

The Tragedy of Open Ecosystems

L. Doyen^{a,*}, A. Cissé^{a,b}, N. Sanz^c, F. Blanchard^b, J-C. Pereau^a

^a*GREThA, UMR CNRS & University of Bordeaux, avenue Léon Duguit, Pessac, France*

^b*IFREMER, Domaine de Suzini, Cayenne, French Guiana, France.*

^c*University of French Guiana, 2091 route de baduel, Cayenne, French Guiana, France*

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 dynamics with inter-specific 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 analytically how harvesting pressure is larger in the non-cooperative case for every species. Then it is examined to what extent gains from cooperation can also be derived for the state of the ecosystem. It turns out that cooperation clearly promotes the conservation of every species when the number of agents is high. When the number of agents remains limited, results are more complicated, especially if a species-by-species viewpoint is adopted. However, we identify two metrics involving the state of every species and accounting for their ecological interactions which exhibit gains from cooperation at the ecosystem scale in the general case. Numerical examples illustrate the mathematical findings.

Keywords: Fish war, Ecosystem, Biodiversity, Bellman optimization, Markov-perfect Nash equilibrium.

JEL Classification: Q20, Q22.

*Corresponding author; Tel. : 33 (0)5 56 84 25 75; Fax : 33 (0)5 56 84 86 47
Email address: luc.doyen@u-bordeaux.fr ()

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. 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 a broader ecosystem-based context remains an open field of research.

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 harvest fraction and a smaller steady-state stock than the cooperative equilibrium. The non-cooperative situation refers to a framework in which each user maximizes their 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 recently been 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) deal with 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 interact. 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

40 relationships, in particular concerning the prey. In the same vein, Datta
41 & Mirman (1999), refining the demand side in a two-species model, also
42 show how results are ambiguous in the sense that they depend on both the
43 preference parameters and the sign of ecological interactions.

44 Generalizing these results based on dynamic games to a general multi-
45 species and multi-agent framework is an important challenge for ecosystem
46 and biodiversity management. This is especially relevant for operationaliz-
47 ing the Ecosystem-Based Fisheries Management (EBFM), which advocates
48 an integrated and bio-economic management of marine resources account-
49 ing for their complexity to promote their sustainability (Pikitch *et al.*, 2004;
50 Sanchirico *et al.*, 2008; Kellner *et al.*, 2011; Doyen *et al.*, 2013). Such a
51 prospect is in line with “models of intermediate complexity”, as proposed in
52 Plaganyi *et al.* (2014). These models of intermediate complexity, such as the
53 dynamic multi-species and multi-agent model studied in the present paper
54 allow to address the ecosystem approach at medium scales for fisheries man-
55 agement. Medium scale means a compromise between very stylized models
56 underlying single species approaches and high dimensional models trying to
57 capture the whole complexity of socio-ecosystems, such as the so-called ‘end-
58 to-end’ modeling (Rose *et al.*, 2010). The intermediate complexity approach
59 is illustrated by recent applied bio-economic works using extended Lotka-
60 Volterra models including Cissé *et al.* (2013) in French Guiana or Hardy *et*
61 *al.* (2013) in the Solomon Islands.

62 In line with these issues, the present article expands the model of Lev-
63 hari & Mirman (1980) to a general multi-species (or multiple groups of
64 species) and multi-agent context. A multi-species Gompertz dynamics as
65 in Mutshinda *et al.* (2009) instead of the seminal Lotka-Volterra dynamics
66 is considered. Such a Gompertz model turns out to be very convenient in
67 mathematical terms. Moreover, fitting again with the Levhari & Mirman
68 (1980) framework, the present study assumes that the overall objective of the
69 agents involved in the harvesting of the ecosystem consists in the maximiza-
70 tion of their discounted utilities derived from the consumption of the differ-
71 ent species. Revisiting the Tragedy of Open Access and over-exploitation
72 issues for a general multi-species ecosystem, the paper addresses two main
73 questions:

- 74 • Is there a gain from cooperation in terms of catch pressure?
- 75 • Is there a gain from cooperation in terms of ecosystem state and bio-
76 diversity?

77 In that regard, the contribution of the paper is threefold. First, analytic

78 results clearly show how cooperation leads to less catch pressure, as com-
79 pared to the non-cooperative case, regardless the number of species in the
80 ecosystem. Second, gains in terms of biodiversity are also clearly elicited
81 whenever the number of agents is high by using the species richness index.
82 Third, even with few agents, two ecosystem and integrated metrics proving
83 an overall gain from cooperation between agents are identified. The first
84 ecosystem metric, relying on ecosystem equilibria, depends only on species
85 interactions, while the second ecosystem criteria, related to the value func-
86 tion of the game, combines both the species interactions and the ecosystem
87 services.

88 The paper is organized as follows: Section 2 presents the bio-economic
89 model based on a multi-species multi-agent dynamics and defines the non-
90 cooperative and cooperative optimality problems. Section 3 is devoted to
91 the analytical results comparing the cooperative and the non-cooperative
92 outcomes in terms of catches, stocks, and biodiversity. Section 4 exemplifies
93 the findings through numerical examples. Section 5 discusses the results and
94 concludes the paper.

95 **2. The bio-economic model**

96 *2.1. The multi-species dynamics*

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

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

102 where r_j stands for the intrinsic growth rate of species j and the coefficient
103 s_{jk} represents the interspecific relationship between species j and k ¹. More
104 specifically, s_{jk} replicates the per capita effect of species k on the growth of

¹The Gompertz dynamics (1) is analogous to that used by Fischer & Mirman (1992) in the two-dimensional case as the equality $x^s = e^{s \log(x)}$ entails that

$$x_j(t+1) = R_j x_j(t)^{\alpha_{jj}} \prod_{k \neq j} x_k(t)^{\alpha_{jk}},$$

105 species j from time t to time $t + 1$. When trophic parameter s_{jk} is positive
 106 and s_{kj} is negative, it means that species k is a prey for predator j . When
 107 s_{jk} and s_{kj} are negative, the two species are in mutual competition. If
 108 both parameters are positive, the two species are in a symbiotic relation.
 109 All diagonal coefficients s_{jj} are supposed to be non-positive $s_{jj} \leq 0$ to
 110 capture the intraspecific competition. The whole set of species interactions
 111 is collected in the squared $(m \times m)$ matrix $S = (s_{jk})$ and the intrinsic growth
 112 rate for species j in the vector $r = (r_j)$. To obtain bounded solutions for
 113 the ecosystem dynamics, it is assumed that $\|S\|_\infty = \max_{j,k} |s_{jk}| < 1$.

