then S_2 can too (Fig. 6b). Thus,

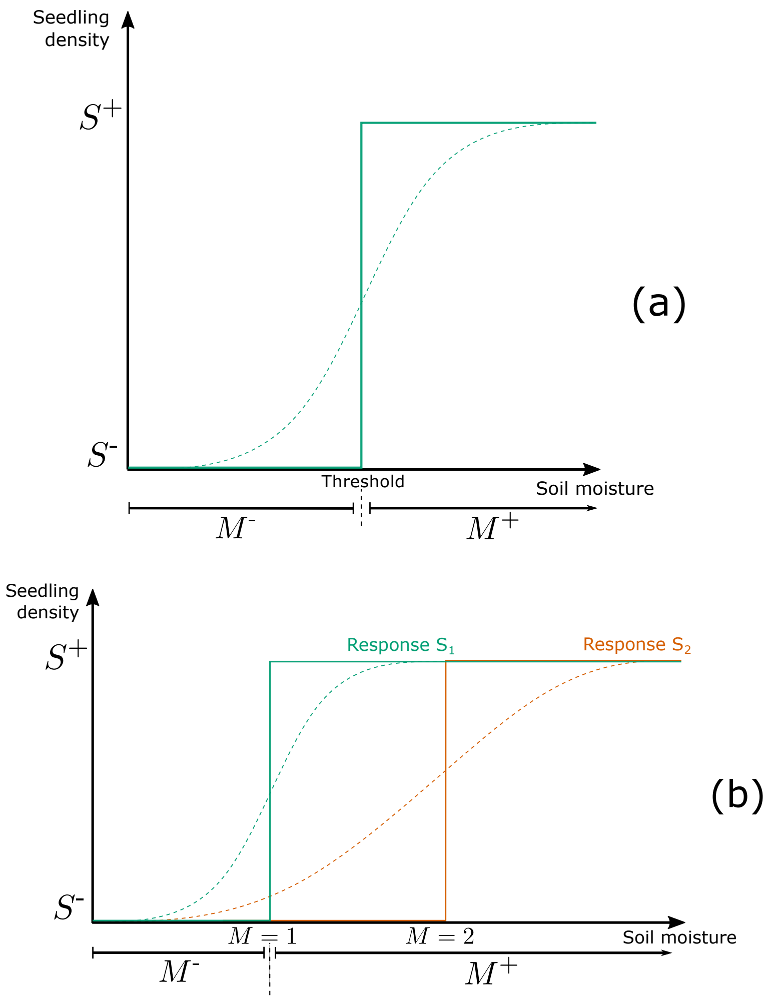


FIGURE 6 – **Threshold-based quantization of continuous dynamics. (a)** : Curves representing the interaction between soil moisture M and seedling density S (and corresponds to the rules $M^+ \to S^+$ and $M^- \to S^-$). The sigmoid curve (dotted line) illustrates one possible monotonically increasing function linking the two variables. The continuous line corresponds to its step-function (Boolean) approximation. For the sake of representation, the threshold between M^- and M^+ is clearly positioned, but may be more fuzzy in reality. **(b)** : Comparison between the Boolean and multivalued representations of interactions. Sigmoid curves represent the effect of soil moisture on the germination of two species S_1 and S_2. In the Boolean abstraction (+ and − intervals on x-axis), there is no difference between specific thresholds. Therefore, if moisture is sufficient for one species, then it is sufficient for all. Inspired from [349].

we have :

$$M^+ \to S_1^+$$

$$M^+ \to S_2^+$$

$$M^- \to S_1^-$$

$$M^- \to S_2^-$$

However, the way rules are executed is not specified yet. When moisture is sufficient (M^+), are rules executed simultaneously or separately ? This choice is likely to strongly impact the modeled dynamics, and should thus be carefully thought. In our example, if rules are are executed simultaneously (synchronously), the Boolean description can miss important trajectories. For instance, soil moisture may be sufficient for S_1 and S_2 to germinate, but hidden variables such as temperature may prevent or delay the germination of one species, thus inducing a non-synchronous response between S_1 and S_2. So how can we represent all qualitatively realistic trajectories, accounting for the effect of hidden variables, while avoiding adding quantitative information or other variables ?

1.3.3 Accounting for uncertainty in the timing of events : the asynchronous update mode

In a given state of an ecological system, several events may occur (for instance, when soil is moist, several plants may germinate). How does the model manage these concurrent events ? This question is related to the way variables change at each computational step, called the update mode [121]. As mentioned in section 1.2.2, variables can be updated synchronously, which is the most common case in ecological models. We mentioned that this is justified in a continuous time perspective where process rates can be adjusted by parameters values, but becomes problematic in a qualitative perspective. We illustrate here the limits of the synchronous update mode using the APT model discussed in section 1.3. When rules of the APT model (Fig. 5b) are executed synchronously (Fig. 7a), the dynamics are deterministic and the $\{APT\}$ state reaches only one stable state ($\emptyset$). However another end state, $\{T\}$, was observed experimentally (see Appendix 1 in [381]). In this case, either model structure (i.e. interactions between variables) is wrong, or the way events are scheduled is inappropriate for the studied phenomenon.

We test the second hypothesis by relaxing all assumptions about the timing of extinctions (determined by interaction strength and population sizes, which are generally uncertain), and execute rules asynchronously, i.e. one by one (Fig. 7b,5c). As each rule changes the state of only one variable, this is similar to the fully asynchronous mode used in Boolean networks [349]. In this asynchronous update mode, transitions are not driven by a global clock synchronizing them, but rather have their own timing. The asynchronous model not only predicts two stable states and four transient states, which are all observed experimentally, but also all observed transitions (unpublished data). Note, however, that some synchronous Boolean Networks also proved insightful for some ecological phenomena [e.g. 56, 300]. Additionally, synchronizing specific events can be relevant as it may more closely match available knowledge. Therefore, in order to make the formalism more flexible for users and in accordance with objective (2), we opt for a *partially synchronous* update mode, in which a rule can update several variables simultaneously (not shown here, but used e.g. in [125]), while rules are still executed one by one. This is similar to semi-synchronic Boolean networks used in [232].

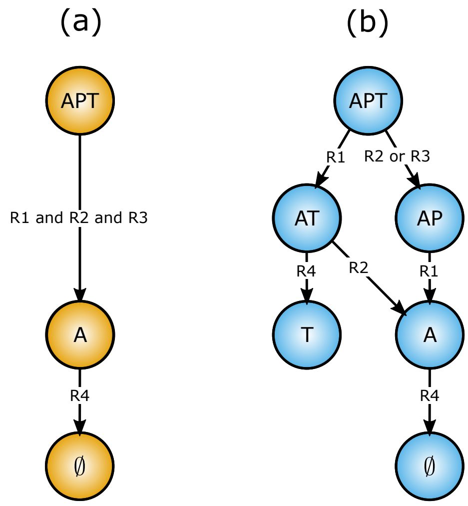


FIGURE 7 – **Comparison of trajectories generated by synchronous and asynchronous update modes derived from the APT model described in Fig. 6. (a)** : In the synchronous update mode, all valid transitions are fired simultaneously. For instance, in the $\{APT\}$ state, rules R1, R2 and R3 are satisfied (see Fig. 6b for rules definitions) and are thus executed simultaneously. The resulting dynamics are thus deterministic and necessarily end up in the empty state $\emptyset$. **(b)** : In contrast, the asynchronous update mode used in EDEN opens an alternative trajectory from the $\{APT\}$ state by separately firing, on one hand R2 or R3, and on the other hand R1, possibly leading to the alternative stable state $\{T\}$ observed in [381] experiments.

1.3.4 Possibilism as a new approach to non-determinism

Assuming that ecological systems are non-deterministic, the trajectory they take depends on several factors, such as events timing or interaction strengths. Generally, only a few alternative trajectories will be frequently observed, thus motivating a probabilistic approach. However, rare events crucially contribute to history in ecological and biological dynamics [212, 130], thus making the exhaustive set of trajectories highly relevant, whatever their probabilities [68, 142, 191]. Therefore, we adopt a possibilistic perspective, in which all the possible long-term trajectories are computed, that is, all changes compatible with the predefined variables and rules, regardless of probabilities. This perspective combines with the asynchronous update mode, which usually opens several alternative trajectories (as in Fig. 7b). It allows assessing all the far-reaching consequences of the occurrence or non-occurrence of a given event (e.g. management action or natural event). Possibilism has been widely exploited in systems biology to study the transient and asymptotic behaviors of regulatory networks in response to various environmental stimuli [238]. It has also been used to disentangle the complex sequences of events leading to a particular outcome, namely a causality analysis, based on counterfactual reasoning [201] which may be useful for ecosystem management and decision support [4]. Note, however, that possibilism is only relevant for a highly aggregated system description. Indeed, a possibilistic description of the behavior of each individual in a population would lead to an enormous and inextricable set of trajectories which would provide little insights, if any.

All the aforementioned properties draw a general picture of EDEN : the qualitative approach implies that only major and discontinuous changes will be considered, while the discrete-event framework implies that these discontinuous changes may occur at possibly irregular time intervals following threshold crossings. Additionally, the asynchronous execution of rules opens alternative trajectories corresponding to contrasted event sequences, which are all computed, in a possibilistic way.

1.3.5 The state-transition graph as the assemblage of model properties

As vegetation succession diagrams [144], States-and-Transitions Models [338, 384], Qualitative Reasoning [305], community assembly models [218, 321, 332] or more recently timed-automata [319], the EDEN approach represents ecological dynamics as a State-Transition Graph.

The topology of this graph provides valuable information about ecological dynamics [321, 332, 387, 125]. A State-Transition Graph generally includes three main topological structures (or *components*), namely Strongly Connected Components, stable states and basins [76] :

— First, a *Strongly Connected Component* (SCC) is a set of mutually reachable states, i.e. any change is reversible. It can be cyclic (only one trajectory, e.g. yellow states in Fig. 8a) or complex (several trajectories, e.g. green states in Fig. 8a) highlighting the presence of one or several feedback loops, respectively. Cyclic SCCs are discrete analogues of limit cycles [275] and have been used in community assembly to define cyclic changes in species community composition [321, 332]. On the other hand, complex SCCs have been observed in cell differentiation [387], rangeland dynamics [208, 338] and geomorphology [283], and have been predicted theoretically [300].

In addition, this concept is crucial in State-and-Transition Models for defining the concept of "state", which is "a sustained equilibrium that is expressed by a specific suite of vegetative communities"[338].

— Second, a *stable state* is a state with no successor (Fig. 8, dark blue state). These have been interpreted as final phenotypes in cell differentiation trajectories [387] or uninvadable communities in community assembly experiments [380].

— Finally, *basins* are defined as sets of states which (1) are not part of a SCC or stable state and (2) all lead to the same SCCs or stable states (Fig. 8, orange and non-terminal blue states). Although they do not have well-known empirical counterparts, a recent model based on protists community disassembly experiments [381] confirmed the relevance of such structures, suggesting their role as sets of transient states with indeterminate fate.

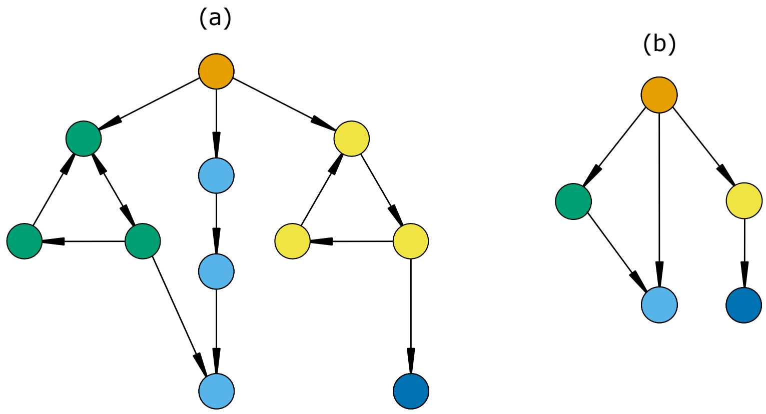


Figure 8 – Illustration of topological structures (or components) in a state-transition graph and its compression in a hierarchical transition graph. (a) : State-transition graph (STG). Each node and edge is a state and a transition, respectively. Node colors indicate which topological structure a state is belonging to. For instance, all yellow states belong to the same SCC. Note that the light blue states represent a set of states necessarily ending in a stable state and thus represent its basin. (b) : Hierarchical transition graph corresponding to the STG) in (a). Each node is a topological structure of the STG, and each transition is necessarily irreversible. The HTG is thus acyclic.

There is no mathematical limit to the size of STGs, EDEN models outputs STGs up to thousands or billions of states [e.g. 124, 223]. Automatic analyses (summarized in [1]) are thus required to disentangle relevant information. They include STG aggregations and model-checking [67]. STG aggregation is related to the identification of transient and persistent sets of states and consist in merging states according to their neighboring relations [30, 97]. On the other hand, model-checking refers to the formal verification of dynamic properties in the set of computed ecosystem trajectories. It is beyond the scope of this paper to provide an exhaustive list of such techniques, so we will present the main analysis techniques.

The main STG aggregation aims to summarize the STG by merging its components (i.e. SCCs, stable states and basins), thus forming a *Hierarchical Transition Graph* ([30], Fig. 8b). In this graph there is a transition between two components (for example between green and blue components in Fig. 7b) only if there is a transition between at least two states belonging to either of these components (Fig. 8a). Nodes of the Hierarchical Transition Graph correspond to transient (basins) and persistent behaviors (SCCs and stable states), while transitions indicate the irreversible changes. Note that the similarity between the definition of SCCs and "states" in the States-and-Transitions modelling framework make the Hierarchical Transition Graph comparable with a States-and-Transitions Model.

On the other hand, model-checking is a verification method that proves automatically if a given State-Transition Graph satisfies a dynamic property, usually expressed as a temporal logic formula [67]. However, the mathematical formalism used for expressing dynamic properties is usually hard to master for ecologists and biologists. Therefore, pre-established properties (called query patterns) already exist in biology [238] and ecology [73]. These query patterns enable asking questions like :

— Is ecosystem collapse avoidable ?
— Is a highly productive ecosystem state reachable and stable ?
— Is this productive state always preceded at some time by e.g. a disturbance ?

While temporal logic has mostly been used in systems biology, seminal applications can be found in agricultural sciences [150, 394, 195] or ecosystem management [73].

Discussion and conclusion

Dynamic ecosystem models aim at predicting temporal changes of ecosystem state variables' values induced by internal system structure or external influences. So far, ecosystem modelling mostly opted for a quantitative approach, generally based on differential equations. However, depending on the objectives, quantitative information may not be necessary, e.g. the search for keystone species [270], study of vegetation succession [257] or qualitative response of ecological communities to press perturbations [41]. Additionally, parameter values are often imprecisely known and may change over time, thus reducing confidence in some model results.

In this regard, qualitative models represent an alternative in data-poor situations. Although less precise, they are no less rigorous and often rely on fewer assumptions, thus increasing the generality of model predictions. They are not meant to replace quantitative models in all situations, but can prove useful in the early steps of the modelling process for generating and rejecting qualitative hypotheses. As they generally display ambiguous predictions, this can also inform ecologists about which processes require quantitative information to provide unambiguous qualitative predictions and which do not.

We have exposed some of the major properties of each modelling method and discussed their limitations according to specific objectives. We expected ecosystem models to (1) grasp the qualitative dynamics of the system of interest, (2) make as few assumptions as possible about interaction parameters and spatial structure, (3) be explanatory and (4) be predictive. We have shown that there is a long tradition of qualitative approaches in ecology, dating back to [54], followed by [70], [204] and [384], to name a few. In particular, after others [e.g. 394, 56, 300], we propose the EDEN modelling approach, which considers discrete events as the basic units of change in qualitative dynamics. An event is a change in system state defined as the crossing of a threshold which delimits different ecological functions of a variable.

We also highlighted some of the assumptions implied by a deterministic view (at least) in qualitative models. As illustrated in Fig. 7 from the rule set in Fig. 5b, the synchronous qualitative models assumes equally fast processes, which is a too strong assumption and can lead reject a model that would be accurate if asynchronous. As a consequence, we suggest considering the asynchronous update mode as a realistic alternative for qualitative models. Note, however, that determinism still enabled to predict important phenomena such as trophic cascades [54]. Probabilistic models also face limitations due to necessary assumptions. Indeed, a probability distribution needs to be chosen for any stochastic process and every choice of probability distribution needs to be justified thus requiring much information. When such information is unavailable or insufficient, we propose possibilistic non-determinism as an alternative. It infers all possible alternative trajectory given a set of premises (rules or equations). Note, however, that the number of possible states grows exponentially with the number of variables or variables values, thus making model computation, analysis and intelligibility challenging. Therefore, possibilism do not prevent modellers from keeping models simple.

We think qualitative models raise important methodological questions in ecological modelling. In particular, the prevalence of quantitative models in spite of the poor quantitative information suggests a confusion between precision and accuracy. For instance, the APT model (Fig. 5) is imprecise (i.e. no numerical values of population size are given), but also highly accurate since all predicted states and transitions are actually observed [381]. This, of course, does not discard quantitative models as relevant tools for explaining complementary aspects of ecological dynamics. It is common to find aspects of ecological phenomena whose explanation require the use of multiple models (what [367] calls model pluralism). Model pluralism is a fact in ecology and should be maintained and promoted. By offering various mathematical expressions to ecological situations, it widens the range of ecological questions one can ask to a particular system and thus helps formulating new ideas.

In this respect, systems biology can be a great source of inspiration for ecology. Its constant dialog with computer sciences contributed to its current spectrum of qualitative-to-quantitative formalisms, from the Boolean to multivalued to hybrid to fully continuous methods [87, 20]. There is a continuous effort to bridge gaps (and not necessarily unify) between existing methods, which is of great interest for explaining natural phenomena. As [204] puts it, talking about qualitative models : “general models are necessary but not sufficient for understanding nature. For understanding is not achieved by generality alone, but by a relation between the general and the particular”. In this respect, mathematical connections between, on one hand, differential equations and, on the other hand, loop analysis [176], logical models [282, 304] or qualitative reasoning models [192] have already been demonstrated. Therefore, if each qualitative model is proved to be a relevant abstraction of specific aspects of quantitative models, it can be possible to draw relevant conclusions with much less information. This is encouraging as modellers can lean on this pluralism for building more robust explanations of natural phenomena.

Chapitre 2

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

2.1 Introduction

African savannas provide many ecosystem services to human societies [224]. Their high primary production support livestock herding and smallholder farming [302], while large mammal populations contribute to large-scale nutrient flows and tourism [163, 231, 326]. The dynamic nature of such systems has been widely acknowledged, with water availability being the primary driver of vegetation [104, 224] (and thus of wildlife, [385]), but also of tourism [198], pastoralism, and rain-fed agriculture. On the other hand, human activities locally retroact on wildlife and vegetation [210, 287]. These feedbacks between social-ecological components thus call for integrated ecosystem management. However, a sound management strategy requires efficient forecasting methods for assessing the possible consequences of changes in environmental conditions. Here, we introduce an innovative modeling 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 [151] or the increase in herbivore populations [149, 327]. So far, many savanna models consider a few variables (e.g., [354]) 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 that are often unavailable or highly costly to obtain [179, 204, 349]. This feature makes difficult for most dynamic models to take qualitative expert knowledge [21] or historical anecdotes [9] 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 [27].

