AN AGE GROUP MODEL FOR THE STUDY OF A POPULATION OF TREES

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Abstract. In this paper, we derive a simple model for the description of an ecological system including several subgroups with distinct ages, in order to analyze the influence of various phenomena on temporal evolution of the considered species. Our aim is to address the question of resilience of the global system, defined as its ability to stabilize itself to equilibrium, when being perturbed by exterior fluctuations. It is shown that a under a critical condition involving growth rate and mortality rate of each subgroup, extinction of all species may occur.

1. Introduction. The study of ecological systems has raised a growing interest in the last decade due to a policy of sustainable development that becomes a crucial point for all governments ([26]). In particular, emergence of evidence for global heating on Earth that has been pointed out by a large community of scientists (see for example [30]) addresses many questions. Among them is the concept of resilience that estimates intrinsic ability of a given system to drive itself into equilibrium, when perturbed with exterior actions forced by human interventions as well as climatic changes.

Questions related to resilience have been raised for a long time ([16], [17], [18], [27]). Many studies investigated the capacity of systems to absorb shocks and maintain a population stability. Lots of them concluded that small variations of input parameters may have huge consequences in various ways ([2], [8], [12], [13], [14], [10], [11]). Therefore, in systems where influence of human activities may be relevant, it becomes essential to take into account intrinsic adaptation that could decrease potential vulnerability in the case of external disturbances ([14]). Three kind of mathematical models are generally used to study resilience and vulnerability: differential equation models, probabilistic graphic models and multi-agent systems ([1], [24], [6], [22]). Resilience studies often request a systemic approach where state variables are disturbed by external forces ([8], [20]) whereas vulnerability is more often associated to multi-agents systems which are based on feedback ([31], [34]). A system including interaction between ecological and human population

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which complexity depends on the type of interactions is known in the literature as a *socio-ecological system* (see [12], [28]). The question of deriving realistic models that include climatology as well as ecological processes and human activity is out of reach, since each of these aspects displays a huge complexity ([21]).

Aiming to study evolution of vegetal populations, different kinds of models for forest ecosystems have been proposed ([7]): age or size structure mathematical models, multi-species models, partial differential equations models or even cellular automata models. In a simplified framework, it is first necessary to study a given ecological system including various competing species when no interaction with the exterior background is considered. Equipped with such a toy-model, it is possible to define the concept of resilience in terms of stability of stationary states that turns out to be crucial since regeneration of forests has various consequences on the preservation of biodiversity, emission of greenhouse gases as well as urbanism concerns or life quality. Our aim is here to present a toy-model governing a population of trees divided into different age subgroups generalizing the classical system first historically detailed in [32] and to analyze the influence of perturbations on persistence of asymptotic stationary states.

This paper is organized as follows: in Section 2, we present some academic models for the study of a given population: the logistic equation and the Lotka-Volterra system for predator-prey models. In Section 3 we derive and mathematically study a general toy-model that governs the dynamics of population for several groups of trees, starting from academic strategies suggested in Section 2. In Section 4, the numerical algorithm is introduced in order to solve numerically the mathematical model and some numerical results are presented and discussed in Section 5.

2. A review of simple models. We now first briefly describe toy models that can be written for idealistic situations before getting a more sophisticated one that will be used for our investigations. For all models that will be presented (see [3] for a complete review), the main concern is to investigate the possibility for solutions to reach a stationary nontrivial state that could be interpreted as an equilibrium of the ecological system. If this state exists, it is necessary to study its stability, that is to check if this equilibrium could persist in presence of external perturbations.