114 When the resource is exploited, the dynamics of species becomes

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

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

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

117 Since harvesting reduces species' stocks, the value $x_j - h_j$ measures the
 118 amount of species j available for growth and species interactions into the
 119 next period. Since the catches cannot exceed the stock, the scarcity con-
 120 straint $0 \leq h_j(t) \leq x_j(t)$ is binding for every species j .

121 2.2. Utility of agents

122 Agents, labeled $i = 1, \dots, n$, potentially harvest and derive ecosystem
 123 services from the catch of the m species. Once again following Fischer &

with $R_j = e^{r_j}$, $\alpha_{jj} = 1 + s_{jj}$ and $\alpha_{jk} = s_{jk}$. Interestingly, such a dynamics can also be related to the usual Gompertz mono-specific dynamics in continuous time (Nobile *et al.*, 1982)

$$\dot{x}(t) = rx(t) \log \left(\frac{K}{x(t)} \right)$$

and its 'Lotka-Volterra' version

$$\dot{x}_j(t) = x_j(t) \left(r_j + \sum_k s_{jk} \log(x_k(t)) \right).$$

Using the first order approximation of $x(t+1)$ with respect to $x(t)$ or assuming that the rate of growth $r_j + \sum_k s_{jk} \log(x_k(t))$ remains constant between period t and $t+1$, we precisely obtain dynamics (1).

124 Mirman (1996) and for the sake of simplicity, the agents are assumed to
 125 be identical in the sense that they have the same preferences regarding
 126 consumption of the different species. More specifically, for every agent i ,
 127 the common one-period utility from consuming the basket of catches $h_i =$
 128 $(h_{i,1}, \dots, h_{i,m})$ is a logarithmic function defined as follows:

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

129 where $a_j \geq 0$ captures the preferences² of agents with respect to species j .
 130 More complex utility function coping with consumer preferences for variety
 131 can be found for instance in Quaas & Requate (2013). Cost of harvesting
 132 (Mesterton-Gibbons, 1993) as well as the demand side (Datta & Mirman,
 133 1999) are not taken into account here. In the context of the ‘fish war’,
 134 examples of asymmetric players can be found in Breton & Keoula (2014)
 135 and Doyen & Perea (2012).

136 In line with Levhari & Mirman (1980) in the mono-species case or Fis-
 137 cher & Mirman (1996) in the two-species case, we aim at designing optimal
 138 feedback or Markov-perfect harvesting rules for each species j such that

$$h_{ij}(t) = F_{ij}(t)x_j(t)$$

139 where $F_{ij}(t)$ measures the harvest fraction at time t . Hereafter the vector
 140 $F_i = (F_{i1}, \dots, F_{im})'$ stands for the transpose vector of harvest fractions. The
 141 harvest fractions in the non-cooperative and cooperative cases are denoted
 142 by $F^{nc}(t)$ and $F^c(t)$ respectively.

143 2.3. Non-cooperative vs cooperative optimality problems

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

²The limit $\lim_{h_i \rightarrow 0} U(h) = -\infty$ of the logarithmic utility when catch of one species vanishes, captures a strong incentive both to the diversity in harvesting and to avoid extinction of every species which is interesting in terms of biodiversity conservation. Of interest is also the fact that this utility function is a case of iso-elastic functions where relative risk aversion is constant. Said differently, the marginal utility of the species $\frac{\partial U}{\partial h_j} = \frac{a_j}{h_j}$ goes to infinity when this species goes to extinction. At the opposite end, the marginal utility of the species goes to zero when its catch is very large.

148 In the non-cooperative context, the maximization program of agent $i =$
 149 $1, \dots, n$ can be written as:

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

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

154 In the cooperative case, the program is given by

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

155 again under the dynamics (2) and the scarcity constraint $0 \leq F_{ij}(t) \leq 1$.

156 3. Results

157 3.1. Non-cooperative optimal harvest

To obtain the Markov-perfect Nash (or feedback) solution of this dynamic game (see Dutta & Sundaram (1992); Basar & Older (1995)), we assume that player i believes that the other players use a feedback Markovian strategy (Long, 2010). The Bellman equation corresponding to this optimization problem is

$$\begin{aligned} V_i(x) &= \max_{F_i=(F_{i1}, \dots, F_{im})'} \left\{ U(h_i) + \rho V_i \left(G \left(\left(\left(1 - F_i - \sum_{l \neq i} F_l \right) x \right) \right) \right) \right\} \\ &= \max_{F_i} \left\{ a' \log(F_i x) + \rho V_i \left(G \left(\left(\left(1 - F_i - \sum_{l \neq i} F_l \right) x \right) \right) \right) \right\} \end{aligned} \quad (7)$$

158 where $a = (a_1, \dots, a_m)'$ stands for the $(m \times 1)$ -size transpose vector of preference
 159 parameters of the utility function (4). Using dynamic programming
 160 and assuming the uniqueness of the value function V_i solution of (7), the
 161 optimal catch rate F_{ij}^{nc} can be identified for every agent i as displayed in the
 162 following proposition 1. The proof can be found in Appendix A.1. At this
 163 stage, it is convenient to introduce the notation M for the matrix:

$$M = I + S' \tag{8}$$

164 where I denotes the identity matrix (m, m) . Such a matrix M plays a key
 165 role in the multi-species dynamics. The following notation w is also useful
 166 for the vector:

$$w = (I - \rho M)^{-1} a. \tag{9}$$

167 For the vector w to make sense, it is assumed that

$$I - \rho M \text{ is invertible}^3. \tag{10}$$

168 It turns out that w can be considered as a vector of ‘shadow’ prices for the
 169 different species. This vector w is indeed a marginal value in the sense that
 170 it is a derivative of the value function V with $\frac{\partial V}{\partial \log(x)} = w$ as proved⁴ in
 171 Appendix A.1. The bio-economic interpretation of this vector w is elab-
 172 orated hereafter especially in Section 3.6. The proposition related to the
 173 non-cooperative optimal harvest fraction reads as follows:

174 **Proposition 1.** *Assume that there is a unique value function solution of*
 175 *Nash-Bellman equations (7). Assume also that matrix S is such that condi-*
 176 *tion (10) holds true and that $(Mw)_j > 0$ for every species j . Then the ag-*
 177 *gregate non-cooperative optimal harvest fraction for all species $j = 1, \dots, m$*
 178 *is given by*

$$F_j^{nc}(t) = F_j^{nc} = \frac{na_j}{na_j + \rho(Mw)_j}. \tag{11}$$

179

180 Let us first point out that this optimal harvest fraction $F_j^{nc}(t) = F_j^{nc}$ is
 181 not time-dependent for every species. Although the optimal strategy defined

³This 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 $\det(S) > 0$.