In contrast, qualitative modeling such as state-and-transition models [384], loop analysis [205], qualitative reasoning [46], Boolean Networks [300, 126], or timed automata [394] enable using expert-knowledge and require few or no quantitative information for model conception. They have proven useful for assessing the effect of press perturbations on whole interaction networks [82], providing recommendations for rangeland management [34], modeling cerrado dynamics [305, 333], or modeling the dynamics of fish communities in response to fisheries management [394]. Qualitative modeling enables building models when numerical data are not available [205, 303, 176] while assuring more general predictions (sensu [227]) due to comparable quantitative models. Indeed, where a quantitative model would require precise parameter values to make predictions, a qualitative model with comparable variables, internal relations, and objectives will require less information for providing the same qualitative predictions [46]. This in turn makes its qualitative predictions more (or totally) independent of parameter values, and thus keeps them valid when parameters change over time or between locations [282]. Its lower reliance on quantitative data also facilitates the integration of multiple and heterogeneous components and relations from various knowledge sources [159, 290, 304]. Moreover, quantitative predictions are not always required. For instance, if one simply wants to determine whether it is possible that a given ecosystem reaches a particular state (e.g., a more biodiverse or socially desirable state) [101], then qualitative predictions can be sufficient, which does not preclude including quantitative aspects in further analyses. A qualitative perspective is also a convenient way to study long-term dynamics by averaging short-term quantitative variations [126]. 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 [34], or rule-based models generating complex dynamics from simple “if-then” rules [333]. This facilitating role is especially useful for decision-makers which may seek robust and easily interpretable results for designing management actions.

However, most qualitative modeling frameworks are constrained by several assumptions or methodological limitations [78]. Limitations, for instance, include (depending on the chosen method) determinism, assumptions about parameters values, and the form of interactions, the inability to make predictions of unobserved system states, or the tendency to produce ambiguous (undeterminate) predictions [78]. These limitations thus call for an innovative modeling framework.

Discrete-event models [61] have shown their ability to provide understanding and recommendations for ecosystem management [73, 394]. These models represent system components as discrete (and often Boolean) variables while 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 cell differentiation [1] or response to cancer treatments [24]. In ecology, they have been used to model the assembly of plant-pollinator networks [56], their response to extinctions [58], and their invasibility [57], but also spatialized predator-prey dynamics [135] and ecosystem services assessment [124, 223]. Importantly, they are able to qualitatively grasp key features of ecosystem behavior, such as the bistable behavior of budworm-forest dynamics [300] or bush encroachment in some Ethiopian savannas [346], without requiring precise parameterization. In addition, like most qualitative models, they provide a graphical and intuitive representation of social-ecological dynamics ([e.g. 300]), thus improving communication of complex phenomena towards the non-scientific public such as stakeholders and students [35]. Finally, their co-evolution with computer science contributed to the development of efficient analysis techniques such as model-checking [67], which could be highly relevant for social-ecological applications [346].

In this study, we introduce the Ecological Discrete-Event Network (EDEN) modeling framework [125] for modeling 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 that 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 [34]. In contrast with existing rule-based models of vegetation dynamics [284], an EDEN model computes all possible trajectories and can thus account for rare events and their far-reaching effects [130].

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., [39, 267, 310]), we built a 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 aimed to answer three research questions, namely : (Q1) Did these changes in environmental conditions induce irreversible ecosystem transitions ? ; did they modify the set of existing (Q2) vegetation types and transitions and (Q3) socio-economic profiles and transitions, and why (i.e., which rules drove these vegetation and socio-economic changes) ? Although vegetation dynamics are influenced by spatial structure [207], the model presented here is spatially implicit, assuming that it still enables to test the following hypotheses.

We tested the following hypotheses : (Hypothesis 1) Permanently changing environmental conditions will induce an irreversible change (i.e., impossibility to reach back the initial savanna state) ; (Hypothesis 2) as water availability is known to modulate woody plant recruitment [47], 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 [63], including livestock and thus pastoralism. Finally, (Hypothesis 3) 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). After presenting the study site and data collection, we introduce the EDEN framework (i.e., the formalism and analysis tools) and the savanna model in more details. Results show that water availability directly and indirectly influences vegetation and socio-economic transitions, with herbivores often mediating this influence. Then we discuss the realism of such predictions and their policy implications.

2.2 Materials and Methods

2.2.1 Study Area

We performed surveys in the savannas of the Arusha region, northern Tanzania, which is representative of many savannas of East Africa. 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 [127]. Two sites were surveyed, the Gelai plains and Meru savanna, in order to get a broad view of northern-Tanzanian savannas. Vegetation was diverse, ranging from open grassland to wooded savannas. The Gelai plains ($2°47'52.1``S$, $36°06'03.1''E$) are grassy plains located between 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 agriculture and pastoralism are practiced [168]. We did not find any fire scars on tree trunks nor charcoals attesting to recent fire on any site. More information about the sites we surveyed is available in Appendix A.1.

2.2.2 Data Requirements and Collection

All data collections aimed to determine which qualitative changes related to research questions could occur in the system. For instance, elephants are known to topple trees, which makes woodlands shift into more open savanna [200]. This qualitative change of interest can then be included in the model.

Information about system structure and events was obtained through field surveys and a literature review. Field surveys consisted of informal discussions [236], namely open and semi-structured interviews and focus groups. Interviewed stakeholders consisted of NGOs (e.g., Istituto Oikos), scientists, and farmers, who also guided us during field surveys. First, these discussions were aimed to provide a comprehensive understanding of the system's main components and relations between them (focused on present day). More justifications about the choice of variables is given in Appendix A.2. Then, we determined whether these components exhibit (or have exhibited) contrasting qualitative states in the past or in neighboring regions or districts. In order to keep the model simple, we sought to only determine two qualitative states (i.e., active/inactive or present/absent). The qualitative state of a component was defined by its ability to perform a function. For instance, surface water is active (or present) when it is able to sustain at least one herbivore population. When such a relation between state and function was not available, the qualitative state of a component was defined by stakeholder claims. Finally, once qualitative states of a component have been determined, we sought to understand under which conditions for a component to change its state (i.e., which components must be present/absent for a given component to change).

The same process was done for the literature review by searching for studies highlighting the qualitative aspects of social-ecological system dynamics.

2.2.3 The EDEN Modeling Framework

EDEN is a modeling framework relying on a qualitative discrete-event approach to model system dynamics. Variables are Boolean and their values are modified by *"if-then" rules* representing social-ecological events (e.g., seasonal shifts, drastic changes in population density or droughts). Therefore, system dynamics consist of discrete states and transitions. "If-then" rules are executed one at a time (i.e., asynchronously), which implies that several alternative trajectories may be opened from a given state (dynamics are non-deterministic). Since rules are not assigned a probability value (non-probabilistic) and dynamics are non-deterministic, the EDEN framework is called possibilistic (i.e., non-probabilistic non-determinism) as all possible trajectories are computed given the predefined rules and initial state. Each of these properties are further detailed and justified in the following.

2.2.3.1 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 [80, 349]. 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 a variable response. As a simple ecological illustration, consider seed germination (the variable) triggered by soil moisture (the driver) [152]. Above a given (and often unknown [80]) 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 modeler defines a set of variables, their initial value, and the set of "if-then" rules, as has been done previously in other models [305, 333, 284]. The specific method applied here follows the work of [125].

2.2.3.2 "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 2.1). 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 2.1) for (formal details about rule execution, see [125]). The execution of a rule in a given state produces a *transition* resulting in a new system state (Fig. 9).

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 [121], 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 for 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 A.2). Moreover, priority rules (called *constraints*) can be used to model fast processes (discussed in Appendix A.3).

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 [68, 191]. A possibilistic model is thus a non-deterministic, yet non-probabilistic, model.

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

TABLE 2.1 – 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.

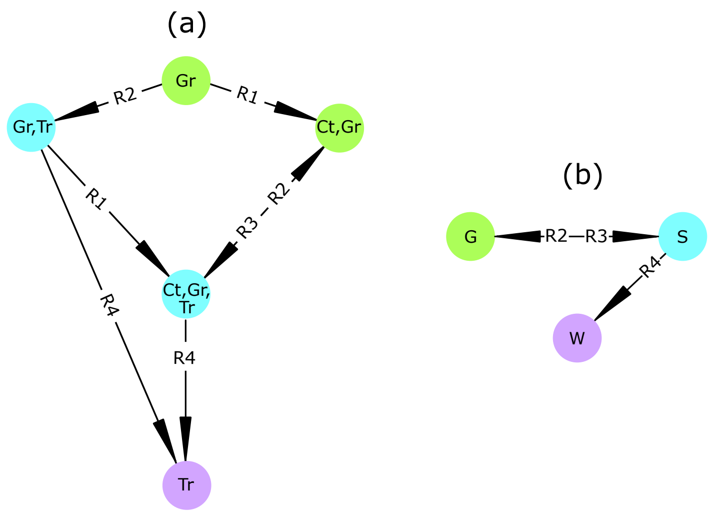


FIGURE 9 – Transition graphs of the "Grasses-Trees-Livestock" toy model (Table 2.1). (**a**) State-Transition Graph (STG) depicting every reachable states and transitions from the initial state, with node labels corresponding to active variables `Gr` (Grasses), `Tr` (Trees), and `Ct` (Cattle). (**b**) 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).

2.2.3.3 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. 9a). A STG may include topological structures representing cyclic behaviors, transient states, or stable states [125]. Here, we mostly focused on the concept of a 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. 9a, e.g., states $\{\texttt{Ct,Gr}\} and \{\texttt{Ct,Gr,Tr}\}$ form a SCC). Therefore, any ecosystem change within a SCC is reversible, either directly (as in Fig. 9a) 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*. These concepts are illustrated below through a simple model.

In Fig. 9a, 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 2.1), this oscillation could be interpreted as a periodic control of woody plants by livestock. The bottom-most state is an attractor as it has no successor. Since it is composed of only one state, it thus forms a stable state. Details on STG computation have been discussed in another study [125].

2.2.4 Model Description

The 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).

2.2.4.1 Scales

Model spatial and temporal scales were constrained by research questions. Spatial and temporal ranges over which model prediction remain valid were not precisely defined. Regarding temporal scale, the lower temporal bound of model predictions is approximately a few weeks to a month (i.e., the duration of the most rapid transitions, such as a season shift). The upper temporal bound is not strictly defined : Model predictions are no longer valid as soon as new events or new variables emerge in the system such that the phenomena of interest (e.g., vegetation transitions) are modified at the considered spatial scale. This upper bound is thus, by definition, unknown. Regarding the spatial scale, as we consider socio-economic activities, the lower spatial bound is defined by agriculture, pastoralism, and tourism, which require a minimal area to co-occur (and whose exact value is unknown and probably variable). As for the temporal upper bound, the upper spatial bound is defined by the appearance of new events or variables.

2.2.4.2 Model Variables and Rules

The model included 13 biotic, abiotic, and socio-economic variables (Table 2.2), 49 rules, and 8 constraints representing system transitions (Table A.1 and A.2). 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. For details on the choice of other variables, see Appendix A.2. The chosen initial state (i.e., the initial valuation of variables, Table 2.2) was aimed to represent the state of the Meru savanna when field surveys were performed.

Table 2.2 – 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	+

2.2.5 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 were developed. The first two scenarios are related to surface water availability. Indeed, as Africa currently undergoes persistent changes in annual rainfall, these are expected to affect surface water reserves and indirectly modify ecosystem structure and functioning [63, 89]. Therefore, we defined the *"dry period"* and *"wet period"* scenarios to simulate the effect of permanently insufficient and sufficient surface water resources, respectively. This was done by adding a constraint maintaining the "surface water" variable inactive (`Sw-`) or active (`Sw+`), respectively (Table A.1). The last two scenarios are related to the presence of herbivore functional groups. Indeed, herbivores are known as a major driver of vegetation change, with grazers and browsers having contrasting effects on vegetation dynamics [334]. Therefore, we defined the *"no grazers"* and *"no browsers"* scenarios to simulate the effect of each group's local extinction. This was done by adding a constraint maintaining inactive either grazers (`Ct-, Gz-`) or browsers (`Go-, Bw-, El-`), respectively (Table A.1).

2.2.6 State-Transition Graphs Analyses

First, to assess whether changes in environmental conditions induced irreversible ecosystem transitions (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, [30]). 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). For an illustration of the correspondence between STG and HTG, see Fig. 21. 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. 19). Therefore, to assess whether changes in environmental conditions modified the set of vegetation and socio-economic transitions (Q2 and Q3, respectively), 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 [97], i.e., groups of disjoint states characterized by specific state properties. Here, partitions were vegetation types (characterized by the presence/absence of grasses and trees) and socio-economic profiles (characterized by the presence/absence of agriculture, pastoralism, and tourism) (Table 2.3). In order to compare vegetation and socio-economic transitions between the reference and other scenarios, we used such partitions to draw *summary graphs* (see [97], for detailed procedure) (Fig. 9b).

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. 9b). Summary graphs of vegetation types and socio-economic activities were called the vegetation summary graph and socio-economic summary graph, respectively. Differences between the summary graphs of the various scenarios were then explained by determining which rules drove transitions from the analysis of the rule set.

TABLE 2.3 – Vegetation and socio-economic partitions. Each partition consists of several groups that 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- ∧ Gr-
	Grassland (G)	Tr- ∧ Gr+
	Savanna (S)	Tr+ ∧ Gr+
	Woodland (W)	Tr+ ∧ Gr-
Socio-economic profiles	APT	Cr+ ∧ (Ct+ ∨ Go+) ∧ To+
	AP	Cr+ ∧ (Ct+ ∨ Go+) ∧ To-
	AT	Cr+ ∧ (Ct- ∨ Go-) ∧ To+
	AP	Cr+ ∧ (Ct+ ∨ Go+) ∧ To-
	PT	Cr- ∧ (Ct+ ∨ Go+) ∧ To+
	A	Cr+ ∧ (Ct- ∨ Go-) ∧ To-
	P	Cr- ∧ (Ct+ ∨ Go+) ∧ To-
	T	Cr- ∧ (Ct- ∨ Go-) ∧ To+
	∅	Cr- ∧ (Ct- ∨ Go-) ∧ To-

2.3 Results

2.3.1 General Observations

Scenarios had highly contrasted State-Transition Graphs (Table A.3). 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 State-Transition Graph. Its attractor was small (three states) and was thus characterized in detail (Fig. 22).

2.3.2 Vegetation Transitions

In all scenarios, the initial state had savanna vegetation (Table 2.3). In the reference model (Fig. 10a), bare soil and grasslands were both reachable from any other vegetation type (Fig. 20). Once reached, bare soil could only be colonized by grasses before trees to invade. Vegetation transitions were driven by herbivores and water availability. Rules responsible for these vegetation transitions in Fig. 10 can be visualized in Fig. 20 and are detailed in Table A.2.

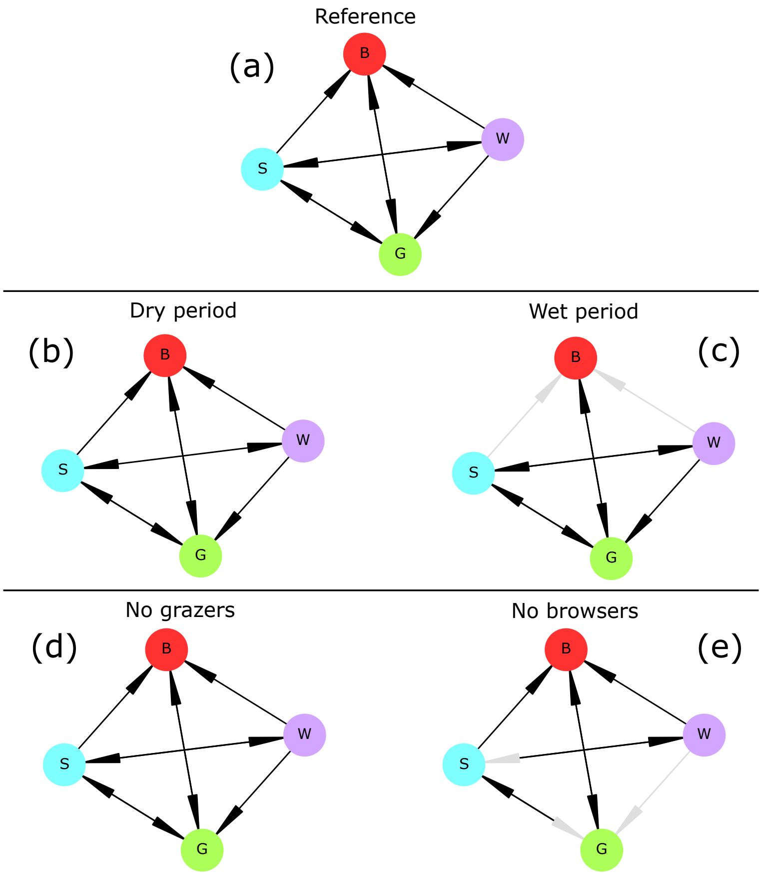


FIGURE 10 – **Vegetation transitions for each scenario.** Vegetation summary graphs for (**a**) the reference scenario, (**b**) the "dry period", (**c**) the "wet period", (**d**) "no grazers", and (**e**) "no browsers". Node labels indicate vegetation types as defined in Section 2.2.6, with B : Bare soil ; G : Grassland ; S : Savanna, and W : Woodland. Node colors are arbitrary and correspond to vegetation types. Grayed out edges are absent from the graph and highlight differences relative to reference scenario. Grayed out arrow tips (e) indicate when a bidirectional transition becomes unidirectional.

In the "dry period" scenario (Fig. 10b), the lack of surface water did not modify vegetation transitions. However, the system experienced sequences of irreversible transitions (Fig. 11a) towards a regime of seasonal grassland (Fig. 22) in which woody plants were unable to colonize due to the lack of groundwater (R33). Such drought-induced transitions were (logically) absent from the "wet period" scenario (Fig. 10c), in which tree mortality was only due to browsing (R29 to R31). In the "no grazers" scenario (i.e., without cattle and wild grazers, Fig. 10d), vegetation transitions were not modified. 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 still be induced by drought-related rules (R6 and R13), the transitions were maintained, although not necessarily by the same drivers. Finally, the "no browsers" scenario (Fig. 10e) was the inverse of the "wet-period" scenario : Drought (R13) was the only factor driving tree mortality (C8), implying that both trees and grasses died (C8) thus only leading to bare soil. The transition from woodland to savanna which resulted from the competitive advantage of grasses over trees in presence browsers was no longer possible.