2.1. A single population model. We begin with a simple model in a specific context: we aim to consider the time evolution of the number $R = R(t)$ of trees in a given surface. This population involving individuals of the same kind (meaning that there is no differentiation between two given trees) is subject to mortality that can be explained by many causes: natural mortality, human exploitation, presence of pathogen species and climate change, each of them being characterized by a specific mortality rate. Of course, more efforts should be paid to quantify in a realistic way the influence of the climate involving spatial inhomogeneity, nonlocal effects as well as stochastic phenomena. Even if the assumption that a global heating could uniformly increase the general mortality seems quite simplistic, it may be relevant in a toy-model. A population that is influenced only with total mortality rate $m$ would by governed by the Malthusian linear model

$$R' = -mR$$

that would lead the population to extinction at infinite time, since $R(t) = e^{-mt} R(0)$. In a similar way, one finds the model $R' = g \times R$ that involves the growth rate of trees $g$; unfortunately, it leads to unbounded values for the tree population which
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does not fit the realistic dynamics of a given forest area. The growth of the trees is then modelled by the logistic evolution equation

\[ R' = gR \left( 1 - \frac{R}{K} \right) \]  

(1)

(see [32]) where \( K \) stands for the maximal occupation, that prevents unboundedness of the tree population. Indeed, when \( R \) is close to \( K \), growth coefficient \( 1 - \frac{R}{K} \) becomes close to zero and the growing effect is slowed down. At this stage, it can be seen that a fluctuation of the growth rate will not affect the long time asymptotics of the population. This will be observed in the numerical section.

Taking into account these two contributions leads to the single equation

\[ R' = gR \left( 1 - \frac{R}{K} \right) - mR. \]  

(2)

In this reduced model, the population of trees is only affected by mortality and growth that appear as constant rate contributions, even if they may include a non-deterministic part. Eq. (2) admits two equilibrium states:

\[ R^*_{1} = 0 \] (the trivial one) and \( R^*_{2} = K(1 - m/g) \) (the nontrivial one). It can be first noticed that taking into account intrinsic mortality gives a nontrivial equilibrium smaller than \( K \). Furthermore, \( R^*_{2} \) becomes nonphysical when \( m > g \).

It is observed that Eq. (2) appears as Ricatti-type differential equation \( R' = \alpha R^2 + \beta R \) (with \( \alpha = -g/K \) and \( \beta = g - m \)), that can be explicitly solved. Indeed, setting \( u = 1/R \) leads us to the linear equation \( u' = -\left( \beta u + \alpha \right) \), which finally gives the solution of the initial problem as

\[ R(t) = \frac{\beta R_0}{(\beta + R_0\alpha)e^{-\beta t} - \alpha R_0} = \frac{(g - m)KR_0}{(K(g - m) - gR_0)e^{-(g-m)t} + gR_0}. \]  

(3)

From this, we deduce that if \( g > m \), then \( R \) attains equilibrium value \( R^*_{2} \) as \( t \) tends to \(+\infty\). Moreover, this state is stable since starting with \( R_0 \in [0, R^*_{2}] \), the solution is such that \( R'(t) > 0 \). When \( g < m \), the population \( R \) tends to the trivial stationary state \( R_{1}^* \) for any choice of \( R_0 \). It suggests that if the mortality increases and becomes larger than \( g \), the population of trees extincts at infinite time. This is somehow logical for this model where only one species is considered.

2.2. A Lotka-Volterra model. We now also take into account a population \( P \) of pathogens. Indeed, as observed in biological or ecological systems, the mortality of trees increases with the density of pathogens. This can be modelled by considering that mortality defined in the previous model is now proportional to \( P \). We then find the equation governing the evolution of \( R \) as

\[ R' = g_R R \left( 1 - \frac{R}{K} \right) - m_R R P. \]

It means that the intrinsic growth of \( R \) is counterbalanced by a mortality that increases with the number of pathogens. In order to obtain a closed system, one has to add the equation of evolution for \( P \) that writes

\[ P' = g_P R P - m_P P, \]

involving mortality \( m_P \) and growth rate \( g_P \); the total growth of pathogens \( g_P R \) thus depends on the population of trees. Consequently, pathogens cannot grow in the absence of trees, whereas in the absence of pathogens, the population of trees is simply governed by the logistic equation. This system is well-known and referred as a predator-prey model (see [33] for pioneering works in this context). Depending on the initial value \((R_0, P_0)\), convergence to an equilibrium point or extinction of
the tree population can occur. This model may be ill-adapted in systems for which the mortality of trees caused by pathogens is negligible.

