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The tragedy of ecosystems in open-access

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La tragédie des écosystèmes en accès libre

Résumé

Cet article étudie le rôle joué par la coopération dans la soutenabilité d'un écosystème exploité. L'analyse s'appuie sur un modèle bio-économique fondé sur une dynamique multi-espèces à la Gompertz avec compétition interspécifique en présence de plusieurs exploitants. La comparaison des stratégies optimales obtenues dans les cas coopératifs et non coopératifs permet de réinterpréter la tragédie en accès libre et la sur-exploitation des ressources dans un cadre multi-espèces. Les résultats montrent d'abord que les prélèvements sont plus élevés dans le cas non coopératif pour toutes les espèces. Ils soulignent aussi comment la coopération peut induire des gains pour l'écosystème en termes d'espèce et de biodiversité. Il est montré que la coopération favorise la biodiversité quand le nombre d'exploitants est élevé. En revanche, un nombre restreint d'exploitants conduit à des résultats plus ambigus si l'analyse est menée espèces par espèces. Cependant, un indicateur fondé sur la valeur de l'écosystème est proposé pour mesurer le gain de la coopération dans le cas général. Des exemples numériques illustrent les résultats analytiques.

Mots-clés : Pêcherie, Ecosystème, Biodiversité, Optimisation, Equilibre de Nash.

The tragedy of ecosystems in open-access

Abstract

This paper investigates the role played by cooperation for the sustainable harvesting of an ecosystem. To achieve this, a bio-economic model based on a multi-species Gompertz dynamics with interspecific relationships and multi-agent catches is considered. A comparison between the non cooperative and cooperative optimal strategies is carried out. Revisiting the tragedy of open-access and over exploitation issues, it is first proved how harvesting pressure is larger in the non cooperative case for every species. Then it is examined to what extent gains of cooperation can also be derived for the state of the ecosystem. It turns out that cooperation clearly promotes the biodiversity when the number of agents is high. By contrast, when the number of agents remains limited, results are more ambiguous especially if a species by species viewpoint is adopted. However, an indicator is proposed at the ecosystem scale to highlight the gain of cooperation in the general case. Numerical examples illustrate the analytical findings.

Keywords: Fish war, Ecosystem, Biodiversity, Optimization, Nash equilibrium.

JEL: Q20, Q22

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1. Introduction

Cooperation is crucial for the sustainable management of renewable resources, exploited ecosystems and biodiversity as stressed by the well-known tragedy of the commons (Hardin, 1968). Game theory is a particularly relevant modeling tool to study such issues because it provides important quantitative and qualitative insights into the strategic interactions between users exploiting a common renewable resource as in Kaitala & Munro (1995); Hannesson (1997); Kaitala & Lindroos (2007); Finus (2001) to quote a few. However, as pointed out by Bailey *et al.* (2010), the majority of game-theoretic models have been applied to single stocks. Notable exceptions exist such as the study of predator-prey models (Mesterton-Gibbons, 1996) but the use of game theory in broader ecosystem-based context remains an open research field.

In the extensive game theory literature applied to fisheries, the dynamic model of Levhari & Mirman (1980) provides a solid framework for analyzing the consequences of users' strategies on the resource in open-access fisheries. Using a dynamic Cournot-Nash solution, these authors show that the non cooperative equilibrium yields a higher catch mortality rate and a smaller steady-state stock than the cooperative equilibrium. The non-cooperative situation refers to a framework in which each user maximizes its own intertemporal utility without taking into account other users' utility. By contrast, in the cooperative case, users jointly define a harvesting strategy. The result of Levhari & Mirman (1980) illustrates the famous tragedy of over-exploitation of resources in open access (Dutta & Sundaram, 1993). Between these two extreme cases, full cooperation and no cooperation, the sustainability of partial cooperation has been recently studied by Kwon (2006); Breton & Keoula (2011) or Doyen & Pereau (2012).

Expanding the approach of Levhari & Mirman (1980), the works of Fischer & Mirman (1992, 1996) allow for the interaction between two different species of fish, including prey-predator relations, symbiotic interactions and mutual competition. Contrary to Levhari & Mirman (1980), the model of Fischer & Mirman (1992) assumes that users do not compete for the same stock, each user targeting only one specific and exclusive species. Thus externalities only arise from ecological interactions and interspecific mechanisms. In Fischer & Mirman (1996), this assumption is relaxed since both the users and species interplay. In the case of only positive (or symmetrically negative) interspecies relationships characterizing a symbiotic network, results show that, without cooperation, there is always overfishing as compared to the cooperative case. Results are ambiguous in the case of predator-prey

relationships, in particular concerning the prey. In the same vein, Datta & Mirman (1999), refining the demand side in a two-species model, also show how results are ambiguous in the sense that they depend on both the preference parameters and the sign of ecological interactions. Thus, generalizing this approach to a general multi-species and multi-agent framework is an important challenge in the area of ecosystem and biodiversity management. This is especially relevant for operationalizing the Ecosystem-Based Fisheries Management (EBFM) which advocates an integrated and bio-economic management of marine resources accounting for their complexity to promote their sustainability (Pikitch *et al.*, 2004; Sanchirico *et al.*, 2008; Doyen *et al.*, 2013). Such a prospect is in line with “models of intermediate complexity” as proposed in Plaganyi *et al.* (2014). These models of intermediate complexity, such as the dynamic multi-species and multi-agent model investigated in the present paper allow to address the ecosystem approach at medium scales for fisheries management. By medium scale modeling is meant a trade-off between very stylized models like single species approaches and high dimensional models trying to capture the whole complexity of socio-ecosystems such as the so-called ”end-to-end” modeling (Rose *et al.*, 2010). The approach of intermediate complexity is illustrated by recent applied works using extended Lotka-Volterra models including Cissé *et al.* (2013) in French Guiana or Hardy *et al.* (2013) in Solomon Islands.

In line with these issues, the present article extends the model of Levhari & Mirman (1980) to a general multi-species (or multi-groups of species) and multi-agent context. A multi-species Gompertz dynamics as in Mutshinda *et al.* (2009) instead of the seminal Lotka-Volterra dynamics is considered. Such a Gompertz model turns out to be very convenient in mathematical terms. Moreover, fitting again with Levhari & Mirman (1980) framework, the present study assumes that the overall objective of the agents involved in the harvesting of the ecosystem consists in the maximization of their discounted utilities derived from the consumption of the different species. Revisiting the tragedy of open-access and over exploitation issues, the paper addresses two main questions:

- Is there a gain of cooperation in terms of catch pressure ?
- Is there a gain of cooperation in terms of ecosystem state and biodiversity ?

The paper is organized as follows. Section 2 presents the bio-economic model based on a multi-species multi-agent dynamics and define the non-cooperative and cooperative optimality problems. Section 3 presents the

analytical results especially comparing the cooperative and the non cooperative solutions both in terms of catches, stocks and biodiversity. Section 4 illustrates the findings through numerical examples. Section 5 discusses the results and concludes.

2. The bio-economic model

2.1. The multi-species dynamics

The two-species model of Fischer & Mirman (1992, 1996) is extended to a multi-species general framework with a Gompertz function in discrete time inspired by Mutshinda *et al.* (2009). Thus, for each species $j = 1, \dots, m$, the dynamics of the state $x_j(t)$ (biomass, abundance, ..) of the species is described by

$$\begin{aligned} x_j(t+1) &= G_j(x_1(t), \dots, x_m(t)) \\ &= x_j(t) \exp \left\{ r_j + \sum_{k=1}^m s_{jk} \ln(x_k(t)) \right\}. \end{aligned} \quad (1)$$

where r_j stands for the intrinsic growth rate of species j and the coefficient s_{jk} represents the interspecific relationship between species j and k . More specifically s_{jk} replicates the per-capita effect of species k on the growth of species j from time t to time $t+1$. When trophic parameter s_{jk} is positive and s_{kj} is negative, it means that species k is a prey for predator j . When s_{jk} and s_{kj} are negative, the two species are in mutual competition. If both are positive, the two species are in symbiotic relation. All coefficients s_{jj} are supposed to be non positive $s_{jj} \leq 0$ to capture the intraspecific competition. The whole set of species interactions is collected in the squared ($m \times m$) matrix $S = (s_{jk})$ and the intrinsic growth rate for species j in the vector $r = (r_j)$. To get bounded solutions for the ecosystem dynamics, it is assumed that $\|S\|_\infty = \max_{j,k} |s_{jk}| < 1$.