⁴The intuition for the value function to have a log-linear form, namely to be a linear combination of the logarithm of the states $\log(x)$ arises, first, from the form of the utility function $U(x) = a' \log(x)$, which is also linear in $\log(x)$, and, second, from the linearity of the dynamics with respect to the (transformed) state $\log(x(t))$. However, the dynamics is not linear in control, namely catch H or harvest rate F , which makes it possible to use usual first-order optimality conditions in the dynamic programming equation.

182 in terms of harvest rate does not depend on time, catches $h_{ij}(t)$ fluctuate
 183 throughout time for every species due to stock variations and species inter-
 184 actions.

185 Let us now comment on the condition $(Mw)_j > 0$ involved in Propo-
 186 sition 1. This condition justifies compliance with the scarcity constraint
 187 $0 \leq F_j^{nc} < 1$ since the discount factor is strictly positive ($0 < \rho$). The
 188 condition $(Mw)_j > 0$ can be rewritten for a given species j as

$$(1 + s_{jj})w_j + \sum_{k \neq j} s_{kj}w_k > 0, \quad (12)$$

189 where the w_j coefficients depend both on ecological parameters (the in-
 190 terspecies parameters S) and on the economic parameters (the preference
 191 parameters a and the discount factor ρ). Assuming that the weights w_j have
 192 closed levels in the sense that $w_j \approx w_k$, a condition similar to Fischer & Mir-
 193 man (1992) can be derived stating that the sum of the direct effect given by
 194 $(1 + s_{jj})$ and the indirect effect given by $\sum_{k \neq j} s_{kj}$ on the evolution of the
 195 biomass of species j has to be positive. Condition (12) always holds true
 196 when all the species are in a symbiotic relation ($s_{kj} > 0 \forall k$) and the weights
 197 w_j are positive. With only one species and assuming that $s_{11} = \frac{-r}{\log(K)}$ where
 198 K denotes the carrying capacity, condition (12) reads $\log(K) > r$, meaning
 199 that the carrying capacity K is large enough as compared to the intrinsic
 200 growth, which generally occurs.

201 To be in line with the paper of Fischer & Mirman (1996), we assume
 202 for a moment that the number of species is reduced to $m = 2$ species. The
 203 computation of ‘prices’ w through definition (9) yields

$$w_1 = \frac{a_1(1 - \rho(1 + s_{22})) + \rho s_{21}a_2}{\Delta}, \quad (13)$$

$$w_2 = \frac{a_2(1 - \rho(1 + s_{11})) + \rho s_{12}a_1}{\Delta}, \quad (14)$$

where

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

204 stands for the determinant of matrix $I - \rho M = I - \rho(I + S')$. The interpre-
 205 tation of this vector w in bio-economic terms is developed in particular in
 206 Section 3.6. The marginal values w_j imply the following harvesting mortality
 207 for the two species:

$$F_1^{nc} = \frac{n\Delta}{(n - (n - 1)\rho(1 + s_{11}))(1 - \rho(1 + s_{22})) + \rho s_{21} \left(\frac{a_2}{a_1} - (n - 1)\rho s_{12}\right)}, \quad (15)$$

$$F_2^{nc} = \frac{n\Delta}{(n - (n - 1)\rho(1 + s_{22}))(1 - \rho(1 + s_{11})) + \rho s_{12} \left(\frac{a_1}{a_2} - (n - 1)\rho s_{21}\right)}. \quad (16)$$

208 Such relations for two species highlight the complexity and non-linearity
 209 underlying the optimal catch rates with respect to the ecological parameters
 210 as well as the discount factor and the number of agents.

211 3.2. Cooperative optimal harvest

212 In the cooperative case, again using dynamic programming, the harvest
 213 fractions F_j^c can be identified as displayed by the following proposition. They
 214 again involve the preferences a , the vector w defined by (9), and the matrix
 215 M related to species interactions and defined by (8).

216 **Proposition 2.** *Postulate the assumptions of Proposition (1). Then the*
 217 *optimal aggregated cooperative harvest fractions for all species $j = 1, \dots, m$*
 218 *are given by*

$$F_j^c(t) = F_j^c = \frac{a_j}{a_j + \rho(Mw)_j}. \quad (17)$$

219

220 Proposition 2 is a direct consequence of Proposition (1) with only one
 221 player $n = 1$ in the non-cooperative context. In particular, in the two-species
 222 case, the harvest fractions become

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

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

223

224 Although the formulation of these catch rates is simpler than the non-
 225 cooperative one in (16), it remains highly non-linear, in particular because
 226 of the determinant $\Delta = \det(I - \rho M)$.

227 *3.3. The Tragedy of the Commons revisited*

228 Comparing the optimal harvest fractions in both non-cooperative (11)
 229 and cooperative (17) cases leads to the following proposition. It points out
 230 the overall gain from cooperation in terms of catch pressure in the sense
 231 that, for every species, the optimal harvesting rate is strictly higher in the
 232 non-cooperative case as compared to the cooperative context.

233 **Proposition 3.** *Postulate the assumptions of Proposition (1). If the num-*
 234 *ber of agents is strictly greater than one, for all exploited species j , the*
 235 *aggregate optimal non-cooperative harvest fraction is strictly larger than the*
 236 *aggregate optimal cooperative harvest fraction :*

$$n > 1 \implies F_j^{nc} > F_j^c. \quad (18)$$

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

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

239 since $n > 1$, $Mw > 0$ and $\rho > 0$. This result is a generalization in a multi-
 240 species and ecosystem context of the well-known Tragedy of Open Access. It
 241 stresses that harvesting pressure on every species involved in the ecosystem
 242 is strictly greater when the agents fail to cooperate.