Here, several kinds of stationary solutions can be obtained: trivial state \((R^*, P^*, 1) = (0, 0)\), nontrivial one \((R^*, 2, P^*, 2) = (\frac{mR}{gP}, \frac{gP}{mR} (1 - \frac{mP}{gP}R))\) and the semitrivial one \((R^*, 3, P^*, 3) = (K, 0)\). For the study of the stability of these states, we compute the Jacobian matrix of the system

\[
J = J(R^*, P^*) = \begin{bmatrix}
g_R (1 - \frac{2R}{K}) & -m_R P^* \\
g_P P^* & g_P R - m_P
\end{bmatrix}.
\]

The analysis of the spectrum of \(J\) provides informations about the stability of the stationary state \((R^*, P^*)\). Indeed, \(J(0, 0)\) is diagonal with eigenvalues \(\{r_R, -m_R\}\) and it is found that the trivial state is unstable. For the nontrivial state, it is found that the two eigenvalues have negative real parts if \(1 - \frac{mP}{gP}K > 0\) which suggests that once again, the nontrivial equilibrium is stable for small enough mortality \(m_R\), but also here for large enough growth rate of pathogens. Logically, the semitrivial state becomes stable when \(m_P > g_P K\) showing a bifurcation phenomenon occurring at critical mortality \(m_P^* = g_P K\). It means that large mortality of pathogens drives the population of trees to attend its maximal occupation value \(K\) and causes the extinction of pathogens.

3. A age group model. We now intend to obtain a new model based upon simple considerations made in the previous Section, involving different subclasses of trees depending on their ages.

It is possible to distinguish among the total population \(R\) several subclasses of trees (young, intermediate and old trees) located at distinct areas and that do not match the same properties. For example, growth rates are not the same for young trees and old trees. Moreover, it is assumed here that the dynamical evolution of individuals in a given subclass is the same. Let \(Y\), \(I\) and \(O\) respectively stand for the population of young, intermediate and old trees in the region under study. We infer that young trees become intermediate ones and then turn into old ones. Even if old trees are assumed to die, they will have an influence on the population of young trees due to a cyclic turnover effect: once the old trees have died, natural germination processes give birth to new generations of young trees. Indeed, the growth rate of population of intermediate (respectively old) trees is driven by the population of young (respectively intermediate) trees with growth rate \(g_I\) (respectively \(g_O\)), whereas the growth rate of population of young trees depends on the population of old ones by means of renewal growing rate \(g_Y\). We also assume that the maximum occupation is not the same for each population; we thus define \(K_Y\), \(K_I\) and \(K_O\) as occupations for young, intermediate and old trees. Finally, we prescribe specific values for mortalities \(m_Y\), \(m_I\) and \(m_O\), each of them being a consequence of natural mortality \((n)\), mortality by pathogens \((p)\), mortality by climate \((c)\) and mortality by human exploitation \((e)\). Note that in general, the population of young trees may be affected by various animal species, which justifies the choice of considering age groups in the modelization of the ecological system. It would be also possible to add a noisy contribution \(\epsilon\) taking into account nondeterministic fluctuations of mortality. It means that for each population, we have \(m = m_n + m_p + m_c + m_e + \epsilon\). We then consider the system
Furthermore, one has for all time $t$

\begin{equation}
\begin{aligned}
Y' &= g_Y O \left( 1 - \frac{Y}{K_Y} \right) - m_Y Y \\
I' &= g_I Y \left( 1 - \frac{I}{K_I} \right) - m_I I \\
O' &= g_O I \left( 1 - \frac{O}{K_O} \right) - m_O O.
\end{aligned}
\end{equation}

This model is relevant in forests often cut into three different areas, each of them containing a given subclass population. It has been inspired from the SIRS model (see [3], [5]) for the concern of epidemiology. In this approach, the forest is considered as uniform, that is with no spatial differentiation or interaction. Consequently, the dynamics of the three age group populations at a given spatial location is not affected by the neighboring ones. This is somehow simplistic in heterogeneous media where population of given subgroups can depend on the localization.