When the resource is exploited, the dynamics of species j become

$$\begin{aligned} x_j(t+1) &= G_j(x_1(t) - h_1(t), \dots, x_m(t) - h_m(t)), \\ &= (x_j(t) - h_j(t)) \exp \left\{ r_j + \sum_{k=1}^m s_{jk} \ln(x_k(t) - h_k(t)) \right\}, \end{aligned} \quad (2)$$

where $h_j(t)$ stands for the harvest of species j induced by n agents at time t namely

$$h_j(t) = \sum_{i=1}^n h_{ij}(t). \quad (3)$$

Since harvesting reduces the species stocks, the value $(x_j - h_j)$ measures the amount of species j available for growth and species interactions into the next period. Since the catches cannot exceed the stock, the scarcity constraint $0 \leq h_j(t) \leq x_j(t)$ applies for every species j .

2.2. Utility of agents

Agents labeled by $i = 1, \dots, n$ potentially harvest and derive ecosystem services from the catch of the m species. The agents are assumed to have identical preferences. For every agent i , the one-period utility from consuming the basket of species $h_i = (h_{i,1}, \dots, h_{i,m})$ is a logarithmic function defined as follows

$$U_i(h_i) = U(h_i) = U(h_{i,1}, \dots, h_{i,m}) = \sum_{j=1}^m a_j \ln(h_{ij}), \quad (4)$$

with $a_j \geq 0$ for every species j . More complex utility function coping with consumer preferences for variety can be found for instance in Quaas & Requate (2013). Cost of harvesting (Mesterton-Gibbons, 1993) as well as the demand side (Datta and Mirman, 1999) are not taken into account here.

Following Levhari & Mirman (1980) in the mono-species case or Fischer & Mirman (1996) in the two-species case, we aim at designing optimal linear feedback or Markov-perfect harvesting rules for each species j such that

$$h_j(t) = F_j(t)x_j(t)$$

where $F_j(t)$ measures the harvesting mortality rate at time t . Hereafter the vector $F = (F_1, \dots, F_m)'$ stands for the transpose¹ vector of catch mortality rate. The harvesting mortality rates in the non cooperative and cooperative cases are denoted by $F^{nc}(t)$ and $F^c(t)$ respectively.

2.3. Non-cooperative vs cooperative optimality problems

We aim at comparing the solutions in terms of states or controls of the non-cooperative and cooperative versions of the problem consisting in maximizing the intertemporal sum of discounted utilities of multi-species catches.

¹Let us recall that the notation $'$ stands for the transpose operator. The transpose of any matrix M is defined by $M'_{ij} = M_{ji}$. Recall also the useful properties $(M + N)' = M' + N'$ and $(M * N)' = N' * M'$.

In the non cooperative context, the maximization program of agent $i = 1, \dots, n$ can be written as:

$$\max_{F_{i,1}(t), \dots, F_{i,m}(t)} \sum_{t=0}^{\infty} \rho^t U(h_{i,1}(t), \dots, h_{i,m}(t)) \quad (5)$$

subject to the dynamics (2) and the scarcity constraint $0 \leq F_{ij}(t) \leq 1$. The common one-period discount factor is denoted by ρ with $0 \leq \rho \leq 1$. The solution of this dynamic game will be considered in the Markov-perfect Nash sense as clarified in the following sections.

In the cooperative case, the program is given by

$$\left\{ \begin{array}{l} \max_{F_{1,1}(t), \dots, F_{1,m}(t)} \\ \dots \\ F_{n,1}(t), \dots, F_{n,m}(t) \end{array} \right. \sum_{t=1}^{\infty} \rho^t \sum_{i=1}^n U(h_{i,1}(t), \dots, h_{i,m}(t)), \quad (6)$$

again subject to the dynamics (2) and the scarcity constraint $0 \leq F_j(t) \leq 1$.

3. Results

3.1. Non-cooperative optimal mortality rate

To obtain the Markov-perfect Nash solution of this dynamic game, we assume that player i believes that the other players use a stationary linear Markovian strategy (Long, 2010). The Bellman equation corresponding to this optimization problem is

$$\begin{aligned} V_i(x) &= \max_{F_i=(F_{i1}, \dots, F_{im})} \left\{ U(h_i) + \rho V_i \left(G \left(\left(\left(1 - F_i - \sum_{l \neq i} F_l \right) x \right) \right) \right) \right\} \\ &= \max_{F_i=(F_{i1}, \dots, F_{im})} \left\{ A'(\ln(F_i x)) + \rho V_i \left(G \left(\left(\left(1 - F_i - \sum_{l \neq i} F_l \right) x \right) \right) \right) \right\}. \end{aligned}$$

where $A = (a_1, \dots, a_m)'$ stands for the $(m \times 1)$ -size transpose vector of preference parameters of the utility function (4). Using dynamic programming, the optimal catch mortality F_{ij}^{nc} can be identified for every agent i as displayed in the following Proposition 1. The proof can be found in Appendix A.1. At this stage, it is convenient to introduce the notation B for the matrix

$$B = I + S' \quad (7)$$

where I denotes the identity matrix (m, m) . The following notation D is also useful for the vector

$$D = (I - \rho B)^{-1} A. \quad (8)$$

For the vector D to make sense, it is assumed that

$$I - \rho B \text{ is invertible}^2. \quad (9)$$

It turns out that D can be considered as a vector of shadow prices for the different species since it is proved in Appendix A.1 how D is a marginal value of the value function V in the sense $\frac{\partial V}{\partial \ln(x)} = D$. The bio-economic interpretation of this vector D is elaborated hereafter especially in subsection 3.7. The proposition related to the non-cooperative optimal mortality rates reads as follows.

Proposition 1. *Assume that matrix S is such that condition (9) holds true and that $(BD)_j > 0$ for every species j . Then the aggregate noncooperative optimal harvesting mortality rate for all species $j = 1, \dots, m$ is given by*

$$F_j^{nc}(t) = \frac{na_j}{na_j + \rho(BD)_j}. \quad (10)$$

Let us first point out that this optimal mortality rate $F_j^{nc}(t)$ is steady for every species. Thus the harvesting strategy does not depend on time although catches fluctuate throughout time for every species because of the stock variations and species interactions.

Let us now comment on the condition $(BD)_j > 0$ involved in the Proposition 1. This condition warrants the compliance with the scarcity constraint $0 \leq F_j^{nc} < 1$ since the discount factor is strictly positive ($0 < \rho$). The condition $(BD)_j > 0$ can be rewritten for a given species j as

$$(1 + s_{jj}) D_j + \sum_{k \neq j} s_{kj} D_k > 0, \quad (11)$$

where the D_j coefficients depend both on the ecological parameters (the growth rates and the interspecies parameters) and on the economic parameters (the preference parameters and the discount factor). Assuming that

²This is not a too demanding requirement. Typically when $\rho \approx 1$, it means that S is invertible which is the case for most trophic networks. For instance, in the two species case, we have $S = \begin{pmatrix} - & + \\ - & - \end{pmatrix}$ and thus $\det(S) > 0$.

the values D_j are closed in the sense that $D_j \approx D_k$, a condition similar to Fischer & Mirman (1992) can be derived stating that the sum of the direct effect given by $(1 + s_{jj})$ and the indirect effect given by $\sum_{k \neq j} s_{kj}$ on the evolution of the biomass of species j has to be positive. Condition (11) always holds true when all the species are in symbiotic relation ($s_{kj} > 0 \forall k$) and the weights D_j are positive. With only one species and assuming that $s_{11} = \frac{-r}{\ln(K)}$ where K denotes the carrying capacity, condition (11) reads $\ln(K) > r$ meaning that the carrying capacity K is large enough as compared to the intrinsic growth which generally occurs.