243 *3.4. How cooperation promotes biodiversity with many agents*

244 At this stage, we can wonder whether the gains from cooperation stressed
 245 in Proposition 3 in terms of catches can induce better stocks for species $x(t)$
 246 or better biodiversity levels or better ecosystem states. It turns out that the
 247 results are more complicated in terms of stock as compared to harvest. In
 248 particular, the findings depend on the number of agents. We first focus on
 249 the simplest case where the number of agents is very high. Such a situation is
 250 mathematically stylized by considering that the number of agents converges
 251 towards infinity $n \rightarrow +\infty$ as in numerous works on dynamic games. In
 252 particular, Wiszniewska-Matyskiel (2002) relates such an assumption to a
 253 continuum of players. In a similar modeling context, Mesterton-Gibbons
 254 (1993) shows that the stock associated with the non-cooperative outcome
 255 converges to the bio-economic equilibrium (or open access stock) with nil
 256 payoffs for the agents when their number converges towards infinity.

257 Let us first point out that in the non-cooperative case the aggregate
 258 harvest fraction identified in Proposition 1 increases with the number of

259 players⁵. More specifically, whenever $n \rightarrow \infty$, it turns out, as soon as
 260 $a_j > 0$, that $F_j^{nc} \rightarrow 1$ implying the depletion of every exploited stock and
 261 thus the erosion and loss of biodiversity. This result corresponds to the
 262 following proposition.

263 **Proposition 4.** *Postulate the assumptions of Proposition (1). When the*
 264 *agents are numerous and do not cooperate, the exploited species (species*
 265 *such that $a_j > 0$) collapse in the following bio-economic sense:*

$$a_j > 0 \implies \lim_{n \rightarrow +\infty} x_j^{nc}(t) = \lim_{n \rightarrow +\infty} h_j^{nc}(t) = 0, \quad \forall t \geq 1. \quad (19)$$

266 By contrast, when agents do cooperate, the global catches of each species
 267 do not depend on the number of players as claimed by Proposition 2. Thus,
 268 when the number of agents is large, only the individual harvests as part of
 269 the aggregated harvest are reduced. In other words, the stocks and their
 270 dynamics are not altered by a high number of agents in the cooperative case.
 271 We then obtain the following condition as proved in Appendix A.2.

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

$$\lim_{n \rightarrow +\infty} x_j^c(t) > 0 \quad \forall t \geq 1, \forall j \quad (20)$$

275

276 We deduce that the number of surviving species in the cooperative con-
 277 text is larger as compared to the non-cooperative case. In other words,
 278 species richness is strictly greater in the cooperative context for a large
 279 number of agents. This result, captured by Proposition 6 below, is a way
 280 to revisit the Tragedy of Open Access in multi-species, multi-agent, and
 281 ecosystems contexts. It is convenient to introduce the species richness index

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

⁵This results from the computation of the ratio

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

since $(Mw)_j > 0$ for every species j and $\rho > 0$.

282 where $\mathbb{1}_{\mathbb{R}_+^*}$ means the characteristic (Boolean) function of strictly positive
 283 reals⁶.

284 **Proposition 6.** *Postulate the assumptions of Proposition (1). Assume also*
 285 *that at least one species is harvested namely that there exists $a_j > 0$. Con-*
 286 *sider a strictly positive initial state $x_0 > 0$. When the numerous agents do*
 287 *cooperate, the ecosystem is more diverse in the sense that at every time $t > 0$*

$$\text{SR} \left(\lim_{n \rightarrow +\infty} x^c(t) \right) > \text{SR} \left(\lim_{n \rightarrow +\infty} x^{nc}(t) \right) \quad (21)$$

288

289 Although numerous other biodiversity metrics such as the Shannon or Simp-
 290 son index are proposed in the ecological literature, species richness is one of
 291 the most popular because it informs on extinction risks in a very simple man-
 292 ner. Thus Proposition 6 points out that the biodiversity in the ecosystem
 293 is directly altered when many agents exploiting it fail to cooperate. There-
 294 fore, it is another analytical proof of the tragedy of unregulated access. The
 295 ecological viewpoint underlying Proposition 6 constitutes an original contri-
 296 bution in that vein, especially in a multi-species and ecosystem context.

297 3.5. How cooperation promotes biodiversity with few agents

298 When the number of agents is limited, Section 4, which is dedicated to
 299 numerical examples, shows how some species (typically mesopredator) can
 300 benefit from non cooperation. In other words, if the comparison between
 301 cooperative and non-cooperative outcomes is only carried out species by
 302 species, the gains from cooperation for the stocks and states of the ecosys-
 303 tem are more ambiguous. Here, we proceed differently and exhibit a first
 304 aggregated metric for stocks to assess the gains induced by cooperation.
 305 This first ecosystem indicator relies on the equilibria and steady states for
 306 the optimal solutions. Using dynamics (2), stationary states x_* are charac-
 307 terized for every species j by

$$0 = \log(1 - F_j) + r_j + \sum_{k=1}^m s_{jk} \log(x_*)_k + \sum_{k=1}^m s_{jk} \log(1 - F_k)$$

⁶The characteristic function is defined by

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

This reads in matrix form:

$$-S \log(x_*) = r + (I + S) \log(1 - F)$$

308 Assuming that matrix S is invertible, this yields:

$$\log(x_*) = -S^{-1}r - (I + S^{-1}) \log(1 - F)$$

309 In line with that formulation at equilibrium, let us consider the following
310 ecosystem metric:

$$\text{ER}(x) = \exp\left(\sum_{j=1}^m \gamma_j \log(x_j)\right) = \exp\left(\gamma' \log(x)\right) \quad (22)$$

311 where the vector γ is defined by

$$\gamma = -(1, \dots, 1) \cdot (I + S^{-1})^{-1} \quad (23)$$

312 and $(1, \dots, 1)$ means the unit vector of dimension m . The exponential in
313 definition (22) guarantees that the metric $\text{ER}(x)$ is a positive index. Here-
314 after we name this index ER the ecosystem richness in comparison to the
315 species richness used previously. A gain from cooperation can be derived for
316 this ecosystem richness as follows:

317 **Proposition 7.** *Assume that matrices S and $I + S^{-1}$ are invertible. At*
318 *equilibrium, the cooperative management of the ecosystem performs better*
319 *than the non-cooperative management in the sense that*

$$\text{ER}(x_*^c) \geq \text{ER}(x_*^{nc})$$

320

321 A detailed proof is given in Appendix A.3. The intuition for the proof
322 relates to the difference:

$$\log(x_*^c) - \log(x_*^{nc}) = -(I + S^{-1}) \log\left(\frac{1 - F^c}{1 - F^{nc}}\right)$$

323 and catch pressure inequality $F^c < F^{nc}$ underlying Proposition 3.

