

Modelling of “ the evolution ” of ecosystems

Thi Thu Tam Nguyen

▶ **To cite this version:**

Thi Thu Tam Nguyen. Modelling of “ the evolution ” of ecosystems. Life Sciences [q-bio]. 2018. dumas-02138940

HAL Id: dumas-02138940

https://dumas.ccsd.cnrs.fr/dumas-02138940

Submitted on 24 May 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L’archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d’enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives| 4.0 International License

AGROCAMPUS OUEST

CFR Angers ☑ CFR Rennes

Terre, Écosystèmes et Sociétés

Année universitaire : 2017 - 2018 Spécialité : Ingénieur Agronome Spécialisation (et option éventuelle) : Modélisation en Écologie	**Mémoire de fin d'études** ☑ d'Ingénieur de l'Institut Supérieur des Sciences agronomiques, agroalimentaires, horticoles et du paysage ☐ de Master de l'Institut Supérieur des Sciences agronomiques, agroalimentaires, horticoles et du paysage ☐ d'un autre établissement (étudiant arrivé en M2)

Modelling of « the evolution » of ecosystems

Par : Thi Thu Tam NGUYEN

Soutenu à Rennes le 14 Juin 2018

Devant le jury composé de :

Président : Cédric Wolf

Maîtres de stage : Manuel Blouin et Cédric Gaucherel

Enseignant référent : Frédéric Hamelin

Autres membres du jury : Manuel Plantegenest

Les analyses et les conclusions de ce travail d'étudiant n'engagent que la responsabilité de son auteur et non celle d'AGROCAMPUS OUEST

Ce document est soumis aux conditions d'utilisation «Paternité-Pas d'Utilisation Commerciale-Pas de Modification 4.0 France» disponible en ligne http://creativecommons.org/licenses/by-nc-nd/4.0/deed.fr

Synthèse du rapport de stage

Introduction

La théorie évolutionniste de Darwin (Darwin, 1859) est résumée en trois éléments principaux : les pressions sélectives de l'environnement, la variation des caractères impliquant la variation de la valeur sélective des vivants face à ces pressions et la transmission de cette variation à leur descendance (Ellegren & Sheldon, 2008). Ainsi, ce concept évolutionniste est jusqu'à ce jour définie pour des composantes vivantes. De plus, la sélection naturelle – le moteur principal de l'évolution, est montré avoir lieu à plusieurs niveaux d'organisation de l'écosystème, des molécules jusqu'aux communautés (Goodnight, 1990a). Si l'écosystème comprend non seulement l'ensemble des organismes vivants dans un habitat donné mais aussi la totalité des facteurs physiques, voire anthropiques qui y présentent des effets non négligeables (Tansley, 1935), est-ce possible de parler de « l'évolution » d'un écosystème ? Si oui, comment est-elle définie, en adaptant la définition actuelle de l'évolution pour la décrire à ce niveau supérieur et complexe ?

1. Contexte biologique :

D'une part, les mécanismes de l'évolution sont très divers. Jablonka *et al* (2006) parle d'une évolution en 4 dimensions, dont génétique (sélection naturelle et dérive génétique), épigénétique (transmission des caractères non génétiques acquis au cours de la vie), comportementale et symbolique (chez les humains). Étudier l'évolution au niveau de l'écosystème demande donc de connaître cette diversité, qui présente non seulement des effets spécifiques mais aussi des propriétés d'émergence importantes.

De plus, la sélection peut avoir lieu à des niveaux supérieurs que les espèces et populations, par exemple la sélection de groupe (Goodnight & Stevens, 1997), ou de communauté (Goodnight, 1990a).

D'autre part, modéliser un écosystème nécessite de prendre en compte à la fois ses composantes biotiques et abiotiques. Ainsi, tous les interactions, trophiques ou non-trophiques (compétition, mutualisme, amensalisme, commensalisme), interviennent dans les dynamiques de l'écosystème. De plus, les interactions au niveau supérieur (interactions entre deux espèces mais modulées par les autres, Bairey *et al*, 2016) ainsi que des propriétés de la structure des interactions (Thebault & Fontaine, 2010) ont des effets non négligeables sur l'évolution. Ces interactions non trophiques sont pourtant très peu discutées dans la littérature (Ings *et al*, 2009), et si elles sont inclues, il existe peu d'études qui traitent plusieurs types d'interactions dans le même système. Dans ce cas, ces différents réseaux d'interactions sont donc supposés indépendants, or une même espèce peut être concernée par de différentes interactions

simultanément (Fontaine *et al*, 2011). Quant aux facteurs environnementaux, ces variables sont très peu étudiées dans les dynamiques des écosystèmes et très souvent associées avec les perturbations externes, donc considérées comme indépendants du système (Dambacher *et al*, 2007; Reum *et al*, 2015). Pourtant, quand les composantes de l'écosystème se développent et s'interagissent, certaines peuvent disparaître et puis réapparaître, ce qui peut changer radicalement l'état de l'écosystème. Dans ce cas, l'écosystème doit être considéré comme un dynamique système avec une dynamique structure (Giavitto & Michel, 2003).

Étudier les dynamiques et « l'évolution » possible d'un écosystème demande donc un modèle susceptible de capturer sa complexité (dont la diversité des composantes, l'organisation à plusieurs niveaux et les dynamiques des interactions et de leurs structures), en discutant les évolutions possibles de la totalité du système. Nous supposons que l'utilisation des modèles qualitatives comme le réseau Petri (Gaucherel & Pommereau, soumis en 2017) ou les réseaux Booléens (Gaucherel *et al*, 2017) est une solution pertinente pour simplifier cette complexité et ses dynamiques sans perdre des propriétés.

2. Les objectifs du stage :

Nous cherchons à utiliser l'approche du réseau Petri pour décrire et comprendre les dynamiques d'un écosystème microbien et son évolution, en utilisant deux cas d'étude : les communautés microbiennes avec des évènements de sélection artificielle au niveau écosystémique, et le cycle de l'azote dans des communautés en biofilm. L'objectif principal de ce travail est donc de choisir des approches expérimentales et de modélisation susceptibles de décrire et de montrer (ou de contribuer à montrer) qu'un écosystème « évolue » et de quelle nature est cette évolution. Les questions sont donc posées pour chaque modèle proposé dans ce travail. Dans le premier cas d'étude, si la sélection au niveau écosystémique est imposée, est-ce que les effets sont exactement les mêmes que ceux de la sélection à des niveaux plus bas ? Le deuxième modèle traite deux questions principales : comment le cycle de l'azote est maintenu avant l'apparition de certaines bactéries spécifiques (qui arrivent plus tard dans l'histoire évolutive) ? et l'oxygène est-il une contrainte cruciale pour ce cycle de l'azote ?

Matériels et méthodes

1. Approches expérimentales :

a. Sélection artificielle à l'échelle écosystémique

Cette expérience a pour but d'étudier les effets de la sélection artificielle dans un écosystème microbien issu d'un centre d'épuration en France, en considérant les émissions de CO_2 comme le caractère sélectionné. Les communautés microbiennes de cet écosystème sont séparées en deux groupes avec deux méthodes de traitements différents : contrôle et sélection.

Pour générer la génération suivante, trois communautés sont sélectionnées dans chaque groupe, de manière aléatoire dans le groupe contrôle ou selon les émissions de CO_2 dans le groupe sélection pour être assemblées et produire la descendance. La composition en unités génétiques est déterminée à certaines générations pour calculer les coefficients de corrélation à partir de l'abondance de différentes unités génétiques et construire par la suite des matrices de cooccurrence pour montrer et analyser la structure des interactions écologiques.

b. Évolution du cycle de l'azote : rôle du processus d'Anammox et de l'oxygène

Notre deuxième modèle est basé sur le cycle de l'azote où l'azote existe sous différentes formes chimiques et la conversion d'une molécule à une autre est réalisée par un gène spécifique, par exemple le gène nifH pour la fixation de l'azote atmosphérique. Parmi les processus biologiques (la fixation, l'assimilation, l'ammonification, la nitrification, la dénitrification, …), le processus d'Anammox (Oxydation anaérobique de l'ammonium) représente un rôle important dans la production du diazote gazeux. Décrivant la conversion de NH_4 et NO_4 en diazote (et de l'eau, non représenté dans ce modèle), cette conversion est découverte plus tard par rapport aux autres, mais est responsable d'une libération significative de N_2, entre 30-50% de sa production totale. Étudier les effets de ce processus est donc intéressant en termes d'évolution car cela existe seulement chez certaines bactéries.

De plus, l'oxygène est aussi essentiel pour ce cycle, comme un donneur d'électron pour certains processus, donc doit être pris en compte dans ce modèle.

2. Utilisation d'un modèle discret pour décrire l'évolution d'un écosystème

Les modèles qualitatifs discrets semblent d'être une solution pertinente pour étudier notre sujet, car ils permettent de simplifier la complexité du système due à la hiérarchie de ses niveaux d'organisation. De plus, il est possible, avec cet outil, d'étudier les dynamiques de l'écosystème et toutes ses trajectoires possibles résultant des processus et/ou des interactions écologiques. Nous pourrons par la suite identifier certaines dynamiques spécifiques du système (l'apparition ou la disparition de certaines espèces, les états de collapses ou autres types de stabilités structurales).

a. Définition intuitive du modèle par un graphe

Un système peut être modélisé comme un graphe composé des composantes (nœuds) et des liens (flèches/arcs) entre ces composantes. Un exemple d'un système de proie-prédateur simple est présenté à la Fig. 3.

Pour un écosystème, toutes les composantes matérielles, soit biotique ou abiotique ou anthropogénique sont représentées par des nœuds, et sont reliées entre elles par des flèches. Chaque nœud peut avoir un des deux états Booléen : « On » si la composante est présente dans

le système ou « Off » si elle est absente dans le système à un instant. On définit alors l'état du système entier comme une combinaison des nœuds absents et présents à cet instant. Par conséquent, le nombre d'états possible du système peut atteindre $2^{\#noeuds}$, et donc augmente exponentiellement avec le nombre de nœuds.

Les liens entre une paire de nœuds définie leurs changements, définies à partir des processus bioécologiques, physicochimiques ou socioéconomiques et représentent les interactions entre les composantes du système étudié. Une règle est composée de 2 parties : Une condition et une réalisation. Elle est appliquée si l'état du système satisfait sa partie de condition, cette application modifie par la suite l'état de certains nœuds en fonction de la partie de réalisation de cette règle.

Ainsi, une fois appliquée, chaque règle faire modifier système d'un état à un autre. On définit alors l'espace des états comme l'ensemble des états du système accessibles par les règles définies à partir d'un état initial spécifique. Normalement, la taille de l'espace d'état est plus petit que le nombre d'états possibles ($2^{\#noeuds}$), car les règles rendent impossibles certaines combinaisons de présences et absences des composantes avec ses conditions d'application.

La définition formelle d'un modèle qualitatif est expliquée dans la partie B- II- 2. Suggested discrete qualitative model – Petri net.

b. Définition formelle d'un modèle de réseau de Petri marqué

Un réseau de Petri marqué est un tuple $N \stackrel{\text{def}}{=} (S, T, W, M)$ tel que :

- $S=\{s_1, s_2, \ldots, s_n\}$ est un ensemble fini de places;
- $T=\{t_1, t_2, \ldots, t_n\}$, disjoint de S, est l'ensemble fini de transitions;
- $W: (S\times T)\cup(T\times S) \rightarrow N$ est la fonction de poids définissant les flèches;
- $M \in S^*$ est le marquage qui est un multi-ensemble de places représentant l'état du réseau de Petri

La conversion du modèle qualitatif précédemment défini se fait de manière suivante :

- Chaque nœud peut être représenté par 2 places dans le réseau Petri (pour les états « On » et « Off ») ;
- Chaque règle est traduite en une (ou plusieurs) transitions(s) ;
- Chaque état du système est défini par un marquage du réseau de Petri (le jeton que contient chaque place).

L'illustration de cette conversion pour le modèle simple de proie-prédateur est présentée dans la Fig. 7.

- Place et marquage du réseau

Pour chaque nœud, deux places e^+ (pour nœud « On ») et e^- (pour nœud « Off ») sont créées correspondantes à deux états de ce nœud. Les jetons sont alors distribués entre ces différentes places pour définir l'état initial du nœud. Si le nœud e est initialement présent dans le système, la place e^+ contient alors un jeton (on dit que cette place est marquée), alors que la place e^- n'est pas marquée et pourrait avoir un jeton plus tard au cours de la simulation. Cette distribution de jetons dans les places différentes décrit le marquage du réseau. Les transitions vont par la suite permettre la circulation des jetons entre les différentes places et modifier alors le marquage du graphe, donc de l'état du système entier.

- Normalisation des règles

Les règles doivent être explicites et non ambiguës avant d'être converties en transitions. Par exemple, quand on a une règle simple comme A+ >> B -, cela veut dire que :

- La partie de condition ne dépend pas de l'état de B ;
- L'état de A n'est pas modifié par sa réalisation.

Pourtant pour une machine de calcul, cela doit être réécrit pour être le plus exhaustif et le plus rigoureux possible. C'est pour cela que nous devons écrire deux règles au lieu d'une seule :

A+, B+ >> A+, B-

et A+, B- >> A+, B-

Cette procédure de normalisation est généralisée à chaque règle $r \stackrel{\text{def}}{=} (\alpha^+, \alpha^-, \omega^+, \omega^-)$ en deux étapes :

- Réécrire la condition comme $C \stackrel{\text{def}}{=} \{(\alpha^+ \cup x, \alpha^- \cup (\chi \backslash x), \omega^+, \omega^-) | x \in 2^x\}$ où $\chi \stackrel{\text{def}}{=} \omega \backslash \alpha$ avec $\alpha \stackrel{\text{def}}{=} \alpha^+ \cup \alpha^-, \omega \stackrel{\text{def}}{=} \omega^+ \cup \omega^-$ (ajouter les états des nœuds touchés par la réalisation), donc pour l'exemple ci-dessus C = {A+, B+ >> B-; A+, B- >>B-}
- Réécrire la réalisation comme $Z \stackrel{\text{def}}{=} \{(\alpha^+, \alpha^-, \omega^+ \cup (\alpha^+ \backslash \omega), \omega^- \cup (\alpha^- \backslash \omega) | (\alpha^+, \alpha^-, \omega^+, \omega^-) \in C\}$ (ajouter les états des nœuds concernés dans la condition mais non modifies par la réalisation), donc pour l'exemple ci-dessus Z={A+, B+ >> A+, B-; A+, B- >> A+, B-}.

- Des règles aux transitions

Une fois normalisées, les règles peuvent être traduites en transitions de Petri.

Chaque transition t de T est définie par sa précondition $\overleftarrow{t}$ and sa post-condition $\vec{t}$ telles que : $\overleftarrow{t} \stackrel{\text{def}}{=} \sum_{s \in S} W(s,t) \times \{s\} \in S^*$ and $\vec{t} \stackrel{\text{def}}{=} \sum_{s \in S} W(t,s) \times \{s\} \in S^*$ où S* est l'ensemble de tous les multi-ensembles (i.e. l'état du système).

Ces définitions correspondent à la condition et la réalisation des règles normalisées respectivement. Ainsi, la transition t est applicable à un marque M si $\overleftarrow{t} \leq M$. Si c'est le cas, t va être appliquée et conduire à un nouveau marquage M' défini avec :

$$M' \stackrel{\text{def}}{=} M - \overleftarrow{t} + \vec{t}$$, noté M[t⟩M'.