To get more connections with the paper of Fischer & Mirman (1996), assume for a while that the number of species is reduced to $m = 2$ species. The computation of “prices” D through definition (8) yields

$$D_1 = \frac{a_1(1 - \rho(1 + s_{22})) + \rho s_{21} a_2}{\Delta}, \quad (12)$$

$$D_2 = \frac{a_2(1 - \rho(1 + s_{11})) + \rho s_{12} a_1}{\Delta}, \quad (13)$$

where

$$\Delta = \det(I - \rho B) = (1 - \rho(1 + s_{11}))(1 - \rho(1 + s_{22})) - \rho^2 s_{21} s_{12}$$

stands for the discriminant of matrix $I - \rho B = I - \rho(I + S')$. The values of D implies the two species harvesting mortalities³

$$F_1^{nc} = \frac{n\Delta}{(n - (n - 1)\rho(1 + s_{11}))(1 - \rho(1 + s_{22})) + \rho s_{21} \left(\frac{a_2}{a_1} - (n - 1)\rho s_{12}\right)}, \quad (14)$$

$$F_2^{nc} = \frac{n\Delta}{(n - (n - 1)\rho(1 + s_{22}))(1 - \rho(1 + s_{11})) + \rho s_{12} \left(\frac{a_1}{a_2} - (n - 1)\rho s_{21}\right)}. \quad (15)$$

Such relations for two species highlight the complexity and non linearity underlying the optimal mortalities with respect to both the ecological parameters, the discount factor and the number of agents.

3.2. Cooperative optimal mortality rate

In the cooperative case, using again the dynamic programming and optimality conditions, the mortality rates F_j^c can be identified as displayed by the following Proposition. They involve again the preferences A , the vector D defined by (8) and the matrix B related to species interactions and defined by (7).

³Similar expressions are obtained by Fischer & Mirman (1996) using the following notation $\alpha_i = 1 + s_{ii}$ and $\beta_i = s_{ij}$ for $i, j = 1, 2$ and $i \neq j$.

Proposition 2. *Postulate the same assumptions than in Proposition (1). Then the optimal aggregated cooperative catch mortality rate for all species $j = 1, \dots, m$ are given by*

$$F_j^c(t) = \frac{a_j}{a_j + \rho(BD)_j}. \quad (16)$$

The proof of the previous Proposition 2 is explained in Appendix A.2.

It can be emphasized that these mortality values in the cooperative case correspond to the non cooperative values with only one player $n = 1$. In particular, in the two species case, the harvesting mortality rates become

$$F_1^c = \frac{\Delta}{(1 - \rho(1 + s_{22})) + \rho s_{21} \left(\frac{a_2}{a_1}\right)},$$

$$F_2^c = \frac{\Delta}{(1 - \rho(1 + s_{11})) + \rho s_{12} \left(\frac{a_1}{a_2}\right)}.$$

Although the formulation of these mortalities is simpler than the non cooperative one in (15), it remains highly non linear especially because of the determinant $\Delta = \det(I - \rho B)$.

3.3. The tragedy of the commons revisited

Comparing the optimal catch mortality rates in both non cooperative (10) and cooperative (16) cases entails the following Proposition. It points out the overall gain of cooperation in terms of catch pressure in the sense that, for every species, the optimal harvesting mortalities are strictly larger in the non cooperative case as compared to the cooperative context.

Proposition 3. *Postulate the same assumptions than in Proposition (1). If the number of agents is larger than one, for all species j , the aggregate optimal non cooperative harvesting mortality rate is strictly larger than the aggregate optimal cooperative harvesting mortality rate :*

$$n > 1 \implies F_j^{nc} > F_j^c. \quad (17)$$

The proof of the previous assertion stems from the following formulation for the mortality

$$F_j^{nc} = \frac{a_j}{a_j + \frac{\rho}{n}(BD)_j} > \frac{a_j}{a_j + \rho(BD)_j} = F_j^c$$

since $n > 1$, $BD > 0$ and $\rho > 0$. This result is a generalization in a multi-species and ecosystem context of the well-known tragedy of open-access. It stresses that the harvesting pressure on every species involved in the ecosystem is strictly larger when agents fail to cooperate.

3.4. Sensitivity analysis

We here investigate the impact on the catch mortalities of different major parameters. The sensitivity analysis with respect to the number of player n in the non cooperative case relies on the computation of the ratio

$$\frac{F_j^{nc}(n+1)}{F_j^{nc}(n)} = \frac{a_j + \frac{\rho}{n} (BD)_j}{a_j + \frac{\rho}{n+1} (BD)_j} > 1 \quad (18)$$

since $(BD)_j > 0$ for every species j and $\rho > 0$. It shows that non cooperative mortality rate increases with the number of agents. Regarding the gain of cooperation, it can be claimed that this benefit is enhanced with the number of agents because

$$(F_j^{nc}(n+1) - F_j^c) - (F_j^{nc}(n) - F_j^c) = F_j^{nc}(n+1) - F_j^{nc}(n) > 0 \quad (19)$$

This property will be used in proposition 5.

Regarding the sensitivity with respect to preferences a_k , it is proved⁴ in Appendix A.3 that when ρ is close enough to zero and the number of agents is high, we have for $k \neq j$

$$k \text{ is a predator of } j \implies \frac{\partial (F_j^{nc} - F_j^c)}{\partial a_k} > 0 \quad (20)$$

In other words, whenever k is a predator of prey j and the number of agents is high, the gain of cooperation is strengthened with an increasing preference for the predator k . Symmetrically, whenever k is a prey of species j , the gain of cooperation is reduced with a higher preference for the prey k . As regards the direct impact of preferences on each species captured by the derivative $\frac{\partial F_j}{\partial a_j}$, the sign turns out undetermined in the general case.

The impact of the discount factor also appears to be ambiguous in the sense that

$$\frac{\partial F_j^{nc}}{\partial \rho} \leq 0 \text{ and } \frac{\partial F_j^c}{\partial \rho} \leq 0$$

⁴The proof crucially relies on the relation

$$(I - \rho B)^{-1} = \sum_{k=0}^{\infty} (\rho B)^k = I + (\rho B) + (\rho B)^2 + \dots$$

as proved by the two following examples. First when considering interspecies interactions in the form

$$S = \begin{pmatrix} -0.5 & -0.2 & -0.1 \\ 0.4 & -0.1 & 0.4 \\ 0.3 & 0.3 & -0.2 \end{pmatrix}$$

together with preferences $A = (2, 1, 0)'$ and a discount factor $\rho = 0.9$, we obtain that

$$D \approx \begin{pmatrix} 8 \\ 9.5 \\ 11 \end{pmatrix}, \quad BD > 0, \quad \frac{\partial F_j^{nc}}{\partial \rho} > 0.$$

By contrast when

$$S = \begin{pmatrix} -0.4 & 0.4 & -0.1 \\ 0.2 & -0.4 & 0.1 \\ 0.2 & -0.5 & -0.1 \end{pmatrix}$$

and $A = (2, 1, 0)'$ with a discount factor $\rho = 0.9$, we derive that

$$D \approx \begin{pmatrix} 7.4 \\ 7.8 \\ 0.1 \end{pmatrix}, \quad BD > 0, \quad \frac{\partial F_j^{nc}}{\partial \rho} < 0.$$

Numerical illustrations in the section 4 and especially Table 1 show to what extent the preference for the future affects in a complex way the whole ecosystem in terms of catches, stocks and biodiversity.

3.5. *How cooperation promotes biodiversity with many agents*

At this stage, we can wonder whether the gains of cooperation stressed in Proposition 3 in terms of catches can induce better stocks for species $x(t)$ or better biodiversity levels or better ecosystem states. It turns out that results critically depend on the number of agents. We first focus on the case where the number of agents is very high. This situation is mathematically stylized by considering that the number of agents converges towards infinity.