As the following result states, this model stands for a well-posed dynamical system:

**Theorem 3.1.** Let $(Y_0, I_0, O_0) \in \mathbb{R}^3$ be such that $0 < Y_0 < K_Y$, $0 < I_0 < K_I$ and $0 < O_0 < K_O$. Then system (4) admits a unique solution $(Y(t), I(t), O(t))$ defined for all times, that satisfies $(Y(0), I(0), O(0)) = (Y_0, I_0, O_0)$. Furthermore, one has for all $t \geq 0$ the bounds $0 < Y(t) < K_Y$, $0 < I(t) < K_I$ and $0 < O(t) < K_O$.

**Proof.** First, local well-posedness of (4) for any prescribed Cauchy data $(Y_0, I_0, O_0)$ follows from the classical Cauchy-Lipchitz theorem that holds since (4) involves a polynomial contribution that is locally Lipschitzian with respect to space.

Let us now assume that $0 < Y_0 < K_Y$, $0 < I_0 < K_I$ and $0 < O_0 < K_O$ and let $T$ stands for the local existence time of the solution of (4). We then show that each component satisfies the same bounds. For this, let us consider for example $t_* := \inf \{ t \in ]0, T[ : Y(t) = K_Y \}$. If $t_* < +\infty$, the first equation of (4) then implies that $Y'(t_*) = -m_Y K_Y < 0$. Using a first-order Taylor expansion around $t_*$, one would find that

$$Y(t) = K_Y - m_Y K_Y (t - t_*) + O(t - t_*)$$

which implies that $Y(t_* - \epsilon) = K_Y + m_Y K_Y \epsilon + o(\epsilon)$, contradicting the definition of $t_*$ since one has $Y(t_* - \epsilon) > K_Y$ for $\epsilon \ll 1$. We conclude that $t_*$ cannot be finite, leading us to the bound $Y(t) < K_Y$ for each $t < T$. This argument can also be used for $I$ and $O$.

We show in a similar way that each component also remains strictly positive at all times, claiming that if one of the subgroup population vanishes at some finite time $t_*$, its derivative would be strictly positive at that time. Note that extinction of all populations at the same time $t_* > 0$ is excluded by a uniqueness argument, claiming that $(0, 0, 0)$ is a global solution of (4).

Finally, these bounds grant global well-posedness of (4) by classical ODE arguments. This achieves the proof.

We now look for stationary states of system (4), that is $(Y_*, I_*, O_*)$ such that

$$\frac{g_Y O_*}{m_Y} \left( 1 - \frac{Y_*}{K_Y} \right) = Y_*, \quad \frac{g_I Y_*}{m_I} \left( 1 - \frac{I_*}{K_I} \right) = I_*, \quad \frac{g_O I_*}{m_O} \left( 1 - \frac{O_*}{K_O} \right) = O_*.$$

This is a nonlinear quadratic-like system that we solve by substitution, after rescaling the variables for the sake of convenience. Setting $\beta_Y = (m_Y K_Y)/(g_Y K_O)$,
\( \beta_1 = \frac{(m_I K_I)}{(g_Y K_Y)} \) and \( \beta_O = \frac{(m_O K_O)}{(g_O K_I)} \), it is found that rescaled quantities \( y_* = \frac{Y_*}{K_Y}, i_* = \frac{I_*}{K_I} \) and \( o_* = \frac{O_*}{K_O} \) (appearing as fraction of occupation of each subgroup) solve the reduced equations

\[
(1 - y_*)o_* = \beta_Y y_*, \quad (1 - i_*)y_* = \beta_I i_* \quad (1 - o_*)i_* = \beta_O o_*. \]

At this point, we have to notice that assuming that one of the stationary value vanishes leads us to \((y_*, i_*, o_*) = (0, 0, 0)\) in the case where all intrinsic mortalities are not zero. It means that as opposed to the previous models, one cannot have here a “semi-trivial” state consisting in the persistence of one single population. Expressing two quantities in terms of the third one explicitly gives the expected solutions. We then find

\[
y_* = \frac{1 - \beta_Y \beta_I \beta_O}{1 + \beta_Y (1 + \beta_I)}, \quad i_* = \frac{1 - \beta_Y \beta_I \beta_O}{1 + \beta_I (1 + \beta_Y)} \quad \text{and} \quad o_* = \frac{1 - \beta_Y \beta_I \beta_O}{1 + \beta_O (1 + \beta_Y)}
\]

which enables us to compute the values of \((Y_*, I_*, O_*)\) with respect to original parameters. We notice that when mortalities are set equal to zero, the nontrivial state is simply given by \((Y_*, I_*, O_*) = (K_Y, K_I, K_O)\).