À partir de ces définitions, une transition t_r, est ajoutée au réseau de Petri pour chaque règle normalisée $r \stackrel{\text{def}}{=} (\alpha^+, \alpha^-, \omega^+, \omega^-)$ telle que :

- $W(e^+,t_r) \stackrel{\text{def}}{=} 1$ pour tout $e \in \alpha^+$
- $W(e^-,t_r) \stackrel{\text{def}}{=} 1$ pour tout $e \in \alpha^-$
- $W(t_r,e^+) \stackrel{\text{def}}{=} 1$ pour tout $e \in \omega^+$
- $W(t_r,e^-) \stackrel{\text{def}}{=} 1$ pour tout $e \in \omega^-$
- $W(t_r,p) \stackrel{\text{def}}{=} 0$ pour chaque place p

- Espace d'états et le graphe de marquage

Puisque l'état du système correspond au marquage du réseau de Petri, l'espace d'état est représenté en utilisant le graphe de marquage de ce réseau. Dans ce graphe, les sommets sont les états du système et les flèches représentent les transitions permettant le passage d'un état à un autre (Fig. 8).

- Réalisme du modèle – définition des contraintes

L'application des règles mènent à autant de chemins possibles que de règles applicables, permettant au modèle d'explorer tous les états possibles à partir de l'état initial. Pourtant, appliquer une règle indépendamment de certains d'autres peut provoquer le passage du système à des états irréalistes (par exemple un état avec certaines espèces vivantes sans aucun habitat). On introduit ainsi la notion de contrainte pour prévenir le modèle à ne pas présenter de tels états. Étant similaire à une règle, une contrainte est aussi composée d'une condition et une réalisation, et empêcher le modèle à montrer des états non réalistes avec présence en même temps deux ou plus composantes qui ne peuvent pas coexister en réalité, ou une composante qui ne peut pas exister sans les autres.

L'espace d'états peut être étudié et analysé en définissant et identifiant l'état initial, les points de collapses, les stabilités structurales et les bassins. Il peut être représenté sous plusieurs formes : en complet avec tous les états possibles : en compact quand les états transitifs (par contraintes) sont enlevés ; en fusionnant les états appartenant à une même stabilité ou un même point de collapse,…. Par la suite, nous utilisons des outils d'analyse statistiques (comme l'AFC, l'ACP) pour étudier l'abondance de chaque composante de l'écosystème pour comprendre les différentes trajectoires en fonction des états initiaux différents, ….

Résultats

1. Modèle 1 : Sélection artificielle des communautés microbiennes

a. Construction du modèle

Nous avons fait le choix de représenter au moins 3 niveaux d'organisation de notre écosystème microbien (Fig. 9) pour modéliser la sélection au niveau écosystémique et comparer ses effets possibles sur les niveaux inférieurs (niveau des individus et des unités génétiques). Les composantes, biotiques ou abiotiques, impliquant dans ces différents niveaux sont représentées comme des nœuds dans notre modèle. De plus, nous avons ajouté un nœud « experimenter » pour introduire la sélection artificielle dans ce modèle.

Les règles et les contraintes décrivent des processus ayant lieu dans cet écosystème microbien. Les règles explicitent les corrélations possibles (positives ou négatives) entre les bactéries et/ou entre les unités génétiques, ainsi que la sélection artificielle impliquant à l'échelle écosystémique. Les contraintes permettent d'appliquer en avance la hiérarchie entre les différents niveaux du système ainsi que la nécessité de nutriments dans le milieu.

Nous réécrivons alors ce modèle avec le formalisme de Petri (cf Results – I-2. Formalism).

b. Espaces d'états et interprétations

Nous avons obtenu un espace d'états complet ainsi qu'un espace d'état réduit en fusionnant des états en 2 stabilités structurales distinctes (suivies de deux bassins). Cet espace d'état réduit montre deux trajectoires possibles pour notre système : la première mène à une stabilité où GU1 et toutes ses bactéries sont absentes du système par sélection artificielle, alors que la deuxième stabilité ne contient GU3 et ses bactéries par corrélation négative entre cette unité génétique avec GU1 (présente s'il n'y a pas de sélection artificielle).

2. Modèle 2 : Évolution du cycle de l'azote

a. Construction du modèle

Les nœuds du modèle représentent toujours les composantes physiques (matérielles) impliquant dans le cycle de l'azote, qui sont soit biotiques (les gènes), soit abiotiques (les différentes formes de l'azote et l'oxygènes). Les règles définissent les processus chimiques permettant les conversions d'une molécule à une autre (ou plusieurs) dans ce cycle (formalisme dans la partie Results – II-2. Formalism). Nous testons pour ce modèle trois scénarios qui correspondent à 3 états initiaux : le premier avec présence de toute molécule et gène, le deuxième en désactivant le processus d'Anammox et le troisième en absence de l'oxygène.

b. Espaces d'états et interprétations

L'espace d'états réduit correspondant au premier scénario est représenté sur la Fig. 12. Nous remarquons une évolution identique à toutes les molécules : leur abondance diminue

graduellement de l'état initial au dernier. De plus, la règle n°16, représentant le processus d'Anammox joue un rôle de court-circuit permettant au système contourner certains états, donc plus de trajectoires possibles en cas de perturbations. Nous confirmons cette remarque en observant le résultat du deuxième scénario, où le processus d'Anammox est désactivé. Nous y retrouvons les mêmes stabilités structurales, mais l'ensemble des court-circuits possibles par Anammox n'est plus présent sur cet espace d'états.

Dans le troisième scénario sans oxygène, le système se termine par un état de collapse (où il n'y a plus d'évolution possible). Avec l'analyse par AFC, l'espace d'états obtenu est séparé par un axe où d'un côté nous observons des états avec présence de N_2 et de l'autre côté des états avec les autres formes de l'azote : NO, NO_2, NO_3, N_2O et NH_4. Ainsi, cet axe définit deux groupes principaux des formes de l'azote dans le cycle : ceux qui sont fixés par les microbes (NO, NO_2,…) ou ceux qui sont libres dans l'environnement (seulement N_2, donc pas de vie possible).

Discussions

Avantages et limites du premier modèle basé sur les émissions de CO2 :

Le premier modèle est une étude préliminaire pour représenter un écosystème avec des interactions diverses entre ces composantes, en ajoutant une sélection artificielle. Il a répondu aux premières demandes d'un modèle discret et qualitatif qui peut inclure à la fois des composantes biotiques et abiotiques ainsi que la succession des niveaux d'organisation de l'écosystème. Nous avons obtenu deux trajectoires possibles correspondant à « l'évolution » de l'écosystème avec ou sans la sélection. Pourtant, ce modèle présente certaines difficultés infranchissables.

Tout d'abord, la règle de sélection a été prédéfinie sans prenant en compte du caractère sélectionné : dans notre modèle, les unités génétiques 2 et 3 sont sélectionnés au profit de l'unité génétique 1, mais cette sélection n'a pas de lien causal avec des émissions quantitatives de CO2 de ces unités. De plus, le réseau d'interactions a été aussi prédéfini et n'a pas pu être modifié durant la simulation. Aussi, nous devions avoir plusieurs écosystèmes dans le même modèle avec les interactions entre eux, afin de comparer les structures différentes, mais cela suppose donc un système beaucoup plus grand et complexe, due à la nature exponentielle combinatoire des interactions entre composantes, que les outils de calcul ne sont pas assez puissants pour maîtriser.

C'est pour ces raisons que nous avons choisi de modéliser un autre système, le cycle de l'azote où la nature qualitative de ce cycle nous permettrait de contrôler complètement les

dynamiques du système. De plus, nous avons développé trois scénarios avec les apparitions graduelles des composantes dans ce cycle pour étudier l'évolution possible d'un tel système.

Comparaison des scénarios du cycle de l'azote :

Le scénario de référence suppose que toutes les composantes du cycle de l'azote sont présentes. Activer ou pas le processus d'Anammox revient à modéliser deux systèmes différents, avec ou sans les bactéries d'Anammox, qui semblent d'apparaître à des périodes différentes dans l'histoire de vie. Notre modèle montre que dans un système sans les bactéries d'Anammox, le cycle de l'azote reste maintenu. Ainsi, cette caractéristique évolutionnaire fournit de nouvelles trajectoires entre des états qui sont déjà présents et permet donc de nouveaux chemins en cas de perturbations, par exemple en absence de certains gènes. De plus, ces bactéries semblent d'être étendue dans plusieurs systèmes marins et d'eau douce, et sa présence explique mieux les données expérimentales sur le cycle de l'azote (Jetten *et al*, 2009). Étudier ce processus présente aussi des intérêts écologiques dans le traitement des eaux usées pour un enlèvement plus efficace de l'ammoniac ou dans la microbiologie industrielle (Kuenen, 2008).

Le troisième scénario caractérisé par l'absence de l'oxygène montre son rôle essentiel dans ce cycle de l'azote. Les résultats, même relativement non significatifs, montre l'efficacité des réseau Petri qualitatifs pour modéliser les systèmes complexes et les appliquer plus tard pour des questions évolutionnaires plus compliquées. Ainsi, l'oxygène n'y est pas modélisé comme un réacteur chimique, nous avons supposé que l'oxygène soit assez abondant (comme réacteur). L'absence de l'oxygène y est prise en compte seulement à travers ses effets sur certains gènes inactifs en anaérobie. Ainsi, notre modèle montre que, en plus de sa contribution aux processus chimiques, les effets de l'oxygène comme un catalyseur de gènes sont essentiels pour le cycle de l'azote.

Avantages et limites du modèle basé sur le cycle de l'azote :

En revenant aux objectifs initiaux du stage, ce modèle a pu inclure les deux types de composantes : biotiques et abiotiques de l'écosystème. Les analyses statistiques et graphiques sont possibles pour interpréter les espaces d'états obtenus. De plus, il permet de comparer des sorties de différents états initiaux du même modèle, ce qui correspond aux différentes périodes dans l'histoire évolutionnaire, comme l'exemple du processus d'Anammox dans le cycle de l'azote. D'ailleurs, cela est aussi un moyen pertinent pour déterminer l'importance de chaque molécule ou gène dans ce cycle de l'azote comme le rôle crucial de l'oxygène que nous avons confirmé dans notre travail.

Cependant, ce modèle préliminaire présente encore certains points faibles à améliorer. Tout d'abord, ce cycle de l'azote n'imite pas encore un écosystème complet. Alors que certaines composantes font partie des vivants (gènes), le cycle ne peut pas exister sans les individus vivants autonomes. Or, ajouter des vivants, par exemple les microorganismes, peut impliquer un modèle plus complexe avec des interactions entre ces gènes et les autres composantes d'un même individu ou entre plusieurs individus ou groupes d'individus. De plus, tous les processus chimiques du cycle sont supposés possibles à 100% dans ce modèle, mais en réalité, certains gènes comme nosZ sont plus abondants que les autres et cette limite n'est pas encore franchissable avec notre outil informatique actuel.

Perspectives

Pour améliorer notre travail jusqu'à présent et répondre mieux aux objectifs posés, il est nécessaire de discuter les deux points principaux : l'utilisation des modèles discrets et qualitatifs ainsi que l'écosystème illustré par ces modèles.

D'une part, les modèles qualitatifs sont pertinents pour simplifier les écosystèmes et ses propriétés, mais certains points doivent être traités de façon qualitative : la règle de sélection devrait être variable au cours de la simulation selon les changements du système au lieu d'être prédéfinie. Des modèles semi-quantitatifs pourraient être donc une solution pertinente pour aborder et analyser non seulement la présence/l'absence des espèces mais aussi leur abondance ; pourtant, ces derniers doivent être utilisés avec précaution pour ne pas perdre tous les avantages de simplification des modèles qualitatifs et pour ne pas exploser le système à cause de sa complexité. Une de nos premières tentatives de modèle semi-quantitatif est d'utiliser le réseau Petri quantitatif tel qu'il y dans chaque composante plusieurs jetons représentant sa quantité relative par rapport aux autres.

D'autre part, en revenant à la pertinence des deux approches expérimentales réalisées au cours de ce travail (Table 2), nous remarquons que les communautés microbiennes (modèle 1) semblent d'être des écosystèmes contrôlables pour analyser et développer un point de vue plus complet de l'évolution à ce niveau, mais présente encre des difficultés pour la modélisation par manque d'information (due aux difficultés des manipulations). Le deuxième système basé sur le cycle de l'azote contient des composantes biotiques et abiotiques ainsi que leur rôle bien défini dans l'écosystème, ce qui est un avantage par rapport au premier modèle. Nous avons réussi à montrer l'importance du processus d'Anammox permettant la stabilité du système avec plus de trajectoires possibles entre les stabilités structurales ainsi que de l'oxygène dont l'apparition augmente la fitness de l'écosystème. Ainsi, cette approche reste intéressante à être développée par la suite pour mieux décrire et comprendre l'évolution à l'échelle écosystémique.

TABLE OF CONTENTS:

A- INTRODUCTION 1

I- Biological context 1

1. Different mechanisms of selection 1
2. Multi-level organization of an ecosystem 2
3. Trophic and non-trophic interactions in an ecosystem 3

II- Internship objectives and main questions to be studied 4

B- MATERIALS AND METHODS 5

I- Experiments 5

1. Artificial selection at the ecosystem level 5
2. Study of the nitrogen cycle: role of the Anammox process and oxygen 6

II- Using discrete model to describe and understand "ecosystem evolution" 7

1. Advantages of discrete and qualitative models 7
2. Suggested discrete qualitative model: Petri net 7
   a. Intuitive definition of the model by a graph 7
   b. Formal definition of a marked Petri net model 11
3. Methodology 15

C- RESULTS 16

I- Artificial selection at the ecosystem level – Model 1 16

1. Model building 16
2. Formalism 17
3. State spaces and interpretation 18

III- The nitrogen cycle: effects of the Anammox process and O_2 – Model 2 19

1. Model building 19
2. Formalism 20
3. State spaces and interpretation 20

D- DISCUSSIONS 23

I- Advantages and limits of the model based on CO_2 emissions – Model 1 23

II- Comparing the different scenarios of the N cycle model – Model 2 24

III- Advantages and limits of the N cycle model – Model 2 25

IV- Perspectives 25

Conclusion

Bibliography

Annexes: (1) Full model 1, (2) Full model 2, (3) Full state space of the second model, (4) Contents of stabilities found in the second model

A- INTRODUCTION

Biological evolution results from random variation in population genetic composition due to mutations or recombination of the genetic material and selective pressions from environmental factors that promote traits better adapting to it (Loreau, 2010). Only living components are supposed to evolve in this conceptual view. Furthermore, natural selection – the main engine of evolution, has been shown to apply at several hierarchical levels, from the molecular to the community one (Goodnight, 1990a). Considering that an ecosystem is composed by both living organisms in a given habitat and all physical components (Tansley, 1935), and often anthropic factors too, could we talk about "the evolution" of an ecosystem? How should the current definition of evolution be adapted to describe evolution at this higher level, if any?

I- Biological context

1. Different mechanisms of selection

The evolution theory of Darwin can be summed up into three main elements (Darwin, 1859) : selective pressures from environment, trait variations that involve fitness variations of organisms facing those pressures, and the transmission of these variations to offspring (Ellegren & Sheldon, 2008). The concept of natural selection is then defined as the mechanism allowing species evolution and influencing selected traits with a genetic basis (heritable traits).

While Darwin mentioned natural selection as the sole engine of evolution, the mechanism of genetic drift has also been shown to occur, with a relative importance which increases in case of small populations. It describes the change in gene frequencies owing to random differences in the survival and fecundity of individuals, as well as to binomial sampling of alleles during meiosis (Lowe *et al*, 2017).