At this stage, we can point out that this ecosystem metric has strong similarities to a trophic index (Pauly & Watson, 2005) advocated for ecosystem management for fisheries in relation to the metaphor of ‘fishing down the food web’. To illustrate this claim, consider the 2D example of a very

simple predator-prey ecosystem where the interactions between species are captured by the matrix

$$S = \begin{pmatrix} 0 & \alpha \\ -\beta & 0 \end{pmatrix}$$

324 where α and β are positive parameters. Using equation (23), we can indeed
 325 compute the vector $\gamma = (\gamma_1, \gamma_2)'$:

$$\gamma = -(1 \ 1)(I+S^{-1})^{-1} = -\frac{1}{1+\alpha\beta}(1 \ 1) \begin{pmatrix} \alpha\beta & \alpha \\ -\beta & \alpha\beta \end{pmatrix} = \frac{1}{1+\alpha\beta}(-\alpha\beta+\beta \ -\alpha\beta-\alpha).$$

326 Since $-\alpha\beta + \beta > -\alpha\beta - \alpha$ and consequently $\gamma_1 > \gamma_2$, such a computation
 327 suggests that the ecosystem richness ER gives more weight to the predator
 328 than to the prey and accounts for their trophic interaction intensity.

329 At this stage, let us emphasize that the numerical examples described
 330 in Section 4 for three-species food webs point out the extent to which the
 331 gains from cooperation can be ambiguous if the analysis is only carried
 332 out species by species. By contrast, the ecosystem richness $ER(x)$ proposed
 333 here is a generic aggregation between species that takes into account for
 334 the structure and intensity of their relationships and exhibits a gain from
 335 cooperation in every case. Interestingly, this indicator ER only depends on
 336 the ecology through the matrix S of interactions between species. However,
 337 the quantitative gain from cooperation $ER(x_*^c) - ER(x_*^{nc})$ is affected by the
 338 economic parameters (the discount rate ρ , the preferences of agents a , and
 339 the number of agents) as it also depends on the spread between the harvest
 340 rates F^c and F^{nc} .

341 Furthermore, it is worth stressing that this gain from cooperation is
 342 only proved for equilibria of the system. The next paragraph also identifies
 343 a global bio-economic index that leads to a gain from cooperation over the
 344 whole optimal trajectory and transient of the state $x(t)$ of the ecosystem.

345 3.6. The value of the ecosystem

346 The marginal value of species underlying the vector w as well as the value
 347 functions V associated with the optimality problems in both cooperative and
 348 non-cooperative cases suggest a way to assess the state $x(t)$ of the ecosystem,
 349 balancing the functional diversity of matrix S related to species interactions
 350 and the ecosystem services relying on preferences a . Indeed, let us consider
 351 the indicator

$$ECOS(x) = w' \log(x) = \sum_j w_j \log(x_j). \quad (24)$$

352 This indicator makes sense in terms of metrics because it can be proved that
 353 $w > a \geq 0$ under the assumptions of Proposition 1 for instance⁷. At this
 354 stage, it is worth examining the vector w for the two-species case displayed in
 355 equation (14) for a predator-prey system. In particular, it can be emphasized
 356 that a species without economic value, typically a prey such that $a_2 = 0$, is
 357 priced in the sense that it gets a strictly positive weight $w_2 > 0$. Such a
 358 result occurs because of the trophic interactions due to $s_{12} > 0$, the economic
 359 utility of predator $a_1 > 0$, and the account of future with discount factor ρ .
 360 In other words, w_2 evaluates the marginal (and indirect here) contribution
 361 of the prey ($j = 2$) to the ecosystem (provisioning) services related to utility
 362 U . More generally, the vector w assesses the marginal contribution to the
 363 ecosystem services U of the different species involved in the ecosystem.

364 Regarding the gains from cooperation, we then can prove that the ecosys-
 365 tem directly benefits from cooperation in the sense of the index ECOS as
 366 follows. To achieve this, an extension of the condition $(Mw)_j > 0$ used in
 367 the propositions below is required.

368 **Proposition 8.** *Postulate that $(M^k w)_j > 0$ for every species j and every*
 369 *integer $k \in \mathbb{N}$. The cooperative ecosystem performs better than the nonco-*
 370 *operative ecosystem at every time t in the sense that*

$$\text{ECOS}(x^c(t)) \geq \text{ECOS}(x^{nc}(t)) \quad (25)$$

371

372 The proof is given in Appendix A.4. The numerical examples and Figures
 373 2, 3, and 4 in Section 4 display the gains from cooperation for this ecosystem
 374 metric ECOS.

375 4. Numerical examples

376 The following simulations illustrate in numerical terms the analytical
 377 findings of the previous section⁸. They especially show to what extent co-
 378 operation favors biodiversity, catches and the whole ecosystem states as

⁷From the very definition of w (eq 9), we derive that $(I - \rho M)w = a$ or equivalently

$$w - a = \rho Mw$$

As $Mw > 0$ then we deduce $w - a > 0$ as expected.

⁸Simulations have been done using the scientific software Scilab 5.5. The numerical codes are displayed in appendix.

379 compared to the non cooperative situation. We focus on the most chal-
 380 lenging case of trophic interactions. Two examples involving three species
 381 are examined. The second example in particular shows how a species can
 382 benefit from non-cooperation and that the comparison between cooperative
 383 and non-cooperative performances based on a species-by-species viewpoint
 384 has to be overcome with more integrated indicators.