Let us first recall from the sensitivity analysis and inequality (18) that in the non cooperative case the aggregate catch mortality rate increases with the number of players. More specifically, whenever $n \rightarrow \infty$, it turns out, as soon as $a_j > 0$, that $F_j^{nc} \rightarrow 1$ implying the depletion of every exploited stocks and thus the erosion of the biodiversity. This result corresponds to the following Proposition.

Proposition 4. *Postulate the same assumptions than in Proposition (1). When the agents do not cooperate and are too many, the exploited species collapses in the following bio-economic sense*

$$\lim_{n \rightarrow +\infty} x_j^{nc}(t) = \lim_{n \rightarrow +\infty} h_j^{nc}(t) = 0, \quad \forall t \geq 1, \forall j \text{ such that } a_j > 0. \quad (21)$$

By contrast, when agents do cooperate, the global catch remains unchanged and only individual mortality rates as part of the aggregated harvest are reduced. We obtain the following condition as proved in Appendix A.4.

Proposition 5. *Postulate the same assumptions than in Proposition (1). Consider a strictly positive initial state $x_0 > 0$. When agents do cooperate, the whole ecosystem persists in the following sense*

$$\lim_{n \rightarrow +\infty} x_j^c(t) > 0 \quad \forall t \geq 1, \forall j \quad (22)$$

We deduce that the number of surviving species in the cooperative context is larger as compared to the non cooperative case. In other words, the species richness is strictly larger in the cooperative context for a large number of agents. This result captured by the following Proposition 6 is a way to revisit the tragedy of open-access in multi-species, multi-agents and ecosystems contexts. We need to introduce the species richness index

$$\text{SR}(x) = \sum_{\text{species } j} \mathbb{1}_{\mathbb{R}_+^*}(x_j)$$

where $\mathbb{1}_{\mathbb{R}_+^*}$ means the characteristic (boolean) function of strictly positive reals⁵.

Proposition 6. *Postulate the same assumptions than in Proposition (1). Assume also that $a_j > 0$ for every species. Consider a strictly positive initial state $x_0 > 0$. When the numerous agents do cooperate, the ecosystem is more diverse in the sense that*

$$\text{SR} \left(\lim_{n \rightarrow +\infty} x^c(t) \right) > \text{SR} \left(\lim_{n \rightarrow +\infty} x^{nc}(t) \right) \quad (23)$$

⁵The characteristic function is defined by

$$\mathbb{1}_{\mathbb{R}_+^*}(x) = \begin{cases} 1 & \text{if } x > 0 \\ 0 & \text{otherwise} \end{cases}$$

Although numerous other biodiversity metrics such as the Shannon or Simpson index are proposed in the ecological literature, the species richness is one of the most popular because it informs on extinction risks in a very simple manner. Thus Proposition 6 points out that the biodiversity in the ecosystem is directly altered when many agents exploiting it fail to cooperate. Therefore, it is another analytical proof of the tragedy of unregulated access. The ecological viewpoint underlying Proposition 6 constitutes an original contribution especially in a multi-species and ecosystem context.

3.6. How cooperation promotes biodiversity with few agents

When the number of agents is limited, a general condition can be derived to assess the gains induced by cooperation in terms of equilibrium and steady state. We need to introduce the (positive) vector $E = \ln(1 - F^c) - \ln(1 - F^{nc})$ depending on the number of agents, utility parameters A , interspecific interactions S and discount factor ρ as follows:

$$E(A, S) = \ln \left(\frac{nA + \rho BD}{A + \rho BD} \right) \quad (24)$$

Proposition 7. *Postulate the same assumptions than in Proposition 1. A necessary and sufficient condition for the cooperative equilibrium x_*^c to be larger than the noncooperative equilibrium x_*^{nc} for every species is given by*

$$x_*^c \geq x_*^{nc} \iff (I + S^{-1})E(A, S) \leq 0 \quad (25)$$

The sign of the vector $(I + S^{-1})E(A, S)$ turns out to be ambiguous in the general case as it depends on a lot of parameters including s_{ij} and a_j . However, in the decoupled case without trophic or interspecific interactions (S is diagonal), condition (25) always holds true because S^{-1} is also diagonal with $(S^{-1})_{ii} = \frac{1}{s_{ii}} < -1$ and thus $1 + (S^{-1})_{ii} < 0$ for every species. As vector $E(A, S)$ is always non negative from Proposition 3, we conclude. Therefore, without interspecific interactions, we recover usual results as in Levhari & Mirman (1980) stressing how cooperation promotes the state of every species and in that sense the whole ecosystem.

Section 4 dedicated later on to numerical examples in more complex context with trophic interactions shows how ambiguous the results can be in the general case if the comparison between cooperative and non cooperative outcomes is only carried out species by species. The next paragraph however identifies a global bio-economic index highlighting the gain of cooperation for the state $x(t)$ of the ecosystem over the whole trajectory.

3.7. The value of the ecosystem

The marginal value of species underlying the vector D as well as the value functions associated with the optimality problems in both cooperative and non cooperative cases suggest a way to assess the state $x(t)$ of the ecosystem balancing the functional diversity of matrix S related to species interactions and the ecosystem services relying on preferences A . Let us indeed consider the indicator

$$\text{ECOS}(x) = D' \log(x) = \sum_j D_j \log(x_j). \quad (26)$$

This indicator makes sense in terms of metrics because it can be proved that $D > A \geq 0$ under the assumptions of Proposition 1 for instance⁶. At this stage it is worth to examine the vector D for the two-species case displayed in equations (13) for a predator-prey system. In particular, it can be noted that a species without economic value (typically a prey $a_2 = 0$) is priced and get a strictly positive weight D_2 because of the trophic interactions due to $s_{12} > 0$, the economic utility of predator $a_1 > 0$ and the account of future with discount factor ρ . In other words, D_2 evaluates the marginal (and indirect here) contribution of the prey ($j = 2$) to the ecosystem (provisioning) services related to utility U . More generally, the vector D assesses the marginal contribution of the different species involved in the ecosystem.

Regarding the gains of cooperation, we then can prove that the ecosystem directly benefits from cooperation in the sense of the index ECOS as follows. To achieve this, an extension of the condition $(BD)_j > 0$ used in the propositions below is required.

Proposition 8. *Postulate that $(B^k D)_j > 0$ for every species j and every integer $k \in \mathbb{N}$. The cooperative ecosystem is larger than the noncooperative ecosystem at every time t in the sense that*

$$\text{ECOS}(x^c(t)) \geq \text{ECOS}(x^{nc}(t)) \quad (27)$$

⁶From the very definition of D we derive that $(I - \rho B)D = A$ or equivalently

$$D - A = \rho BD$$

As $BD > 0$ then we deduce $D - A > 0$ as expected.

The proof is given in Appendix A.6. The numerical examples and the figures 2, 3 or 4 in the following section 4 display the gains of cooperation for this ecosystem metrics ECOS.

4. Numerical examples

The following simulations illustrate in numerical terms the analytical findings of the previous section. They especially show to what extent cooperation favors biodiversity, catches and the whole ecosystem states as compared to the non cooperative situation. We focus on the most challenging case of trophic interactions. We examine a two-species example followed by two three species case studies. The last example shows how ambiguous the results can be in the general case if the comparison between cooperative and non cooperative outcomes is only carried out species by species.

4.1. A two species ecosystem

Consider first the following stylized numerical example involving two species where the predator is labeled species 1 while species 2 stands for the prey. The biological parameters (approximated at 10^{-4}) are defined by

$$r = \begin{pmatrix} -0.0057 \\ 0.0108 \end{pmatrix} \quad S = \begin{pmatrix} -0.0148 & 0.0003 \\ -0.0097 & -0.0187 \end{pmatrix}.$$

where it can be noted that the negative intrinsic growth rate of the predator entails its collapse without the prey.

The economic context is characterized by equal utility coefficients $a_1 = a_2 = 1$, a discount factor $\rho = 0.98$ for three players $n = 3$.