Another view of evolution described by Lamarck concerns changes fulfilled during the individual's life and transmissible to their offspring too (Lamarck, 1809; Ricklefs & Miller, 2005). While this concept first appeared to be opposed to natural selection, it was refined by the introduction and the proof of heredity of acquired traits, i.e. transmission of phenotypical characters/traits acquired by individuals during their life to their offspring (Landman, 1991) Epigenetic transmission is a particular case, which describes changes during processes associated to gene expression (methylation and acetylation of DNA, modifications of histones...), without modifying the DNA sequence and transmissible in cell divisions. Such epigenetic modifications are reversible, and so might be lost after some generations (Danchin, 2013).

In addition of genetic and epigenetic observations, we also observe behaviour and symbolic inheritances (transmission through languages and with other forms of symbolic communication, e.g. in human societies) that complete the four dimensions of evolution (Jablonka *et al*, 2006). Studying the evolution at the ecosystem level requires thus to acknowledge this diversity of evolutionary mechanisms, which may not only show specific effects, but also significant emergent properties.

2. Multi-level organisation of an ecosystem

The concepts of natural selection and biological evolution have usually been applied to populations, but selection has been proved for having effects at several higher levels, for instance in groups of individuals, i.e. populations (Goodnight & Stevens, 1997), or in groups of populations, i.e. communities (Goodnight, 1990a). By definition, a selection level, is a level at which there exists a well-defined set of information, that is transferred during generations – i.e. a selected trait, carried by the avatars, i.e. materials that transfer this information (Gliddon & Gouyon, 1989). Such avatars should share or struggle for the same resources, and thus, the relative success of an avatar has effects on the others.

Selection at the molecular level concerns sequences in genomes and molecular processes allowing the increase of copies of a sequence in a genome. There are numerous, for instance, gene conversion, crossing-over…

Group selection concerns the evolutionary mechanism in which natural selection has effects at the group level, independently of selection at the individual level. Under group selection, an individual from a group could be promoted or not (compared to others), but it allows a higher fitness for the whole group. In some experiments on plants Goodnight & Stevens (1997) took into account contextual traits in addition to selected ones in order to study the group selection. These traits mean group-level phenotypes, includes both the group means of the individual traits and traits only expressed at the neighbourhood or group level. They showed that there was group selection when a component of the individual fitness is allocated to its context.

Selection at the community level, also observed in several studies (Goodnight, 1990a,b), concern differential proliferation and/or extinction of communities and can exhibit a response qualitatively different from that of lower selection levels (Goodnight, 1990b). It may concern the co-evolution of multi-species associations considered as a selection unit (e.g. lichen, which is a symbiosis association of fungi and algae) or a meta-community – i.e. a set of communities linked by migration, extinction and recolonization with divergent selection due to random differences between communities in terms of species composition (Goodnight, 2011).

3. Trophic and non-trophic interactions in an ecosystem

In an ecosystem, we may observe trophic relationships directly like predation, or indirectly like competition, mutualism, amensalism, commensalism. Furthermore, there are also some non-trophic species interactions, for instance between engineer organisms and the others in the same ecosystem, i.e. organisms that impact directly or indirectly resource availabilities for other species, by physically modifying biotic and abiotic materials (Jones *et al*, 1994). Even, higher-order interactions exist, i.e. interactions between two species that can be modulated by others (Sander *et al*, 2015; Bairey *et al*, 2016). Besides, structural properties of these different interaction networks are not the same: while the stability of a trophic network is promoted by compartmented structures, strongly connected and nested architectures enhance community stability in mutualistic networks (Thebault & Fontaine, 2010). Hence, diversity of interactions and their various structures need to be taken into account in any relevant ecosystem model.

Yet, most of current studies on species interactions focus on food webs, and other natures of species interactions are less discussed (Ings *et al*, 2009). Furthermore, links between different interaction natures are confirmed, for instance the modulation of trophic webs by chemical communication (DeAngelis, 2016), but only a few models are integrating interactions of several types within the same network (Melián *et al*, 2009; Mougi & Kondoh, 2012). Separating these interactions within an ecosystem assumes the independence of their networks, while the same species might be involved into different types of interactions simultaneously, or at different life stages (Fontaine *et al*, 2011). Some studies have modelled ecosystems by sign-digraph including both trophic and non-trophic relationships (Dambacher *et al*, 2007; Reum *et al*, 2015), but ecosystem components described in these models are species (or group of species) most of the time, while abiotic factors have an indisputable role in ecosystem structures and dynamics. Even, anthropic activities need to be taken into account due to its crucial effects, usually negative on natural ecosystems, for instance pollution (Henry *et al*, 2004), introduction of new species (Gollasch, 2002), etc. Such variables are crucial to understand interactions related to habitat changes, competition for resources, etc. (Tansley, 1935). When they are included in the model, as in the two above examples (Dambacher *et al*, 2007; Reum *et al*, 2015), they are usually associated with external perturbations, considered as independent (external) and thus modelled as pre-defined assumptions. These assumptions are various, such as important component removals, random additions (Dunne *et al*, 2002). However, when the ecosystem components develop and interact between each other, some might disappear and reappear, which consequently can drastically change the ecosystem state. In this case, ecosystems should be considered as "dynamical systems with a dynamical structure". Such systems have been

identified with variables, (sometimes strongly) modified in time, with the set of these variables and their interactions also changing over time (Giavitto & Michel, 2003). Such dynamical structures can be modelled as ecological "successions" in which pioneer components are progressively replaced by species typical from the climax (Clements, 1936), and modelled by rewriting systems (Lane & Prusinkiewicz, 2002). Systems in these models are defined by an alphabet for the system components, an axiom for the system initial state and a list of production rules for the processes taking place in this system (Dershowitz & Jouannaud, 1990; Giavitto *et al*, 2002). This formalism has been used in biology to describe phenomena such as plant growth (Lindenmayer, 1968; Balduzzi *et al*, 2017) or for the dynamics of agricultural landscapes (Gaucherel *et al*, 2012).

Other models of this category of discrete models, such as Boolean networks and Petri nets might be relevant for this endeavour. There are already some works using these model to describe ecosystem, such as the model of ecosystem development according to its regime shifts using Boolean networks (Gaucherel *et al*, 2017) or the Petri net model to explore trajectories of a termite ecosystem (Gaucherel & Pommereau, submitted in 2017).

Hence, studying ecosystem dynamics and its possible "evolution" needs a model that can capture its complexity (the diversity of system components, the multi-level organisation and the dynamics of system component interactions and structures), while discussing possible evolutions of the whole system. We hypothesize that using discrete qualitative models such as the previously cited ones is an appealing option to simplify the system complexity and dynamics without losing its properties.

II- Internship objectives and main questions to be studied

We aim at applying the Petri net approach (already developed, Pommereau, 2009) to describe and understand ecosystem dynamics. We focused on a microbial ecosystem and its possible evolution, and therefore choose two specific case studies: microbial communities with several artificial selection events at the ecosystem level, and the nitrogen cycle in soil microbial communities.

The main objective of this work is to choose an experimental and modelling approach to describe and prove (or contribute to prove) that an ecosystem "evolves" and to how it is "evolving". The two models that we suggest are based on the two kinds of selections: the natural selection, that is occurring in natural ecosystem, and the artificial selection, issued from human activities in favour of an expected trait (Ricklefs & Miller, 2005). While natural selection is characterized by randomness, the artificial selection is a controllable tool and, as a major

argument for the theory of Darwin, has been proved to be efficient at the community level (Swenson *et al*, 2000; Blouin *et al*, 2015). The first model addresses the central question: "Does evolution by artificial selection at the ecosystem level results only from interactions between genetic units at the community level (there is no variation at the individual level)?". The second model deals with the central question: "Could natural selection at the ecosystem level promote more stable ecosystems?" The first model is based on artificial selection so its effects are controllable while mimicking the natural selection and the second model describes a nowadays ecosystem resulting from several events of natural selection to confirm the experimental data.

B- MATERIALS AND METHODS

I- Experiments

1. Artificial selection at the ecosystem level

This experiment consists to study effects of artificial selection in a microbial ecosystem coming from a water treatment plant in France, while considering the CO_2 emissions as the selected trait. Cultivated in a sterile liquid medium, they are separated into two group corresponding to two different selection methods: control and selection. Each group contains six independent lines of thirty microbial communities. The experimental process is composed by several steps and is repeated twenty times, corresponding to twenty selection events (Fig. 1): (1) 24 hours of incubation, (2) measure of the selected trait, (3) selection of three ecosystems among the 20, (4) reproduction by pooling the three selected ecosystems and (5) inoculation of the offspring generation of 20 ecosystems from the three parental ones. Only the selection step is different in the two treatment groups: three communities are selected (i) randomly in the control group or (ii) for their low CO2 emission in the selection group. Once selected, these three communities are then pooled to produce the offspring. For the last generation, community composition is determined by the T-RFLP analysis providing genetic units profile of the generation in question (Blackwood *et al*, 2007). The correlation coefficients are computed from the abundance of the different genetic units and integrated in the network if significant (Barberán *et al*, 2012). Besides, co-occurrence matrices are built to show and analyse the structure of ecological interactions, by defining correlations between genetic units (Faust & Raes, 2012), and used to build co-occurrence networks describing direct and indirect interactions between genetic units.

Therefore, this experimental evolution experiment relies on ecosystems with biotic components, and the interactions between them are introduced by the correlation between

genetic units. Furthermore, selection is carried out at the ecosystem level, so a relevant experimental study to understand the "evolution" of an ecosystem.

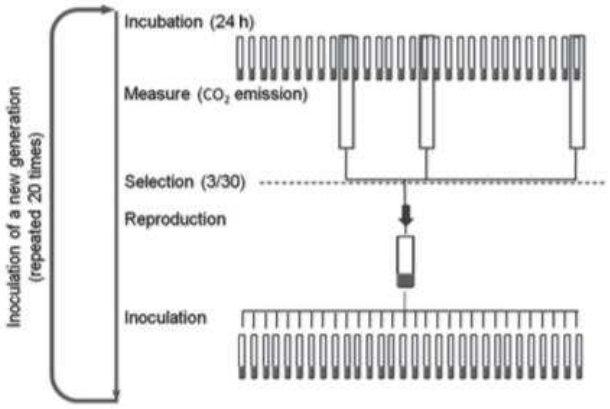


Figure 1: Experimental process. 5 steps are done respectively and repeatedly twenty times: (1) incubation, (2) measure of CO2 emissions, (3) selection, (4) reproduction and (5) inoculation (Blouin *et al*, 2015)

2. Study of the nitrogen cycle: role of the Anammox process and O_2

Our second model is based on the nitrogen cycle (Galloway *et al*, 2004; Carter *et al*, 2012), where nitrogen exists in different chemical forms and the conversion from a molecule to others is carried out with presence of a specific gene, for instance nifH for the fixation of the atmospheric nitrogen (Fig.2). Among these biological processes (fixation, assimilation, ammonification, nitrification, denitrification, …), Anammox (anaerobic ammonium oxidation) process represents an important role in the production of the N_2 gas (Reimann *et al*, 2015). It describes the conversion of NH_4 (ammonium) and NO_4 (nitrite) into dinitrogen (and water, not represented in our graph). This process is discovered lately comparing to the other ones, but is responsible for a significant release of N_2, between 30-50% of its total production (Niftrik *et al*, 2004). Studying the effects of this process is interesting in terms of evolution, since the gene responsible for it only exists in some bacteria.

Besides, oxygen is not shown in this cycle, but still have an essential role. Even by assuming that oxygen, as a substrate for some chemical process, is always available, there is also another role of oxygen as an electron-donor for some processes (mineralisation, nitrification) that needs to be taken into account.

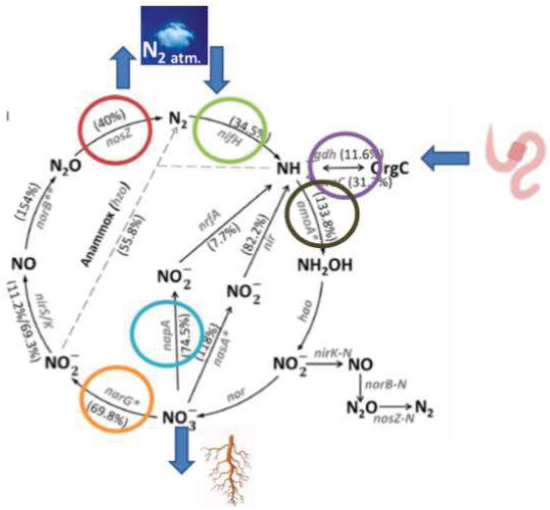


Figure 2: Nitrogen cycle (modified from Carter et al.) of a microbial communitites with nitrogen molecules and genes involving in it, indicated at each arrow, with the probability of each process.

II- Using discrete model to describe and understand "ecosystem evolution"

1. Advantages of discrete and qualitative models:

A model likely to describe dynamics need to represent the complexity of both biotic and abiotic components and their interactions and also its multi-level organisation. Furthermore, evolution concept has to be included in this ecosystem model. Thus, these objectives imply some difficulties to deal with the evolution of an ecosystem. It is possible to apply numeric models based on differential equations (Neumann & Morgenstern, 1944; Gaucherel & Jensen, 2012), while adding the interaction between living and non-living components and the hierarchical relationships between different levels of organization. However, it seems to result a very complex model that is difficult for simulations. Furthermore, these models need exact parameters, and the incertitude of parameter values is responsible for their powerlessness. Using a discrete and qualitative model is then a relevant solution to simplify this complexity of the system. Besides, this kind of model makes it possible to study ecosystem dynamics and all of its possible trajectories dues to ecological processes/interactions. Besides, it allows to identify some particular ecosystem dynamics (appearance/disappearance of some species, collapses, basins or other kinds of structural stabilities). This choice of a qualitative model is particularly relevant when considering present changes in biodiversity: the relevant question is no more "what are the consequences of variation in the size of a given population?" but more "what are the consequences of the disappearance of a given population?".

2. Suggested discrete qualitative model – Petri net

a. Intuitive definition of the model by a graph

- Component, component state and system state

A system can be modelled as a graph containing components (nodes) and links (edges) between these components. As for an ecosystem, no matter its complexity, we can use a multi-

digraph, i.e. a directed graph with parallel edges between the same pair of nodes. Material components of the ecosystem, biotic, abiotic and anthropogenic (e.g. individual, group of individuals, species, environmental factors) are represented by nodes, connected by edges. Each node has two Boolean states: "On" (the component is present in the system, denoted "+") and "Off" (the component is absent from the system, denoted "-"). A state of the whole (eco-)system is then defined by a combination of present and absent nodes. Consequently, the number of possible system states can reach to $2^{\#nodes}$, and so grows exponentially with the number of nodes.

For instance, a simplistic prey-predator system, with two species (with two nodes only) representing predator and prey populations has $2^2 = 4$ possible states (Fig. 3).

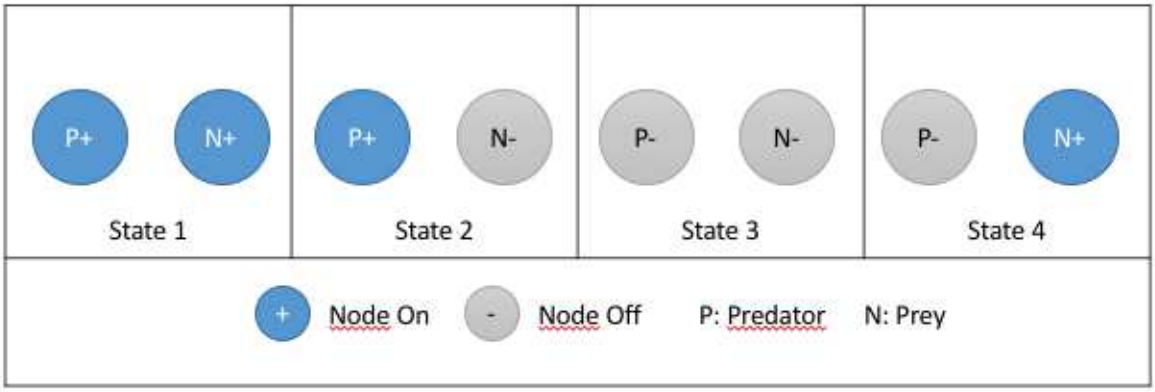


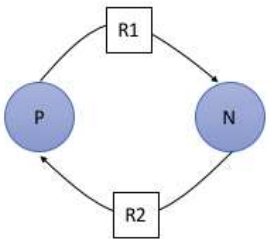
Figure 3: Example of the qualitative model for a simple prey-predator system showing four possible states.