385 *4.1. A three-species ecosystem*

386 Consider a stylized numerical example involving three species in a situ-
 387 ation of omnivory as illustrated by Figure 1: A top predator (species 1), a
 388 mesopredator (species 2) and a prey (species 3) are in trophic interactions.
 389 The biological parameters are (rounded to 10^{-4})

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

390 Note that the predator is not viable without the other species because of its
 391 negative intrinsic growth rate $r_1 < 0$. The economic context is characterized
 392 by a discount factor $\rho = 0.98$ for three players $n = 3$. Utility coefficients
 393 now capture how predators are preferred to preys:

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

394 Using Propositions 1 and 2 to compute the aggregate harvest fraction in
 395 cooperative F^c and non-cooperative F^{nc} cases, we obtain (rounded to 10^{-4})

harvest fractions (%)	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

397 Consequently, Proposition 3, which claims higher catch pressure in the non-
 398 cooperative context, namely $F_j^{nc} > F_j^c$ for every species $j = 1, 2, 3$, is again
 399 confirmed. Moreover, for these numerical values, the steady state for every
 400 species is larger in the cooperative case than in the non-cooperative case
 401 $x_{j,*}^c > x_{j,*}^{nc}$. The top of Figure 2 shows that both the predators $x_1^c(t)$ and
 402 $x_2^c(t)$ as well as the prey $x_3^c(0)$ are better off in the cooperative case over
 403 all the trajectories namely, over a time simulation of 1000 periods. In the
 404 cooperative case, the stock of every species converges towards a positive
 405 equilibrium level $x_{j,*}^c$. By contrast, the top predator $x_1^{nc}(t)$ and the prey

406 $x_3^{nc}(t)$ are jeopardized in the non-cooperative case because the harvesting
 407 pressure is too high. Hence, by reducing the mortality on every species,
 408 cooperation prevents erosion of the prey and loss of the predator. In other
 409 words, species richness performs better in the cooperative context. The
 410 gains from cooperation for biodiversity and the ecosystem are also displayed
 411 at the bottom of Figure 2 through the Simpson index (left)

$$\text{SIMPSON}(x) = 1 - \sum_j \left(\frac{x_j}{\sum_l x_l} \right)^2 \quad (26)$$

412 as well as the ecosystem value ECOS defined previously in equation (24).
 413 It can be observed that both metrics show better score in the cooperative
 414 framework. For the metric ECOS, the simulations confirm Proposition 8.
 415 Hence, cooperation promotes biodiversity and the ecosystem. Increasing
 416 the number of agents n would also reinforce the gain from cooperation as
 417 claimed by Proposition 5.

418 Examining the marginal prices $w \approx (54 \ 51 \ 28)'$ induced by the value
 419 function shows that the trophic relations combined with the intertemporal
 420 viewpoint significantly affect the initial utility preferences underlying a . In
 421 particular, the important marginal contribution of species 2 as compared to
 422 its initial utility weight points out the major role it plays in the ecosystem
 423 functioning as a mesopredator and the indirect effects underlying the trophic
 424 web.

425 4.2. Why cooperation is not sufficient for some species

426 The following example shows how things can be more complicated be-
 427 cause non-cooperation can promote the state of some species in certain cases
 428 where the number of agents remains bounded.

429 Consider a stylized numerical example once again involving three species
 430 $m = 3$ where a top predator (species 1), a mesopredator (species 2) and a
 431 prey (species 3) again engage in a situation of omnivory. The predators
 432 (species 1 and 2) are again assumed to be preferred in terms of economic
 433 demand. As compared to the previous numerical example, the strength of
 434 trophic interactions between species has been reinforced through s_{jk} . Thus
 435 the bio-economic parameters (rounded to 10^{-4}) are

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

436 Figure 3 shows how non cooperation fosters the mesopredator species
 437 contrary to the previous example. The intuition for such a result to occur
 438 is that the extinction of the top predator (species 1) in the non-cooperative
 439 framework promotes the mesopredator (species 2) by limiting its predation
 440 by predator 1 and compensates for the loss of preys (species 3) after a
 441 transition period. Such a situation illustrates the so-called ‘mesopredator
 442 release’ hypothesis (Crooks and Soulé, 2013) where the decline of top preda-
 443 tors in an ecosystem promotes the populations of mesopredators. However,
 444 although species 2 performs better asymptotically in the non-cooperative
 445 case, the computation of usual diversity indicators shows that biodiversity
 446 still benefits from cooperation. For instance, species richness is higher in the
 447 long run with cooperation since the top predator collapses without cooper-
 448 ation. Computing the Simpson index as displayed at the bottom (left) of
 449 Figure 3 also highlights the advantage of cooperation. Similarly, the ecosys-
 450 tem value $ECOS(t)$ (right) displays higher levels for cooperation as expected
 451 from Proposition 8. Furthermore, from Proposition 7 based on the indi-
 452 cator ecosystem richness $ER(x)$, we also know that gains from cooperation
 453 can be exhibited at equilibrium. In other words, we restate the fact that
 454 such a situation of ‘mesopredator release’ is detrimental to biodiversity and
 455 ecosystems.

456 Moreover, when the number of agents significantly increases to $n = 22$,
 457 the non-cooperative benefits on species 2 vanish as shown by Figure 4 be-
 458 cause the mesopredator is also jeopardized by non-cooperative strategies.
 459 This is consistent with Proposition 5 claiming that with a high number
 460 of agents harvesting the ecosystem, species richness is strongly altered by
 461 non-cooperative strategies as compared to cooperative behaviors.

462 As regards ecosystem richness $ER(x)$, when computing the weights γ
 463 underpinning the metric $ER(x)$ as in equation (23), it is of interest to observe
 464 that (rounded to 10^{-3})

$$\gamma = (0.046 \quad 0.031 \quad 0.011)'$$

465 Since $\gamma_1 > \gamma_2 > \gamma_3$, the weights of each species in the indicator strongly re-
 466 late to their trophic levels in the ecosystem in the same vein as the trophic
 467 index (Pauly & Watson, 2005) advocated for ecosystem-based fishery man-
 468 agement.