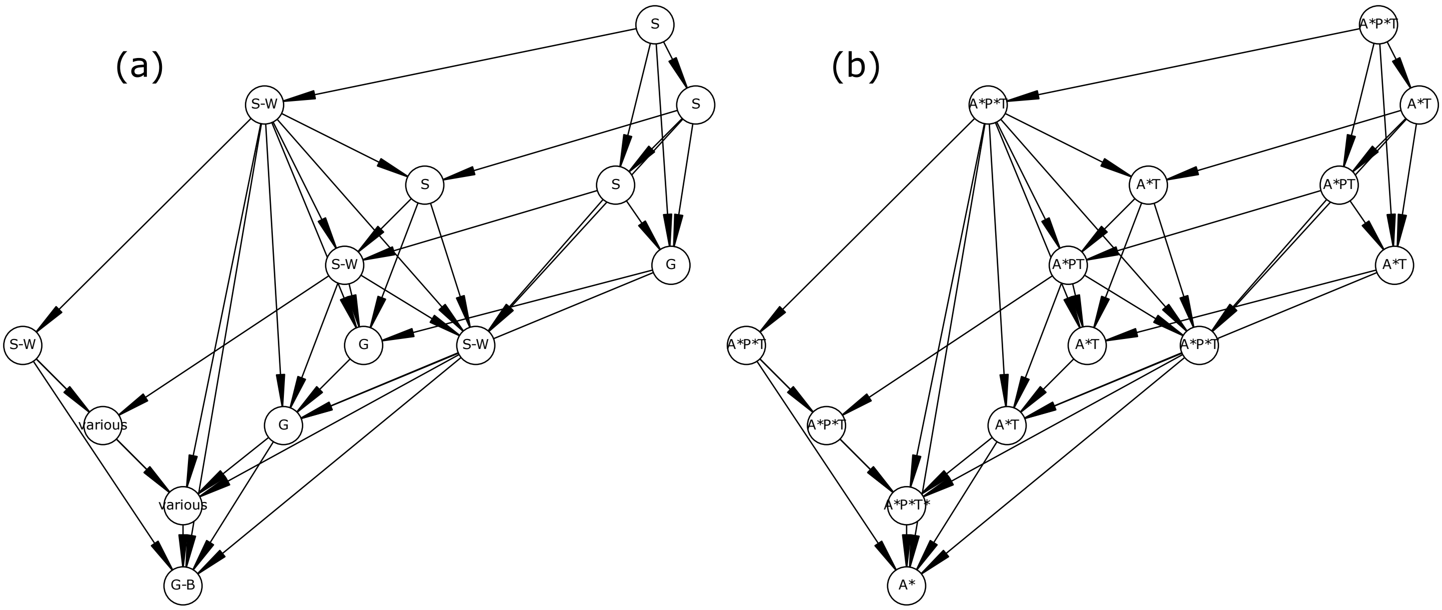


FIGURE 11 – Hierarchical Transition Graph (HTG) of the “dry period” scenario. The same HTG is represented with a focus on either vegetation (**a**) and socio-economic (**b**) dynamics. Graph nodes are SCCs and each transition is, by definition, irreversible. Therefore, dynamics within each node display some form of oscillation. Letters correspond to vegetation types (B : Bare soil ; G : Grassland ; S : Savanna ; W : Woodland) or socio-economic activities (A : Agriculture ; P : Pastoralism ; T : Tourism). In (**a**), node labels either correspond to a stable vegetation type (e.g., “S”) or to an oscillation between two (e.g., “G-B”) or more (“various”) types. In (**b**), node labels correspond to socio-economic activities. An activity can be stable, and is thus noted by a letter (for instance, T in “A*T”). When the activity can change (oscillate) in a SCC, it is noted with a * (as in, A*T, where A is oscillating).

2.3.3 Socio-Economic Transitions

In all scenarios, the initial state had a mixed economy including Agriculture, Pastoralism, and Tourism (APT).

In the reference model (Fig. 12a), the absence of activities (red node, Fig. 12) 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→AP and PT→P were impossible).

In the “dry period” scenario, socio-economic transitions were not modified. However, further analyses showed that pastoralism could be lost and never recover (Fig. 11b). 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 A.1). The system ended up in an attractor in which the only human activity was seasonal agriculture (Fig. 22).

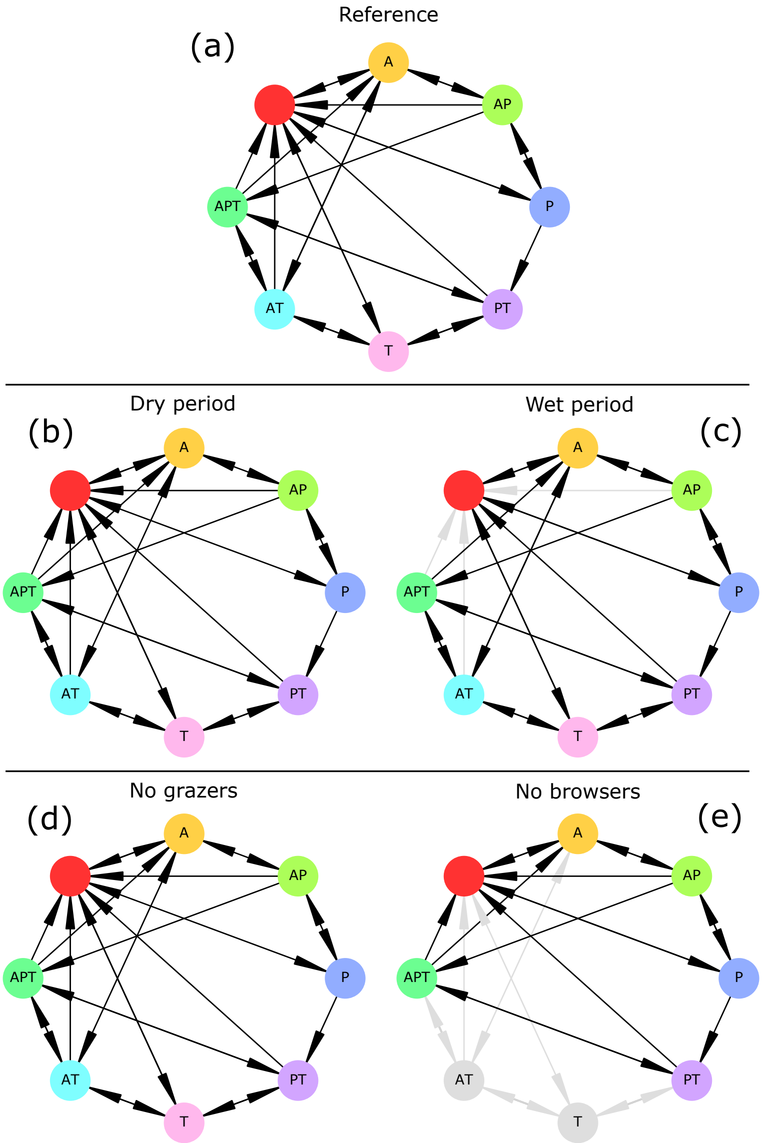


FIGURE 12 – Socio-economic transitions for each scenario. Socio-economic summary graphs for (**a**) the reference scenario, (**b**) the “dry period”, (**c**) the “wet period”, (**d**) “no grazers”, and (**e**) “no browsers”. Node labels indicate socio-economic profiles, i.e., combinations of socio-economic activities A, P, and T, with A : Agriculture ; P : Pastoralism, and T : Tourism. Non-gray node colors are arbitrary and correspond to socio-economic profiles. Grayed out nodes and edges are absent from the graph and highlight differences relative to the reference scenario.

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 surface water is constantly present (`Sw+`) and R6 (which was able to induce these three transitions through constraints C6 to C8 when surface water (`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 cattle (`Ct`), grazers (`Gz`), or carnivores (`Ca`) were active (see constraint C1, Table A.1). However, grazers necessarily became active simultaneously to cattle (R39) and became inactive before or at the same time as cattle (see Table A.2 for rules (in)activating cattle and grazers). Therefore, when cattle became inactive, this implied that grazers already were, which instantaneously made carnivores (C5) (and thus tourists (`To`)) inactive.

2.4 Discussion

In this paper, we applied the Ecological Discrete-Event Network (EDEN) modeling 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 [93, 111, 157, 315, 326]. 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. 9a, the ecosystem may remain inside the SCC (an infinite trajectory) without never reaching the attractor. Therefore, STG reversibility should not be equated with resilience [156], but rather to a potential resilience. Second, our model is possibilistic and may thus include highly unlikely transitions. Therefore, using such models for management recommendations may require assessing the sensitivity of STG reversibility to rare events.

2.4.1 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 socio-economic activities such as pastoralism and especially cattle production [7]. 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 [47, 208].

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. 22). 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 [329, 47]. 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. 10). This was not in agreement with current knowledge as grazing is known to favor trees over grasses [155]. 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 (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 [60, 112, 47, 329, 189]. Browsers contributed to a reduction in woody cover, which confirms current knowledge [374, 336]. These general results support management recommendations about the preservation of wild herbivores for managing vegetation [208].

Fire and soil nutrients, which are not considered here, are well-known drivers of vegetation dynamics [329] and could easily be included in later model versions. 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. Besides, vegetation summary graphs (Fig. 10) share many similarities with State-and-Transition Models [384] which have been extensively used to represent rangeland or savanna dynamics [208, 34].

2.4.2 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 in rainfall frequency and intensity [184, 388]. 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. 22). For the same reasons, wildlife populations declined, thus making tourism disappear. This latter prediction corroborates other findings [183]. On the other hand, increasing water availability ("wet period" scenario) did not prevent any socio-economic profile (Fig. 12). Rather, drought-induced transitions (here, general disruption of all socio-economic 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 the 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 [8]. 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.

2.4.3 From Predictions to Policy Implications

Although our model makes predictions, it is unable to provide management recommendations at this stage. What would be required for doing so ? The first requirement is to find a clear agreement between predicted and observed dynamics for at least one specific location. Here, the agreement between predictions and data is partial (albeit groundwater availability and browsers indeed play a role in vegetation dynamics) and is not sufficient for providing recommendations. Second, even though predictions would be confirmed, management recommendations must benefit stakeholders (e.g., farmers, pastoralists, tourists, or wildlife managers) and thus, must be discussed before being proposed. This is not the case here as the aim of this study is mostly methodological and only involve stakeholders during model conception. Such discussions could however be pursued in the future. This is not an exhaustive list of the requirements for providing management recommendations from model predictions.

Nonetheless, this study provides some tools that may draw the attention of managers to EDEN models. For instance, the summary graphs presented share many similarities with State-and-Transition Models used for rangeland management and national parks [34, 289]. The EDEN framework complements these empirical (i.e., non-formal) models by providing a mechanistic basis to ecosystem transitions and many tools to analyze them.

2.4.4 How to Cope with Model Structure Uncertainty

Generally, the presence or absence of specific variables and relations (i.e., model structure) is not certain and several model structures could correspond to available knowledge or observations. Such uncertainty could result from spatial heterogeneity [226] or temporal changes of interaction networks. Alternative model structures often lead to contrasting dynamics [316, 162] and choosing the right one(s) is challenging. In this study, we considered a single model structure to which we applied four press perturbations manipulating the value of specific variables. However, rules are not equally well supported (Table A.2). Instead of testing all possible alternative model structures (which would generate many ecologically meaningless models), we could use uncertain rules to generate alternative model structures. For instance, we assumed that cattle was able to exclude wild grazers (R22), while the reverse was assumed impossible. One way to assess the role of such uncertain rules (r) would be to exclude them in all possible combinations (2^r) and verify a list of specific dynamical properties (e.g., vegetation transitions) for each of the 2^r corresponding STGs. The same method could be applied to rules definitions. For instance, rule R47 assumes that wild (`Bw`) and domestic (`Go`) browsers should co-occur to enable epidemics to emerge. However, in areas where browsers are now extinct, livestock are still subject to diseases [297]. Therefore, we could split this rule as `R47a: Bw+, Rf+, Sw+ » Bw-, Go-`, and `R47b: Go+, Rf+, Sw+ » Bw-, Go-`. These two rules can also be considered more parsimonious as goats and browsers can be subject to diseases independently of one another. Note that rules R47a and R47b are both general cases of R47 (their conditions include that of R47). Besides, automatically assessing dynamical properties of hundreds or thousands alternative models requires powerful and rigorous analysis tools. For that purpose, the visual analysis of summary graphs would be unworkable and should be replaced by model-checking techniques [346].

2.4.5 The Scope and Verification of EDEN Models

This study showed how the EDEN modeling 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 [67] which enable the automatic exploration of large ecological State-Transition Graphs [346]. 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 [384]. In return, researchers can provide modeling tools to derive predictions from this abundant expert knowledge. Ultimately, this interaction between ecosystem management and modeling may be used to improve management interventions.

2.5 Conclusions

In this study, we proposed the EDEN modeling 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 modeling 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 socio-economic 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.

The EDEN framework is qualitative, which means that it cannot provide precise (i.e., quantitative) predictions. In addition, the model is non-deterministic and non-probabilistic, which implies that its predictions cannot be assigned a probability. However, these two “limitations” have an interesting counterpart : The model does not require quantitative data about parameters describing observed phenomena, and its predictions are robust to changes in parameters or to uncertain measurements. Therefore, they are more general, more parsimonious, albeit less precise and certain. Although rules may be more descriptive than explanatory (e.g., rules driving seasonality), they correspond to observed phenomena, can be easily explained and thus enable the use of expert-knowledge.

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, modeling through an intuitive event-based approach. Such models could find applications in agroecology to assess the long-term impacts of management actions on biodiversity and livelihoods.

Chapitre 3

Farm trajectories in the South Sudanian zone of Burkina Faso : how to achieve a persistent crop-livestock integration ?

3.1 Introduction

Understanding how farm households maintain, accumulate or lose their assets and capabilities is crucial for designing socially and environmentally relevant management policies. To approach this question, it is common to start by discriminating farm types based on their activities, assets and/or objectives [344, 359, 95, 98]. Usually, a few farm types are found to coexist [98] and differ by a few factors (e.g. livestock capital, farm size, market orientation or dependence on non-farm income) [273, 193, 66, 395]. Since the last two decades, farm trajectories (i.e. how a specific farm changes over time) have also received increasing attention [140, 259]. Indeed, as noted by [318], farmers' "livelihoods emerge out of past actions and decisions are made within specific historical and agroecological conditions". Such trajectories depend on the farmers' ability to maintain or enhance their capabilities and assets, to increase their resistance and resilience to stresses and shocks and maintain their natural resource base [59]. In this study, we will draw upon existing knowledge of farm dynamics to model farm trajectories and assess how small farmers can develop a persistent production of food crops, cash crops and livestock.

Observational studies have highlighted the dynamic nature of poverty [55], while others pinpointed major drivers of transition/diversification [259] and the persisting coexistence [351] of multiple household types. One of the most prominent examples are persisting poor households, stuck in a self-reinforcing poverty [16] whose pathways to exit have been studied empirically. Modelling studies also substantially contribute to explain farm trajectories by allowing to formulate and test hypotheses about their drivers [e.g. 99]. Agent-based models are widely used in social-ecological modelling (for a review, see [369]) and are the main type of models for studying livelihood transitions. For instance, an agent-based model predicted that an improved crop management combined with forest protection in Madagascar was able to improve food self-sufficiency and household income, and reduced wealth inequalities [48]. Another agent-based model highlighted the central role of market influence in smallholders livelihood transitions [220]. However, this kind of models generally requires abundant data for parameterization, which are generally unavailable. On the other hand, expert knowledge and qualitative information is abundant for many farm systems. Therefore, a formalism that would handle qualitative information on interactions between system components may ease the modelling process while making predictions more general [204].

The Ecological Discrete-Event Network (EDEN) dynamic modelling framework has been developed with this objective [125]. This framework relies on a discrete-event formalism involving qualitative variables. System states (here, farm types) change through discrete transitions resulting from the application of predefined "if-then" rules. The modelled dynamics are non-deterministic, yet non-probabilistic (i.e. *possibilistic*). Therefore, it computes all possible states and transitions resulting from the successive rule applications. Such qualitative models proved useful in systems biology for modelling regulatory networks [349, 2] and recently emerged in ecology [56, 126, 300] and social-ecological studies [76, 124, 223].

In this paper, we present the model of a farm system [defined by the limits of the sphere of household decision-making, 122] under various scenarios in Southwestern Burkina Faso (West Africa). Using a farm typology [359] and reported farm trajectories [273] from a specific village, we assessed under which scenarios (i.e. combinations of environmental conditions and management practices) model predictions matched observations. Once model predictions were in agreement with observations, we determined which scenarios and events enabled poor farmers to develop a persistent agropastoralism. Based on empirical evidences [e.g. 273], we hypothesized that (H1) the observed farm types were reachable by the poorest farmers (i.e. they can step out of poverty), (H2) livestock was critical for improving livelihood [95] and (H3) the maintenance of soil fertility was associated to an improved livelihood (here, agropastoralism) [95, 352].

3.2 Materials and Methods

3.2.1 Field surveys and study area

Two field surveys were conducted in March and November 2019 in Dano (Ioba Province, Southwestern region). During these surveys, we interviewed researchers, local farmers, NGOs and extension services about farm activities and soil and water management techniques. This area is considered representative of the South Sudanian agroecological zone in Burkina Faso. In this region, climate is characterized by one rainy season running from May to October with a mean annual rainfall of 900 to 1000mm since the 1950's

(Schmengler, 2010). In the last few decades, changes in the precipitation regime increased the vulnerability of rainfed food production, which is the predominant form of agriculture. Additionally, the shortening of fallow periods induces a widespread reduction in soil organic carbon and nutrients. Predominant soil types are Plinthosols, Lixisols, Luvisols, Gleysols [160, 390]. Natural vegetation is a wooded savanna and is mainly driven by water availability, fire and wood collection by local people.

Agriculture is the main activity. Today, traditional crops include sorghum, millet and maize for household consumption, and cotton as the main cash crop. Agriculture and livestock husbandry are generally combined, albeit to different degrees. This region has experienced an important agricultural expansion. This has led to a drastic reduction or abandonment of fallowing and a widespread reduction of soil fertility through water erosion and soil carbon mineralization. Fertility loss, in turn, constrains crop yields and thus agriculture-derived income. To tackle these issues (fertility loss and constraints on income), several management options have been proposed, including crop residue collection, abandonment of dry season free grazing (to reduce outgoing carbon and nutrient fluxes [222], erosion control (by means of stone bunds, diguettes or grass stripes) or non-farm activities which provide complementary incomes which can then be invested in agriculture. When possible, farmers generally tend to complement cash crop production with livestock and manure production, thus adopting an agropastoral livelihood. Livestock provides many services, among which animal traction, production of organic fertilizers (manure) or social-cultural value during traditional ceremonies. Livestock relies on rangelands and fallows in rainy season, and on crop residues in dry season. When fodder is lacking, the wealthiest farmers may send their livestock on transhumance. Some farmers also complement livestock feed with cottonseed cake in dry season. In the last decades, fodder plants have also been highly promoted but are not yet widely adopted.

3.2.2 Farm types

We compared predicted farm types to a farm typology proposed in Koumbia in the Tuy Province (Southwestern Burkina Faso) [359], and farm trajectories (i.e. farms shifting from one type to another) to recent studies performed in the same village [273, 109]. Indeed, we did not find any literature on farm types and trajectories at the southwestern region scale. Despite being limited to one village, Vall's typology [359] overlaps with typologies done in the whole neighboring Ioba Province [344] and elsewhere in Burkina Faso [95]. Consistencies between typologies include e.g. the existence of subsistence-based farm and wealthier agropastoral farms. Other groups such as non-farm based households exists in Ioba and Yatenga [344, 95] and were not reported in Vall's typology [359].

In Koumbia, three main farm types have been identified : agriculture-oriented farms (A), agropastoral farms (AP) and livestock-oriented farms (i.e. breeders, B). Following

[360], agriculture-oriented farms were further refined here in small (A1), medium (A2) and large (A3) farms. A1 includes small subsistence-based farms focusing on food crop production or non-farm activities. They have a few or no draught animal and few or no equipment for animal traction. A2 own a few draught animals and equipment and tend to increase cotton production. A3 cultivate large areas, but still have a limited livestock capital. However, their access to fertilizers allow them to increase grain and crop residues. Agropastoral (AP) farmers focus more on animal production and increase their cattle herds and cotton production. Finally, breeders (B) own relatively small farm areas and large cattle herds. Although they may include a small portion of cereal production for their own consumption, they heavily rely on fodder availability. Note that AP and B types can be split in two sub-types [as in 359] which, however, mostly differ by quantitative aspects (e.g. herd size or cropped area).

3.2.3 Farm trajectories

Five trajectories involving the previously mentioned farm types are identified in the literature [273, 109] : (1) A1 → A2 → A3 → AP ; (2) A1 → A2 → A3 ; (3) A2 → A1 ; (4) B → AP and (5) A1 → A2 → AP. Since trajectory (2) is included trajectory (1), we will not consider trajectory (2). We used these observed trajectories to falsify the model, that is, to verify the existence of farm types and trajectories that were not predicted by the model.

3.2.4 Discrete-event modelling

The EDEN modelling framework relies on a qualitative and discrete-event formalism. A discrete-event framework describes system dynamics in terms of events, i.e. changes possibly occurring at irregular intervals [61].