Using Propositions 1 and 2 to compute the aggregate harvesting mortality rate in the cooperative F^c and non cooperative F^{nc} cases, we obtain (approximated at 10^{-4})

Mortality rates (%)	Species 1	Species 2
cooperative F^c	4.59	3.80
non cooperative F^{nc}	12.63	10.61

Consequently, we recover Proposition 3 which claims that $F_j^{nc} > F_j^c$ for every species $j = 1, 2$. Moreover, for these numerical values, condition $(I + S^{-1})E(A, S) \leq 0$ involved in (25) is satisfied and the steady states for both species are higher in the cooperative case than in the non cooperative case $x_{j,*}^c > x_{j,*}^{nc}$ for $j = 1, 2$. Figure 1 shows that the predator $x_1^c(t)$ and the prey $x_2^c(0)$ perform indeed better in the cooperative case along the

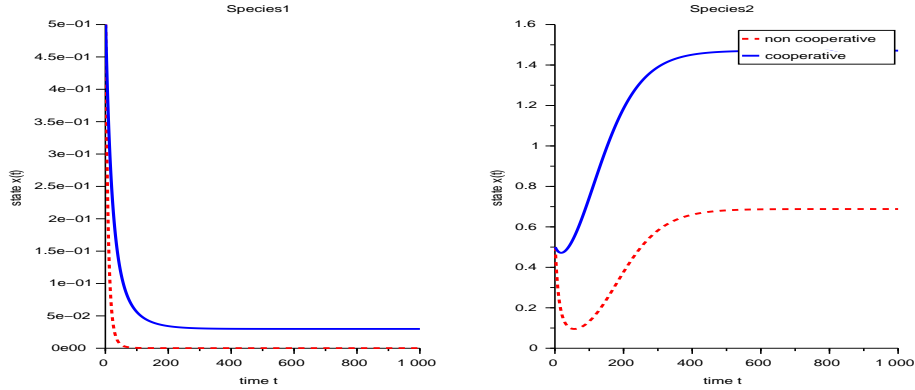


Figure 1: A two species example with trophic interactions and $n = 3$ agents. In blue (solid line) the cooperative trajectories $x_j^c(t)$ for the prey (right) and the predator (left). In red (dotted line) the non cooperative trajectories $x_j^{nc}(t)$. Cooperation performs better for both species. In particular the predator collapses in the non cooperative context. Thus cooperation performs better for biodiversity and the ecosystem.

whole trajectories namely over a time simulation of 1000 periods. In the cooperative case, the stock of the predator decreases from its initial value $x_1^c(0)$ and then converges towards a lower positive equilibrium level $x_{1,*}^c$. By contrast, the predator $x_1^{nc}(t)$ collapses in the non-cooperative case because of the higher harvesting pressure and the lower stock of the prey $x_2^{nc}(t)$ that doesn't allow to maintain the predator stock at viable levels. Hence by reducing the mortality on every species, cooperation prevents the exhaustion of the predator. Hence cooperation favors biodiversity and the ecosystem.

Increasing the number of agents n would also reinforce the gain of cooperation as pointed out by Proposition 5.

Regarding the ecosystem value and the vector D capturing the marginal contributions of species

$$D = (21.74, 26.25)',$$

of interest is the fact that the value of the prey D_2 is strictly larger than the value D_1 although their initial utility value was equal ($a_1 = a_2$). This highlights the indirect positive role played by the prey on the growth of the predator. More globally such a result underlines the complexities underlying the ecosystem functioning and value.

4.2. A three species ecosystem

Consider now another stylized numerical example involving three species where a top predator (species 1), a meso-predator (species 2) and a prey (species 3) are again in trophic interactions. The biological parameters are (approximated at 10^{-4})

$$r = \begin{pmatrix} -0.0026 \\ 0.0392 \\ 0.0644 \end{pmatrix} \quad S = \begin{pmatrix} -0.0218 & 0.0005 & 0.0001 \\ -0.0143 & -0.0153 & 0.0003 \\ -0.0003 & -0.0085 & -0.0161 \end{pmatrix}$$

As in the previous example, the predator is not viable without the other species because of its negative intrinsic growth rate. The economic context is again characterized by a discount factor $\rho = 0.98$ for three players $n = 3$. Utility coefficients now capture how predators are preferred to preys:

$$A = (3 \quad 2 \quad 1)'$$

Using Propositions 1 and 2 to compute the aggregate harvesting mortality rate in cooperative F^c and non cooperative F^{nc} cases, we obtain (approximated at 10^{-4})

Mortality rates (%)	Species 1	Species 2	Species 3
cooperative F^c	5.45	3.91	3.52
non cooperative F^{nc}	14.79	10.88	9.87

Consequently, we recover again Proposition 3 which claims higher catch pressure in the non cooperative context namely $F_j^{nc} > F_j^c$ for every species $j = 1, 2, 3$. Moreover, for these numerical values, condition $(I + S^{-1})E(A, S) \leq 0$ involved in (25) is satisfied and steady states for every species are larger in the cooperative case than in the non cooperative case $x_{j,*}^c > x_{j,*}^{nc}$ for every species j . The top of figure 2 shows that both the predators $x_1^c(t)$ and $x_2^c(t)$ as well as the prey $x_3^c(0)$ are better off in the cooperative case along the whole trajectories namely over a time simulation of 1000 periods. In the cooperative case, the stock of every species converges towards a positive equilibrium levels $x_{j,*}^c$. By contrast, the top predator $x_1^{nc}(t)$ and the prey $x_3^{nc}(t)$ are jeopardized in the non-cooperative case because the harvesting pressure is too high. Hence by reducing the mortality on every species, cooperation avoids the erosion of two species. In other words, the species

richness performs better in the cooperative context. The gains of cooperation for biodiversity and the ecosystem are also displayed in the bottom of Figure 2 through the Simpson index (left)

$$\text{SIMPSON}(x) = 1 - \sum_j \left(\frac{x_j}{\sum_l x_l} \right)^2 \quad (28)$$

as well as the ecosystem value ECOS defined previously in equation (26). It can be observed that both metrics show better performances in the cooperative framework. For the metrics ECOS, the simulations confirms the Proposition 8. Hence cooperation favors biodiversity and the ecosystem. Increasing the number of agents n would again reinforce the gain of cooperation.

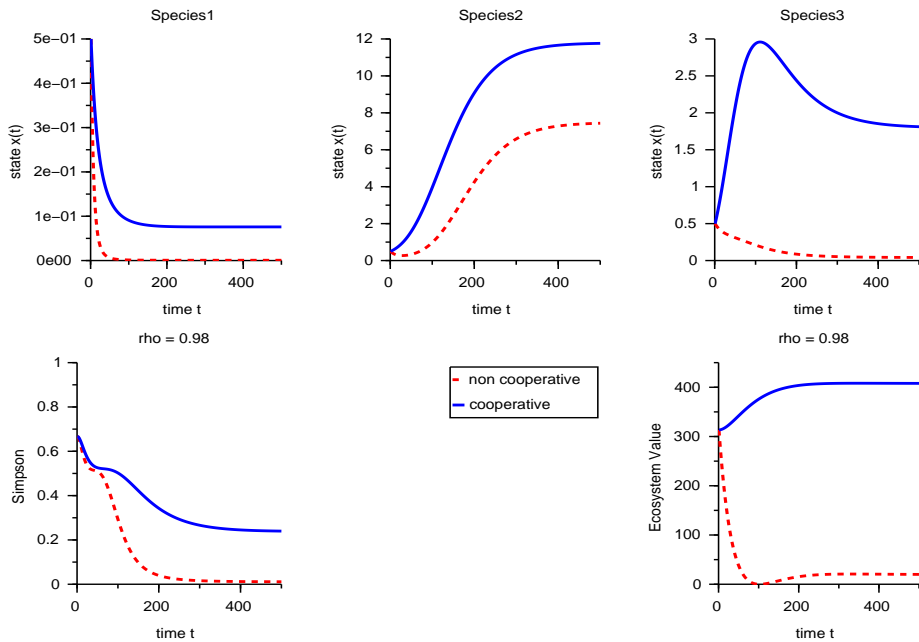


Figure 2: A three species example with trophic interactions. In blue (solid line) the cooperative trajectories. In red (dotted line) the non cooperative trajectories. On the top, stock states $x_j^{nc}(t)$ and $x_j^c(t)$ for the prey (right), the top predator (left) and the meso-predator (center). Cooperation performs better for every species. In particular both the predator and the prey are jeopardized in the non cooperative context. On the bottom the Simpson index and ecosystem index ECOS(t). Thus cooperation also performs better for these metrics.