We now investigate the linear stability of the previously found equilibrium states. The result states as

**Theorem 3.2.** Under the condition \( g_Y g_I g_O > m_Y m_I m_O \), the trivial stationary state \((0, 0, 0)\) is unstable and the nontrivial state \((Y_*, I_*, O_*)\) is stable. When \( g_Y g_I g_O < m_Y m_I m_O \), \((0, 0, 0)\) is stable and \((Y_*, I_*, O_*)\) is unstable.

**Proof.** Investigation of stability of stationary states of (4) relies on the spectrum of the Jacobian matrix of system (4) that writes

\[
J = \begin{bmatrix}
-\left( \frac{g_Y}{K_Y} O_* + m_Y \right) & 0 & g_Y \left( 1 - \frac{Y_*}{K_Y} \right) \\
g_I \left( 1 - \frac{I_*}{K_I} \right) & -\left( \frac{g_I}{K_I} Y_* + m_I \right) & 0 \\
0 & g_O \left( 1 - \frac{O_*}{K_O} \right) & -\left( \frac{g_O}{K_O} O_* + m_O \right)
\end{bmatrix}.
\]

This matrix evaluated at \((Y_*, I_*, O_*) = (0, 0, 0)\) reduces to

\[
J = \begin{bmatrix}
-m_Y & 0 & g_Y \\
g_I & -m_I & 0 \\
0 & g_O & -m_O
\end{bmatrix}.
\]

The eigenvalues \( \lambda \) solve the third-order equation \( P(\lambda) := -(m_Y + \lambda)(m_I + \lambda)(m_O + \lambda) + g_Y g_I g_O = 0 \). In the absence of growth, \( P \) admits the three roots \(-m_Y, -m_I, -m_O\); adding the nonnegative term \( g_Y g_I g_O \) gives a positive root as soon as \( P(0) = g_Y g_I g_O - m_Y m_I m_O > 0 \). It means that for large enough growing rates (that is if \( g_Y g_I g_O > m_Y m_I m_O \)), the trivial equilibrium is unstable. If \( g_Y g_I g_O < m_Y m_I m_O \), third-order polynomial \(-P\) has the form \(-P(\lambda) = \lambda^3 + b\lambda^2 + c\lambda + d\) with strictly positive coefficients and \( d < bc \). Hence, \(-P\) is a Hurwitz polynomial ([19]), which means that all its roots have strictly negative real parts. It follows that \((0, 0, 0)\) is stable and locally attracts the trajectories.

When considering the nontrivial state, it is possible to simplify the expression of \( J \) claiming that

\[
g_Y \left( 1 - \frac{Y_*}{K_Y} \right) = m_Y \frac{Y_*}{O_*}, \quad -\left( \frac{g_Y}{K_Y} O_* + m_Y \right) = -g_Y \frac{O_*}{Y_*}
\]
(and the same for other quantities up to circular permutations). Plugging this gives

\[
J(Y_*, I_*, O_*) = \begin{bmatrix}
-g_Y \frac{O}{Y} & 0 & m_Y \frac{Y}{O} \\
-m_I \frac{I}{Y} & -g_I \frac{I}{Y} & 0 \\
0 & m_O \frac{O}{I} & -g_O \frac{O}{I}
\end{bmatrix}
\]

and eigenvalues of \(J\) now solve

\[-(\lambda + g_Y \frac{O}{Y})(\lambda + g_I \frac{I}{Y})(\lambda + g_O \frac{O}{I}) + m_Y m_I m_O = 0.\]

Following the same idea as for the trivial state, we then find that \((Y_*, I_*, O_*)\) is now stable for \(g_Y g_I g_O > m_Y m_I m_O\) and unstable for \(g_Y g_I g_O < m_Y m_I m_O\). \(\square\)