469 5. Discussion and conclusion

470 This paper adopts an ecosystem-based approach to revisit the Tragedy
 471 of Open Access and over-exploitation issues. More specifically, it provides a

472 bio-economic generalization of the multi-species and multi-agent approach
473 of the ‘fish war’ model of Fisher and Mirman (1992, 1996). This extension
474 stems from the use in discrete time of the multi-species Gompertz dynamics
475 where ecological (typically trophic) interactions between species occur. It
476 enables us to compare both theoretically and numerically the impact of
477 cooperative and non-cooperative harvesting strategies on the ecosystem.

478 Results clearly show that cooperation implies lower harvest fractions
479 than non-cooperation and in this sense less catch pressure over the whole
480 ecosystem. This a first contribution to the well-known issue of the Tragedy
481 of the Commons. Moreover, the gains in terms of biodiversity and ecosystem
482 performance are also clearly highlighted whenever the number of agents is
483 high by using the well-known species richness index. This justifies the title
484 of the paper stressing ‘The Tragedy of Open Ecosystems’ since an open or
485 unregulated ecosystem implicitly induces a non-cooperative situation where
486 the agents exploit the commodities or services delivered by the ecosystem
487 as soon as they benefit from the harvesting of underlying stocks.

488 The gains from cooperation for the ecosystem state turn out to be slightly
489 more tricky when the number of agents remains limited because they de-
490 pend in a complex way on species interactions, species preferences, and
491 future preferences based on the discount factor, as already pointed out in
492 Fischer & Mirman (1996) in the two-species context. The case of trophic
493 relationships is the most difficult to address. In particular, the paper identi-
494 fies situations where mesopredators, namely species of intermediary trophic
495 level, benefit from non-cooperation. Such a configuration exemplifies the so-
496 called ‘mesopredator release’ hypothesis where the erosion of top predators
497 in an ecosystem promotes the populations of mesopredators. However, in
498 the general context, the paper exhibits two ecosystem and integrated criteria
499 proving an overall gain from cooperation between agents.

500 The first ecosystem criterion, named ecosystem richness, relies on ecosys-
501 tem equilibria and depends only on species interactions. Interestingly, this
502 ecosystem metric has strong similarities with the trophic index (Pauly &
503 Watson, 2005) in the sense that it gives greater weight to predators than
504 to preys. The second metric, termed value of the ecosystem, informs on
505 the transients of the trajectories and is based on the value function of the
506 non-cooperative game. It thus depends on both ecological and economic pa-
507 rameters. In particular, the weight of every species in this metric captures
508 the marginal contribution of species to ecosystem services as a whole. For
509 instance preys without direct economic value are positively priced due to
510 their role in ecosystem functioning and their indirect role in production.

511 Stylized numerical examples also show how cooperation promote bio-

512 diversity by preventing predators from collapsing in contrast to the non-
513 cooperative case. The ecological gain is also reinforced by the use of the
514 Simpson biodiversity metric for these simulations. All these results question
515 the choice of relevant biodiversity indicators (Magurran, 1988) to assess the
516 biodiversity performance of harvesting strategies as stressed in Doyen *et al.*
517 (2013). They suggest accounting for explicit biodiversity values as in Brock
518 & Xepapadeas (2003); Kellner *et al.* (2011) or constraints in the optimal
519 control problem. Regarding this last point, another alternative would con-
520 sist in adopting a viable control approach aimed at balancing biodiversity
521 and economic constraints as in Pereau *et al.* (2012).

522 Furthermore, the modeling prospect developed in the present paper is in
523 line with ‘models of intermediate complexity’ as proposed in Plaganyi *et al.*
524 (2014) to operationalize the ecosystem-based approach for biodiversity and
525 ecosystem services management. These models of intermediate complexity,
526 such as the one examined here, make it possible to address the ecosystem
527 approach at an intermediate scale, as a compromise between analytically
528 tractable models such as MEY-MSY approaches (Larkin *et al.*, 2011) for
529 single stocks and very high dimensional and numerical models trying to cap-
530 ture the ‘end-to-end’ complexity of the ecosystem. These latter ‘end-to-end’
531 models are usually characterized by a reduced mathematical understanding
532 and may appear as ‘black boxes’. In particular, the numerous uncertain-
533 ties affecting the mechanisms of such ‘end-to-end’ modeling as well as the
534 difficulties in parameterizing them can significantly alter the reliability of
535 these models for stakeholders. In that respect, the present work paves the
536 way toward the mathematical control of complex decision models for the
537 management of ecosystems and socio-ecosystems.

538 Many improvements to the present game modeling can of course be
539 made. Taking uncertainties into account through a stochastic control frame-
540 work as in DeLara & Doyen (2008) would be worthwhile to reinforce the
541 relevance of the mathematical model used here for operationalizing the
542 ecosystem-based approach. Moreover, using profit and integrating effort
543 costs instead of only considering the utility of catches, would also improve
544 the credibility of the modeling work as a whole by better corresponding
545 to well-known bio-economic MEY targets that can promote the reconcili-
546 ation between economic and ecological goals. Moreover, the heterogeneity
547 of agents should be taken into account. Lastly, it would be interesting to
548 analyze the issue of cooperation in terms of coalition formation models as in
549 Kwon (2006); Breton & Keoula (2011), or Doyen & Pereau (2012) because
550 it would make it possible to refine the results related to the Tragedy of Open
551 Ecosystems between the two extreme cases of cooperative and individualis-

552 tic behaviors and foster analysis in terms of community-based management
553 and governance of socio-ecosystems in the same vein as Ostrom E. (1990).

554 **Acknowledgments**

555 This work has been carried out with the financial support of the Belmont
556 Forum through the SEAVIEW program. IHP (Institut Henri Poincaré)
557 played also a major role during the three-month international program
558 ‘Mathematics of Bio-Economics’ organized in Paris as part of the event
559 ‘Mathematics of Planet Earth 2013’. Support from the PIG CNRS under
560 the ECOPE, VOGUE and GECO research projects has also been important.