Examining the marginal prices $D \approx (54 \ 51 \ 28)'$ induced by the value function shows that the trophic relations combined with the intertemporal

viewpoint significantly affect the initial utility preferences underlying A . In particular, the important marginal contribution of species 2 as compared to its initial utility weight points out its major role in the ecosystem functioning as a meso-predator and the indirect effects underlying the trophic web.

4.3. Why cooperation is not sufficient

The following example shows how things can be complex and ambiguous because non cooperation can promote the state of some species in some cases when the number of agents remains bounded.

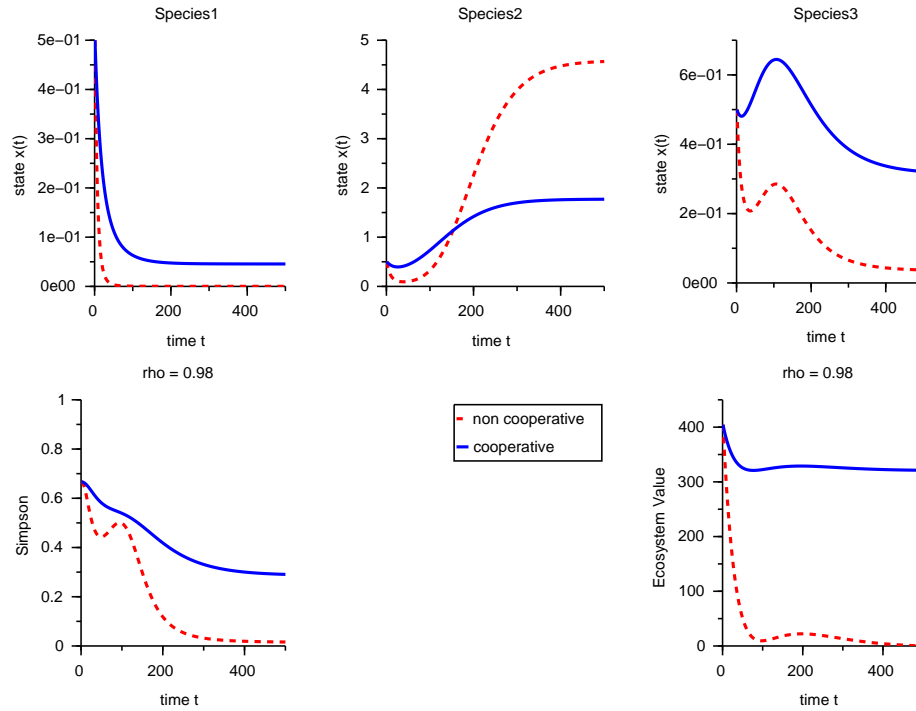


Figure 3: An ecosystem where cooperation is more ambiguous in terms of biodiversity performances. On the top, in blue (solid line) the cooperative trajectories $x_j^c(t)$ for the prey (right), the top predator (left) and the meso-predator (center). In red (dotted line) the non cooperative trajectories $x_j^{nc}(t)$. Non cooperation performs better for meso-predator species. However on the bottom the Simpson diversity index and the value of the ecosystem ECOS show better performances with cooperation.

Consider the stylized numerical example involving again three species $n = 3$ where a top predator (species 1), a meso-predator (species 2) and a prey (species 3) are again in trophic interactions. The predators are again

supposed to be preferred in economic demand terms. As compared to the previous numerical example, the trophic intensity between species has been reinforced through S_{jk} . Thus the bio-economic parameters (approximated at 10^{-5}) are

$$r = \begin{pmatrix} -0.00002 \\ 0.00018 \\ 0.00027 \end{pmatrix} \quad S = \begin{pmatrix} -0.01902 & 0.00072 & 0.00030 \\ -0.01819 & -0.01766 & 0.00054 \\ -0.00757 & -0.01364 & -0.01254 \end{pmatrix} \quad A = \begin{pmatrix} 3 \\ 2 \\ 1 \end{pmatrix}$$

Figure 3 shows how non cooperation fosters the meso-predator species contrary to previous examples. The intuition for such a result to occur is that the extinction of the top-predator (species 1) in the non cooperative framework favors the meso-predator (species 2) by limiting its predation by predator 1 and compensates the loss of preys (species 3) after a transition period. However, although species 2 performs better asymptotically in the non cooperative case, the computation of usual diversity indicators show that biodiversity still benefits from cooperation. For instance, the species richness is higher in the long run with cooperation since the top predator collapses without cooperation. Computing the Simpson index as displayed on the bottom (left) of figure 3 also highlights the advantage of cooperation. Similarly the ecosystem value $ECOS(t)$ (right) displays higher levels for cooperation as expected from the Proposition 8.

Discount factor ρ	Mortality gains of cooperation $F_j^{nc} - F_j^c$			Species contribution D_j			Equilibrium state gaps of cooperation $x_j^{*,c} - x_j^{*,nc}$		
	$j = 1$	$j = 2$	$j = 3$	$j = 1$	$j = 2$	$j = 3$	$j = 1$	$j = 2$	$j = 3$
0.9	0.1	0.1	0.09	22.79	16.42	9.11	0	-0.03	0.01
0.91	0.1	0.09	0.08	24.56	17.84	10.01	0	-0.09	0.01
0.92	0.09	0.08	0.08	26.63	19.51	11.11	0	-0.15	0.02
0.93	0.08	0.08	0.07	29.06	21.54	12.48	0	-0.23	0.03
0.94	0.08	0.07	0.06	31.95	24.01	14.23	0.01	-0.31	0.05
0.95	0.07	0.06	0.05	35.44	27.1	16.54	0.01	-0.42	0.07
0.96	0.06	0.06	0.05	39.72	31.06	19.75	0.02	-0.53	0.1
0.97	0.06	0.05	0.04	45.02	36.23	24.48	0.03	-0.67	0.15
0.98	0.05	0.04	0.03	51.6	43.07	32.15	0.05	-0.81	0.21
0.99	0.05	0.04	0.02	59.82	51.41	46.63	0.07	-0.84	0.24
1	0.04	0.04	0.01	75.03	51.61	83.76	0.11	0.06	-0.54

Table 1: The impact of the discount factor ρ .

At this stage we can question the impact of the discount factor on the outcomes and the sustainability of the ecosystem. Increasing the preference for the future through an increase in the discount factor ρ turns out to entail ambiguous effects as captured by Table 1.

On one hand, it enhances the ecosystem value by significantly increasing the value of the marginal contributions D_j of every species j . In the same vein, examining the impact of ρ on the gains of cooperation $F_j^{nc} - F_j^c$ at the mortality levels, we observe that it decreases with ρ for every species putting emphasis on the fact that the optimal rules between cooperative and non cooperative strategies tend to coincide. However, focusing on the equilibrium state gaps $x^{*,c} - x^{*,nc}$ as used in Proposition 7, we remark that both the meso-predator (species 2) or the prey (species 3) do not always take advantage of higher discount factors because the differences become negative at particular levels illustrating that the cooperative equilibrium is smaller than the non cooperative one. In particular, cooperation is detrimental to the prey with a strong discount factor $\rho = 1$. Again this is induced by the complexities of the trophic web.