In this modelling framework, quantitative parameters are not required. Additionally, in this paper, variables are *Boolean* (i.e. present/absent). This simplification facilitates model conception and increases model robustness to parameter changes [204]. In the following, a present (resp. absent) variable `v` will be noted `v+` (resp. `v-`). The value of all variables at a given time defines a system *state*.

The EDEN framework uses a formalism based on "if-then" rules representing social-ecological events. A rule specifies the *conditions* for an event to occur, and the *consequences* of this event on variables values. For instance, the rule `rainfall » grass` indicates that grass growth (i.e. the event) is conditioned by rainfall. When a system state satisfies a rule condition, this rule is executed and generates a new state. The shift from one state to another is called a *transition*.

Rules are executed one by one (or, technically speaking, asynchronously). As a consequence, when several rule conditions are satisfied, each rule is executed independently and thus opens alternative trajectories. The model is thus *non-deterministic*. Note that no trajectory is “chosen” : all possible trajectories are computed. We call this non-probabilistic non-deterministic approach *possibilism*.

In brief, the EDEN framework is based on a qualitative, asynchronous and possibilistic approach. The model computes all alternative sequences of rules execution. The model output is a State-Transition Graph (STG) whose nodes and edges represent system states and transitions, respectively. Technical details on model functioning are provided in previous works [125].

3.2.5 Definition of the farm model : rules and variables

Model conception was based on information gathered during field surveys and literature review about soil fertility management, non-farm activities, livestock management and crop production. It aimed to address the following questions :

Q1 Are observed farm types and trajectories predicted by the model ?

Q2 For a newly settled and poor farm household, which scenarios and management actions enable improving its livelihood ?

Q3 Under which scenarios is it (im)possible for a poor farm to develop and maintain agropastoralism ?

The model computes farm trajectories (resulting from management actions and ecological events) under various scenarios and favorable climatic, market and safety conditions. Therefore, the model does not include perturbations (e.g. drought, market fluctuations or conflicts). It includes state variables and control variables. While the values of state variables are modified by rules applications, the values of control variables are set in initial state and are not affected by rules. The values of control variables define a scenario. The model includes eight state variables, six control variables (Table 3.1) and 31 rules, including 11 constraints (i.e. rules applied in priority to represent fast and/or mandatory events) (Tables B.1 and B.2).

Following **Q1**, initial variables values are chosen to represent a poor farm (A1, Table 3.2). The seven control variables (plus `Lv`) have unspecified initial values (noted “*”) and can thus be either present or absent (two values). Therefore, $2^7 = 128$ scenarios (i.e. initial states) are considered simultaneously.

3.2.5.1 Definition of farm types and trajectories within the model

Each farm type was defined as a combination of present/absent state variables (Table 3.2) such that each state belongs to a single farm type. However, some states did not match any of the predefined farm type and were thus left uncharacterized. Farm trajectories were defined as sequences of at least two farm types such as A1 → A2, which by the way implies

TABLE 3.1 – **Variables and their initial values in the model.** State variables are changing in the model, while control variables are predefined. The initial values of variables are either "present" (+), "absent" (−), or unspecified (*) when both initial states are considered. Note that livestock (Lv) is the only state variable whose initial value is not specified, because a family can own livestock since its establishment.

Type	Acronym	Variable	Description	Initial value
State variables	`Fe`	Soil fertility	Soil nutrient and organic matter content	+
	`Cr`	Crop residues	Residues from cereals (maize, sorghum, millet)	+
	`Fp`	Fodder plants	Woody or non-woody plants grew for feeding livestock	-
	`Lv`	Livestock	At least two draught animals (generally bovines)	*
	`Ma`	Manure	Sufficient quantity of livestock manure for maintaining soil fertility	-
	`Cc`	Cash crops	Income-generating crops (mostly cotton)	-
	`Ca`	Cropped area	Area used for agricultural production (mostly for cash crops)	-
	`Eq`	Equipments	Animal traction or trucks	-
Control variables	`Flw`	Fallowing	Sufficient fraction of land under natural or managed fallow for maintaining overall soil fertility	*
	`Rg`	Rangelands	Available and sufficiently productive rangelands for maintaining livestock	*
	`CRC`	Crop residue collection	Action of removing crop residues when they are produced	*
	`Fg`	Free grazing	Animals allowed to freely graze crop residues	*
	`EC`	Erosion control	Efficient soil and water conservation measures (e.g. stone bunds, grass stripes or diguettes)	*
	`Nf`	Non-farm income	Gold mining, remittances, wage earning or petty trade	*

that A2 is directly preceded by A1, with no intermediate farm type.

3.2.6 Verification of farm types and trajectories

The verification of the existence of farm types and trajectories in the STG (i.e. the computed states and transitions) was assessed using a temporal logic. Temporal logics express dynamical properties about discrete dynamics [for applications of temporal logic in agricultural or ecological studies, see e.g. 196, 150, 73]. Such temporal properties can be "*currently*, the farm is small (A1)", "the farm *will necessarily* become A1" or "medium-sized farm type (A2) *is possibly preceded by* A1".

Here we chose a temporal logic fitted to the non-deterministic nature of our model : the computation Tree Logic [CTL, 67] expressing whether a temporal property holds for some or for all its futures from a given state.

For instance, one can ask whether an A1 farm *possibly* or *necessarily* leads to an A2 farm or, in other words, whether A2 eventually occurs *for some* (∃) or *for all* (∀) trajectories starting from A1.

These ∃ and ∀ *branching operators* are combined with *temporal operators*, namely X

TABLE 3.2 – **Typology of livelihood types used in the model.** Each livelihood is defined in our model by a specific farm type corresponding to a combination of the six state variables (Table 3.1) based on the literature [359, 360, 361, 273]. Note that control variables are not used for defining farm types.

	Variables					
Livelihood type	Cc	Ca	Ma	Eq	Cr	Lv
A1 (Subsistence farmers)	-	-	-	*	*	*
A2 (Medium farmers)	+	-	-	+	*	+
A3 (Large farmers)	+	+	-	+	+	+
AP (Agropastoralists)	+	*	+	+	+	+
B (Breeders)	-	-	+	*	*	+

(for ne**X**t), F (**F**inally), G (**G**lobally) and U (**U**ntil). Intuitively, these temporal operators express the following properties :

- X : what happens in the immediate next state (e.g. "A2 occurs at the next time step")
- F : what happens at some point in the future (e.g. "A2 occurs at some subsequent step")
- G : what happens from now on and forever in the future (e.g. "A2 remains always present")
- U : a chronological sequence (e.g. "A2 is systematically preceded by A1)

Note that in this paper, we only use qualitative temporal properties, without any quantitative detail about *when* or *how long* a property holds.

Additionally, temporal logic formula can also include logical operators AND (∧), OR (∨) and NOT (¬). All these operators may combine to express more complex properties such as :

$$A1 \ \wedge \ \exists \mathbf{F}(\exists(A3 \ \mathbf{U} \ \forall \mathbf{G}(AP)))$$

which can be translated as "Among *small farmers* (A1), some *can eventually* (∃**F**) become *large farmers which may develop* (∃($A3$ **U**) a *persistent* (∀**G**) *agropastoralism* (AP)". In the following, we will only express properties in English and detail the corresponding CTL formulae in Appendix B.4.

3.2.7 Answering model questions

A CTL formula is tested on a State-Transition Graph using an automated tool called *model-checker*. Using the ITS-tools model-checker [343], we verified the existence of observed farm types and trajectories in the model (**Q1**) (see Tables B.3 and B.5 for detailed CTL formulae). States verifying CTL formulae and transitions between them can then be visualized (Fig. 13).

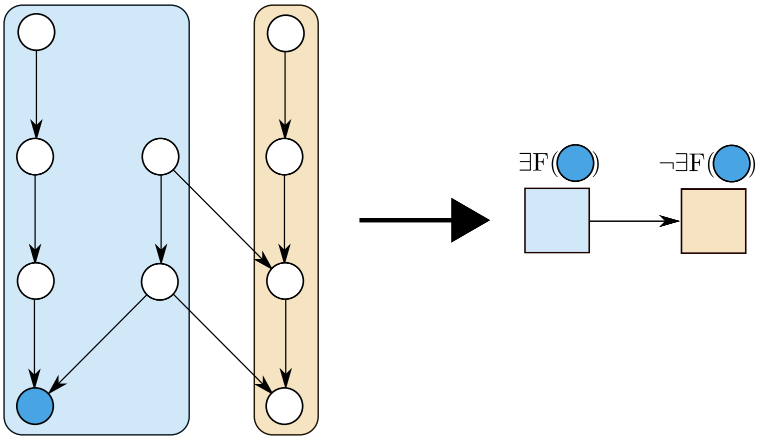


FIGURE 13 – **Translating a CTL formula into a State-Transition Graph.** A state has *state properties* (here, the property "blue" or "white") and *dynamical properties*, i.e. the trajectories it belongs to. Dynamical properties are expressed as CTL formulae. In this illustration, the bottom-left state has the state property "blue". All states can either have the dynamical property "blue is reachable" (∃F(blue), blue shade) or not (¬∃F(blue), brown shade). The CTL formula ∃F("blue") is used to assess which states verify the formula and split the State-Transition Graph accordingly. The resulting graph (right-hand side) thus has two nodes gathering states according to their ability to reach of "blue". In addition, the shape of nodes (here, squares) indicates that they both include a stable state (i.e. a state with no outgoing transition). This graph highlights the fact that the system can permanently lose its ability to reach the property "blue".

Then (**Q2**), we determined for which combinations of control variables an A1 farm can or cannot reach each farm type . This was done in three steps : (1) identifying A1 states for which A2, A3, AP or B farm types were reachable (Table B.3), (2) obtaining the values of control variables for each of these states (which is a "OR of ANDs" Boolean expression) and (3) simplifying this Boolean expression (see Fig. 23 for details on methodology). Finally (**Q3**), we defined "persistent agropastoralism" as CTL formula (Appendix B.4) and assessed under which scenarios (i.e. control variables) and management actions (i.e. transitions) an A1 farm cannot, can or necessarily develops persistent agropastoralism.

3.3 Results

3.3.1 Comparing observations and model predictions

3.3.1.1 Farm types

All farm types (A2, A3, AP and B) were reachable from A1 (Fig. 14). However, they were reachable under scenarios which can be summarized as `[Lv ∧ (Flw ∨ Rg) ∧ (CRC ∨ Fg)] ∨ [Nf ∧ (Flw- ∨ Fg)]`, where variables noted "-" are absent (and present otherwise), ∧ and ∨ mean "AND" and "OR", respectively (see Table B.3 for detailed reachability conditions for each farm type). In other words, livestock (`Lv`), or non-farm income (`Nf`)

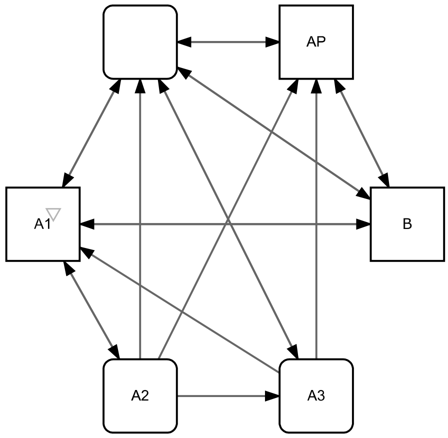


FIGURE 14 – **Farm types and transitions.** Each node in this STG corresponds to a *set of states* of the same farm type and each edge corresponds to a farm transition. A path corresponds to a livelihood trajectory. Squares include at least one stable state (i.e. states with no outgoing transition). Rounded squares include no stable state. The triangle indicates all initial states are A1 farms.

to purchase it, is a prerequisite. This had to be combined with a sufficient and available fodder in rainy season (`Rg` ∨ `Flw`) and dry season (`CRC` ∨ `Fg`). Alternatively, fallow is not practiced, fodder plants (`Fp`) may be developed (rule `R19`, Table B.2). Otherwise, fallows must be combined with free grazing to ensure fodder provision all year long.

Livestock capital (be it inherited or purchased by non-farm income) and fodder management thus determine the ability of A1 farmers to improve their livelihood. If these initial conditions are not satisfied, A1 farmers cannot change. Some predicted farm types were absent from Vall's typology, such as those based on non-farm activities, and were gathered within the A1 farm type.

3.3.1.2 Farm trajectories

In this section, we discuss farm trajectories and transitions (i.e. trajectories between two farm types), which we will generically refer to by the term "trajectory". All observed trajectories were predicted by the model. Trajectories A1→A2 and B→AP were driven by an increase in cash crop production, A3→AP by an increase in manure production, A2→A3 by an increase in cropped area and A2→A1 by fertility loss (Table B.4).

Trajectories A2→A3, A3→AP and B→AP were possible in scenarios `[(Flw ∨ Rg) ∧ (CRC ∨ Fg)] ∨ [Flw- ∧ Nf]` (Table B.5), i.e. if either (1) fodder is sufficient (in dry and wet season) for feeding livestock or, (2) in an intensive context (`Flw-`), if non-farm income is sufficient for purchasing livestock (and if fodder plants production is developed before soil fertility loss).

Trajectories A1→A2→A3→AP and B→AP were interruptible, i.e. it was always possible for the trajectory to be diverted or reversed. In particular, it was always possible for medium farmers (A2) to fall down (i.e. not to become large farmers). Therefore, some events should be avoided for an household to step out, which are discussed in the next section.

3.3.2 How (not) to reach a persistent agropastoralism ?

The ability for A1 farmers to reach a persistent agropastoralism (AP for short) was context-dependent (Table 3.3). In particular, three main factors determined this reachability : (1) the ownership or ability to purchase livestock (by means of non-farm income), (2) the ability to feed livestock all year long and (3) the ability to maintain/recover soil fertility. We partitioned scenarios according to whether they enabled A1 farmers to impossibly, possibly or necessarily reach AP.

TABLE 3.3 – **Reachability of a persistent agropastoralism under various scenarios.** Each scenario is a specific combination of management techniques (i.e. control variables). A control variable noted "-" is absent, otherwise it is present. Note that `Lv` is not a control variable, but can either be present or absent in initial states, and is thus included in scenarios (Table 3.1).

Reachability of AP	Scenarios	Interpretation
Impossible	`Flw, CRC-,Fg-` `Flw, Lv-, Fg-`	The farm practices fallowing, but does not own cattle, or dry season forage is lacking, thus making husbandry unsustainable.
	`Flw-, Nf-, Rg-` `Flw-, EC-`	Without fallows and neither erosion control nor rangelands and income for purchasing livestock, agropastoralism is unreachable.
	`Nf-, Lv-` `Nf-, CRC-, Fg-`	Without income and neither livestock nor dry season forage, agropastoralism is unreachable.

Possible (not necessary)	`Flw-, EC, Nf`
	`Flw-, EC, Lv, Rg, CRC`
	`Flw-, EC, Lv, Rg, Fg`
		Fallows are insufficient for feeding livestock and preventing soil fertility loss, which is limited by erosion control techniques. In addition, the household either own livestock (which requires rainy and dry season forage) or is engaged in non-farm activities which allows to purchase livestock.

Necessary	`Flw, CRC, Lv`
	`Flw, Fg, Lv`
	`Flw, Fg, Nf`
		Fallows prevent soil fertility loss and provide forage in rainy season, while free grazing or crop residue collection contribute to dry season feeding. Here, cattle is either initially owned or can be purchased by means of non-farm income.

First, we focused on initial states possibly reaching AP (yellow area, Fig. 15). In these states, the farm does not practice fallowing (`Flw-`) and used of erosion control techniques (`EC`) (Table 3.3). To keep AP reachable, the farm has to prevent the irreversible loss of soil fertility (Table 3.3, which requires purchasing agricultural equipment in order to apply organic inputs (crop residues or manure) (rules R25-28, Table B.2). Indeed, soil fertility is necessary for developing and maintaining cash crop (R20) and food crop production. Food crops provide dry season fodder to livestock (which produces manure) through crop residues (R3-R6). They also are a precondition for producing fodder plants (R19), which are an alternative feeding source for livestock (R11-12). Note that, in these

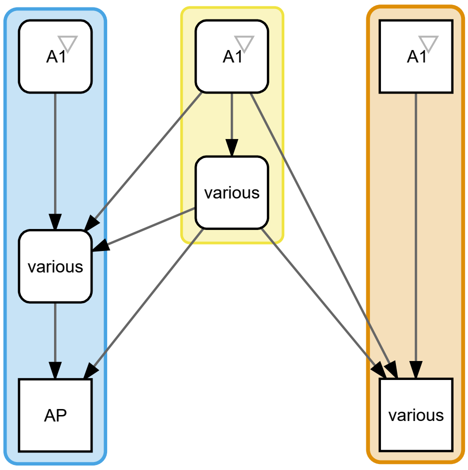


FIGURE 15 – **Transitions between reachability sets of persistent agropastoralism.** A reachability set is a set of states sharing the same dynamical properties (here, whether it *cannot/can/will lead to* or *is* persistent agropastoralism). Each node in this STG corresponds to a set of states belonging to initial states (marked with a triangle) and/or to the same reachability set. Node labels correspond to farm types, with "various" indicating that the corresponding set of states includes several farm types. Each edge corresponds to a transition between two reachability sets. Squares include at least one stable state (i.e. states with no outgoing transition). Rounded squares include no stable state.

states which possibly reach AP, soil fertility can be lost but can always be restored as long as sufficient manure can be applied (R23, Table 3.4) (result not shown). Once soil fertility is developed, the continuous application of manure using agricultural equipment prevents soil fertility loss (R25-27). From this moment, AP becomes necessary (blue area, Fig. 15). Alternatively, AP could become unreachable (shifting from yellow to brown states) by losing soil fertility before the acquisition of agricultural equipment and the development of manure production (result not shown).

Second, scenarios necessarily leading to AP involved practicing fallowing (which prevents soil fertility loss and feeds livestock in rainy season), having a source of dry season fodder and the ownership/ability to purchase livestock (Table 3.3).

Finally, scenarios preventing persistent agropastoralism were highly heterogeneous (see Table 3.3 for a detailed description).

3.4 Discussion

3.4.1 Farm types and trajectories

Our study uses a qualitative and discrete-event modelling framework - named EDEN - to infer farm types and trajectories in Southwestern Burkina Faso. Based on knowledge from scientific literature, field observations and interviews of experts, it describes

TABLE 3.4 – **Rules driving transitions between reachability sets.** Due to the various contexts in which a transition may occur, it may be driven by one (e.g. Possible → Impossible) or several phenomena (e.g. Possible → Necessary). See Table B.2 for rules description.

Transition	Rule(s) and Interpretation
Possible → Impossible	R26, R27, R28 (Soil fertility loss)
Possible → Necessary	R13, R14, R17 (Development of manure production) R23 (Soil fertility restoration) R30, R31 (Purchase of agricultural equipment)

which farm types a small farm (noted A1) can reach and how to reach them. This answer is twofold, as it both includes the specific events responsible for a given transition and the scenarios in which they may occur. Model predictions were compared with observed trajectories in the Koumbia village, which is located in the Tuy Province (southwestern region, Burkina Faso).

Our model predicted that A1 farm type (i.e. the initial farm type) was able to reach medium (A2) and large (3) agricultural farms, agropastoralists (AP) and breeders (B), which does not invalidate hypothesis H1. It also predicted farm types which were not observed in Koumbia, but reported elsewhere in the region [344], such as household oriented towards non-farm activities (which were merged with A1 farms for the sake of clarity). Predicted farm types overlapped with those described in other farm typologies in West-Africa [100, 311, 344, 193, 95] or elsewhere in sub-Saharan Africa [e.g. 353]. The consistency of model predictions with West-African farm typologies involving unobserved farm types in Koumbia [e.g. 344] could be assessed in a future study.