- Processes – Rules

The edges between pair of nodes define their changes. An edge between two nodes exists when at least one explicit rule is relating them. These rules can be bio-ecological, physicochemical and/or socio-economic (sub-)processes, and thus represent the interactions between components of the studied ecosystem. A rule is made up of two parts: a condition and a realization. It is applied when the system state satisfies its condition part – the rule is then "enabled". If enabled, this application will then modify the state of the nodes according to its realization part – the rule is then "fired". By convention, each rule is written as, "name: condition >> realization".

In the example of the prey-predator system, two rules can be defined: "the predator eats the prey" (R1) and "the predator dies when the prey is absent" (R2) (Fig. 4). In case of the first rule, predator and prey must both be present (so is the condition part of R1) and it then leads to the disappearance of the prey from the system (so is the realization part of R1). Similarly, the

absence of the prey is a condition of the second rule, and the disappearance of the predator its realization.



Rule	Condition	Realization
R1: P+, N+ >> N-	On: {P, N}, Off: {}	On: {P}, Off: {N}
R2: N-, P+ >> P-	On: {P}, Off: {N}	On: {}, Off: {N,P}

Figure 4: Multidigraph of the prey-predator system and the table of conditions and realizations of its two rules.

- State space

When a rule is fired, the states of ecosystem component are modified by following its realization, and so is the whole system state. Hence, the system will switch from one state to another one after each application of the rules. The state space is defined as the set of accessible system states by all defined rules and from one specific initial system state. Usually, the size of this state space is smaller than the number of possible system states ($2^{\#nodes}$), because rules have specific application conditions that make some combination of present and absent nodes impossible (i.e. rules reduce the potential state space).

Going back to the prey-predator system, if the initial state is composed by the presence of both predator and prey components (state 1), R1 can be fired and make the system shifting to a new state in which only predator remains present (state 2). The condition of R2 is then satisfied and when R2 is fired, the system reaches a third state in which both predator and prey are absent (state 3). Here, neither of the two rules can be enabled anymore, and so the system cannot change anymore. The state 4 mentioned in Fig.3 is thus never reached with this set of rules and initial state (Fig. 5). The corresponding state space of this simple model is summarised in the figure 6.

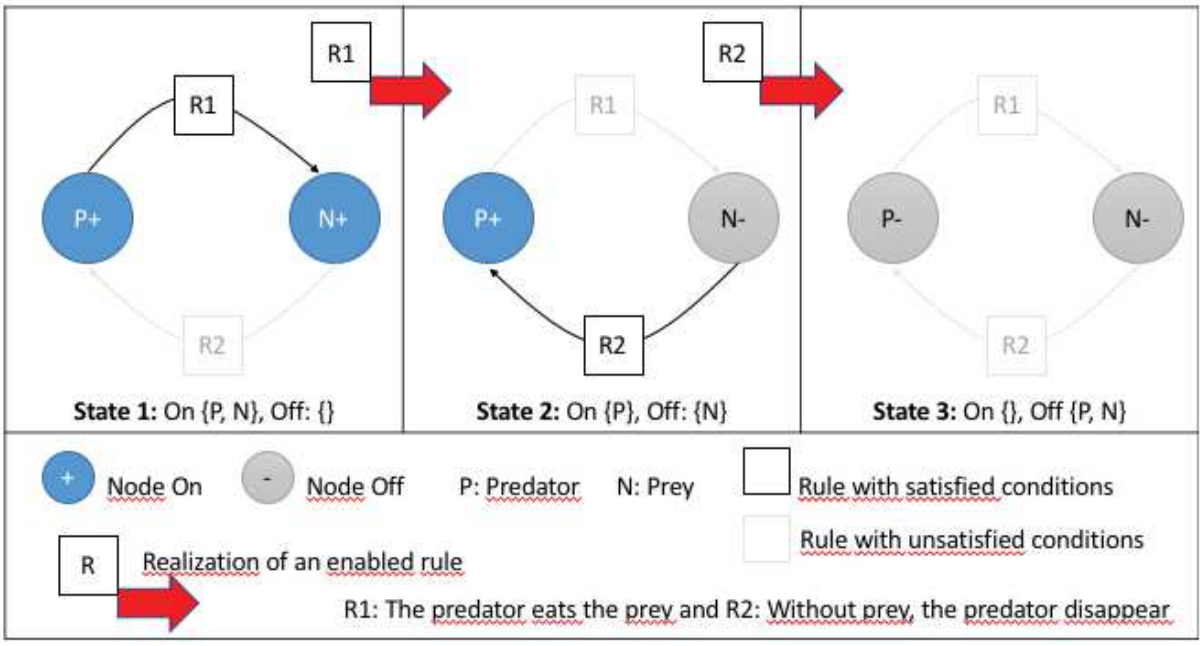


Figure 5: Successive states of the prey-predator model example.



Figure 6: State space of the prey-predator model

- Formal definition of this qualitative model

Based on the above explanations, the ecosystem can be defined as a triplet (E, s_0, R) such that:

- E is the set of nodes composing the ecosystem;
- $s_0 \subseteq$ E is the initial state (i.e. the set of all the nodes supposed to be initially "On");
- R is the set of rules;

One state s of the system is defined as a subset of E that is a set of all the "On" nodes at this state.

A rule r is defined as:

$$r \stackrel{\text{def}}{=} (\alpha^+, \alpha^-, \omega^+, \omega^-) \subseteq E^4,$$

such that $\alpha^+ \cap \alpha^- = \omega^+ \cap \omega^- = \emptyset$ and

- α^+ is the set of "On" nodes in the condition part of the rule,
- ω^+ is the set of "On" nodes in the realization part of the rule,

- α^- is the set of "Off" nodes in the condition part of the rule,
- ω^- is the set of "Off" nodes in the realization part of the rule.

The rule r is enabled at a state s $\subseteq$ E iff $(\alpha^+ \subseteq s) \wedge (\alpha^- \cap s = \emptyset)$, i.e. if and only if all the "On" nodes in the condition part of r are present in s and all the "Off" nodes of r are absent in s. If it is, r will be fired and the system will reach a new state $s' \stackrel{\text{def}}{=} (s \setminus \omega^-) \cup \omega^+$, i.e. all the "Off" nodes of the realization part will be removed from the previous state and besides, the "On" nodes of the realization part that were not in the previous state will be added in the new one.

The state space is then the smallest graph (V, G) made of vertices (V) and edges (G) such that:

- The initial state is in V
- For each s $\in$ V and a rule r such as s → s', s' $\in$ V and there is an edge (s,r,s') $\in$ G.

Furthermore, the rule-topology of a node e in the graph can be defined as a tuple T that contains its incoming and outcoming rules such as $T_e = (In_e^+, In_e^-, Out_e^+, Out_e^-)$ where:

$$In_e^+ = \{(\alpha^+, \alpha^-, \omega^+, \omega^-) \in R | e \in \omega^+\}, In_e^- = \{(\alpha^+, \alpha^-, \omega^+, \omega^-) \in R | e \in \omega^-\},$$

$$Out_e^+ = \{(\alpha^+, \alpha^-, \omega^+, \omega^-) \in R | e \in \alpha^+\}, Out_e^- = \{(\alpha^+, \alpha^-, \omega^+, \omega^-) \in R | e \in \alpha^-\},$$

i.e. In_e^+ is the set of rules that active the node e, In_e^- the set of rules that inactive e, Out_e^+ the set of rules where "e is On" is one of theirs conditions, Out_e^- the set of rules where "e is Off" is one of theirs conditions.

Therefore, in order to apply this graph and analyse its results, we use a marked Petri net as an informatic tool (Pommereau, 2009; Reisig, 2013).

b. Formal definition of a marked Petri net model

A marked Petri net is a tuple $N \stackrel{\text{def}}{=} (S, T, W, M)$ such that:

- S={s_1, s_2, …, s_n} is a finite set of places;
- T={t_1, t_2, …, t_n}, disjoint from S, is the finite set of transitions;
- W: (S×T)∪(T×S) → N is the weight function that defines arcs;
- M $\in$ S* is the marking, that is, a multiset of places representing the state of the Petri net.

The triplet (E, s_0, R) can be then converted into a Petri net by considering that:

- Each node of E is represented by two places in the Petri net (for the "on" and "off" states);
- Each rule of R is translated into one (or several) transition(s);

- The state s of the system is defined by the Petri net marking (i.e. the token carried by each place).

Using the simple prey-predator example, its multidigraph can be converted into a marked Petri net (Fig. 7).

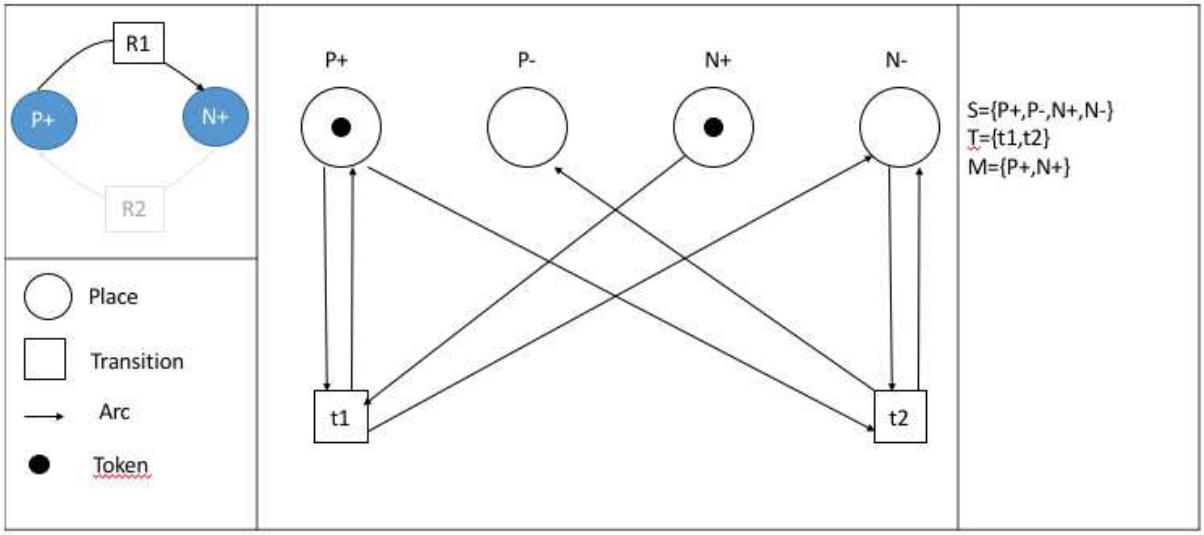


Figure 7: A marked Petri net featuring the example of a simple prey-predator system.

- Place and net marking

For each node e ∈ E, two places are created, corresponding to two states of e, e^+ for the "On" state and e^- for the "Off" state. Tokens are then distributed between these different places, in order to define the initial node state. If the node e is in the initial state s_0, the place e^+ will hold a token (i.e. be marked), otherwise e^- will not and may later have a token. This token distribution in various places describes the net marking. Transitions will then allow tokens to circulate between places, and to modify the graph marking, thus the whole system state.

- Rule normalization

Rules need to be explicit and unambiguous before being converted into transitions. For instance, users write a simple rule as A+ >> B- meaning that:

- The condition part does not depend on the state of B,
- The state of A will not be modified by its realization.

But for the computation machine, it should be re-written to become as exhaustive and rigorous as possible. Therefore, we need to write two rules instead of one: A+, B+ >> A+, B- and A+, B->> A+, B-.

This normalization procedure is generalized to any rule $r \stackrel{\text{def}}{=} (\alpha^+, \alpha^-, \omega^+, \omega^-)$ by two steps:

- Re-writing the condition part as $C \stackrel{def}{=} \{(\alpha^+ \cup x, \alpha^- \cup (\chi \backslash x), \omega^+, \omega^-) | x \in 2^x\}$ where $\chi \stackrel{def}{=} \omega \backslash \alpha$ with $\alpha \stackrel{def}{=} \alpha^+ \cup \alpha^-, \omega \stackrel{def}{=} \omega^+ \cup \omega^-$, i.e. adding the states of nodes affected by the realization of this rule, so for the previous example C = {A+, B+ >> B-; A+, B- >>B-}
- Re-writing the realization part as $Z \stackrel{def}{=} \{(\alpha^+, \alpha^-, \omega^+ \cup (\alpha^+ \backslash \omega), \omega^- \cup (\alpha^- \backslash \omega) | (\alpha^+, \alpha^-, \omega^+, \omega^-) \in C\}$, i.e. adding the states of nodes mentioned in the condition part but not modified by the realization part of this rule, so for the previous example Z={A+, B+ >> A+, B-; A+, B- >> A+, B-}.

- From rules to transitions

Once normalized, rules can be translated into Petri net transitions.

Each transition t ∈ T is defined by its pre-condition $\overleftarrow{t}$ and its post-condition $\vec{t}$ such as:

$\overleftarrow{t} \stackrel{def}{=} \sum_{s \in S} W(s,t) \times \{s\} \in S^*$ and $\vec{t} \stackrel{def}{=} \sum_{s \in S} W(t,s) \times \{s\} \in S^*$ where S* is the set of all the multi set (i.e. system state).

These definitions correspond to the condition and the realization of normalized rules, respectively. Therefore, the transition t is enabled at a marking M if $\overleftarrow{t} \leq$ M. If so, t will be fired and lead to a new marking M' defined as:

$$M' \stackrel{def}{=} M - \overleftarrow{t} + \vec{t} \text{ and denoted as M[t⟩M'.}$$

Going back to the prey-predator model, the corresponding Petri net transitions are rigorously defined (Table 1).

Multidigraph			Petri net		
Name	Condition	Realization	Name	Pre-condition	Post-condition
R1	α^+: {P, N}, α^-: {}	ω^+: {P}, ω^-: {N}	t_1	$\overleftarrow{t_1} = \{P^+, N^+\}$	$\overrightarrow{t_1} = \{P^+, N^-\}$
R2	α^+: {P}, α^-: {N}	ω^+: {}, ω^-: {P, N}	t_2	$\overleftarrow{t_2} = \{P^+, N^-\}$	$\overrightarrow{t_2} = \{P^-, N^-\}$

Table 1: Rules and corresponding Petri net transitions of the simple prey-predator system.

Based on these definitions, a transition t_r, is added to the Petri net for each normalised rule $r \stackrel{def}{=} (\alpha^+, \alpha^-, \omega^+, \omega^-)$ such that:

- $W(e^+, t_r) \stackrel{def}{=} 1$ for all $e \in \alpha^+$
- $W(e^-, t_r) \stackrel{def}{=} 1$ for all $e \in \alpha^-$
- $W(t_r, e^+) \stackrel{def}{=} 1$ for all $e \in \omega^+$
- $W(t_r, e^-) \stackrel{def}{=} 1$ for all $e \in \omega^-$
- $W(t_r, p) \stackrel{def}{=} 0$ for any other place p

- State space and marking graph

Since the state of the system corresponds to the Petri net marking, the state space is represented by using the marking graph of this net. In this graph, vertices (V) are states of the system and edges (G) represent the transitions allowing the switch from one state to another (Fig. 8).