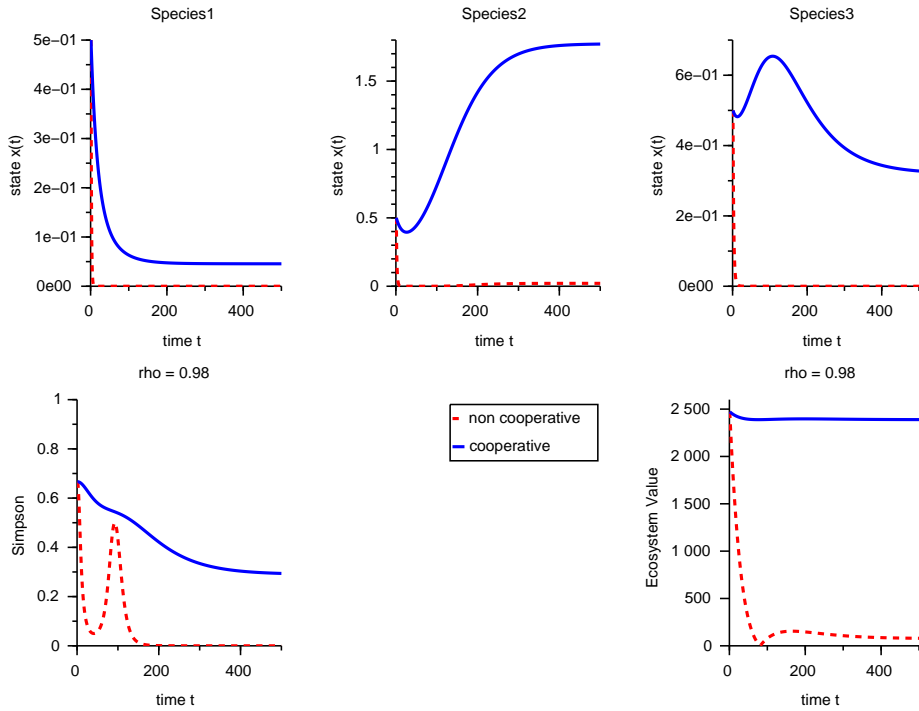


Figure 4: When the number of agents increases to $n = 22$: The ecosystem performs better with cooperation in terms of biodiversity performances. In blue (solid line) the cooperative trajectories $x_j^c(t)$ for the prey (right), the top predator (left) and the meso-predator (center). In red (dotted line) the non cooperative trajectories $x_j^{nc}(t)$. Cooperation performs better for every species, the Simpson diversity index and the ecosystem value ECOS.

However, when the number of agents significantly increases to $n = 22$, the non cooperative gains vanish as shown by figure 4 because the mesopredator is also jeopardized by non cooperative strategies. This is consistent with Proposition 5 claiming that with a high number of agents harvesting the ecosystem, the species richness is strongly altered by non cooperative strategies as compared to cooperative behaviors.

5. Discussion and conclusion

This paper adopts an ecosystem based approach to revisit the tragedy of open-access and over-exploitation issues. More specifically, it provides a bio-economic generalization of the multi-species and multi-agents approach of the fish-war model of Fisher and Mirman (1992, 1996). This extension stems from the use in discrete time of the multi-species Gompertz dynamics where ecological (typically trophic) interactions between species occur. It enables us to compare both theoretically and empirically the impact of cooperative and non cooperative harvesting strategies on the ecosystem.

Results clearly show that cooperation implies lower harvesting mortality rate than non cooperation and in this sense less harvesting pressure over the whole ecosystem. This a first contribution to the well-known issue of the tragedy of the commons. Moreover, the gains in terms of biodiversity and ecosystems performances are also clearly highlighted whenever the number of agents is high. This justifies the title of the paper stressing "the tragedy of open ecosystem" since an open or unregulated ecosystem implicitly entails a non cooperative situation where the agents exploit the commodities or services delivered by the ecosystem as soon as they benefit from the harvesting of underlying stocks. The gains of cooperation turn out to be more tricky for the ecosystem state when the number of agents remains limited because it depends in a complex way on species interactions, on species preferences and on future preferences based on the discount factor as already pointed out in Fischer & Mirman (1996) in the two species context. The case of trophic relationships is the most difficult to address. However, the paper identifies an ecosystem value relying on the marginal contribution of every species proving the gains the cooperation between agents in a general context. In line with this, stylized numerical examples also show how cooperation can promote biodiversity by preventing predators to collapse in contrast to the non cooperative case. The ecological gain is also reinforced by the use of the Simpson biodiversity metrics for these simulations. All these results question the choice of relevant biodiversity indicators (Magurran, 1988) to assess the biodiversity performances of harvesting strategies

as stressed in Doyen *et al.* (2013). It suggests the account of explicit biodiversity value as in Brock & Xepapadeas (2003) or constraints in the optimal control problem. Regarding this last point, another alternative would consist in adopting a viable control approach aimed at balancing biodiversity and economic constraints as in Pereau *et al.* (2012).

Furthermore, the modeling prospect developed in the present paper is in line with "models of intermediate complexity" as proposed in Plaganyi *et al.* (2014) to operationalize the ecosystem based approach for biodiversity and ecosystems services management. These models of intermediate complexity, such as the one examined here allow to address the ecosystem approach at medium scales in the sense of a trade-off between analytically tractable models as MEY-MSY approaches (Larkin *et al.*, 2011) for single stocks and very high dimensional and numerical models trying to capture the "end-to-end" complexity of the ecosystem at play. These latter "end-to-end" models are usually characterized by reduced mathematical understanding and may appear as "black boxes". In that respect, the present work paves the road toward the mathematical control of complex decision models for the management of ecosystems and socio-ecosystems.

Many improvements of the present game modeling are of course possible. The account of uncertainties through a stochastic control framework as in DeLara & Doyen (2008) would be worthwhile to reinforce the relevance of the mathematical model used here for operationalizing the ecosystem based approach. Moreover, using profit and integrating effort costs instead of only considering utility of catches, would also improve the reliability of the whole modeling work by fitting more with well known bio-economic MEY targets promoting the reconciliation between economic and ecological goals. Moreover the heterogeneity of agents should be taken into account as in Cissé *et al.* (2013). Lastly, it would be interesting to analyze the issue of cooperation in terms of coalition formation models as in Kwon (2006); Breton & Keoula (2011) or Doyen & Pereau (2012) because it would make possible the refinement of the results related to the tragedy of open ecosystems between the two extreme cases of cooperative and individualistic behaviors and favors an analysis in terms of community based management and governance of socio-ecosystems.

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Appendix A. Proofs

Appendix A.1. Proof of Proposition 1

First set the vector $y(t) = \ln(x(t)') = (\ln(x_1), \dots, \ln(x_m))'$. Taking the logarithm of ecosystem dynamics (2) controlled by the harvesting mortalities $F = (F_1, \dots, F_m)'$ gives the linear dynamics written in matrix form

$$y(t+1) = r + B' \ln(1 - F) + B'y(t). \quad (\text{A.1})$$

where we use the notation $B = (I + S)'$ as defined in equation (7). Using the change of variable from $x(t)$ to $y(t)$, Bellman equation corresponding to the non cooperative optimization problem (5) can be written as follows

$$V_i(y) = \max_{F_i} \left\{ A'(y + \ln F_i) + \rho V_i(\ln(G((1 - F_i - F_{-i})x))) \right\}.$$

where F_{-i} stands for the aggregate catch mortalities of players different than i . Using the dynamics (A.1), it reads

$$V_i(y) = \max_{F_i} \left(A' \ln F_i + A'y + \rho V_i(r + B' \ln(1 - F_i - F_{-i}) + B'y) \right).$$

Assuming that the value function takes the linear form $V_i(y) = C + D'y$ where C and D are vectors of size $(m \times 1)$, we obtain

$$V_i(y) = \max_{F_i} \left(\begin{array}{c} A'y + A' \ln F_i + \rho C \\ + \rho D' \left(r + B' \ln(1 - F_i - F_{-i}) + B'y \right) \end{array} \right).$$

First order optimality conditions give for every species j

$$\frac{a_j}{F_{ij}} = \frac{\rho (BD)_j}{1 - F_{ij} - F_{(-i)j}}$$

We deduce that users are identical in the sense that $F_{ij} = F_j$ for every i . Thus $F_{(-i)j} = (n-1)F_{ij}$ and we obtain

$$F_{ij}^{nc} = \frac{a_j}{na_j + \rho (BD)_j}.$$

The aggregate non-cooperative harvesting rate is

$$F_j^{nc} = \frac{na_j}{na_j + \rho (BD)_j}.$$

as required. The scarcity constraint $F_j^{nc} \leq 1$ is satisfied because of assumption $\rho (BD)_j > 0$.