The model also predicted all observed farm trajectories. Livestock ownership (or non-farm income to purchase it) was crucial for A1 farms for improving their livelihood (Tables B.3 and B.5) as it justifies and helps acquiring agricultural equipment for increasing cash crop production. This is in agreement with reported drivers in southwestern Burkina Faso [273, 312] and is also confirmed by studies highlighting the role of non-farm income such as remittances, gold mining or petty trade for enabling agricultural investments in rural areas [17]. Note, however, that livestock requires sufficient fodder all year long, and thus necessitates available and sufficient fodder during wet (rangelands or fallows) and dry season (crop residues through free-grazing or crop residue collection). Such fodder could also come from fodder plants production such as mucuna (*Mucuna sp.*), cowpea (*Vigna unguiculata*) or local trees and shrubs such as *Faidherbia albida* or *Pterocarpus erinaceus* [358, 323].

Only three farm types (A1, B and AP) were able to persist (square nodes, Fig. 14). Persistence here refers to the inability for a farm to change. This model property cannot be rigorously compared with data from Koumbia as (1) farm type persistence (persistence or resilience) should considered in face of challenges [234] and (2) only the occurrence of farm types and trajectories is described in existing literature. Yet, farm type history has been estimated from farmers interviews and it appears that 50% of agropastoral farms are > 50 years old and 80% of pastoral farms are < 10 years old [273]. Such aggregated statistics cannot be used for model validation. However, individual farm data could exhibit patterns relating farm longevity with their history (past investments and activities), thus providing historical data which could be compared with model trajectories.

3.4.2 Reaching and maintaining agropastoralism

Demographic pressure and the resulting agricultural expansion have led African smallholder to reduce or abandon fallowing as a soil management technique. However, high mineralization rates observed in the tropics [378] quickly deplete soil organic matter and put crop production at risk. As a response, many farmers have developed a form of mixed-farming or agropastoralism involving (cash and food) crop and livestock production in which livestock is used as a source of income, as a tool for tillage and transport and as source of organic amendments for improving and maintaining soil fertility [240, 146].

As this form of agropastoralism represents an improvement compared with subsistence farmers livelihood, we determined the conditions under which it is impossible, possible or necessary for such small farmers to develop a persistent agropastoralism. Persistent agropastoralism was possibly (not necessarily) reachable if farmers (1) adopted erosion control techniques, (2) owned livestock or had means to purchase it (e.g. non-farm income) and (3) if fodder was sufficient and available all year long. This was achieved by maintaining rainy season pastures (rangelands or fallows) and dry season fodder (crop residue production and collection or free grazing), or alternatively, by producing fodder plants. However, these conditions were not sufficient *per se*, as the lack of organic inputs could lead to an irreversible soil fertility loss. Farmers thus have to develop their capacity to rebuild soil fertility and prevent its depletion. For that purpose, the farm has to produce sufficient manure (or any appropriate organic input) and purchase appropriate equipment for transporting and applying these organic inputs. In this case, the persistence of most endowed farms was thus closely linked to the persistence of soil fertility, which is consistent with current knowledge [352, 16].

3.4.3 Limitations and perspectives

3.4.3.1 Disturbances and resilience

Our model is a preliminary step for understanding farm dynamics in an undisturbed context. However, economic shocks [259], climate change [171], extreme weather events [243], political instabilities or health-related issues are known to impact livelihood dynamics [225]. Additionally, authors have promoted resilience as a relevant concept for managing farm systems [84, 306]. However, the concept of resilience is intrinsically linked to that of shock (or perturbation) [376]. Hence, as our model does not include perturbations, it cannot assess the resilience of farm systems. Yet, methods used in this study remain valid for resilience-related questions as disturbances can easily be represented in the EDEN framework e.g. as new rules, as it has been done in a previous study [76].

3.4.3.2 Interactions between farms

Our model implicitly includes the effect of neighboring farms, as in rule R27 in which free grazing implicitly prevents the maintenance of mulch in dry season, and may thus induce soil fertility loss if fallowing is not practiced and manure is not applied. Yet, spatial interactions between farms could be more deeply investigated. For instance, we could model several neighboring farms and observe stable configurations. It has been showed [221] how between-farms nutrients transfers induced by free grazing are mostly beneficial to big cattle owners, which may be detrimental to poor farmers' crop production. Therefore, we could assess under which scenarios multiple interacting farms could improve their respective livelihood and coexist. A spatialized version of the EDEN framework has already been developed [202] and could be used in this investigation.

3.4.3.3 Towards a more quantitative approach

In its current form, the EDEN modelling framework does not consider the probability of states and transitions. For instance, the production of fodder plants has not been widely adopted in southwestern Burkina Faso [358]. Yet, we could assign a low (conditional) probability to this event (rule R19, Table B.2). This may make model more relevant for management recommendations, but would (1) require more data for model conception, (2) add new assumptions, (3) overlook the effect or rare events and (4) perhaps reduce model robustness and reliability. This explains why, as a first step, this possibilistic model is adequate for addressing our the questions we raised in this study. Additionally, Boolean variables prevent from ranking variables responses to a given condition. For instance, the model makes no assumption regarding differences in soil fertility requirement between fodder plants and cash crops. However, the former may include Fabaceae and thus have lower nitrogen requirements. Multivalued variables (taking values 0, 1, 2...) could fix this issue, as each value would correspond to a fertility interval to which various crop species would respond differently. Yet, in biology, Boolean models have shown to preserve some properties of continuous ones [albeit under specific conditions, 304, 85], and can thus be seen as a first step towards a better understanding agroecosytem dynamics and self-organization.

3.4.3.4 Going beyond livelihood studies

This work assesses the long-term effects of the combination of management practices on economic status of rural households in Burkina Faso. Although the model investigates the effect of human actions on soil fertility, the combined socio-economic and ecological viability [or coviability, 18] remain unexplored. Yet, this region of Africa experiences a widespread environmental degradation [65] whose relations to farmers' livelihoods have already been pointed [306, 65]. Therefore, future works should explicitly include environmental degradation and biodiversity loss, thus tackling the problem of social-ecological coviability.

3.5 Conclusions

In this paper, we developed a qualitative, discrete-event and possibilistic model of farm trajectories in southwestern Burkina Faso. Available data were in agreement with model predictions. Additionally, we determined under which scenarios such trajectories may occur. For the trajectory from small farmers to agropastoralists, the model highlighted the crucial role of livestock as a source of organic inputs and workforce. The application of livestock manure required appropriate equipment (e.g. cart). Livestock should be combined to efficient techniques for maintaining soil fertility. For this purpose, applying organic inputs, and especially livestock manure, is crucial and requires appropriate equipment (e.g. carts). Manure production is over-determined by fodder production, either through rangelands and crop residues, or fodder plants (e.g. fodder crops and shrub banks). Therefore, in a favorable economic and environmental context (i.e. without climatic disturbance, no pest and no disease), our model suggests that the persistence of agropastoralism relies on three pillars : erosion control, fodder availability and the ability to apply sufficient manure.

Discussion Générale

L'objectif initial de ce travail consistait à proposer une approche de modélisation pour répondre à la question : *un état (ou ensemble d'états) d'un écosystème est-il atteignable ? Et pourquoi ?* Des méthodes existantes en informatique théorique, notamment utilisées en biologie [**?**], et récemment proposées en écologie [56, 300, 125] et en agronomie [394, 73, 150] peuvent fournir un cadre conceptuel et technique pertinent pour répondre à ces questions. Cette thèse montre que l'approche de modélisation EDEN (pour *Ecological Discrete-Event Networks*), inspirée de ces travaux et formalisée dans [285, 286], s'est avérée capable de répondre à cette question générale ainsi qu'à d'autres plus spécifiques, illustrées sur des socio-écosystèmes subsahariens semi-arides.

Cette discussion générale revient d'abord sur l'approche EDEN, en précisant son origine conceptuelle et en rappelant ses fondements théoriques. Les principaux résultats obtenus dans les chapitres 2 et 3 sont ensuite rappelés et rapprochés d'autres travaux employant également l'approche EDEN sur des biomes [246] similaires mais avec des objectifs écologiques légèrement différents. L'adéquation empirique des résultats obtenus pour chaque système est évaluée pour les autres systèmes étudiés (i.e. ce qui est valable pour l'Afrique de l'Est est-il valable à l'Ouest et réciproquement ?). Nous tenterons ensuite d'interpréter les résultats obtenus dans l'ensemble des travaux employant l'approche EDEN et d'en dégager des propriétés générales caractérisant les écosystèmes. Les apports et limites de cette approche sont discutés, et des propositions de solutions sont apportées à ces dernières. L'application de l'approche EDEN à d'autres champs de l'écologie que ceux étudiés dans cette thèse est abordée, ainsi que les apports mutuels entre EDEN et les approches de modélisation d'autres domaines du vivant. Je conclus enfin et discute l'apport mutuel de cette nouvelle approche de modélisation à l'écologie et à l'informatique.

3.6 L'approche EDEN : fondements théoriques, applicabilité et utilité pour l'étude des écosystèmes

L'approche EDEN hérite d'une conception dans laquelle les fluctuations de densité des composants de l'écosystème se compensent et/ou peuvent être lissées sur le long terme, laissant ainsi apparaître les variations les plus importantes, telles que des apparitions et disparitions. De cette vision découle une perspective qualitative des dynamiques. Ces travaux trouvent leur origine dans des réflexions sur les systèmes vivants et accueillants le vivant [126, 123]. Dans cette perspective centrée sur le long terme, les événements de la dynamique de l'écosystème résultent d'opérations de lecture de l'information du réseau d'interaction écologique entre composants biotiques et abiotiques. L'opération de lecture réalisée par un composant consiste notamment en l'évaluation de l'adéquation de ce composant dans ce réseau. L'information est déterminée par la structure du réseau (sa topologie) et par la nature des composants qui le constituent. Selon cette conception, cette information conditionne les événements de l'écosystème, événements qui rétroagissent sur le réseau en modifiant parfois sa topologie (i.e. son contenu informationnel).

Cette conception et les propriétés qu'elle propose est complétée par des arguments techniques détaillés dans le chapitre 1 [78].

La première propriété essentielle d'EDEN est la nature qualitative des variables. Cette description qualitative, par l'imprécision qu'elle offre, favorise la prise en compte de connaissances provenant de différentes sources (e.g. littérature, mesures empiriques ou dires d'experts) et de précision différentes.

En effet, la représentation par événements discrets, bien que supposant l'existence de seuils dans les interactions entre les composants, n'en suppose pas les valeurs numériques. Ces événements, qui modélisent des franchissements de seuils, marquent l'acquisition et/ou la perte par les composants de nouvelles fonctions (e.g. sociales, écologiques ou économiques) dans l'écosystème.

Ces événements peuvent avoir des causes internes comme externes au système (e.g. climat, immigrations, perturbations externes, interactions biotiques). Ces causes peuvent être conçues comme des flux (i.e. des interactions) dont les vitesses sont souvent mal (ou in-)connues [173]. Ces vitesses, représentées par les paramètres du modèle, influencent l'ordre des événements et l'on sait que cet ordre est susceptible de modifier les états atteignables [119, 64]. L'exécution asynchrone des règles pallie cette limite dans les connaissances en calculant l'ensemble des ordres d'occurrence possibles des événements, ce qui réduit la sensibilité du modèle à cet ordonnancement. Bien que cela puisse représenter une perte d'information (on ne sait pas quel chemin va prendre le système), cette propriété accroît la parcimonie du modèle en imposant des contraintes minimales sur les ordres des événements (on sait quels chemins peut prendre le système). Elle permet en outre de prédire de nombreuses trajectoires inobservées [86]. La pertinence de l'asynchronie pour décrire les dynamiques non-déterministes d'extinction d'espèces de protistes observées expérimentalement a été illustrée avec le modèle APT présenté dans le chapitre 1, et dans un autre article auquel j'ai participé [86].

Le fait que l'approche EDEN génère l'ensemble des ordres des événements et leurs possibles trajectoires nous a amené à la nommer possibiliste, c'est-à-dire à la fois non-déterministe et non-probabiliste. Le terme “possibiliste" se retrouve en métaphysique (sous différentes versions [292], [206]), en mathématiques (théorie des possibilités, [392]) et en sociologie du risque ("*worst case thinking*", [69]), avec des sens différents dans chacun d'eux. Considérer les possibles (d'un modèle donné) discrimine les états que le système peut ou ne peut pas atteindre. La première étape de validation de ce type de modèle est donc bien posée : tous les comportements observés du système étudié – dans les limites imposées par les variables et événements considérés – doivent être inclus dans les prédictions du modèle. Dans cette thèse, le possibilisme présenté par l'approche EDEN concerne un *modèle spécifique* dont les éléments (variables et règles) sont fixés au préalable. De plus, les variables présentent un nombre fini de valeurs, menant donc à un espace des possibles lui-même fini.

3.7 Principaux résultats écologiques obtenus par l'approche EDEN

3.7.1 Influence de la disponibilité en eau et des communautés d'herbivores sur les transitions de végétation et socio-économiques

Dans le deuxième chapitre, nous avons montré comment la disponibilité en eau de surface modifie l'atteignabilité de certains états de l'écosystème de savane et la possibilité de certaines transitions de végétation [76]. Son mode d'action est double : d'une part, le manque d'eau en surface réduit les réserves souterraines et empêche le maintien des plantes ligneuses à enracinement profond, laissant les herbacées dont la période de croissance et de vie aérienne est limitée à la saison des pluies ; d'autre part, il empêche le maintien des herbivores, dont ceux de type *browser* consommant les plantes ligneuses et dont la présence empêche la fermeture du milieu. Ces résultats suggèrent qu'il est important dans la gestion de la végétation de tenir compte de la gestion de l'eau de surface qui, bien que n'étant pas directement utilisable par les plantes, peut avoir des conséquences en présence des herbivores. Les transitions socio-économiques, en particulier celles impliquant l'élevage et le tourisme, sont également sensibles à cette ressource du fait de la dépendance du bétail (dont dépend l'élevage) et de la faune sauvage (dont dépend le tourisme) à cette eau de surface. Ce modèle indique non seulement si les états d'intérêt (les quatre types de végétation et les huit profils socio-économiques) sont atteignables dans chaque scénario, mais également si les transitions de végétation et socio-économiques sont préservées entre les scénarios. La façon dont chaque scénario modifie les états atteignables et les transitions possibles peut être expliquée à partir de la connaissance de l'ensemble des règles, i.e. quels événements déterminent l'effet d'un scénario donné (le "pourquoi" de notre question centrale).

3.7.2 Trajectoires de rétablissement en réponse à une éruption volcanique dans différentes conditions économiques

Dans un autre travail, nous avons étudié les conséquences d'une éruption explosive du mont Meru (nord-Tanzanie) sur les activités humaines et la végétation aux alentours du volcan. Nous nous sommes en particulier demandés si les activités humaines peuvent (1) se rétablir, (2) dans quel(s) ordre(s) et (3) si ce rétablissement pouvait dépendre d'une aide financière extérieure [75]. Le mont Meru est un volcan explosif inactif depuis 1910 et qui a plusieurs fois présenté des fumerolles durant le XXème siècle. La région dans laquelle il se situe abrite plus d'un million de personnes, laquelle se concentre dans les districts sur ses flancs. Une éruption explosive pourrait donc avoir des conséquences dévastatrices pour cette population [185]. Le modèle construit ici est donc une expérience *in silico* pour prévoir les effets, mais surtout les voies de rétablissement des écosystèmes avoisinants après une éruption explosive. Il s'agit du premier modèle EDEN “spatialisé", qui décrit les trajectoires de quatre “sous-écosystèmes" en interaction par des échanges matériels et monétaires. Un modèle de référence a d'abord été conçu pour étudier la dynamique de la région en l'absence d'éruption volcanique. Nous y avons ensuite appliqué une éruption sous deux scénarios : avec et sans aide financière extérieure (e.g. de l'État ou d'Organisations Non Gouvernementales). Dans ces deux scénarios, l'agriculture et l'élevage sont les deux activités à pouvoir se rétablir en premier. Si une aide financière est apportée, le tourisme peut se rétablir, ce qui est impossible sans aide financière en raison de l'incapacité à reconstruire les infrastructures routières.

3.7.3 Influence du mode de gestion et des conditions environnementales sur l'embroussaillement des pâturages dans le Borana (Éthiopie)

Un troisième travail auquel j'ai contribué – plus méthodologique cette fois – porte sur un écosystème semi-aride Est-Africain [346]. A partir de la ressemblance entre les *States-and-Transition Models* (STMs) utilisés en écologie des pâturages et les systèmes de transitions utilisés en informatique [180], nous avons proposé d'utiliser les outils de vérifications formelle (model-checking, [67]) pour évaluer certaines propriétés dynamiques formalisées par des formules de logiques temporelles. Les logiques temporelles, comme la logique temporelle arborescente (ou CTL pour *Computer Tree Logic*), ont été développées en informatique pour vérifier l'absence d'erreurs dans les programmes. Elles permettent de formaliser les relations de précédence entre des états. Ces relations peuvent, par le biais *query patterns* [239] de différents types (atteignabilité, conséquence, séquence, invariance), exprimer des comportements recherchés du système dans le graphe états-transitions.

A partir de connaissances issues de la littérature, un modèle EDEN d'un pâturage du sud de l'Éthiopie (Borana) mimant des STMs connus [208] a été construit. Ce modèle est ensuite utilisé pour évaluer la capacité du pâturage à s'embroussailler (*bush encroachment*) et sous quelles conditions de gestion cela pouvait se produire. Il a un rôle illustratif dans cet article méthodologique, mais son analyse révèle des résultats écologiquement pertinents (au moins) pour le Borana. Bien que le rôle de l'herbivorie dans l'embroussaillement des pâturages soit variable selon les localités [26], le modèle prédit que le pâturage par le bétail est une condition nécessaire mais non suffisante à l'embroussaillement. Il prédit également que, dans certaines conditions, l'agriculture peut être un moyen pour lutter contre l'embroussaillement. D'autres propriétés dynamiques plus complexes d'intérêt socio-écologique sont formulées et leur conditions d'existence sont données par le modèle.

3.7.4 Trajectoires des exploitations agricoles du sud-ouest du Burkina Faso et conditions d'atteignabilité et de durabilité de l'agropastoralisme

Dans le troisième chapitre, nous nous sommes intéressés aux exploitations agricoles d'Afrique de l'ouest (Dano, dans la province de Ioba du Burkina Faso) et à leurs fonctionnements sur le long terme [77]. J'ai eu la chance d'effectuer deux déplacements en 2019 dans la zone soudanienne du Burkina Faso et du Ghana, le second de plus d'un mois en autonomie (Novembre-Décembre 2019), pour étudier plus finement ces fonctionnements locaux. J'ai ainsi élaboré, aidé des collègues africains, un modèle du type EDEN décrivant la dynamique d'une exploitation agricole générique soumise à différents scénarios décrivant différentes combinaisons de conditions environnementales et de modes de gestion. Ici, une trajectoire décrit la manière dont une exploitation passe d'un type à l'autre en accroissant/diminuant son capital [140, 317]. Ce modèle s'appuie sur des typologies et des trajectoires d'exploitations identifiées à Koumbia dans la province du Tuy [273], à proximité de notre site d'étude. Le modèle prédit les types d'exploitations observés ainsi que les trajectoires entre eux, ce qui offre une première validation du modèle.