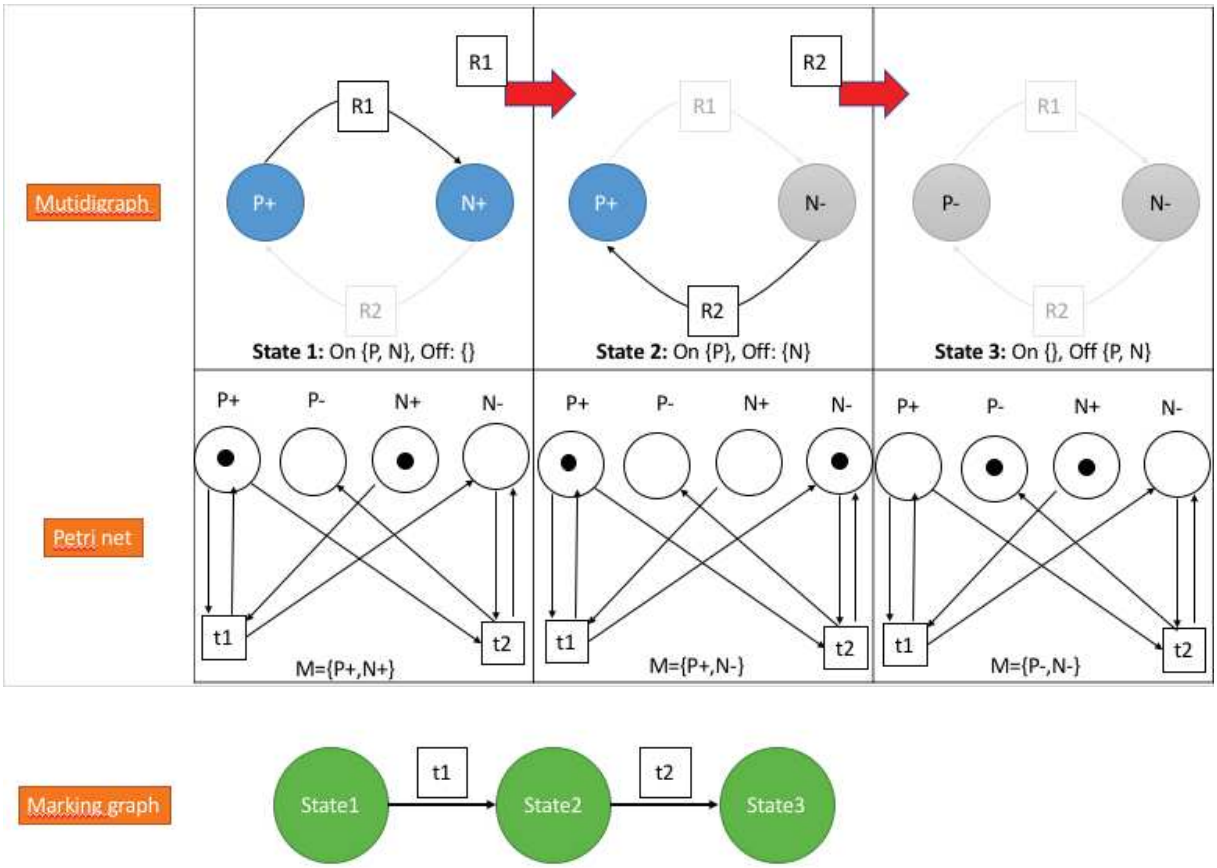


Figure 8: System states as multidigraph and the corresponding marked Petri net, with the corresponding state space as the marking of the net.

Formally, the marking graph of N is defined as the smallest graph $N[t\rangle \stackrel{def}{=} (V, G)$ such that $M \in V$ and, for all $M' \in V$ such that $M'[t\rangle M''$ for a transition $t \in T$, we also have $M'' \in V$ and $(M', t, M'') \in G$.

- Model realism – Constraint definition

Rules firing can lead to as many paths as rules enabled, allowing this model to explore all possible states from an initial system. However, firing a rule independently of some others may lead the system to reach unrealistic states (e.g. say, with species without any habitat). The notion of constraint is thus introduced in order to stop the model from modelling such states and paths. Similar to a rule, a constraint also has a condition and realization parts, and prevents the model to show non-realistic states where two or more components cannot coexist, or one cannot exist

without others. But these instable states still be possible by applying some rules that concern only some components but not the others not mentioned in it. Going back to the previous example, the state 2 is in fact impossible in reality, predators cannot exist without presence of prey. R2: “the predator dies when the prey is absent” must be then a constraint C1. Therefore, the state 2 still exist in the state space, but become a transitive state, while the two others are stable states.

- Study of a state space

To study the state space, some specific states are then identified and defined:

- The initial state is a distinguished state I in S. By definition of a state space, every other state is reachable from I
- Deadlocks D include state that has no successor (d) in the state space and states that every path starting from it always arrived at d.
- A structural stability is a maximal subset of the state space such that there is at least one path between every pair of nodes in this stability.
- A basin is a maximal set of states B such that all the states in B allow to reach exactly the same deadlock or structural stability.

With these specific components, the state space can be represented in several forms:

- Full state space with all the possible states,
- Compact state space where transitive states (due to constraints) are removed,
- Merged graph: full graph where states belonging to the same stability or deadlock or basin are merged into a single component,
- Compact merged graph: compact graph where states are merged into a single state space component

Furthermore, for exploring the state space, other statistical analysis tools are possible, such as AFC, ACP, … on the abundance of each ecosystem node in each stability, depending on the model in order to understand each component of the merged state graph, or different trajectories of the ecosystem changes according to initial state, ….

3. Methodology

To model the two study cases previously mentioned, we apply the Petri net by defining for each of these two nodes and rules allowing interactions between ecosystem components.

The first model consists to describe a microbial ecosystem with 3 levels of living organization and interactions between them, while taking into account abiotic components as nutrients or excretions.

The second model describes the nitrogen cycling in biofilm communities. We test three different scenarios corresponding to 3 initial states. The first one represents a situation where all genes and molecules are initially present (reference scenario, supposedly corresponding to the present-day situation), the second one describes the nitrogen cycle without Annamox bacteria and the last one concerns for the cycle without oxygen, in order to show the effects of these two elements in the nitrogen cycle (Kuenen, 2008; Zerkle *et al*, 2017).

C- RESULTS

I- Artificial selection at the ecosystem level – Model 1

1. Model building

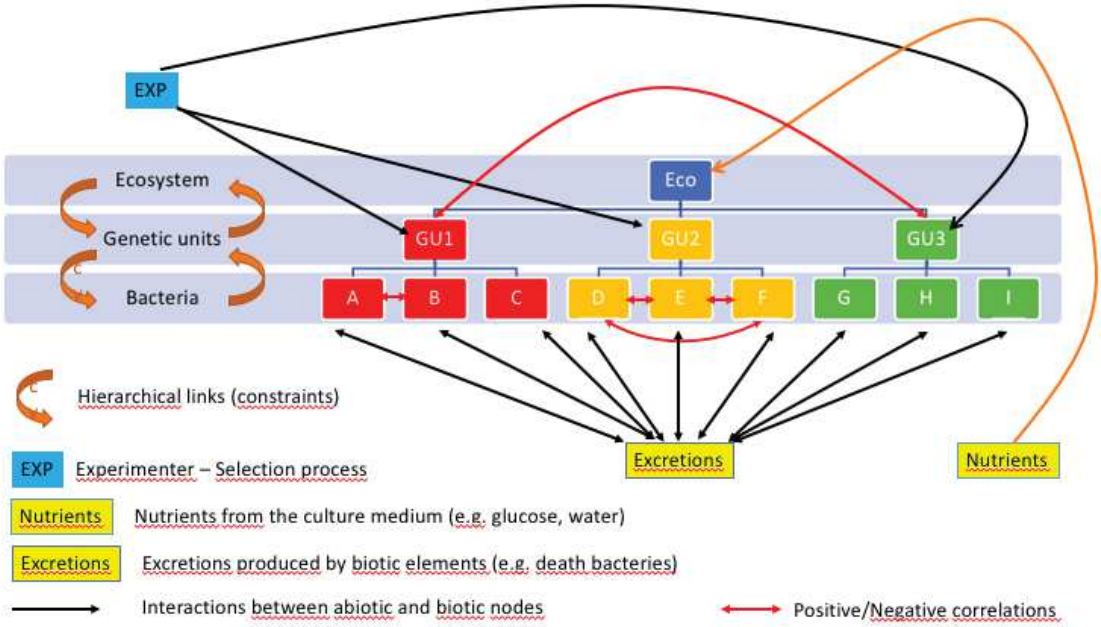


Figure 9: Ecosystem graph for the microbial community model. Nodes are represented in rectangular and processes/rules in arc (orange for constraints, black for interactions between biotic and abiotic factors and red for correlation between livings). Nodes in yellow represent abiotic components. For the other, nodes for bacteria belonging to the same genetic unit have the same colour.

a. *Choice of nodes*

In order to model the selection at the ecosystem level and compare its possible effects to those at lower levels (individual and *genetic units* level), we chose to represent at least three levels as components (nodes) in our model (Fig. 9). In this first model, we chose to represent three bacteria only into each genetic unit, and three genetic units in the ecosystem. As we are interested in both biotic and abiotic components of the ecosystem, non-living ecosystem components are also modelled. Here, nutrients represent both the culture medium (e.g. glucose and water) and oxygen, both of them are essential for the survival of bacteria. Besides, living components produce excretions (e.g. bacteria deaths) which then become nutrient resource for

others. A last important component of the modelled system is the experimenter, here used for applying the artificial selection at the genetic unit level.

b. Choice of rules and constraints

Rules and constraints describe the processes taking place in this ecosystem and are represented as oriented edges in the fig. 9. The release of excretions when a bacteria death occurs is modelled (Fig. 9, black arrows), and it is then associated to the bacteria reappearance. We model artificial selection by the experimenter node that can remove one of the present genetic units according to some criteria (i.e. the selected trait). In particular, rules play the role to explicit the correlation between bacteria at the same organization level: for instance, if bacteria A and B are present together, then remove B at the next simulation step since A and B cannot co-exist (e.g. illustration of the competitive exclusion between A and B, Blouin et al., 2015). It has been shown that such correlations are the results of the above artificial selection experiment on bacterial community (cf. Materials and Methods).

We also include constraints in this model, understand some rules that are compulsory and applied first (at the beginning of each simulation step). The hierarchy between different levels of this system need to be a constraint justifying the instantaneous death of lower levels when higher levels are dying. For instance, bacteria A, B and C will be killed (turned off) when GU1 is killed by artificial selection (Fig. 9). The presence of nutrients is also a constraint for the survival of the whole ecosystem.

The initial state assumes that all nodes are present (set to "On" or +). Predefined correlations, positive and negative, are added (as rules) between bacteria and between genetic units. For the artificial selection, since the selected trait in the experiment (Blouin et al, 2015) is a quantitative trait (CO_2 emissions), we have to pre-define a qualitative selection rule, for instance the selection of GU2 and GU3 with the removal of GU1.

2. Formalism

We rewrite then the system according to the formalism of Petri net, for example:

- Places: S = {Eco, GU1, A, Nut, exc, …}
- Constraints:
    - Essential resources: Nut- >> Eco –
    - Imbrication/Hierarchy:

      Eco- >> GU1-, GU2-, GU3-

      GU1-, GU2-, GU3- >> Eco-

      GU1- >> A-, B-, C-

      A-, B-, C- >> GU1-

…

- Rules (processes/relationships):
    - Negative (positive) correlations: A+ >>B-, exc+, GU1+ >> GU3-, exc+
    - Use of excretions: exc+, A- >> exc-, A+
    - Selection: Exp+, GU1+, GU2+, GU3+, Nut+ >> GU1-, exc+

(cf Annex 1 for the full model)

3. State spaces and interpretation

As a result, we obtain a full state space with 145 states and 405 Petri net transitions (Fig. 10). When states belonging to the same structural stability or basin are merged into one, we obtain the merged state space with an initial stability, two basins and two additional stabilities (Fig. 11).

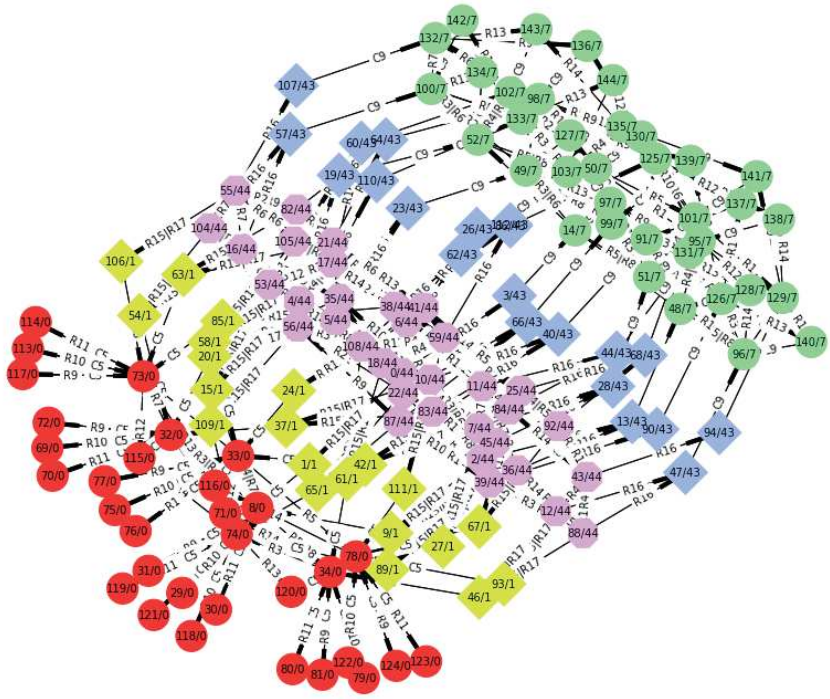


Figure 10: Full state space of the genetic unit model, with different colours and forms representing different components: basin (diamond), initial stability (hexagon) and other structural stabilities (round).

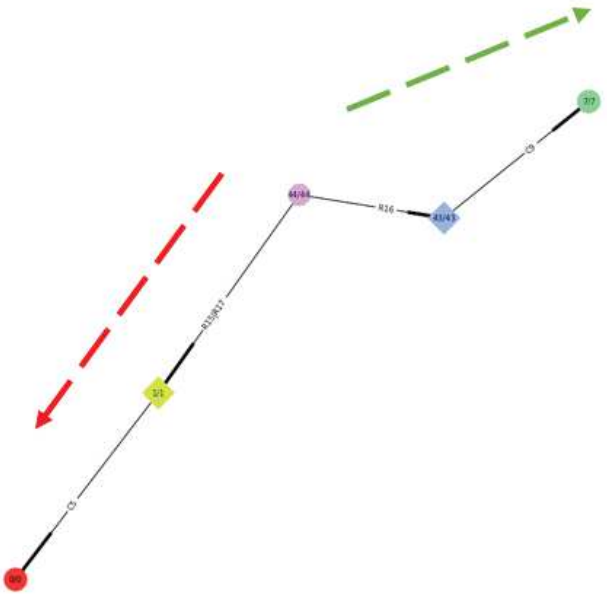


Figure 11: Merged graph of the genetic unit model, diamond component representing basin, hexagon for initial stability and round for other stabilities. The two dashing edges show the two possible fates of the ecosystem evolution.

Inside the two structural stabilities (without the initial states), some nodes that are always Off (absent), in all the included states. The red stability has GU1 and its bacteria (A, B, C) absent due to the effect of artificial selection. The green stability has GU3 and its bacteria (G, H, I) absent and removed by negative correlation with the genetic unit one, since these two are both initially present. Hence, we observe two possible fates for the ecosystem (Fig. 11, dashed arrows with the corresponding colours), depending on the genetic unit killed.