Consequently, a bifurcation occurs for critical value of parameters \(g_Y g_I g_O = m_Y m_I m_O\). This suggests that the growth parameters have to be large enough to make the solution converge to nontrivial equilibrium value. We also notice that if the condition \(g_Y g_I g_O > m_Y m_I m_O\) holds, then \(\beta_Y \beta_I \beta_O < 1\) and all stationary populations are positive. We deduce that in the unstable case \(g_Y g_I g_O < m_Y m_I m_O\) (that means for large mortalities), \((Y, I, O)\) tends to \((0, 0, 0)\). In this case, the nontrivial equilibrium state is nonphysical since the populations are found negative. Note that for our concern, the study of linear stability is sufficient since for dynamical system (4), linear stability implies local asymptotic stability.

This implies that for a given age group, if the growth decreases or if the mortality increases when all other growth and mortality parameters are prescribed, the whole population goes to extinction. This appears as a consequence of the circular dependence of each subgroup that is assumed in the model. It points out that a specific action such as parasitic invasion for a given group may have dramatic consequences for the whole population at large timescales.

4. **Presentation of the numerical method.** All models that have been previously addressed in the last Section appear as autonomous dynamical systems. It is convenient for the sake of simplicity to assume that we start from initial time \(t = 0\) and that temporal dynamics is investigated until final time \(T\) (that can be several centuries). The model then expresses as general system

\[
\begin{align*}
Y'(t) &= F(Y(t)), \quad t \in [0, T] \\
Y(0) &= Y_0
\end{align*}
\]  
(5)

where \(Y(t) \in \mathbb{R}^N\) is the vector containing all the species, starting from initial state \(Y_0\). Due to the complexity of (5), it is necessary to use a numerical method in order to compute an approximation of \(Y\). A lot of efforts have been paid to design very accurate schemes for the numerical resolution of (5). A well-known strategy (see [15]) relies on the use of a timestep, say \(\delta t\) and the integral form of (5) that writes

\[
Y(t_{n+1}) = Y(t_n) + \int_{t_n}^{t_{n+1}} F(Y(s)) \, ds,
\]

where we set \(t_n = n \delta t\) for \(n = 0, \ldots, N = T/\delta t\). At this stage, it is possible to use numerical integration formulas in order to calculate the numerical approximation \(Y_n\) of \(Y(t_n)\) for each \(n\), using an induction relation. A standard numerical scheme is obtained using the trapezoidal rule leading to the fourth-order Runge-Kutta method that writes
\[
\begin{align*}
Y_{n+1} &= Y_n + \frac{\delta t}{6} \left( p_{n,1} + 2(p_{n,2} + p_{n,3}) + p_{n,4} \right) \\
p_{n,1} &= f(Y_n), \quad p_{n,2} = f(Y_n + \delta t p_{n,1}/2) \\
p_{n,3} &= f(Y_n + \delta t p_{n,2}/2), \quad p_{n,4} = f(Y_n + \delta t p_{n,3}),
\end{align*}
\]

initialized with \(Y_0 = Y(0)\). By fourth-order, it is meant that error between the exact solution and the computed one is of magnitude \(C\delta t^4\), when constant \(C\) only depends on the exact solution. This error estimate shows the efficiency of this method that does not afford drastic requirements on the timestep size in order to obtain an accurate numerical solution. Let us mention that numerical accuracy is essential when investigating long-time asymptotics for the solutions of the model.

In these simulations, it is possible to deal with parameters that may depend on time: for example, we can prescribe values of mortality that includes nondeterministic fluctuations caused by exterior factors such as climatic perturbations. Our numerical code easily handles these possible changes.

5. **Numerical results.** We now present a few numerical simulations that have been performed for previously derived models.

5.1. **The logistic system.** We first numerically illustrate that equilibrium state \(R_* = K\) of (1) is not affected by fluctuations of growth rate \(g\) caused by external perturbations such as parasitic invasions or global warming.