Cette adéquation empirique acquise, le modèle détermine ensuite parmi les 126 scénarios possibles, lesquels permettent aux petits agriculteurs d'accroître leur capital (i.e. acquisition d'équipement de travail du sol, d'animaux de trait, production de cultures de rente et accroissement des surfaces cultivées). Plus loin dans l'étude, nous avons déterminé les scénarios dans lesquels un petit agriculteur peut, va ou ne peut pas atteindre un agropastoralisme persistant. Les transitions de bifurcation (i.e. rendant un état inatteignable ou nécessairement atteignable) prédites par le modèle consistent à passer un seuil dans la production de fumure animale et dans le matériel agricole disponible pour l'épandre, permettant ainsi de maintenir et reconstituer la fertilité si celle-ci est perdue.

3.7.5 Généralisation des résultats entre les modèles

Dans les chapitres 2 et 3, l'approche EDEN a été utilisée pour évaluer les conséquences de différents scénarios sur l'atteignabilité de certains états, transitions et trajectoires des écosystèmes étudiés. Ces scénarios avaient pour objectif de représenter des changements permanents des conditions environnementales (e.g. disponibilité en eau et en pâturages ou présence d'herbivores) ou des pratiques de gestion de l'agriculture ou de l'élevage (e.g. pratique de la vaine pâture, prévention de l'érosion ou application de fumure animale). Malgré leurs différences, ces écosystèmes sont soumis à des contraintes hydriques comparables et abritent tous deux des populations rurales dépendantes de l'agriculture et de l'élevage pour vivre. Par conséquent, nous allons tenter d'évaluer l'adéquation empirique des résultats d'un modèle au système correspondant à l'autre modèle (i.e. comparer les résultats du chapitre 2 aux données d'Afrique de l'Ouest et réciproquement pour le chapitre 3 avec l'Afrique de l'Est).

3.7.5.1 D'Afrique de l'Est en Afrique de l'Ouest

Les savanes du nord de la Tanzanie et de la zone soudanienne (occidentale) du sud-ouest du Burkina Faso sont caractérisées par une importante fraction de plantes ligneuses [188]. Elles diffèrent cependant par les facteurs influant sur leurs dynamiques. En effet, là où les herbivores non-domestiques peuvent jouer un rôle majeur dans les transitions de végétation en Afrique de l'Est [155], leur rôle est aujourd'hui minime en Afrique de l'Ouest du fait de leur rareté en zone soudanienne [350]. Par conséquent, il est donc peu probable que la disponibilité de l'eau de surface (points d'eau courante ou stagnante) telle qu'étudiée dans le chapitre 2 ait la même importance pour la dynamique de la végétation en Afrique de l'Ouest. L'absence de grandes populations d'herbivores sauvages en savane soudanienne pourrait permettre de faire un parallèle avec les scénarios *no grazers* et *no browsers* du chapitre 2. Ainsi, si les prédictions de ces scénarios étaient valides en savane soudanienne, les transitions d'ouverture (i.e. de forêt à savane et de savane à prairie) devraient être impossibles. Ce n'est pas ce qui est observé. En effet, l'expansion de l'agriculture est responsable d'une ouverture rapide de la végétation [272]. Ce mécanisme n'est pas pris en compte dans le modèle du chapitre 2, bien qu'il soit également actif en Afrique de l'Est [53]. De plus, les feux d'origine anthropique jouent également un rôle important dans la dynamique de la végétation des savanes soudaniennes [350], rôle qui était négligé dans le mode du chapitre 2 (car absent des sites observés en Tanzanie). Par conséquent, les résultats du chapitre 2 nous semblent difficilement applicables aux savanes soudaniennes du sud-ouest du Burkina Faso sans des modifications substantielles.

3.7.5.2 D'Afrique de l'Ouest en Afrique de l'Est

La majorité des exploitations agricoles d'Afrique subsahariennes peut être classée en un petit nombre de catégories [98, 320]. On sait que les typologies d'exploitations d'Afrique de l'est donnent des résultats proches de celles réalisées en Afrique de l'ouest [352, 345, 359]. Ces régions sont soumises à des transformations comparables (appauvrissement des sols, expansion des cultures au détriment des pâturages,[272]) qui poussent les producteurs vers des stratégies similaires comme la diversification des revenus (extra agricoles notamment) [237] ou l'orientation vers une agriculture de rente [344] ou le maraîchage [137]. De plus, certaines trajectoires d'exploitations décrites en Afrique de l'Est semblent, en première analyse, correspondre à celles décrites en Afrique de l'Ouest [352]. Puisque le modèle du chapitre 3 présente une bonne adéquation empirique aux données d'Afrique de l'Ouest (et notamment de Koumbia), il est donc possible que ses prédictions concernant les conditions d'atteignabilité d'un état agropastoral persistant puissent valoir pour certaines exploitations d'Afrique de l'Est. Il ne s'agit cependant à ce stade que de suppositions et requiert une comparaison rigoureuse de ces prédictions à des données de trajectoires d'exploitations d'Afrique de l'Est.

3.7.5.3 Résultats généraux

Les deux systèmes modélisés sont malgré tout très différents, ce qui rend illusoire toute comparaison rigoureuse. On peut cependant dégager certains résultats communs aux modèles construits jusqu'ici, indépendamment des systèmes modélisés.

Un premier constat est l'absence de centralisation des événements : chaque composant de l'écosystème réagit de façon autonome à l'état de certains autres et cette réponse n'est pas “dictée" par une entité centrale [106]. Ainsi, le déroulement d'un processus comme la transition de savane en forêt requiert la coordination de différents composants (e.g. la disponibilité de l'eau, des nutriments, la présence de certaines espèces de plantes ainsi que la présence/absence de certains herbivores). De plus, chaque composant est susceptible de présenter un délai dans sa réponse. Ainsi, selon que la réponse soit immédiate ou différée, l'avenir d'un écosystème pourra être modifié. On peut donc considérer les écosystèmes comme des systèmes distribués (ou répartis) pour lesquels des outils sont adaptés, comme l'approche EDEN, les modèles logiques ou les réseaux de Petri [286].

Un deuxième constat est le grand nombre de dynamiques alternatives prédites par les modèles. Cet apparent non-déterminisme est lié au nombre de composants agissant sur leur environnement de façon concurrente (i.e. indépendante). Par exemple, deux événements A et B affectant des populations différentes d'un même écosystème sont concurrents s'ils peuvent se dérouler séquentiellement (i.e. un à la fois) dans n'importe quel ordre ou parallèlement (i.e. simultanément). L'exécution asynchrone d'événements concurrents est responsable de leur entrelacement. Si ces les événements A et B n'étaient pas indépendants mais causalement liés, il n'y aurait qu'une seule trajectoire possible (A puis B) car le premier événement précéderait nécessairement le second et l'inverse serait impossible. Ainsi, le grand nombre de trajectoires alternatives prédites par nos modèles suggère une forte indépendance des événements dans un écosystème. Nous reviendrons sur cette propriété par la suite.

Un troisième constat est la dépendance de la dynamique des écosystèmes aux chemins qu'ils prennent. Bien que présente dans les deux chapitres, cette propriété est particulièrement visible dans le modèle du chapitre 3. La capacité pour une même petite exploitation agricole à devenir et rester agropastorale dépend de l'ordre des événements qu'elle rencontre (Fig. 16). Ainsi, le type d'exploitation agropastoral peut devenir inatteignable si la fertilité du sol est perdue avant l'acquisition d'équipements agricoles et le développement de la production de fumure animale. Ces résultats suggèrent donc que cet écosystème a donc une propriété d'historicité, et en particulier présente une dépendance aux événements passés [101, 356]. Ce résultat corrobore d'autres travaux indiquant que la dépendance aux chemins advient notamment en présence d'état stables alternatifs [119, 342].

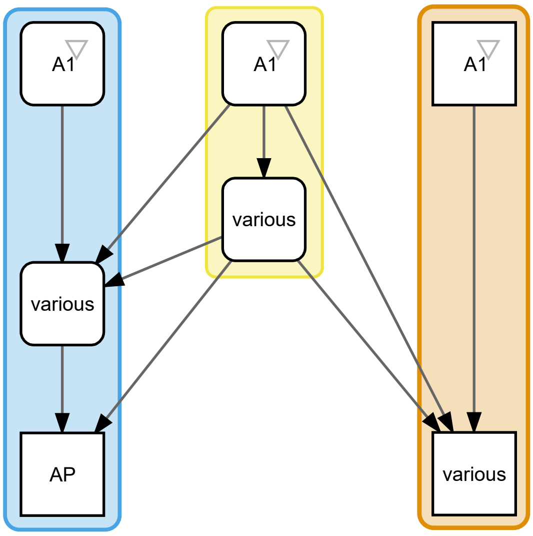


FIGURE 16 – **Dynamique des exploitations agricoles.** Chaque ensemble de couleur englobe des états possédant des propriétés dynamiques similaires. Par exemple, dans l'ensemble bleu, l'agropastoralisme persistant (AP) est nécessairement atteint. Tirée du chapitre 3.

3.8 Apports et limites de l'approche EDEN

3.8.1 Apports

Les formalismes traditionnellement utilisés pour modéliser la dynamique des écosystèmes (i.e. équations différentielles ou aux différences ou, plus rarement, modèles individus-centrés) calculent leurs comportements pour certaines valeurs de paramètres. Les approches possibilistes comme EDEN complètent ces approches en prédisant l'ensemble des comportements qualitatifs possibles pour un ensemble donné de variables et de règles. Cela permet en outre d'identifier les états "structurellement" stables, i.e. stables indépendamment des valeurs de paramètres [86]. Le corollaire de la capacité de ces modèles à prédire l'ensemble des dynamiques possibles est la capacité à conclure à l'impossibilité de certains comportements. Cette information peut se révéler cruciale pour guider l'action de gestionnaires en mettant en évidence les changement qualitatifs nécessaires pour atteindre un état impossible, comme l'ajout de nouveaux composants et/ou événements.

Dans les autres formalismes traditionnels de l'écologie, le modèle ne présente souvent pas de solution analytique (i.e. on ne connaît pas le comportement du système pour toute valeur de variables et de paramètres). L'atteignabilité d'un état est alors déterminée par l'emploi de simulations numériques, ce qui restreint la connaissance des comportements possibles (à noter toutefois l'existence de solutions analytiques pour des modèles individu-centrés, [74]). De plus, la complexité du modèle induit souvent un effet "boîte noire" [170] limitant l'intelligibilité des résultats et les explications dérivées par le modèle [366]. En outre, certains modèles EDEN prédisent des oscillations potentiellement transitoires qui ont également été observés en dynamique des pâturages [384, 338], voir aussi [364] pour les écosystèmes lacustres) et en écologie des communautés, où ils correspondent à des successions cycliques d'états stables liés par des invasions [199] [119]. Ainsi, l'approche possibiliste que nous proposons permet d'explorer les trajectoires possibles du système étudié, autant que certaines de ses dynamiques transitoires.

La représentation des trajectoires sous forme de graphe états-transitions est répandue et historique dans certains domaines de l'écologie [70, 218, 384]. Elle constitue un outil efficace pour communiquer les résultats aux non-spécialistes [33] et permet l'emploi d'analyses du *model-checking* pour évaluer des propriétés dynamiques complexes et d'y apporter des éléments d'explication [346, 285]. L'acquisition de telles informations, bien qu'accessibles par d'autres approches, est grandement facilitée par le formalisme et les outils composant l'approche EDEN.

3.8.2 Limites et perspectives d'amélioration

L'approche EDEN ne va pas sans quelques limites qui sont discutées dans cette section. Tout d'abord, l'absence d'information quantitative (variables, paramètres, probabilités ou durées) empêche toute réponse à des questions d'ordre quantitatif, i.e. associées à des seuils ou intervalles de valeurs (e.g. il faut au moins X composantes ou une densité supérieure à Y ou Z années pour observer cet état). De plus, les approches qualitatives plus courantes en écologie comme l'analyse de graphes orientés (*loop analysis*, [205]) ne sont pas directement comparables aux modèles EDEN. En effet, une règle d'un modèle EDEN peut exprimer l'effet possiblement conjoint d'un ensemble de variables (condition de la règle) sur un autre ensemble de variables (réalisation de la règle). Le graphe représentant un modèle comprenant de telles règles est donc un hypergraphe orienté, dans lequel une arête (ou hyperarête) lie plus de deux noeuds entre eux. Les relations entre variables ne se font donc pas "une à une" mais potentiellement de "groupe à groupe". Par conséquent, les traditionnelles analyses de graphe ne sont pas directement applicables à de tels hypergraphes ou, si elles le sont, n'apportent pas nécessairement la même information. Cela n'empêche pas que certains résultats de *loop analysis* soient en accord avec certains modèles EDEN, mais de telles connexions restent toutefois à explorer.

Enfin, à ce jour, les modèles EDEN se focalisent essentiellement sur l'échelle populationnelle dans laquelle les individus formant les populations ne sont considérés qu'implicitement (l'approche "agrégée" discutée en introduction). Ils ne peuvent donc pas fournir d'explication *bottom-up*, i.e. expliquant les changements d'états qualitatifs d'une population comme phénomènes émergeant du comportement collectif d'individus [90]. Il est toutefois envisageable de modéliser l'émergence de phénomènes à l'échelle écosystémique résultant d'interactions entre des populations, ce qui est une piste de recherche pour de futurs travaux.

3.8.2.1 Identifier et acquérir les données nécessaires à l'élaboration d'un modèle EDEN

Dans l'approche EDEN, une fois la question de recherche clairement formulée et les variables pertinentes identifiées, deux informations centrales sont requises : les états qualitatifs des variables et les conditions de passage de l'un à l'autre (leurs transitions). Ces informations peuvent provenir de différentes sources, comme littérature scientifique, le terrain ou des séries temporelles mesurées, et être collectées de diverses manières.

La description des systèmes en termes d'états qualitatifs et de transitions est rare en écologie. Ainsi, lorsque ces informations sont indisponibles, la première étape consiste à déterminer, pour chaque variable, l'existence de fonctions socio-écologiques qualitativement différentes, généralement associés à des intervalles de densités (i.e. quels changements ce composant permet/empêche-t-il lorsqu'il est rare ou abondant ?). Ce fut le cas dans le chapitre 3 où le bétail de trait n'acquiert ses fonctions de traction et de production de fumure animale qu'au-delà d'un certain nombre d'individus par exploitation agricole (qui est variable selon la taille des exploitations). Si une comparaison modèle-observations est envisagée, ces états qualitatifs doivent être comparables aux données mesurées (i.e. à partir de combien d'individus peut-on dire que cette composante est rare ?). Pour reprendre l'exemple précédent, les exploitations ne possédant pas assez d'animaux de trait pour assurer les fonctions précédemment citées doivent donc être identifiables empiriquement.

Cette méthode présente l'avantage de permettre au modélisateur d'utiliser un grand nombre d'articles dont les résultats sont présentés de façon hétérogène. Cependant, sa limite fondamentale est sa forte sensibilité aux articles trouvés, à la formulation des états qualitatifs et à la définition des transitions. Pour réduire cette sensibilité et accroître la reproductibilité du processus de modélisation, il faut concevoir un (des) processus de modélisation standardisé(s) [139]. Sans prétendre à l'exhaustivité, cela peut passer par (1) l'automatisation de la collecte des articles ressources, (2) la conservation de la trace des recherches effectuées et/ou (3) la conservation d'extraits de textes pertinents en vue d'une justification plus rigoureuse des variables et des règles. Des discussions détaillées existent sur ce sujet [139].

De premières avancées ont été engagées par notre équipe et présentées dans deux articles. Le premier s'appuie sur les *State-and-Transition Models* [384] qui représentent les dynamiques de l'écosystème par des successions d'états qualitatifs et de transitions (décrites par leurs conditions et conséquences). Il est alors possible, en transformant la description verbale des états en un "découpage" par variables, de transcrire les états et transitions observées en un modèle EDEN (Fig. 17) [346]. Le second article s'appuie sur un réseau d'interaction écologique (décrit dans [381]). Les arêtes du réseau sont transformées en règles "si-alors" et les dynamiques prédites sont comparées à celles observées. L'observation de comportements non prédits par le modèle initial (i.e. s'appuyant exclusivement sur le réseau décrit dans [381]) a ensuite permis de réfuter ce dernier et ainsi d'inférer des interactions écologiques initialement inconnues ou incertaines [86].

Comme j'ai pu le vérifier lors de mes séjours en Afrique de l'Ouest dans le cadre du projet SESASA, le choix des sources d'information sur le terrain est fortement conditionné par les contraintes matérielles de la prospection (e.g. moyens de déplacement, disponibilité des personnes, accessibilité des lieux ou relations entre le guide et les autres acteurs). L'effet de ces contraintes sur l'incertitude des connaissances expertes obtenues doit être pris en compte dans l'élaboration du modèle. Les techniques d'élicitation des connaissances doivent être améliorées de façon à pouvoir comparer les résultats entre différentes interviews et ainsi valider (au moins partiellement) les connaissances obtenues. Le développement de méthodes rigoureuses pour la collecte de données issues d'experts pour l'écologie fait l'objet de recherche (voir la synthèse de [102]), et une attention particulière

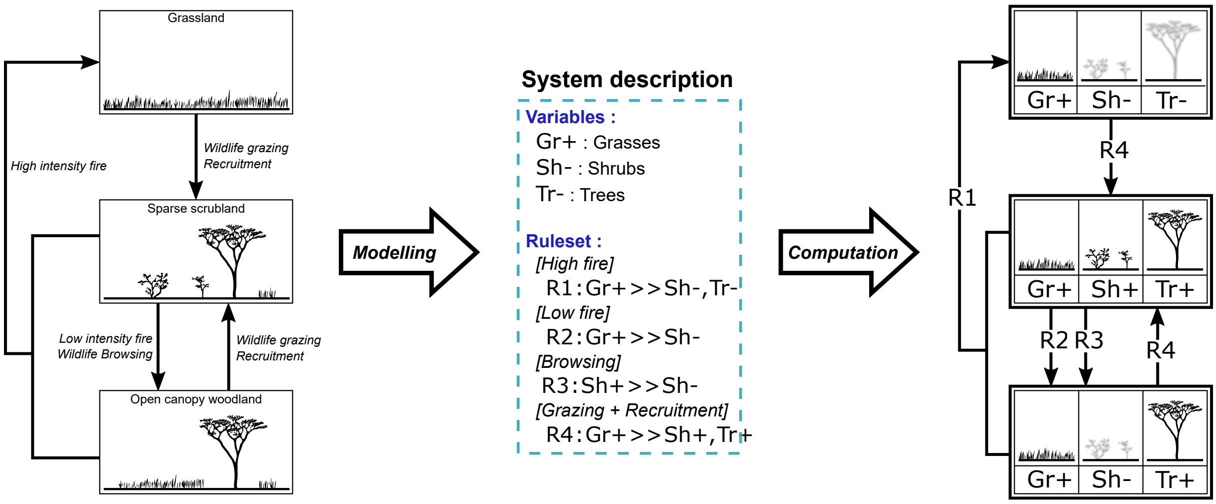


FIGURE 17 – **Illustration d'une traduction d'un *State-and-Transition Model* en modèle EDEN.** La description verbale des types de végétation et de leurs transitions (à gauche) est traduite en un ensemble de variables et de règles (au centre), donnant ensuite lieu à un graphe états-transitions équivalent (à droite)

doit être portée à ces travaux pour consolider les résultats de modélisation.

Les séries temporelles sont plus rares et peuvent autant contribuer à l'inférence qu'à la validation des modèles [31]. En particulier, l'observation des états passés (trajectoires) du système étudié permet de valider l'atteignabilité des états calculés. En revanche, la validation de la stabilité des états peut nécessiter un suivi plus long car le lien entre la durée d'un état et sa stabilité est plus difficile à définir [169, 108].