II- The nitrogen cycle: effects of Anammox process and O_2 – Model 2

1. Model building

a. Choice of nodes

As in the previous model, nodes of this second model represent all the material (physical) components involved into the nitrogen cycle, concerning both abiotic (nitrogen molecules and oxygen) and biotic (genes) entities.

b. Choice of rules

We define each process involved in this nitrogen cycling as a rule. For instance, the following rule model the fixation of atmospheric nitrogen: N2+, nifH+ >> NH4+, N2-. In other words, atmospheric nitrogen is fixed by microorganisms and creates ion NH4 when the gene nifH is present. All the signs used for rules and initial states stand for the presence (+) or the absence (-) of molecules or genes, not for the sign of the mentioned ions. In this preliminary

version of the model, we not yet defined any constraint, and each process is considered as possible (all the processes are assumed to be possible with the same probability at 100%).

As a reminder, three scenarios corresponding to three different initial states will be tested. The first simulation includes the presence of all genes and molecules (reference scenario), the second one describes the nitrogen cycle without Annamox bacteria and the last one is characterized by the absence of oxygen as a catalyser for processes of mineralization (R3) and nitrification (R4, R5, R6, R7).

2. Formalism

We formalize the nitrogen cycle model according to the formalism of Petri net:

- Places: S = {N2, NH4, nifH, gdh, O2, …}
- Rules (processes/relationships):
  - Fixation: N2+, nifH+ >> NH4+, N2-
  - Assimilation: NH4+, gdh+ >> Norg+, NH4-

(cf Annex 2 for the full model)

3. State spaces and interpretation

Three simulations corresponding to the three different initial states (scenarios) previously defined are modelled to analyse this microbial ecosystem.

a. Reference scenario of the N cycle model

We obtain, for this scenario, 255 states in the full state space, and 1984 Petri net transitions (Annex 3). When states belonging to the same stability are merged into one component, we obtain the merged state space with seven stabilities, one of them including the initial state (Fig. 12). The list of always present and always absent nodes in each stability is detailed in Annex 4.

When computing the abundance of each molecule in a stability along to the merged state space, we observe the same evolution for all of them: their abundance gradually declines from the first stability (initial state) to the last one (n° 0). Besides, the rule n° 16 (Anammox process) acts as a short-circuit allowing the system to bypass some states. For instance, the system in the reference scenario switches from the stability n° 6 to the n° 5 before reaching n° 4, but the rule n° 16 allows the direct path from n° 6 to n° 4.

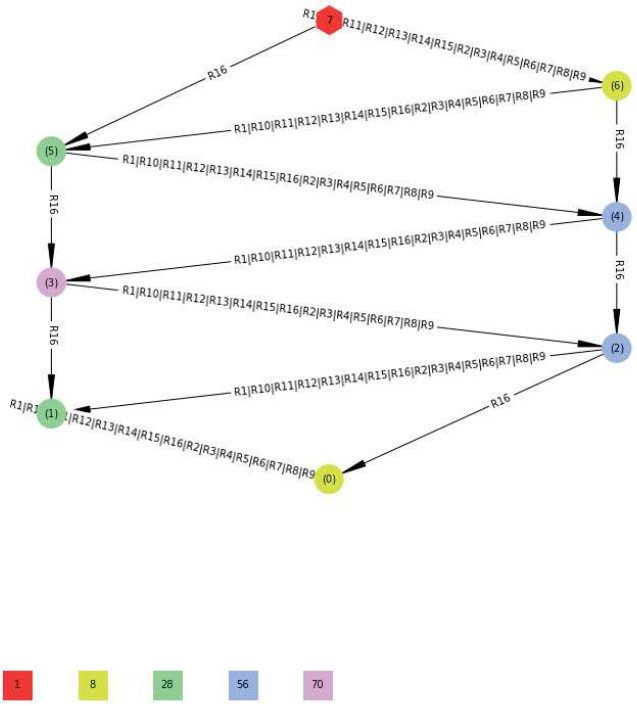


Figure 12: Merged graph for the nitrogen cycling model in the reference scenario. The hexagon (on top) represents the stability including the initial state, the disks represent different stabilities, plotted downward according to causality. Oriented arrows represent the rule(s) allowing switching from a stability to the next one. The colour scale corresponds to the size of each stability (i.e. the number of states it includes)

b. N cycle without anammox process

If we remove the Anammox process by turning off the ecosystem component (node) standing for the gene *hzo*, we observe the same set of components in the merged state space. Yet, in this scenario, the short-circuit allowing bypassing some states is absent, since the rule n° 16 is absent too. Hence, the annamox process is involved in the system dynamics and might improve it by providing new paths, but there still be the same stabilities in the state space.

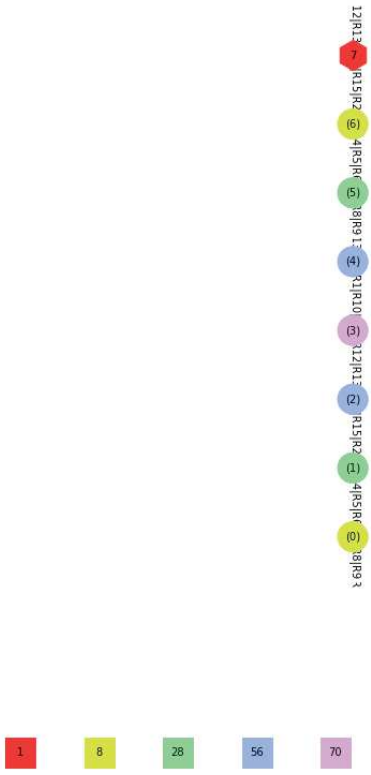


Figure 13: Merged state space for the nitrogen cycling model, in the scenario without the annamox process, plotted downward according to causality. The hexagon represents the initial stability, rounds of different colours represent other stabilities and oriented arrows for the rule(s) allowing to switch from a stability to another. The colour palette corresponds to the number of states in each stability.

c. N cycle without Oxygen

Oxygen is not a nitrogen-based molecule, but its presence impacts in the cycle dynamics too. If Oxygen is removed from the initial state (node O_2 Off), the state space has now 64 states belonging to the same deadlock (Fig.14). Hence, the presence of Oxygen has a significant and even crucial impact on the nitrogen cycle.

With the AFC analysis, we obtained five first dimensions, each of them explains 18,3% of the data. For the two first dimensions, NH_2OH and Norg appear at the centre of the graph (Fig. 15), since these molecules are present in every state (i.e. no possible process may consume these molecules due to lack of Oxygen). The first AFC dimension split the full state space into two areas, one with N_2 presence, the other one with the other molecules: NO, NO_2, NO_3, N_2O and NH_4. Thus, this first axis distinguishes the two main groups of nitrogen molecules in the cycle: either fixed by microbes (NO, NO_2, …) or released in the environment (only N_2, so no possible life).

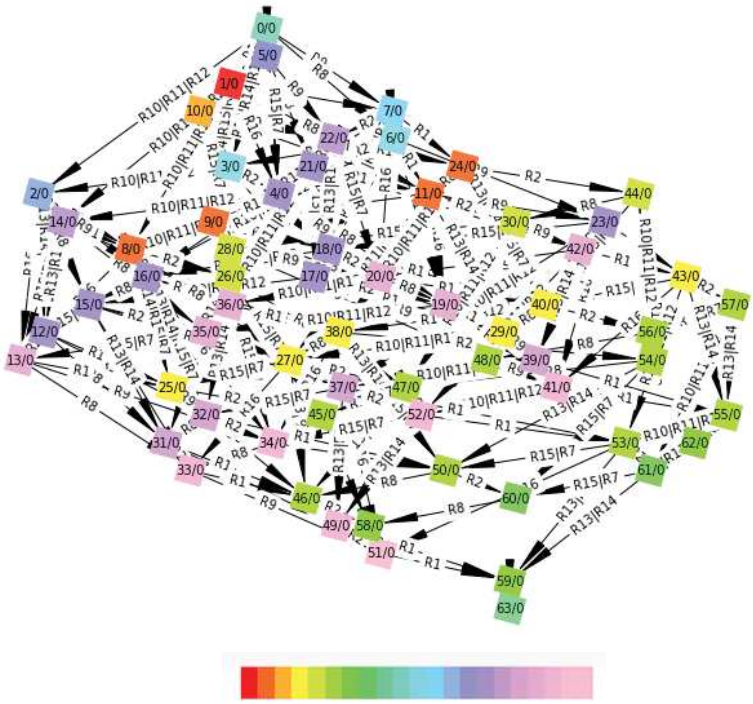


Figure 14: Full state space of the nitrogen cycling without O2 presence, plotted downward according to causality. Squares represent deadlock states (all states are here merged into one unique deadlock). The colour scale describes coordinates of each state along to the first dimension of the AFC analysis, from the lowest (red) to the highest (rose) values.

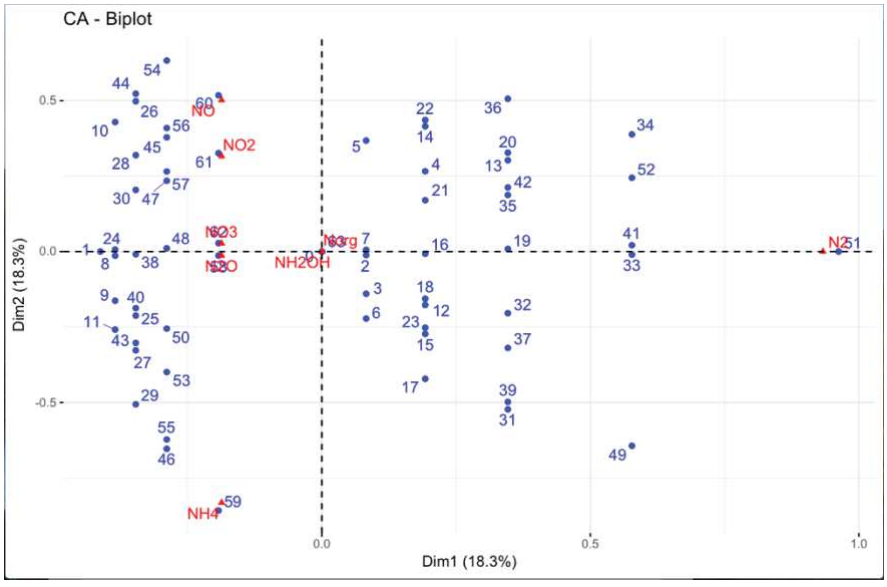


Figure 15: Results of the AFC analysis for the N cycle in the without Oxygen scenario: blue points stand for the system states (with their identifiers), while red points stand for involved molecules on the same AFC space.

D- DISCUSSIONS

I- Advantages and limits of the model based on the CO_2 emissions (Model 1)

The first model based on the CO_2 emissions was a preliminary trial to represent and model an ecosystem with various interactions between its components, aiming at exploring artificial selection of ecosystems. It fulfilled the first requirements to model a discrete and qualitative model that can include both living components and abiotic (environmental) components at successive levels of organization. As results, we computed two possible trajectories for the ecosystem "evolution", according to the application of the selection process.

Meanwhile, we discovered in this modelling task some limits that we cannot overcome. First, to predefine a rule for selection should take into account that the selected genetic units might depend on the selected trait: in our model, GU2 and GU3 are selected among the three units, but this selection has no causal link with the CO2 emissions of these units, a quantitative trait. In addition, the interaction network cannot be modified during the simulation in the case of our qualitative model. Also, we should have several ecosystems in the same model, in order to compare different structures, but this constraint supposes a much more complex and larger system that the computer could not handle (due to the exponential combinatorial nature of genetic unit interactions).

For these prohibitive reasons, we chose to model another system such as the nitrogen cycle, in which the qualitative nature of the cycle should allow us to fully control the system dynamics. In addition, to study the possible evolution of such system, we developed three scenarios with gradual appearance of components into this complex N cycle.

II- Comparing the different scenarios of N cycle model (Model 2)

The reference scenario assumes the presence of all N cycle components. Activating or not the Anammox process can be considered as a modelling of two different systems, with or without Anammox bacteria, that might appear in different periods in the Life evolution. Our model shows that in a system without Anammox bacteria, the nitrogen cycle can still be maintained. Yet, this evolutionary feature (Anammox bacteria) provides new trajectories between already present states, thus allowing new paths in case of perturbations, for instance in case of absence of some genes. Furthermore, these bacteria seem to extend their presence in many anaerobic marine and freshwater system, and its presence explains most the current experimental data on nitrogen cycle (Jetten *et al*, 2009). Studying this process present also some ecological interests in wastewater treatment aiming to a more efficient removal of ammonia-nitrogen or in industrial microbiology (Kuenen, 2008).

The third scenario modelling the absence of Oxygen demonstrates its essential role in the nitrogen cycle. Yet, without oxygen, the current nitrogen cycle is not maintained, any transformation is possible, thus no possible life. In fact, it has been shown that the appearance

of oxygen on Earth had totally changed the nitrogen cycle, in particular its oxidative part (Thomazo *et al*, 2011). Although relatively trivial, this result illustrates the efficiency of qualitative Petri nets to model complex systems and to later apply them to more complex evolutionary questions. Yet, this model does not chemically model Oxygen, and we assume here that Oxygen is abundant enough (as a substrate). In our model, Oxygen absence is taken into account only through its qualitative effects on aerobic bacteria. Hence, our model shows that, more than its contribution to chemical processes, the effects of Oxygen as a catalyser of genes is essential for the maintaining of the N cycle. In reality, there exists a minimum oxygen layer in the ocean where oxygen is very poor (Sewell & Fage, 1948) causing stress for organisms and these oxygen-minimum zones (OMZ) continue to be expanded in the tropical oceans (Stramma *et al*, 2008). Studying the impacts of oxygen on the nitrogen cycle is then interesting to understand effects of these OMZ and their spread.

III- Advantages and limits of the N cycle model (Model 2)

1. Advantages

As a discrete and qualitative model, the N cycle model also includes both abiotic and biotic components of the system, as required in our initial objectives. The model outputs are state spaces with presence/absence of system components, thus easy to interpret with statistical and graphic tools. Furthermore, it allows to compare the outcomes of different initial states within the same model corresponding to different periods of the evolutionary history, as the example of the Anammox path in the nitrogen cycling (Fig. 13). Further, we could develop different scenarios to test the role of each gene or molecule in this N cycle, as the crucial role of Oxygen that we tested in our study (Fig. 14).

2. Limits

Meanwhile, this preliminary model still shows some limits to be improved. First, the nitrogen cycle is not mimicking an ecosystem yet. While some components come from living beings, like genes, the cycle cannot exist on his own, without autonomous living individuals. Even more, including living individuals, for instance microorganisms, would lead to complicate the model with interactions between these genes and other components of the same individual, and further, between several individuals or groups of individuals. Besides, all the processes in this model are assumed to be possible at the same probability (100%), but some genes like nosZ (responsible for reduction of N_2O) are more abundant than the other ones (Graf *et al*, 2014). So far, such objectives are not yet reachable.

IV- Perspectives:

Going back to the main objective aimed at the start, to build a model that define and describe the evolution at the ecosystem level, our current work is not yet completed. It is necessary to discuss the two main points: the use of discrete and qualitative model; the ecosystem to take into account.

On the one hand, qualitative models seem to simplify ecosystem and its properties, but there exist some points that need to be quantitatively explored, for instance the selection rule should not be pre-defined but vary during simulation according to system changes. Semi-quantitative models could then be a relevant path to explore this problem. In these models, there will be not only the presence and absence of a component that are analysed, but also some indications for its abundance. However, semi-quantitative models should be used with precaution not to lose all the advantages of simplification of a qualitative model and to explode the system due to its complexity. We had already worked on a first semi-quantitative model using counting machine methods, but some difficulties were detected but cannot be fixed. A relevant idea is to use quantitative Petri net model with more than one token in a component standing for its relative quantity comparing to the others, that we cannot yet develop by lacking of time.