In Figure 1 is plotted the temporal evolution of \(R\) in three different cases. In the first one (plot (a)), \(g\) is constant and equal to 1 (note that in this case, the solution of (1) is explicitly known). In the second one (plot (b)), previous growth rate value is reduced to 0.2 between \(t = 3\) and \(t = 10\). In the third one (plot (c)), we set \(g = 1\) if \(t \leq 3\) and \(g = 0.2\) if \(t \geq 3\). In these plots, it is observed that equilibrium state \(R_*\) is not modified by the growth rate perturbation, since \(R_*\) does not depend on \(g\). However, we notice that the rate of convergence to \(R_*\) is driven by the constant asymptotic growth rate \(g_*\) (\(g_* = 1\) in (a) and (b), \(g_* = 0.2\) in (c)) that is involved in explicit formula (3) for large enough times.

![Figure 1](image-url)
5.2. The intermediate model. We now consider Eq. (2) that takes into account both growth rate $g$ and mortality rate $m$. We have performed simulations when mortality is perturbed by parasitic invasion as well as global heating. We present here various simulations starting with the same initial population and considering the same growth rate $g = 1$. In Figure 2, we plot temporal evolution of $R$, first with constant mortality $m = 1$, then with a mortality that punctually increases to $m = 1.2$ between $t = 20$ and $t = 40$. It is clearly pointed out that the asymptotic state $R_{*,2}$ is not affected by the mortality fluctuation.

![Figure 2](image1.png)

**Figure 2.** Time evolution of $R$ in two different cases: (a) $m = 1$; (b) $m = 1.2$ between $t = 20$ and $t = 40$ and $m = 1$ elsewhere. The asymptotic state $R_{*,2}$ is not perturbed by mortality fluctuation.

In Figure 3, we now present the results obtained with long-time perturbations of the mortality. First, we performed a computation of $R$ when considering a mortality magnified to 1.2 from $t = 20$. Logically, it leads to a convergence to a modified equilibrium state $R_{*,2} < R_{*,2}$. When dealing with larger mortality $m = 2$, we find that population $R$ tends to zero at large times. It means that a large mortality drives the ecological system to extinction.

![Figure 3](image2.png)

**Figure 3.** Time evolution of $R$ in two different cases: (a) $m = 1.2$ for $t \geq 20$; (b) $m = 2$ for $t \geq 20$. In the first case, the asymptotic state $R_{*,2}$ is perturbed, in the second case, extinction occurs at large times.
5.3. The subgroup toy-model. We first illustrate here stability results obtained for the solutions of (4) For this aim, we show the time evolution of \((Y,I,O)\), for various values of parameters. Recalling that nontrivial equilibrium state \((Y^*, I^*, O^*)\) has been obtained, we numerically check its stability for two different regimes computed with \(K_Y = K_I = K_O = 1\), starting with the same initial state \((0.1, 0.2, 0.3)\): the first one has been taken until final time \(T = 20\) with growth rates greater than mortalities for each subgroup. We have set \(g_Y = 3\), \(g_I = 1\), \(g_O = 0.5\), \(m_Y = 1\), \(m_I = 0.8\), \(m_O = 0.2\) ensuring that stability condition given in Theorem 3.2 is fulfilled. A second test has been performed until the same final time with \(g_Y = 1\), \(g_I = 1\), \(g_O = 0.6\), \(m_Y = 1.5\), \(m_I = 1\), \(m_O = 0.2\). Here, we have chosen a mortality that is greater than the growth rate for young trees, that could turn out as the consequence of an invasion by parasites. As observed in Figure 4, all populations reach stable equilibrium \((Y^*, I^*, O^*)\) even if for the second simulation (presented in the right side), it is not clear that young trees could survive in this context where \(m_Y > g_Y\). However, the presence of old trees enhances increase of population of young ones by means of the effective growth \(g_Y O\): large enough values of \(O\) enforces stabilization of \(Y\) to equilibrium.

![Figure 4](image-url)

**Figure 4.** Time evolution of \((Y,I,O)\) for the two stable cases \(g_Y = 3\), \(g_I = 1\), \(g_O = 0.5\), \(m_Y = 1\), \(m_I = 0.8\), \(m_O = 0.2\) (left) and \(g_Y = 1\), \(g_I = 1\), \(g_O = 0.6\), \(m_Y = 1.5\), \(m_I = 1\), \(m_O = 0.2\) (right) \((Y:\) black, \(I:\) blue, \(O:\) red).