3.8.2.2 Étudier la structure causale des événements dans un écosystème

L'approche EDEN caractérise les états par leur atteignabilité et par les relations de précédence possible/nécessaire entre eux. Il est en revanche plus difficile, dans la forme actuelle de ces modèles, de savoir si, pour atteindre un état donné, il existe une (nécessité) ou plusieurs trajectoires alternatives (contingence) ou encore si certaines portions de trajectoires sont nécessaires tandis que d'autres sont contingentes. Une telle information serait cruciale pour mettre en place des actions de gestion efficaces [131]. Or, l'exécution asynchrone des règles génère un grand nombre de transitions entrelacées donnant lieu à de nombreuses trajectoires alternatives, et rendant une telle interprétation difficile. Dans la mesure où les modèles EDEN peuvent être représentés comme des réseaux de Petri [125, 286], une solution consisterait à simplifier ces dynamiques complexes en factorisant les parties communes d'un graphe états-transitions. Cela permettrait notamment de mettre en évidence le “degré" d'indépendance des événements en comparant le graphe états-transitions asynchrone et sa forme factorisée. Ces factorisations sont appelées réductions d'ordres partiels et peuvent être réalisées grâce à des dépliages de réseaux de Petri

[230], une piste que notre équipe a déjà entreprise.

3.8.2.3 Vers un rapprochement du qualitatif et du quantitatif

Nous avons montré que la mise à jour simultanée de plusieurs variables (synchronie, ou sémantique synchrone) dans un modèle booléen peut empêcher de prédire certains comportements observés (chapitre 1, [121]). On peut donc dans ce cas faussement conclure à l'absence de certains comportements (risque de faux négatif). Une sémantique totalement asynchrone, dans laquelle on ne change la valeur que d'une seule variable à la fois, offre une première solution. Cependant, cette sémantique ne décrit pas non plus tous les comportements qualitatifs possibles. Cela a été montré en précisant quantitativement un modèle booléen par des variables multivaluées (i.e. faites de plus de deux valeurs, comme 0, 1 et 2) [282]. Une autre sémantique, qualifiée de *Most Permissive* (MP), a donc été élaborée et proposée pour dépasser cette limite [282]. Alors que les modèles traditionnels décrivent les variables booléennes par leurs valeurs "inactive" et "active" (0/1), la sémantique MP ajoute deux nouvelles valeurs "ambigües" : "croissante" et "décroissante". Cet ajout ainsi que les règles de transition (e.g. de "inactive" à "croissante") de la sémantique MP garantissent qu'aucun raffinement multivalué (y compris continu) d'un modèle booléen ne prédira des comportements qu'un modèle MP n'aurait pas déjà prédit. Un travail d'adaptation de la sémantique MP au formalisme de l'approche EDEN est également prévu.

3.9 Applications possibles futures en écologie

3.9.1 Écologie des communautés

D'importants points communs avec l'écologie des communautés ont été identifiés, plus spécifiquement avec la théorie de l'assemblage de communautés [56, 321, 380, 332] et des successions écologiques [211]. Toutes deux ambitionnent de comprendre les conditions d'invasion/de coexistence des espèces. De nombreux travaux ont utilisé des graphes pour représenter les successions d'états résultant des invasions successives dans une communauté [119, 321, 332, 199]). Une telle représentation est possible avec l'approche EDEN, dépassant la seule représentation en proposant une modèle à la fois formel et intelligible des dynamiques d'invasions et d'extinctions d'une communauté (Fig. 18).

De telles questions ouvrent la voie à l'emploi des logiques temporelles pour analyser les dynamiques d'assemblage. De plus, la recherche de règles d'assemblage [71, 382] pourrait trouver une traduction intuitive dans un formalisme de règles de réaction [368] tel qu'utilisé dans l'approche EDEN [285].

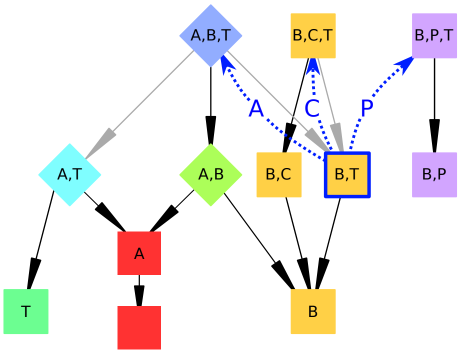


FIGURE 18 – **Dynamique d'une communauté de protistes.** Les transitions en pointillé sont les invasions et les transitions pleines les extinctions. Les lettres correspondent aux espèces. Les carrés correspondent aux attracteurs et à leur bassin et les losanges sont les états pouvant atteindre différents attracteurs. Tiré de [86].

3.9.2 L'écologie des pâturages et l'agroécologie

Il est possible de reproduire les trajectoires de certains State-and-Transition Models (STMs) par des règles "si-alors" exécutées de façon asynchrone (Fig. 17) [346]. De plus, la représentation des dynamiques sous forme de graphes est un point commun entre les modèles d'écologie des pâturages et les modèles EDEN. Cependant, là où ces graphes constituent des représentations schématiques des connaissances disponibles, nous avons montré l'intérêt des logiques temporelles pour analyser les propriétés dynamiques exhibées par de tels graphes. Le graphe n'est alors plus un simple outil de représentation, mais une véritable structure de données capable de livrer des informations difficilement accessibles par d'autres moyens. Les STMs sont un outil central de la gestion des parcs naturels aux États-Unis d'Amérique [337] et ailleurs. Un projet de cartographie exhaustive et de description des transitions de végétation est actuellement en cours en Australie avec *The Australian Ecosystems Models Framework*. Ces modèles sont donc précieux dans les relations des sociétés à leur environnement et gagneraient à disposer d'outils d'analyse rigoureux [**?**]. Les approches du type d'EDEN pourraient contribuer à de tels objectifs, et bénéficieraient en retour d'applications utiles à leurs améliorations. Enfin, initialement développés en écologie des pâturages, les STMs ont récemment fait leur apparition en agroécologie [**?**]. De telles applications des STMs à de nouvelles questions d'ordre agronomique pourraient également bénéficier des outils de l'approche EDEN, comme a commencé à le montrer le chapitre 3 de cette thèse.

3.9.3 Autres applications en écologie

L'ensemble des travaux menés par notre équipe montre que l'approche EDEN, et les approches qualitatives à événements discrets en général [300, 197], sont applicables au-delà des écosystèmes étudiés dans cette thèse. Entre 2016 et 2021, plus de 15 études ont employé l'approche EDEN sur une grande variété de systèmes (termitières [125], réseaux trophiques

[110] et socio-écosystèmes austraux [346, 77, 76, 202, 276] et boréaux [116, 124, 223, 324, 14], communautés expérimentales de protistes [86] et de bactéries [253]) la plupart étant à ce jour non publiées. Une grande diversité de questions de recherche et d'échelles spatiales (du microcosme à l'échelle régionale) et temporelles (du mois au siècle) ont été explorées. Certaines études ont mobilisé de nouveaux outils, notamment pour spatialiser les modèles en faisant généralisant l'approche EDEN a de multiples unités spatiales en interaction [202, 75], soit en employant de nouveaux formalismes comme les transformations de graphe [116, 128] dans lesquels les unités spatiales ne préexistent pas nécessairement mais peuvent être générées, ouvrant la voie à de la modélisation de méta-écosystèmes [214]. Forts de cette multitude d'expériences hétérogènes, il serait intéressant de réexaminer ces travaux, leurs objectifs et leurs résultats afin d'en étudier les limites et d'en réévaluer les conclusions. Ces limites une fois identifiées pourraient aider à l'élaboration de méthodes de modélisation standardisées.

3.9.4 Biologie des systèmes

Si l'approche EDEN est novatrice en écologie, de par ses concepts fondateurs, son formalisme et ses méthodes associées, des approches similaires sont anciennes et trouvent leurs origines en biologie des systèmes [339, 179, 347]. Les méthodes utilisées en biologie des systèmes sont de plus bien développées et répondent aux objectifs des biologistes [250]. Il se pourrait cependant que les questions écologiques impulsent des questions originales. En effet, la plupart des questions d'écologie formulées dans cette thèse ne sont pas centrées sur des attracteurs du système étudié. Ainsi, l'intérêt porté aux transitions de végétation (chapitre 2) et d'exploitation (chapitre 3) ne prend pas en considération la stabilité de ces états, au sens habituel et quantitatif de la discipline [260]. Cette perspective marque un contraste avec les questions traditionnelles de la biologie des systèmes, dont l'intérêt pour les attracteurs est fort, et justifié par l'étude des dynamiques de différenciation cellulaires se stabilisant en phénotypes [249]. En ce sens, on peut considérer les questions de l'écologie, qui mettent l'accent sur les trajectoires et l'existence d'états "stables" transitoires [364, 119], comme complémentaires à celles de la biologie. Les questions présentes en écologie font toutefois écho aux questions liées à la reprogrammation cellulaire, i.e. à la capacité pour une cellule de passer d'un état différencié à un autre par des actions e.g. thérapeutiques [143, 51]. On peut également noter la similitude de forme dans la recherche d'atteignabilité d'un attracteur souhaitable (agropastoral en agroécologie, e.g. non-cancéreux en biologie [296]), en particulier par la recherche de bassins faibles et forts [186]. L'existence de questionnements communs – comme différents – par leur forme peut être un moteur heuristique dans la manière de formuler ces questions de recherche et d'y apporter des réponses.

3.10 Conclusion

La question de la capacité d'un écosystème à atteindre un état, souhaitable ou non, fait écho à de nombreux enjeux contemporains. On peut aujourd'hui répondre à cette question par différents moyens, au sein desquels la modélisation joue un rôle central. Si de nombreuses méthodes de modélisation existent et permettent d'étudier cette question, beaucoup sont limitées, notamment par l'information requise pour y répondre. Dans cette thèse, j'ai développé une approche de modélisation innovante, nommée EDEN, capable de s'attaquer à cette question. Cette approche est qualitative. Elle repose sur un formalisme à événements discrets représentant les événements de l'écosystème par des règles "si-alors" décrivant les conditions d'occurrence et les conséquences chaque événement. Une à une, ces règles calculent l'ensemble des états atteignables par l'écosystème modélisé, chaque état succédant au précédent par une transition. A partir d'une connaissance qualitative des événements, l'approche EDEN permet de statuer sur l'inatteignabilité de certains états ainsi que sur les relations temporelles entre eux. Pour ce faire, elle s'appuie sur des outils issus de l'informatique théorique comme les logiques temporelles utilisées pour exprimer de manière formelle et univoque des propriétés dynamiques de l'écosystème étudié. J'ai illustré la capacité de cette approche à répondre à des questions appliquées d'écologie et d'agroécologie en modélisant des socio-écosystèmes semi-arides subsahariens. J'ai d'une part évalué l'impact de changements environnementaux durables sur la dynamique de la végétation et des activités humaines dans une savane tanzanienne, le modèle indiquant un rôle majeur indirect de l'eau de surface sur la dynamique de la végétation. Dans une deuxième étude, j'ai déterminé les conditions dans lesquelles une exploitation de petits agriculteurs en zone soudanienne du Burkina Faso pouvait développer un agropastoralisme persistant sur le long terme, en maintenant à la fois la fertilité des sols et sa production animale et végétale. L'atteignabilité d'un tel agropastoralisme persistant est conditionnée par l'acquisition de matériel agricole, le maintien de ressources fourragères et l'accroissement du cheptel bovin. Dans les deux études, les résultats obtenus sont qualitatifs, sous la forme de graphes représentant les états et transitions du système étudié. Ces résultats sont intelligibles et les dynamiques prédites sont expliquées par les états qui les précèdent et les transitions qui y mènent. Jusqu'à présent, l'écologie a peu bénéficié des avancées de l'informatique théorique. Or, on a très tôt constaté une forte synergie entre la biologie des systèmes et l'informatique, l'une fournissant des questions, l'autre des méthodes et des concepts pour y répondre. L'écologie, qui est une des sciences du vivant les mieux formalisées, pourrait devenir le moteur d'une telle synergie. Les concepts voyageant d'une science à l'autre ouvrent ainsi la voie à des avancées en informatique autant qu'à de nouvelles théorisations en écologie.

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Annexe du chapitre 2

A.1 Study Area Description

Gelai plains are located in the East African Rift, south of Lake Natron, and are part of the Tarangire-Manyara ecosystem [242] 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 [295] and vegetation changes are mainly driven by water availability and herbivory [310, 11]. Mean annual precipitation strongly varies seasonally and inter-annually [127]. This high variability constrains primary, but also secondary production since the Gelai plains are important calving grounds for wildebeest populations [242]. 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 [127]. 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, characterized by the respective roles of agriculture and pastoralism during the year [168]. Villages and local authorities manage socio-economic activities by allowing water resources use, preventing overgrazing, and regulating 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, which is located south to the mount Meru.

A.2 Model Variables

A.2.1 How We Chose Variables

The choice of variables was constrained by (spatial and temporal) scales and research questions. Rainfall was chosen to represent the seasons (`Rf+` : rainy season ; `Rf-` : dry season), while surface water (`Sw`) and groundwater (`Gw`) were defined according to their role for plants and animals, which are crucial for addressing our research questions. Indeed, surface water is used by wildlife and livestock for watering, while groundwater is assumed to be mostly used by trees and not by grasses, following the "two-layer hypothesis" [377, 379, 154]. Soil moisture was included in earlier versions but was removed since it is highly correlated to rainfall events. We chose to keep the wildlife component simple in this first model, by considering the dominant functional groups known to affect either herbivore populations (`Ca` : carnivores), trees (`Bw` : browsers ; `El` : elephants), or grasses (`Gz` : grazers). These four groups are present and abundant in east Africa, and are known to exert a pressure on plant dynamics, which justifies their presence in the model (they would have been absent if we aimed to model a present-day west African savanna, where many of these mammals have gone extinct). The pastoral component (`Ct` : cattle ; `Go` : goats) is restricted to livestock. Pastoralists were mentioned in earlier versions, but their close dependence on livestock (and reciprocally, livestock depends on pastoralists) made their explicit representation useless for our research questions. The same reasoning applies for farmers with crops. In addition, the fact that these two human groups are implicit enables to account for agropastoral households (families both practicing farming and livestock husbandry). On the other hand, tourists are not related to a specific production (livestock or crops) and were thus represented by themselves. The vegetation component was represented by grasses (`Gr`) and trees (`Tr`) to keep the model simple. We initially included tree saplings in order to represent intermediate tree life stages but finally kept them implicit as vegetation transitions were well represented by these two variables.

A.2.2 How to Make This Choice More Replicable ?

The first way to improve the choice of variables is to make it standardized and replicable. This includes (non-exhaustively) automated (i.e., replicable) literature reviews and standardized field surveys (with rigorous protocols for observations and interviews). Once collected in the literature and in the field, information must be selected according to research objectives. This includes identifying events in the literature, i.e., changes in the qualitative state of a variable, which amounts to its discretization (in our case, in two values + and −). Standardized discretization methods have been discussed in systems biology. From this standardized collection and discretization of data, rules can be built.

A.3 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 A.1 – 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-`		

TABLE A.2 – 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.	[111]
R2	Bw+, Rf-, Tr+	Gr+, Rf+, Sw+		[111]
R3	El+, Rf-, Tr+	Gr+, Rf+, Sw+		[111]
R4	Go+, Rf-, Tr+	Gr+, Rf+, Sw+		[111]
R5	Rf-, Tr-	Gr+, Rf+, Sw+		[111], 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.	[10]
R12	Rf-	Sw-		[10]
R13	Rf-, Sw-	Gw-		[10]
R14	Ct+, Rf-	Gr-	In dry season, non-managed livestock may overgraze the area.	[314]
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 wild preys, carnivores may attack livestock if wildlife populations are low.	[245]
R20	Bw-, Ca+, Gz-	Go-		[245]
R21	Rf-, Sw-	Bw-, El-, Go-	Low water availability may lead browser and generalist herbivores to leave the area.	[383, 331]
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.	[93]
R29	Go+	Gr+, Tr-	All browsers may strongly affect woody plants cover and favor grasses.	[268]
R30	El+	Gr+, Tr-		[200, 268, 335]
R31	Bw+	Gr+, Tr-		[13, 203, 268]
R32	Bw-, El-, Go-, Gr+, Gw+, Rf+	Tr+	In rainy season, the absence of browsers may promote tree recruitment.	[93]
R33	Gr+, Gw+, Rf-, Tr+	Gr-	In dry season, trees maintain a higher productivity than grasses due to their deeper root system.	[111]
R34	Rf+	Cr+	In rainy season, rainfall and surface water enable rain-fed farming as well as animals watering. In dry season, groundwater pumping enable irrigated agriculture and watering livestock.	[330, 219]
R35	Gw+, Rf-	Cr+		[178]
R36	Gw+, Sw-, Tr+	Go+		[62]
R37	Sw+, Tr+	Bw+, El+, Go+		FO
R38	Gw+, Sw-, Gr+	Ct+		[62]
R39	Sw+, Gr+	Ct+, El+, Gz+		FO
R40	El+	Cr-	Elephants may destroy crop fields.	FO and [326]
R41	Gz+	To+	Wildlife and traditional pastoral culture may attract tourists.	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.	[141]
R48	Ct+, Gz+, Rf+, Sw+	Ct-, Gz-	Grazers may die from diseases.	[141]
R49	Rf+	Cr-	In rainy season, pest may destroy crops.	[134]

A.4 Model Scenarios

Table A.3 – 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

As mentioned in Table A.1, 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.

A.4.1 Reference

The STG of reference scenario has 482 states (Fig. 19) 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. 10 and 12).

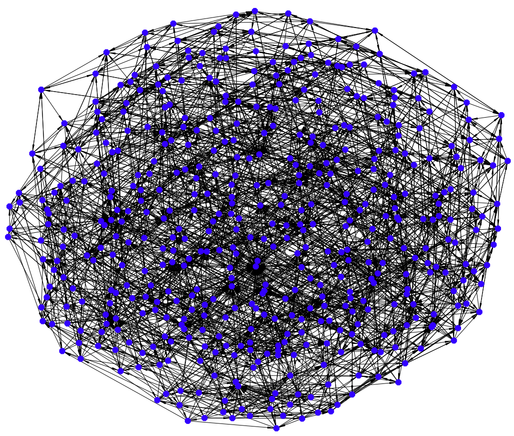

Figure 19 – STG of the reference scenario. Graph nodes and edges represent ecosystem states and transitions, respectively. This STG consists of 482 states and 2640 transitions. Nodes color is arbitrary.