On the other hand, it is also important to discuss the pertinence of the two experimental approaches used in this work (Table 2). Microbial communities (Model 1) seem to provide controllable ecosystems to analyse and develop a more complete view of evolution at the ecosystem level, but there still exist some difficulties for modelling it, by lacking of information. For instance, in the first model based on artificial selection, correlations between genetic units are identified without causality, and furthermore, these data are not available at every generation due to experiment difficulties. The nitrogen cycle provides an interesting system with both biotic and abiotic components and theirs well-defined roles in the ecosystem, that was not satisfied in the first model. We succeeded to prove that the appearance of Anammox process promoted the system stability, by adding possible trajectories between structural stabilities and that the appearance of oxygen increases the ecosystem fitness, i.e. its capacity to avoid the collapse state with only N_2. Hence, this experimental approach is relevant to be more developed in order to describe and understand the evolution at the ecosystem level.

Requirements of the model	Model 1 - CO_2 emissions in microbial communities	Model 2 - Nitrogen cycle with genes and molecules
Including both biotic and abiotic components	Yes	Yes
Multi-level organisation	Yes	No
Controllable information	Incomplete	Almost satisfied
Including selection process	Yes	No

Table 2: Comparison of the two models built in this work, by using the requirements of a model for describing the evolution at the ecosystem level

Conclusion

In conclusion, our work through this internship built two different models based on two different kinds of selection. The first one (model 1), based on the artificial selection on microbial communities, seems not to be adapted to describe the evolution at the ecosystem level due to its limits that we cannot afford. The second one (model 2) mimicking the natural selection through the nitrogen cycle is by the way a relevant approach to demonstrate and describe the ecosystem evolution. The objectives determined by this internship are not yet reached, but our results showed although the capacity of our modelling tools to do it soon, by developing the possible perspectives detailed above.

Bibliography:

Avery DD, Penn PE (1976) Interaction of salicylate and body temperature changes caused by injections of neurohumours into the anterior hypothalamus: possible mechanisms in salicylate antipyresis. *Neuropharmacology* **15**: 433–438.

Bairey E, Kelsic ED, Kishony R (2016) High-order species interactions shape ecosystem diversity. *Nature Communications* **7**: 12285, doi:10.1038/ncomms12285.

Balduzzi M, Binder BM, Bucksch A, Chang C, Hong L, Iyer-Pascuzzi AS, Pradal C, Sparks EE (2017) Reshaping Plant Biology: Qualitative and Quantitative Descriptors for Plant Morphology. *Frontiers in Plant Science* **8**: doi:10.3389/fpls.2017.00117.

Barberán A, Bates ST, Casamayor EO, Fierer N (2012) Using network analysis to explore co-occurrence patterns in soil microbial communities. *The ISME Journal* **6**: 343–351, doi:10.1038/ismej.2011.119.

Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystems (Malden, MA: Blackwell Pub).

Bijma P, Wade MJ (2008) The joint effects of kin, multilevel selection and indirect genetic effects on response to genetic selection. *Journal of Evolutionary Biology* **21**: 1175–1188, doi:10.1111/j.1420-9101.2008.01550.x.

Blackwood CB, Hudleston D, Zak DR, Buyer JS (2007) Interpreting Ecological Diversity Indices Applied to Terminal Restriction Fragment Length Polymorphism Data: Insights from Simulated Microbial Communities. *Applied and Environmental Microbiology* **73**: 5276–5283, doi:10.1128/AEM.00514-07.

Blouin M, Karimi B, Mathieu J, Lerch TZ (2015) Levels and limits in artificial selection of communities. *Ecology Letters* **18**: 1040–1048, doi:10.1111/ele.12486.

Bose KS, Sarma RH (1975) Delineation of the intimate details of the backbone conformation of pyridine nucleotide coenzymes in aqueous solution. *Biochem Biophys Res Commun* **66**: 1173–1179.

Carter MQ, Xue K, Brandl MT, Liu F, Wu L, Louie JW, Mandrell RE, Zhou J (2012) Functional Metagenomics of Escherichia coli O157:H7 Interactions with Spinach Indigenous Microorganisms during Biofilm Formation. *PLoS ONE* **7**: e44186, doi:10.1371/journal.pone.0044186.

Dambacher JM, Brewer DT, Dennis DM, Macintyre M, Foale S (2007) Qualitative Modelling of Gold Mine Impacts on Lihir Island's Socioeconomic System and Reef-Edge Fish Community. *Environmental Science & Technology* **41**: 555–562, doi:10.1021/es0610333.

Danchin É (2013) Avatars of information: towards an inclusive evolutionary synthesis. *Trends in Ecology & Evolution* **28**: 351–358, doi:10.1016/j.tree.2013.02.010.

Darwin C (1859) On the Origin of Species.

DeAngelis KM (2016) Chemical communication connects soil food webs. *Soil Biology and Biochemistry* **102**: 48–51, doi:10.1016/j.soilbio.2016.06.024.

Dershowitz N, Jouannaud J-P (1990) Rewrite Systems. In Formal Models and Semantics, (Elsevier), pp. 243–320.

Devol AH (2003) Solution to a marine mystery: Nitrogen cycle. *Nature* **422**: 575–576, doi:10.1038/422575a.

Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* **5**: 558–567, doi:10.1046/j.1461-0248.2002.00354.x.

Ebisu S, Kato K, Kotani S, Misaki A (1975) Isolation and purification of Flavobacterium alpha-1,3-glucanase-hydrolyzing, insoluble, sticky glucan of Streptococcus mutans. *J Bacteriol* **124**: 1489–1501.

Ellegren H, Sheldon BC (2008) Genetic basis of fitness differences in natural populations. *Nature* **452**: 169–175, doi:10.1038/nature06737.

Faust K, Raes J (2012) Microbial interactions: from networks to models. *Nature Reviews Microbiology* **10**: 538–550, doi:10.1038/nrmicro2832.

Fontaine C, Guimarães PR, Kéfi S, Loeuille N, Memmott J, van der Putten WH, van Veen FJF, Thébault E (2011) The ecological and evolutionary implications of merging different

types of networks: Merging networks with different interaction types. *Ecology Letters* **14**: 1170–1181, doi:10.1111/j.1461-0248.2011.01688.x.
Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP, Asner GP, Cleveland CC, Green PA, Holland EA, Karl DM, Michaels AF, Porter JH, Townsend AR, Vosmarty CJ (2004) Nitrogen Cycles: Past, Present, and Future. *Biogeochemistry* **70**: 153–226, doi:10.1007/s10533-004-0370-0.
Gaucherel C, Boudon F, Houet T, Castets M, Godin C (2012) Understanding Patchy Landscape Dynamics: Towards a Landscape Language. *PLoS ONE* **7**: e46064, doi:10.1371/journal.pone.0046064.
Gaucherel C, Jensen HJ (2012) Origins of evolution: Non-acquired characters dominates over acquired characters in changing environment. *Journal of Theoretical Biology* **304**: 111–120, doi:10.1016/j.jtbi.2012.02.028.
Gaucherel C, Théro H, Puiseux A, Bonhomme V (2017) Understand ecosystem regime shifts by modelling ecosystem development using Boolean networks. *Ecological Complexity* **31**: 104–114, doi:10.1016/j.ecocom.2017.06.001.
Giavitto J-L, Godin C, Michel O, Prusinkiewicz P (2002) Computational models for integrative and developmental biology. In Actes Du Colloque Modélisation et Simulation de Processus Biologiques Dans Le Contexte de La Génomique, (Autrans, France), p. 43.
Giavitto J-L, Michel O (2003) Modeling the topological organization of cellular processes. *Biosystems* **70**: 149–163, doi:10.1016/S0303-2647(03)00037-6.
Gliddon CJ, Gouyon P-H (1989) The units ofselection. *Trends in Ecology & Evolution* **4**: 204–208, doi:10.1016/0169-5347(89)90074-8.
Gollasch S (2002) The Importance of Ship Hull Fouling as a Vector of Species Introductions into the North Sea. *Biofouling* **18**: 105–121, doi:10.1080/08927010290011361.
Goodnight CJ (1990a) EXPERIMENTAL STUDIES OF COMMUNITY EVOLUTION I: THE RESPONSE TO SELECTION AT THE COMMUNITY LEVEL. *Evolution* **44**: 1614–1624, doi:10.1111/j.1558-5646.1990.tb03850.x.
Goodnight CJ (1990b) EXPERIMENTAL STUDIES OF COMMUNITY EVOLUTION II: THE ECOLOGICAL BASIS OF THE RESPONSE TO COMMUNITY SELECTION. *Evolution* **44**: 1625–1636, doi:10.1111/j.1558-5646.1990.tb03851.x.
Goodnight CJ (2000) Heritability at the ecosystem level. *Proceedings of the National Academy of Sciences* **97**: 9365–9366, doi:10.1073/pnas.97.17.9365.
Goodnight CJ (2011) Evolution in metacommunities. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**: 1401–1409, doi:10.1098/rstb.2010.0290.
Goodnight CJ, Stevens L (1997) Experimental Studies of Group Selection: What Do They Tell US About Group Selection in Nature? *The American Naturalist* **150**: S59–S79, doi:10.1086/286050.
Graf DRH, Jones CM, Hallin S (2014) Intergenomic Comparisons Highlight Modularity of the Denitrification Pathway and Underpin the Importance of Community Structure for N2O Emissions. *PLoS ONE* **9**: e114118, doi:10.1371/journal.pone.0114118.
Henry F, Amara R, Courcot L, Lacouture D, Bertho M-L (2004) Heavy metals in four fish species from the French coast of the Eastern English Channel and Southern Bight of the North Sea. *Environment International* **30**: 675–683, doi:10.1016/j.envint.2003.12.007.
Ings TC, Montoya JM, Bascompte J, Blüthgen N, Brown L, Dormann CF, Edwards F, Figueroa D, Jacob U, Jones JI, Lauridsen RB, Ledger ME, Lewis HM, Olesen JM, van Veen FJF, Warren PH, Woodward G (2009) Review: Ecological networks - beyond food webs. *Journal of Animal Ecology* **78**: 253–269, doi:10.1111/j.1365-2656.2008.01460.x.
Jablonka E, Lamb MJ, Zeligowski A (2006) Evolution in four dimensions: genetic, epigenetic, behavioral, and symbolic variation in the history of life (Cambridge, Mass.: MIT Press).
Jallon JM, Risler Y, Iwatsubo M (1975) Beef liver L-Glutamate dehydrogenase mechanism: presteady state study of the catalytic reduction of 2.oxoglutarate by NADPH. *Biochem Biophys Res Commun* **67**: 1527–1536.

Jetten MSM, Niftrik L van, Strous M, Kartal B, Keltjens JT, Op den Camp HJM (2009) Biochemistry and molecular biology of anammox bacteria. *Critical Reviews in Biochemistry and Molecular Biology* **44**: 65–84, doi:10.1080/10409230902722783.
Jones CG, Lawton JH, Shachak M (1994) Organisms as Ecosystem Engineers. *Oikos* **69**: 373, doi:10.2307/3545850.
Kuenen JG (2008) Anammox bacteria: from discovery to application. *Nature Reviews Microbiology* **6**: 320–326, doi:10.1038/nrmicro1857.
Lamarck J-B (1809) Philoquesophie zoologique.
Landman OE (1991) The Inheritance of Acquired Characteristics. *Annual Review of Genetics* **25**: 1–20, doi:10.1146/annurev.ge.25.120191.000245.
Lindenmayer A (1968) Mathematical models for cellular interactions in development I. Filaments with one-sided inputs. *Journal of Theoretical Biology* **18**: 280–299, doi:10.1016/0022-5193(68)90079-9.
Loreau M (2010) From populations to ecosystems: theoretical foundations for a new ecological synthesis (Princeton: Princeton University Press).
Lowe WH, Kovach RP, Allendorf FW (2017) Population Genetics and Demography Unite Ecology and Evolution. *Trends in Ecology & Evolution* **32**: 141–152, doi:10.1016/j.tree.2016.12.002.
Melián CJ, Bascompte J, Jordano P, Krivan V (2009) Diversity in a complex ecological network with two interaction types. *Oikos* **118**: 122–130, doi:10.1111/j.1600-0706.2008.16751.x.
Mills GC, Alperin JB, Trimmer KB (1975) Studies on variant glucose-6-phosphate dehydrogenases: G6PD Fort Worth. *Biochem Med* **13**: 264–275.
Mougi A, Kondoh M (2012) Diversity of Interaction Types and Ecological Community Stability. *Science* **337**: 349–351, doi:10.1126/science.1220529.
Neumann J von, Morgenstern O (1944) Theory of Games and Economic Behavior.
Niftrik LA, Fuerst JA, DamstÃ© JSS, Kuenen JG, Jetten MSM, Strous M (2004) The anammoxosome: an intracytoplasmic compartment in anammox bacteria. *FEMS Microbiology Letters* **233**: 7–13, doi:10.1016/j.femsle.2004.01.044.
Pommereau F (2009) Algebras of coloured Petri nets and their applications to modelling and verification.
Reimann J, Jetten MSM, Keltjens JT (2015) Metal Enzymes in 'Impossible' Microorganisms Catalyzing the Anaerobic Oxidation of Ammonium and Methane. In Sustaining Life on Planet Earth: Metalloenzymes Mastering Dioxygen and Other Chewy Gases, P.M.H. Kroneck, and M.E. Sosa Torres, eds. (Cham: Springer International Publishing), pp. 257–313.
Reisig W (2013) Understanding Petri Nets (Berlin, Heidelberg: Springer Berlin Heidelberg).
Reum J, Ferriss B, McDonald P, Farrell D, Harvey C, Klinger T, Levin P (2015) Evaluating community impacts of ocean acidification using qualitative network models. *Marine Ecology Progress Series* **536**: 11–24, doi:10.3354/meps11417.
Ricklefs RE, Miller GL (2005) Écologie (Bruxelles: De Boeck).
Sander EL, Wootton JT, Allesina S (2015) What Can Interaction Webs Tell Us About Species Roles? *PLOS Computational Biology* **11**: e1004330, doi:10.1371/journal.pcbi.1004330.
Sewell RBS, Fage L (1948) Minimum Oxygen Layer in the Ocean. *Nature* **162**: 949–951, doi:10.1038/162949a0.
Stanley SM (1975) A theory of evolution above the species level. *Proc Natl Acad Sci USA* **72**: 646–650.
Stramma L, Johnson GC, Sprintall J, Mohrholz V (2008) Expanding Oxygen-Minimum Zones in the Tropical Oceans. *Science* **320**: 655–658, doi:10.1126/science.1153847.
Swenson W, Wilson DS, Elias R (2000) Artificial ecosystem selection. *Proceedings of the National Academy of Sciences* **97**: 9110–9114, doi:10.1073/pnas.150237597.
Tansley AG (1935) The Use and Abuse of Vegetational Concepts and Terms. *Ecology* **16**: 284–307, doi:10.2307/1930070.
Thebault E, Fontaine C (2010) Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science* **329**: 853–856, doi:10.1126/science.1188321.