The vector D is obtain by identification with the form of the value function $V(y) = C + D'y$. We obtain⁷

$$A' + \rho D'B' = D',$$

or equivalently $D = (I - \rho B)^{-1} A$.

Appendix A.2. Proof of Proposition 2

We proceed in the same manner than for Proposition 1. The value function associated to the Bellman equation is

$$V(y) = \max_{F_j} \left(A' \ln F + A'y + \rho V \left(r + (I + S) \ln(1 - F) + B'y \right) \right),$$

which can be rewritten as follows by assuming that the value function take the form $V(y) = C + D'y$ with C and D vectors of size $(m \times 1)$

$$V(y) = \max_{F_j} \left(\begin{array}{c} A' \ln F + A'y + \rho C \\ + \rho (D'r + D'B' \ln(1 - F) + D'B'y) \end{array} \right).$$

⁷The computation of the term C^{nc} is omitted.

First optimality condition gives

$$\frac{a_j}{F_j} - \frac{\rho(BD)_j}{1 - F_j} = 0 \Leftrightarrow F_j^c = \frac{a_j}{a_j + \rho(BD)_j}.$$

The condition $F_j^c \leq 1$ is again induced by the assumption $(BD)_j \geq 0$. We obtain the same value for vector D using an identification mechanism for the value function. The value functions for the cooperative and non cooperative cases differ only through the constant C .

Appendix A.3. Proof of sensibility with respect to utility preferences a

To compute the sensitivity with respect to preferences a_k ($k \neq j$), we first write

$$F_j^{nc} = \frac{n}{\left(n \vec{1} + \rho B(I - \rho B)^{-1} \frac{A}{a_j}\right)_j}.$$

We deduce that

$$\frac{\partial F_j^{nc}}{\partial a_k} = - \frac{n \rho (B(I - \rho B)^{-1})_{jk}}{a_j \left(n \vec{1} + \rho B(I - \rho B)^{-1} \frac{A}{a_j}\right)_j^2}$$

We use the relation

$$(I - \rho B)^{-1} = \sum_{k=0}^{\infty} (\rho B)^k = I + (\rho B) + (\rho B)^2 + \dots$$

to claim that $B(I - \rho B)^{-1} = \frac{1}{\rho}((I - \rho B)^{-1} - I)$. When ρ is close enough to zero, we obtain that $(I - \rho B)^{-1} \approx I + \rho B$ and thus we have

$$\text{sign} \left(\frac{\partial F_j^{nc}}{\partial a_k} \right) \approx -\text{sign}(B_{jk}) = -\text{sign}(S'_{jk}) \quad (\text{A.2})$$

Therefore, if k is a predator of j , we obtain that $\text{sign}(\frac{\partial F_j^{nc}}{\partial a_k}) < 0$ and consequently that an increase in the preference for this predator k dampens the catch pressure on the prey j .

Moreover, we can prove that

$$0 \leq \frac{\frac{\partial F_j^{nc}}{\partial a_k}}{\frac{\partial F_j^c}{\partial a_k}} = \frac{n \left(\vec{1} + \rho B(I - \rho B)^{-1} \frac{A}{a_j} \right)_j^2}{\left(n \vec{1} + \rho B(I - \rho B)^{-1} \frac{A}{a_j} \right)_j^2}.$$

For a high number of agents $n \rightarrow \infty$, we have $\sqrt{\frac{1}{n}} \left(\rho B (I - \rho B)^{-1} \frac{A}{a_j} \right)_j < 1$ and consequently

$$0 \leq \frac{\frac{\partial F_j^{nc}}{\partial a_k}}{\frac{\partial F_j^c}{\partial a_k}} \leq 1.$$

For a predator k of a prey j , the previous inequality reads

$$\frac{\partial F_j^{nc}}{\partial a_k} \geq \frac{\partial F_j^c}{\partial a_k}$$

which the desired relation.

Appendix A.4. Proof of Proposition 5

In the cooperative case, we know from Proposition 2 that

$$F_j^c(t) = \frac{a_j}{a_j + \rho(BD)_j}. \quad (\text{A.3})$$

Consequently from assumption $BD > 0$, we derive that

$$F_j^c(t) < 1, \forall j$$

Assume now for a while that $\lim_{n \rightarrow +\infty} x_j^c(1) = 0$. From Gompertz dynamics (1), it implies that

$$x_j^c(0) = 0 \text{ or } F_j^c(0) = 1 \text{ or } \exp \left(1 + r_j + \sum_{k=1}^m s_{jk} \ln(x_k(0)(1 - F_k^c(0))) \right) = 0$$

This is contradictory since the initial state $x_j^c(0)$ is supposed to be strictly positive in all of its components and the exponential is also strictly positive.

We proceed iteratively to get the assertion for every time $t = 2, \dots$

Appendix A.5. Proof of Proposition 7

Using dynamics (A.1), the steady states $x(t+1) = x(t) = x_*$ are characterized for every species j by

$$-\sum_{k=1}^m s_{jk} \ln(x_*)_k = \left(1 + \sum_{k=1}^m s_{jk} \right) \ln(1 - F_j) + r_j$$

Assuming that S is invertible, this reads in matrix form:

$$\ln(x_*) = -S^{-1}L$$

with $L = r + B' \ln(1 - F)$ where the notation $\ln(x)$ means the vector of logarithms by species namely $(\ln(x))_j = \ln(x_j)$. The comparison between biomass in the cooperative x_*^c and non cooperative x_*^{nc} cases yields

$$\ln(x_*^c) - \ln(x_*^{nc}) = -S^{-1}(L^c - L^{nc}).$$

Substituting the expression of L^c and L^{nc} yields the Proposition 7.

Appendix A.6. Proof of Proposition 8

Consider the optimal cooperative $x^c(t)$ and non cooperative $x^{nc}(t)$ trajectories starting from the same initial state x_0 . Let us prove that

$$\text{ECOS}(x^{nc}(t)) \leq \text{ECOS}(x^c(t)), \forall t = 0, 1, \dots$$

Taking the logarithm formulation of equation (2), we can derive by iteration that

$$y(t) = B^{t'}y_0 + \sum_{s=0}^{t-1} B^{s'}r + \sum_{s=1}^t B^{s'} \ln(1 - F)$$

We deduce that

$$\text{ECOS}(x^{nc}(t)) - \text{ECOS}(x^c(t)) = D' \sum_{s=1}^t B^{s'} (\ln(1 - F^{nc}) - \ln(1 - F^c))$$

since the cooperative and non cooperative initial states $y_0^{nc} = y_0^c$ coincide. Using matrix properties, the difference reads as follows

$$\begin{aligned} \text{ECOS}(x^{nc}(t)) - \text{ECOS}(x^c(t)) &= \sum_{s=1}^t D' B^{s'} \left(\ln(1 - F^{nc}) - \ln(1 - F^c) \right) \\ &= \sum_{s=1}^t (B^s D)' \left(\ln(1 - F^{nc}) - \ln(1 - F^c) \right) \end{aligned}$$

The assumption of Proposition 8 guarantees that vector $B^s D$ is positive for every species j and every time s . Moreover, from Proposition 3 related to the gain of cooperation for mortalities, the difference $\ln(1 - F^{nc}) - \ln(1 - F^c)$ is always non positive for every species j . We conclude.

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