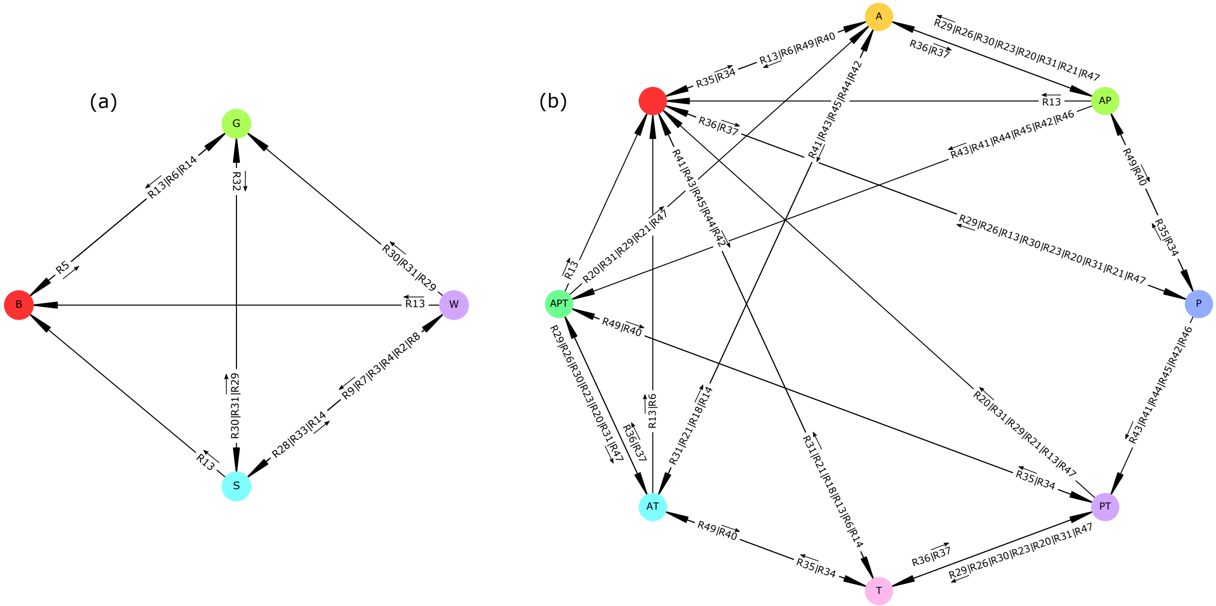

FIGURE 20 – Vegetation and socio-economic summary graphs of the reference scenario. Summary graphs (**a**,**b**) are the same as Fig. 10 and Fig. 12, respectively, and indicate the rules involved in each transition. In (**a**) node labels indicate vegetation types as defined in Section 2.2.6, with B : Bare soil ; G : Grassland ; S : Savanna, and W : Woodland, while in (**b**) they indicate socio-economic profiles, i.e., combinations of socio-economic activities A, P, and T, with A : Agriculture ; P : Pastoralism, and T : Tourism.
Small arrows associated to each transition labels (rules) indicate to which transition are associated the considered group of rules (see Table A.2 for details about rules).

A.4.2 "Dry Period" Scenario

A.4.2.1 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, [30]). 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). It is an acyclic graph focusing only irreversible aspects of system dynamics (Fig. 21).

A.4.2.2 The Attractor

The "dry period" attractor is not a stable state and is not cyclic. Some authors have proposed to call it a *complex attractor* (i.e., involving intertwined cycles [251]). Indeed, while the whole attractor is a cycle, it also comprises two small cycles (R5-R6 and R34-R49) (see Table A.2 for rules details). Ecologically, this attractor represents an ecosystem regime in which periodic rainfall drives a seasonal grassland and enables a rain-fed agri-

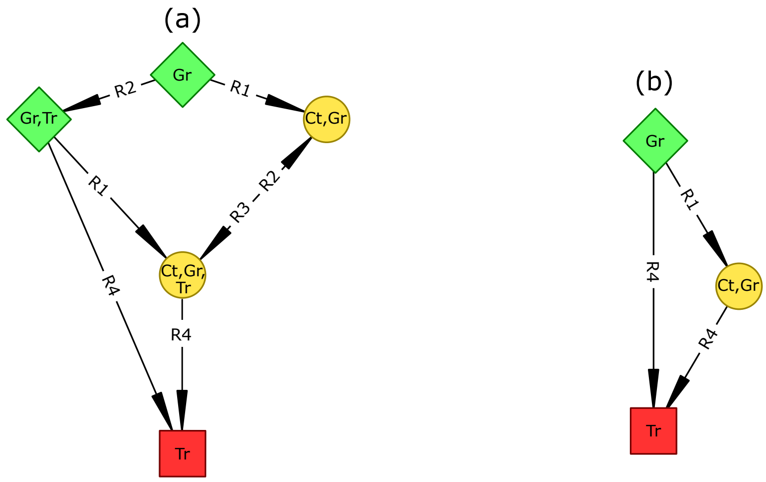

FIGURE 21 – Comparison between the STG and HTG of the "Grasses-Trees-Cattle" toy model. (**a**) This STG is the same as Fig. 9a and rules are those from Table 2.1. In (**b**), green lozenges nodes belong to a basin, yellow round nodes belong to a SCC and the red square node to a stable state (i.e., a 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. Node labels correspond to active variables `Gr` : Grasses, `Tr` : Trees, and `Ct` : Cattle. Note that in (**b**) node labels correspond to variables that are present in all states of the topological structure (i.e., SCC, basin or stable state). For instance, `Tr` oscillates in the yellow SCC in (**a**) and is thus not mentioned in the corresponding yellow node in (**b**).

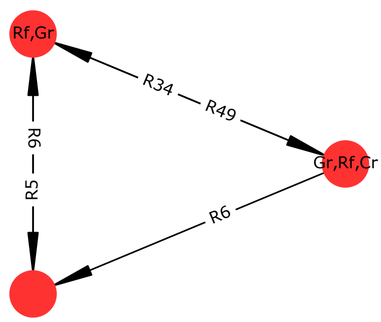

FIGURE 22 – STG of the attractor of the "dry period" scenario. Graph nodes and edges represent ecosystem states and transitions, respectively. Node labels correspond to active variables, with `Rf` : Rainfall, `Gr` : Grass, and `Cr` : Crops. Edge labels correspond to rules driving transitions (see Table A.2). Node color is arbitrary.

culture. 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 the rainy season is necessarily followed by a dry season, and reciprocally (i.e., to apply a fairness constraint on seasonality).

Annexe B

Annexe du chapitre 3

B.1 Model rules

The model includes 31 “regular” rules and 11 constraints. Constraints are executed in priority to other rules. See [125] for formal definition of (reaction) rules.

In this model, and in contrast with other studies [223, 124, 125, 76], we chose to make as few assumptions as possible about parameters and thus opted for rules including a single variable update at a time (except in constraints).

In contrast with our previous studies, we studied the “full” graph, i.e. the graph including all states (satisfying constraints or not). Indeed, in previous studies, states satisfying constraints were removed prior to analysis as they represented ecologically unrealistic or too transient states. This was not the case here as considering a state as “unrealistic” is (at least partially) arbitrary and we aimed at a maximally parsimonious model.

Table B.1 – **Set of constraints.** Constraints with the same realization (i.e. the same effect) are gathered within the same multirow.

N°	Condition	Realization	Description	References
C1	`Fe-, Ma-, Cr`	`Cr-`	Crop residue productions requires a sufficient fertility or manure inputs with equipment for collecting, transporting and applying it.	[23, 22]
C2	`Fe-, Eq-, Cr`			[23, 22]
C3	`Lv-`	`Ma-`	Manure requires livestock to be produced.	Common sense
C4	`Fe-`	`Fp-`	Fodder plants require a fertile soil (and food crops have priority over fodder crops).	[187]
C5	`Cr-`			
C6	`Eq-`	`Cc-, Ca-`	Without fertility or animal traction or draught animals, cropped area must be reduced, which reduces cash crop production.	
C7	`Lv-`			
C8	`Fe-`			Assumption
C9	`Rg-, Flw-, Fp-`	`Lv-, Ma-, Eq-, Ca-`	Without rainy season forage or dry season forage, the livestock herd (and components depending on it) cannot be sustained.	
C10	`CRC-, Fg-, Fp-`			
C11	`Cr-, Fg-, Fp-`			

TABLE B.2 – **Initial conditions for reaching each farm type.** caption

N°	Condition	Realization	Description	References
R1	Fe	Cr	Soil fertility or manure may increase crop residues yield.	[22]
R2	Ma, Eq			[23]
R3	Cc, Flw-, Rg, Cr, Eq, CRC	Lv	If forage (fallows or rangelands in rainy season and freely grazed or collected crop residues in dry season, or fodder plants in both) and income (from the sale of cash crops or non-farm activities) are sufficient, then livestock may be purchased. Crop residues production is assumed sufficient in neighboring farms.	[36, 94]
R4	Nf, Flw-, Rg, Cr, Eq, CRC			[297]
R5	Cc, Flw, Cr, Eq, CRC			[297]
R6	Nf, Flw, Cr, Eq, CRC			[297]
R7	Cc, Flw-, Rg, Fg			[297]
R8	Nf, Flw-, Rg, Fg			[297]
R9	Cc, Flw, Fg			[297]
R10	Nf, Flw, Fg			[297]
R11	Cc, Fp			[187]
R12	Nf, Fp			[187]
R13	Lv, Rg, Cr, Eq, CRC	Ma	If livestock and forage (in all seasons) are present, then manure can be produced.	[222, 96, 297]
R14	Lv, Rg, Fg			[297]
R15	Lv, Flw, Cr, Eq, CRC			[297]
R16	Lv, Flw, Fg			[297]
R17	Lv, Fp			[187, 297]
R18	Lv, Cr, Eq	Ca	Animal traction enables farmers to increase cropped area.	[148]
R19	Fe, Flw-, Cr	Fp	Soil fertility enables farmers to produce fodder plants.	[187]
R20	Eq, Lv, Fe, Cr	Cc	Soil fertility and animal traction enable farmers to produce cash crops. Cash crop producers are assumed to also produce food crops (and thus crop residues).	[181, 182]
R21	Flw	Fe	Organic matter should be incorporated (through fallowing or organic amendments such as crop residues or manure) and erosion controlled for restoring soil fertility.	[221]
R22	EC, Fg-, Eq, Cr, CRC-			[23, 88]
R23	EC, Eq, Ma			[136]
R24	Flw-, EC-	Fe-	Without erosion control, continuous cultivation nor organic input nor equipment, may reduce fertility	
R25	Flw-, Cr-, Ma-			[88]
R26	Flw-, Eq, CRC, Ma-			[88]
R27	Flw-, Fg, Ma-			
R28	Flw-, Eq-			
R29	Cc, Lv, Cr	Eq	Income enables purchasing agricultural equipment. Note that every equipment (cart, plough, etc.) requires livestock.	[148, 147]
R30	Nf, Lv, Cr			[148, 147]
R31	Lv, Cr			[148, 147]

B.2 Farm types

The reachability of each farm type from initial states was assessed using CTL. We recall that initial states were all A1 farm types. A farm type is said reachable if there exists at least one trajectory leading to this farm type, at some point in the future. This corresponds to the formula $\exists F(\varphi)$, where φ is the farm type of interest.

If we consider all initial states, some can reach a particular farm type, some cannot. The table B.3 summarizes the scenarios (i.e. the combinations of control variables) under which each farm type is reachable. In general, the scenarios for reaching a farm type are displayed as a disjunctive normal form (i.e. an "OR of ANDs").

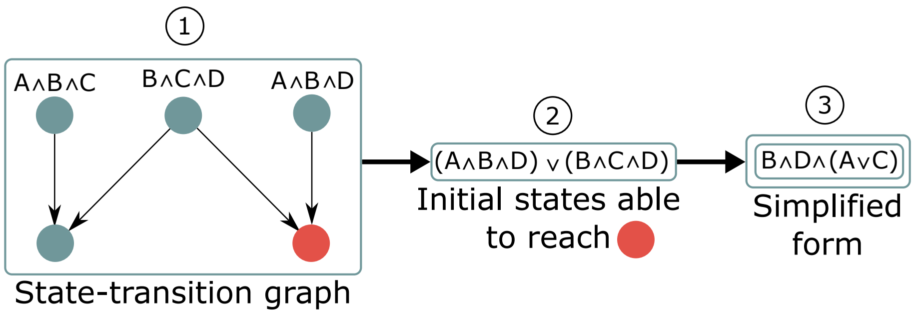

FIGURE 23 – **Procedure for determining scenarios satisfying a dynamical property.** Following STG computation (step 1), the model-checker enables determining the values of control variables in the set of initial states satisfying the property (here, the reachability of the red state). This set of control variables valuations is a boolean formula. This boolean formula is immediately simplified using SymPy [233] to obtain a disjunctive normal form (an OR of ANDs) (step 2). This disjunctive normal is further simplified by hand to get a more compact expression (step 3).

For instance, A2, A3, AP and B are reachable under six disjoint scenarios : `(Flw, CRC, Lv)|(Rg, CRC, Lv)|(Flw, Fg, Lv)|(Rg, Fg, Lv)|(Flw-, Nf)|(Fg, Nf)`, where "," is the logical AND and "|" the logical OR. This can can be further simplified, as in Table B.3, in `[Lv,(Flw|Rg),(CRC|Fg)]|[Nf,(Flw- | Fg)]`.

TABLE B.3 – **Scenarios for which farm types are reachable.** Farm types A2, A3, AP and B were reachable under the same scenarios.

Farm type	CTL formula	Management scenarios
$A2\|A3\|AP\|B$	$\neg\exists F(A2\|A3\|AP\|B)$	`[Nf-,(Flw-,Rg-)|(CRC-,Fg-)|Lv-]	[Flw,Fg-,(CRC-|Lv-)]`
A2 A3 AP B	$\exists F(A2)$ $\exists F(A3)$ $\exists F(AP$ $\exists F(B)$	`[Lv,(Flw|Rg),(CRC|Fg)]	[Nf,(Flw-|Fg)]`

Note that these management scenarios *do not* guarantee reaching a farm type, at least for two reasons : on a logical perspective, a state verifies the formula $\exists F(\varphi)$ if there is a trajectory from that state to φ, which does not mean that all trajectories lead to φ. On the "interpretative" perspective, the fact that a trajectory exists does not mean that the system will take it. Indeed, depending on the meaning of transitions, the system could remain in the current state for an arbitrary time, or take another trajectory, depending on management choices or on unspecified social-ecological constraints at a given moment.

Therefore, these conditions are *necessary but not sufficient conditions* for reaching each farm type.

B.3 Farm trajectories

TABLE B.4 – **Rules and constraints driving farm transitions.**

Source	**Destination**	**Rules and constraints**
A1	B	R13, R14, R15, R16, R17
	transient	R18
	A2	**R20**
A2	**A1**	**C10**
	transient	C11, C12, C13
	AP	R13, R14, R15, R16, R17
	A3	**R18**
A3	transient	C1, C11, C12
	A1	C10
	AP	**R13, R14, R15, R16, R17**
transient	A1	C8, C9, C10, C11, C12, C13
	B	C10
	A3	R20
	AP	R20
AP	B	C10
	transient	C11, C12
B	A1	C11, C12, C13
	transient	R18
	AP	**R20**

Each state-transition graph is associated to a transition table detailing every transition. This includes which rule(s) is responsible for each transition, and the label of these rules (e.g. which variables are affected, which type of event or probability). The label of a rule has no impact on the dynamics and is just indicative.

B.3.1 Conditions of trajectories

Any transition is a shift from a set of states to another. For instance, A2 $\rightarrow$ A3 is transition from states A2 to A3. States belonging to a same farm type share some characteristics (see Table 3.2) but differ for unspecified variables (noted $*$ in Table 3.2). For instance, A2 and A3 may differ for variables `Fe, Cr` and `Fp`.

TABLE B.5 – **Scenarios enabling/preventing each farm transition.** Each transition between X and Y (i.e. $X \rightarrow Y$) is expressed as $X \land \exists(X \text{ U } Y)$, where $\neg$, $\land$, $\lor$ and U represent the logical NOT operator, the logical AND operator, the logical OR operator and the "until" temporal operator, respectively. Each management scenario is a combination of control variables (except `Lv`) and corresponds to a set of initial states. For management scenarios, AND and OR operators are noted "`,`" and "`|`", respectively. Transitions are grouped when they are enabled or disabled by the same scenario. In the "rules" column, R13-17 is a shortcut for all rules between R13 and R17.

<table>
<tr><th>Signification</th><th>CTL formula</th><th>Trajectory</th><th>Management scenarios</th><th>Rules</th></tr>
<tr><td rowspan="3">Conditions of possibility</td><td>$A1 \land \exists(A1 \text{ U } A2)$</td><td>$A1 \rightarrow A2$</td><td><code>[Lv,(Flw|Rg),(CRC|Fg)] |</code>
<code>[Nf,(Flw-|Fg)]</code></td><td>R20</td></tr>
<tr><td>$A2 \land \exists(A2 \text{ U } A3)$
$A3 \land \exists(A3 \text{ U } AP)$
$B \land \exists(P \text{ U } AP)$</td><td>$A2 \rightarrow A3$
$A3 \rightarrow AP$
$B \rightarrow AP$</td><td><code>[(Flw|Rg),(CRC|Fg)] | [Flw-,Nf]</code></td><td>R18
R13-R17
R20</td></tr>
<tr><td>$A2 \land \exists(A2 \text{ U } A1)$</td><td>$A2 \rightarrow A1$</td><td><code>[Flw-,(Rg|Nf),(CRC|Fg)] |</code>
<code>[Flw-,Nf,EC-]</code></td><td>R24, R26, R27</td></tr>
<tr><td rowspan="4">Conditions of impossibility</td><td>$A1 \land \neg\exists(A1 \text{ U } A2)$</td><td>$A1 \nrightarrow A2$</td><td><code>[(Fg-,CRC-)|Flw-] |</code>
<code>[(Lv-,Fg-)|Nf-]</code></td><td></td></tr>
<tr><td>$A2 \land \neg\exists(A2 \text{ U } A3)$
$A3 \land \neg\exists(A3 \text{ U } AP)$</td><td>$A2 \nrightarrow A3$
$A3 \nrightarrow AP$</td><td><code>[Flw-,(Rg|Nf),(CRC|Fg)] | (Flw-,Nf,EC-)</code></td><td></td></tr>
<tr><td>$B \land \neg\exists(P \text{ U } AP)$</td><td>$B \nrightarrow AP$</td><td><code>[(Flw-,Rg,CRC)|Fg] | [Flw-,Nf]</code></td><td></td></tr>
<tr><td>$A2 \land \neg\exists(A2 \text{ U } A1)$</td><td>$A2 \nrightarrow A1$</td><td><code>[(Flw,CRC)|Fg] |</code>
<code>[Flw-,CRC-,Fg-,Nf,EC]</code></td><td></td></tr>
</table>

As in section B.3.1, we determined management scenarios enabling/preventing each farm trajectory. In the case of $A2 \rightarrow A3$, this amounts to find states in A2 which can lead to A3 without leaving A2 (i.e. medium farmers becoming "directly" large farmers, that is, without becoming breeders before).

B.4 How (not) to reach a sustainable agropastoralism ?

Sustainable agropastoralism was defined as ∀G(AP). Reachability sets ("possible", "impossible" and "necessary") detailed in Table 3.3 are state properties. These have been formulated in CTL as follows : states for which it is impossible to reach a sustainable agropastoralism (AP) were expressed as $\neg\exists F(\forall G(AP)$; states for which it is possible but not necessary to reach a sustainable AP were expressed as $\exists F(\forall G(AP) \wedge \neg(\neg\exists F(\forall G(\neg AP))$; states for which it is necessary to reach a sustainable AP were expressed as $\neg\exists F(\forall G(\neg AP)$ (see Table 3.2 for definition of AP).

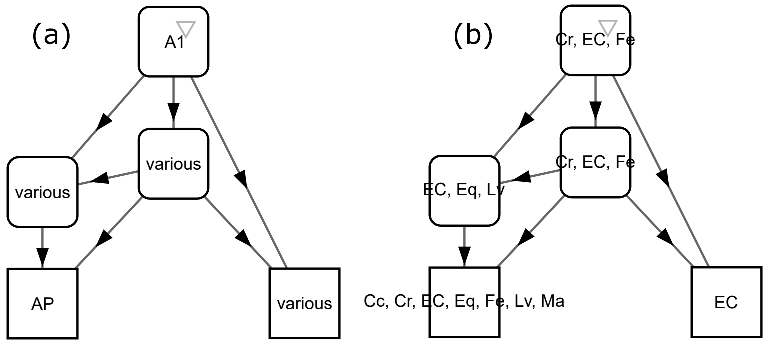

FIGURE 24 – **Dynamics from initial states from which sustainable agropastoralism is possible but not necessary**. Node labels in (a) : farm types ; in b : present variables. The node with an inverted triangle gathers all initial states and square nodes include at least one stable state.

Livestock is crucial for reaching a sustainable agropastoralism. Indeed, farms which necessarily become agropastoral have agricultural equipment (`Eq`) and livestock (Fig. 24.