Thomazo C, Ader M, Philippot P (2011a) Extreme 15N-enrichments in 2.72-Gyr-old sediments: evidence for a turning point in the nitrogen cycle: Extreme 15N-enrichments in 2.72-Gyr-old sediments. *Geobiology* **9**: 107–120, doi:10.1111/j.1472-4669.2011.00271.x.
Thomazo C, Ader M, Philippot P (2011b) Extreme 15N-enrichments in 2.72-Gyr-old sediments: evidence for a turning point in the nitrogen cycle: Extreme 15N-enrichments in 2.72-Gyr-old sediments. *Geobiology* **9**: 107–120, doi:10.1111/j.1472-4669.2011.00271.x.
Wiesmann UN, DiDonato S, Herschkowitz NN (1975) Effect of chloroquine on cultured fibroblasts: release of lysosomal hydrolases and inhibition of their uptake. *Biochem Biophys Res Commun* **66**: 1338–1343.
Zerkle AL, Poulton SW, Newton RJ, Mettam C, Claire MW, Bekker A, Junium CK (2017) Onset of the aerobic nitrogen cycle during the Great Oxidation Event. *Nature* **542**: 465–467, doi:10.1038/nature20826.

Annex 1: The full model based on CO_2 emissions

Nodes

N°	Nodes	Names	Category	Initial state
1	Eco1	Ecosystem	Ecosystem	On (+)
2	GU1	Genetic unit 1	Genetic unit	On (+)
3	GU3	Genetic unit 2	Genetic unit	On (+)
4	GU4	Genetic unit 3	Genetic unit	On (+)
5	Ind1	Individual 1	Individual	On (+)
6	Ind2	Individual 2	Individual	On (+)
7	Ind3	Individual 3	Individual	On (+)
8	Ind4	Individual 4	Individual	On (+)
9	Ind5	Individual 5	Individual	On (+)
10	Ind6	Individual 6	Individual	On (+)
11	Ind7	Individual 7	Individual	On (+)
12	Ind8	Individual 8	Individual	On (+)
13	Ind9	Individual 9	Individual	On (+)
14	nut	Nutrients	Resources	On (+)
15	exc	Excretions	Resources/Products	Off (-)
16	EXP	Experimenter	Selection process	On (+)

Constraints

N°	Constraints	Process
1	nut- >> Eco1-	Without nutrients, the whole ecosystem is dead
2	Eco1- >> GU1-,GU2-,GU3-	Imbrication of GU1, GU2, GU3 by the ecosystem
3	GU1-,GU2-,GU3- >> Eco1-	Imbrication of GU1, GU2, GU3 by the ecosystem
4	GU1- >> Ind1-,Ind2-,Ind3-,exc+	Imbrication of Individuals 1, 2, 3 by the GU1
5	Ind1-,Ind2-,Ind3- >> GU1-,exc+	Imbrication of Individuals 1, 2, 3 by the GU1
6	GU2- >> Ind5-,Ind4-,Ind6-,exc+	Imbrication of Individuals 4, 5, 6 by the GU2
7	Ind5-,Ind4-,Ind6- >> GU2-,exc+	Imbrication of Individuals 4, 5, 6 by the GU2
8	GU3- >> Ind7-,Ind8-,Ind9-,exc+	Imbrication of Individuals 7, 8, 9 by the GU3
9	Ind7-,Ind8-,Ind9- >> GU3-,exc+	Imbrication of Individuals 7, 8, 9 by the GU3

Rules

N°	Rules	Process
1	Ind1+ >> Ind2-,exc+	Negative correlation between Ind1 and Ind2
2	Ind2+ >> Ind1-,exc+	Negative correlation between Ind1 and Ind2
3	Ind4+ >> Ind5-,exc+	Negative correlation between Ind4 and Ind5
4	Ind5+ >> Ind4-,exc+	Negative correlation between Ind4 and Ind5
5	Ind5+ >> Ind6-,exc+	Negative correlation between Ind5 and Ind6
6	Ind6+ >> Ind5-,exc+	Negative correlation between Ind5 and Ind6
7	Ind6+ >> Ind4-,exc+	Negative correlation between Ind4 and Ind6
8	Ind4+ >> Ind6-,exc+	Negative correlation between Ind4 and Ind6
9	exc+,nut+,Ind1- >> Ind1+,exc-	Reappearance of Ind1 by using excretions
10	exc+,nut+,Ind2- >> Ind2+,exc-	Reappearance of Ind2 by using excretions
11	exc+,nut+,Ind3- >> Ind3+,exc-	Reappearance of Ind3 by using excretions
12	exc+,nut+,Ind4- >> Ind4+,exc-	Reappearance of Ind4 by using excretions
13	exc+,nut+,Ind5- >> Ind5+,exc-	Reappearance of Ind5 by using excretions
14	exc+,nut+,Ind6- >> Ind6+,exc-	Reappearance of Ind6 by using excretions
15	Exp+,GU1+,GU2+,GU3+,nut+ >> GU1-,exc+	Selection process promoting GU2, GU3 among these three genetic units
16	GU1+ >> GU3-,exc+	Negative correlation between GU1 and GU3
17	GU3+ >> GU1-,exc+	Negative correlation between GU1 and GU3

Annex 2: The full model based on the nitrogen cycle

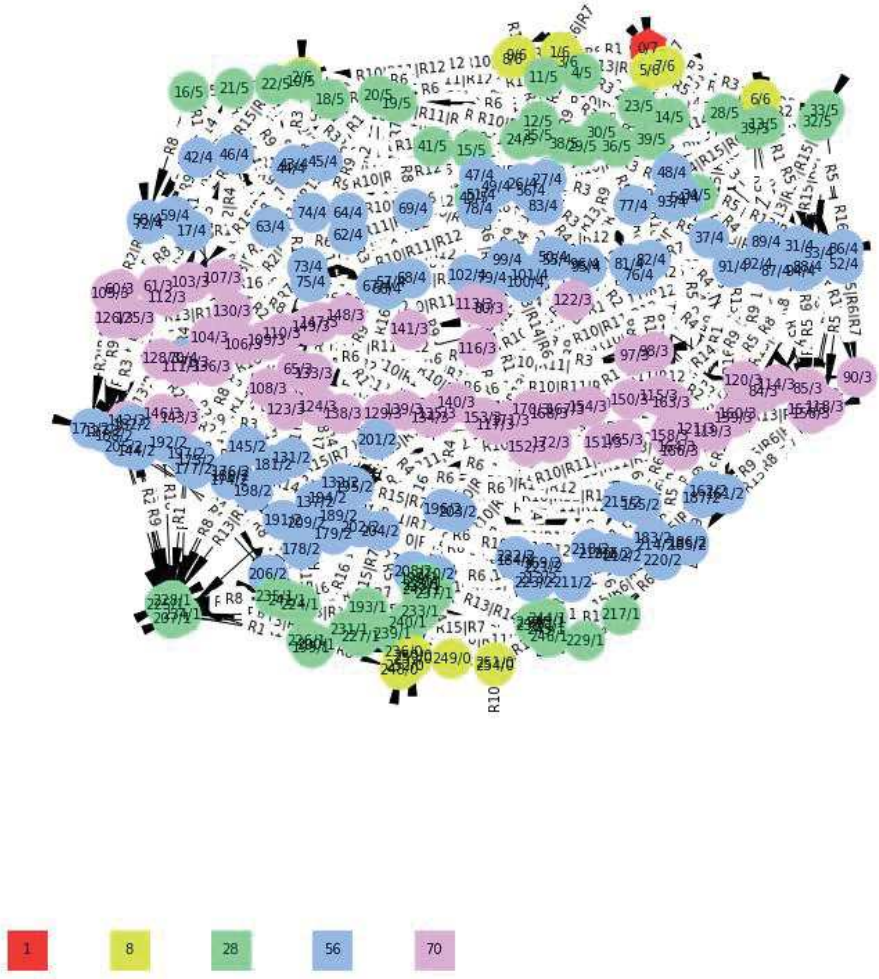
Nodes

N°	Nodes	Category	Initial state		
			Scenario 1	Scenario 2	Scenario 3
1	N2	Molecule	On (+)	On (+)	On (+)
2	NH4	Molecule	On (+)	On (+)	On (+)
3	Norg	Molecule (N organique)	On (+)	On (+)	On (+)
4	NH2OH	Molecule	On (+)	On (+)	On (+)
5	NO2	Molecule	On (+)	On (+)	On (+)
6	NO	Molecule	On (+)	On (+)	On (+)
7	N2O	Molecule	On (+)	On (+)	On (+)
8	NO3	Molecule	On (+)	On (+)	On (+)
9	O2	Molecule	On (+)	On (+)	Off (-)
10	nifH	Gene	On (+)	On (+)	On (+)
11	gdh	Gene	On (+)	On (+)	On (+)
12	ureC	Gene	On (+)	On (+)	On (+)
13	amoA	Gene	On (+)	On (+)	On (+)
14	hao	Gene	On (+)	On (+)	On (+)
15	nirK	Gene	On (+)	On (+)	On (+)
16	norB	Gene	On (+)	On (+)	On (+)
17	nosZ	Gene	On (+)	On (+)	On (+)
18	nor	Gene	On (+)	On (+)	On (+)
19	nasA	Gene	On (+)	On (+)	On (+)
20	napA	Gene	On (+)	On (+)	On (+)
21	nrfA	Gene	On (+)	On (+)	On (+)
22	nir	Gene	On (+)	On (+)	On (+)
23	narG	Gene	On (+)	On (+)	On (+)
24	hzo	Gene	On (+)	Off (-)	On (+)
25	nirS	Gene	On (+)	On (+)	On (+)

Rules

N°	Rules	Process
1	N2+, nifH+ >> NH4+, N2-	Fixation of atmospheric dinitrogen
2	NH4+, gdh+ >> Norg+, NH4-	Assimilation
3	Norg+, ureC+,O2+ >> NH4+, Norg-	Mineralization
4	NH4+, amoA+,O2+ >> NH2OH+, NH4-	Nitrification, hydroxylamine oxidation
5	NH2OH+, hao+,O2+ >> NO2+, NH2OH-	Nitrification, nitritation
6	NO2+, nor+,O2+ >> NO3+, NO2-	Nitrification, nitratation
7	NO2+, nirK+ >> NO+, NO2-	Denitrification, nitrite reduction
8	NO+, norB+ >> N2O+, NO-	Denitrification, nitric oxide reduction
9	N2O+, nosZ+ >> N2+, N2O-	Denitrification, nitrous oxide reduction
10	NO3+, narG+ >> NO2+, NO3-	Denitrification, denitratation
11	NO3+, nasA+ >> NO2+, NO3-	Dissimilatory nitrate reduction to amonium
12	NO3+, napA+ >> NO2+, NO3-	Dissimilatory nitrate reduction to amonium
13	NO2+, nrfA+ >> NH4+, NO2-	Dissimilatory nitrate reduction to amonium
14	NO2+, nir+ >> NH4+, NO2-	Dissimilatory nitrate reduction to amonium
15	NO2+, nirS+ >> NO+, NO2-	Denitrification, denitritation
16	NO2+, NH4+, hzo+ >> N2+, NO2-, NH4-	Anaerobic ammonium oxidation (Anammox)

Annex 3: Full state space of the model based on the nitrogen cycle, for the reference scenario, with different colours and forms representing different components: initial stability (hexagon) and other structural stabilities (round). States having the same colour belong to a same stability. We find out the n° of state and the n° of the stability (state/stability). The colour palette indicates the size (number of states) in each stability



Annex 4: Nodes always present (On) in each stability in the reference model. The scenario without Anammox bacteria has the same stabilities, only the absence of hzo is different from this scenario

Node	On	Off	Size
0	gdh, nosZ, nasA, nor, nir, hzo, O2, nirS, napA, nrfA, nirK, hao, ureC, nifH, narG, norB, amoA		8
1	gdh, nosZ, nasA, nor, nir, hzo, O2, nirS, napA, nrfA, nirK, hao, ureC, nifH, narG, norB, amoA		28
2	gdh, nosZ, nasA, nor, nir, hzo, O2, nirS, napA, nrfA, nirK, hao, ureC, nifH, narG, norB, amoA		56
3	gdh, nosZ, nasA, nor, nir, hzo, O2, nirS, napA, nrfA, nirK, hao, ureC, nifH, narG, norB, amoA		70
4	gdh, nosZ, nasA, nor, nir, hzo, O2, nirS, napA, nrfA, nirK, hao, ureC, nifH, narG, norB, amoA		56
5	gdh, nosZ, nasA, nor, nir, hzo, O2, nirS, napA, nrfA, nirK, hao, ureC, nifH, narG, norB, amoA		28
6	gdh, nosZ, nasA, nor, nir, hzo, O2, nirS, napA, nrfA, nirK, hao, ureC, nifH, narG, norB, amoA		8
7	All nodes are present		1

AGRO CAMPUS OUEST	Diplôme : Ingénieur Agronome Spécialité : Spécialisation / option : Modélisation en Écologie Enseignant référent : Frédéric Hamelin

Auteur(s) : NGUYEN Thi Thu Tam Date de naissance* : 20/01/1995	Organisme d'accueil : INRA Dijon Adresse : 17 rue de Sully, BP 86510
Nb pages : 27 Annexe(s) : 4	
Année de soutenance : 2018	Maîtres de stage : Manuel Blouin et Cédric Gaucherel

Titre français : Modélisation de « l'évolution » des écosystèmes

Titre anglais : Modelling of « the evolution » of ecosystems

Résumé (1600 caractères maximum) : Les écosystèmes évoluent-ils ? Si oui, comment définir et modéliser cette évolution écosystémique ? Un modèle discret et qualitatif inspiré des réseaux de Petri est une méthode pertinente pour prendre en compte la complexité des composantes biotiques (vivantes) et abiotiques (inertes) des écosystèmes, leur organisation à plusieurs niveaux et la diversité de leurs interactions. De tels modèles simplifient le système sans en perdre les propriétés. Il consiste d'abord à représenter l'écosystème comme un graphe, avec les composantes comme des nœuds qui sont liés entre eux par des processus écologiques ou par leurs interactions (arêtes). A partir de cette représentation et d'un formalisme de Petri, nous avons développé deux modèles différents, basés sur une sélection artificielle et naturelle : le premier modélise les communautés microbiennes soumises à une pression de sélection artificielle sur les émissions de CO_2 ; le deuxième modélise le cycle de l'azote en se focalisant sur les processus d'apparition au cours de l'évolution du gène Anammox et de l'oxygène. Le premier modèle n'a pas rempli nos conditions, alors que le deuxième s'est révélé pertinent et mérite d'être mieux étudié à l'avenir. Finalement, bien que nous ne soyons pas encore en mesure de confirmer (ni infirmer) la présence d'évolution de ces écosystèmes, cette étude a montré que les modèles qualitatifs discrets sont probablement intéressants pour cette question.

Abstract (1600 caractères maximum) : Do ecosystems evolve? If yes, how should we define them and test this question? In order to take into account for both abiotic (inert) and biotic (living) components, the multi-level organization and the diversity of interactions of any ecosystem, as well as to model its possible evolution, a discrete and qualitative model such as a Petri net seems to be a relevant method able to simplify the system without losing its properties. It consists in representing ecosystem as a graph, with components as nodes that are linked between them by ecological processes or interactions between nodes (edges). Starting with this representation and with the Petri net formalism, we developed two different models based on artificial and natural selection: the first model on microbial communities with artificial selection based on the CO_2 emissions, and the second model on the nitrogen cycle focusing on the Anammox and O_2 appearance in the course of evolution. The first model is not satisfying our requirements, while the second one seems to be relevant and suggests an in-depth study. Finally, although we are not in the position to confirm (or infirm) the evolution of ecosystems, this study has shown the probable interest to develop qualitative and discrete models to study it.

Mots-clés : evolution, écosystème, réseaux Petri, evolution de l'écosystème, sélection à multi-niveaux

Key Words: evolution, ecosystem, Petri net, ecosystem evolution, multi-level selection

* *Elément qui permet d'enregistrer les notices auteurs dans le catalogue des bibliothèques universitaires*