In view of the previous results, we decide to perturb mortality in order to see how the stable equilibrium can be affected. Here, we only change the value of \(m_I\) and now consider a piecewise linear evolution of the form

\[
m_I = \begin{cases} 
m_{I,1} & \text{if } t < t_1, \\
m_{I,1} + \frac{t - t_2}{t_1 - t_2} (m_{I,2} - m_{I,1}) & \text{if } t_1 \leq t \leq t_2, \\
m_{I,2} & \text{elsewhere},
\end{cases}
\]

It means that we plug a linear increasing of mortality between times \(t_1\) and \(t_2\). We now present the results obtained for two simulations performed with \(t_1 = 40\), \(t_2 = 50\), \(m_{I,1} = 1\) and parameters \(g_Y = 1.2\), \(g_I = 1\), \(g_O = 0.5\), \(m_Y = 0.2\), \(m_I = 1\), \(m_O = 1.5\). In this case, mortality of old trees is greater than the one prescribed for young and intermediate populations. We have set \(T = 200\) in order to investigate...
the asymptotics on a larger timescale. In the first test, we chose $m_{I,2} = 1.4$ for which stability still holds. In Figure 5 (left), it can be shown a first stage where a stabilization seems to occur. When perturbing the mortality, initial equilibrium (plotted in dotted lines) breaks down and a transition phase drives the solution into another stable equilibrium (plotted in dashed lines) given in terms of parameter $m_{I,2}$. It means that in this case, the system turns itself into stable equilibrium. When considering the new value $m_{I,2} = 2$ (that is considering a final mortality twice larger than the initial one), stability condition now fails and Figure 5 (right) shows a bifurcation phenomenon that causes total extinction. Similar results are obtained if other parameters are perturbed.

**Figure 5.** Time evolution of $(Y, I, O)$ when perturbing mortality of intermediate trees: $m_{I,2} = 1.4$ (left) and $m_{I,2} = 2$ (right). In the first case, the system drives itself into another stable nontrivial equilibrium; in the second case, the total population extincts ($Y$: black, $I$: blue, $O$: red).

6. **Discussion and perspectives.** In this work, we have designed a toy-model that governs the evolution of a population of trees that is divided into three age subgroups. This model admits a nontrivial stationary state that can be considered as an equilibrium of the ecological system. It has been mathematically proved that either the decreasing of the growing rate or the increasing of the mortality of a given subgroup (that could be the consequence of environmental perturbations) may affect global equilibrium of the system, since it could lead to a global extinction of all subgroups.

Studies related to mathematical modelling of resilience in socio-ecological systems concept show that disturbances caused by climate change may affect both state variables and parameters ([4]). Thus, it is essential to consider resilience of system to possible repeated, cyclic or stochastic fluctuations of parameters. Furthermore, the dynamics of the system should be investigated on consistent scales with typical ecological ones (several decades for forest ecosystems [16]) as well as short-time feedbacks imposed by human activity, by means of resources management and decision-making process ([29]), which combination with external perturbations may have important consequences on resilience ([23]). All these aspects have been considered in the conception of the present model and will also be taken into account in its future extensions.
Indeed, this model appears as a dynamical system that rules the time evolution of global populations where no spatial fluctuations, that is to say no geographic diversity, are considered. It could be generalized following different strategies. First, a multi-cell model where human exploitation would be included can be written. Indeed, a given plot of land could be exploited giving a sudden decrease of intermediate age group. It could also take into account nondeterministic external disturbances such as thunderstorms striking the forest at small spatial scales. All these contributions could influence the global dynamics of the whole population at large time scales and simulations performed for a large number of stochastic scenarios could point out intrinsic resilience of the global ecological domain. It is also possible to investigate a $N$ subgroups model, where interaction processes are ruled in a similar way and to derive the limit $N \to +\infty$, leading us to a partial differential equation involving the age of trees as an extra continuous variable. All this will deserve a future publication.

The search for adaptation of the system under perturbations is essential and stands for a prerequisite for any model used in socioecology. However, it leads to more complex models where uncertainty for parameters and processes ([9], [25]) may paradoxically increase. The balance between these constraints must therefore be found.

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