561 **References**

- 562 Bailey, M., Sumaila, U. and Lindroos, M., 2010. Application of game theory
563 to fisheries over three decades. *Fisheries Research*, 102: 1-8.
- 564 Basar, T. and Older., G.J., 1995. *Dynamic Non Cooperative Game Theory*.
565 2nd Ed. London: Academic Press.
- 566 Breton, M. and Keoula, M., 2011. Farsightedness in a coalitional great fish
567 war. *Environmental and Resource Economics* 51, 2, 297-315.
- 568 Breton, M. and Keoula, M., 2014. A great fish war model with asymmetric
569 players. *Ecological Economics*, 97:209-223.
- 570 Brock, W. A. and Xepapadeas, A., 2003. Valuing Biodiversity from an Eco-
571 nomic Perspective: A Unified Economic, Ecological, and Genetic Ap-
572 proach. *American Economic Review*, 93(5), 1597-1614.
- 573 Cissé, A., Gourguet, S., Doyen, L., Blanchard, F. and Pereau, J.-C., 2013. A
574 bio-economic model for the ecosystem-based management of the coastal
575 fishery in French Guiana. *Environment and Development Economics*, 18:
576 245-269.
- 577 Crooks, K.R. and Soulé, M.E., 1999. Mesopredator release and avifaunal
578 extinctions in a fragmented system. *Nature*, 400, 563–566
- 579 Datta, L. and Mirman L., 1999. Externalities, Market Power and Resource
580 Extraction. *Journal of Environmental Economics and Management*, 37:
581 233-255.

- 582 DeLara, M. and Doyen, L., 2008. Sustainable Management of Natural Re-
583 sources: Mathematical Models and Methods. Springer.
- 584 Doyen, L., Cissé, A., Gourguet, S., Mouysset, L., Hardy, P.-Y., Béné,
585 C., Blanchard, F., Jiguet, F., Pereau, J.-C. and Thébaud, O., 2013.
586 Ecological-economic modeling for the sustainable management of biodi-
587 versity. *Computational Management Science*, 10: 353-364.
- 588 Doyen, L. and Pereau, J.-C., 2012. Sustainable coalitions in the commons.
589 *Mathematical Social Sciences*, 63(1): 57-64.
- 590 Dutta, P.K and Sundaram, P., 1992. Markovian equilibrium in a class
591 od stochastic game. Existence theorems for discounted and undiscounted
592 models. *Economic Theory*, 2: 197-214.
- 593 Dutta, P.K and Sundaram, P., 1993. The tragedy of commons. *Economic*
594 *Theory*, 3: 413-426.
- 595 Finus, M., 2001. *Game Theory and International Environmental Coopera-*
596 *tion*. Edward Elgar: Cheltenham.
- 597 Fischer, R. and Mirman, L., 1992. Strategic dynamic interaction. *Journal of*
598 *Economic Dynamics and Control*, 16: 267-287.
- 599 Fischer, R. and Mirman, L., 1996. The Complete Fish Wars: Biological and
600 Dynamic Interactions. *Journal of Environmental Economics and Manage-*
601 *ment*, 30: 34-42.
- 602 Hannesson, R., 1997. Fishing as a Supergame. *Journal of Environmental*
603 *Economics and Management*, 32: 309-322.
- 604 Hardy, P.Y., Doyen, L., Béné, C. and Schwartz, A.M., 2013. Food
605 security - environment conservation nexus: a case study of
606 Solomon Islands' small-scale fisheries. *Environmental Development*.
607 <http://www.sciencedirect.com/science/article/pii/S2211464513000584>
- 608 Kaitala, V. and Munro, G.R., 1995. The economic management of high seas
609 fishery resources: Some game theory aspects. In C. Carraro and J.A. Filar
610 (eds.). *Annals of the International Society of Dynamics Games: Control*
611 *and Game-Theoretic Models of the Environment*, Birkhauser, 299-318,
612 Birkhauser, Boston.
- 613 Kaitala, V. and Lindroos, M., 2007. Game Theoretic Applications to Fish-
614 eries, *Handbook of Operations Research in Natural Resources*, Springer,
615 vol 99, Ed by A. Weintraub et al., 201-215.

- 616 Kellner, J., Sanchirico, J., Hastings, A., and Mumby, P. (2011). Optimizing
617 for multiple species and multiple values: tradeoffs inherent in ecosystem-
618 based fisheries management. *Conservation Letters*, 4(1):21–30.
- 619 Kwon, O.S., 2006. Partial International Coordination in the Great Fish War.
620 *Environmental and Resource Economics*, 33: 463-483.
- 621 Larkin, S. L. , Alvarez, S., Sylvia, G. and Harte, M., 2011. Practical Consid-
622 erations in Using Bioeconomic Modeling for Rebuilding Fisheries. OECD
623 Food, Agriculture and Fisheries Working Papers.
- 624 Levhari, D. and Mirman, L., 1980. The great fish war: an example using a
625 dynamic Cournot-Nash solution. *Bell Journal of Economics*, 11: 322-344.
- 626 Long, N.V., 2010. A survey of Dynamic Games in Economics. World Scien-
627 tific Publishing.
- 628 Magurran, A.E., 1988. Ecological Diversity and its Measurement. Croom
629 Helm Limited, London.
- 630 Mesterton-Gibbons, M., 1993. Game-theoretic resource modeling. *Natural*
631 *Resource Modeling*, 7: 93-146.
- 632 Mesterton-Gibbons M., 1996. ‘A technique for finding optimal two-species
633 harvesting policies’. *Ecological Modeling*, 92: 235-244.
- 634 Mutshinda, C., O’Hara, E. and Woiwod I., 2009. What drives community
635 dynamics? *Proceedings B of the Royal Society*, 276, 2923–2929.
- 636 Nobile, A.G., Ricciardi, L.M. and Sacerdote, L., 1982. On Gompertz growth
637 model and related difference equations. *Biol. Cyb.*, 42, 221-229.
- 638 Ostrom E., 1990. *Governing the commons*. Cambridge University Press.
- 639 Pereau, J.-C., Doyen, L., Little, R. and Thébaud O., 2012. The triple bottom
640 line: Meeting ecological, economic and social goals with individual trans-
641 ferable quotas. *Journal of Environmental Economics and Management*,
642 63: 419-434.
- 643 Pauly, D. and Watson, R., 2005. Background and interpretation of the ‘Ma-
644 rine Trophic Index’ as a measure of biodiversity. *Philos. Trans. R. Soc. B*
645 *Biol. Sci.*, 360, 415-423.

- 646 Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bon, R., Conover,
647 D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D.,
648 Link, J., Livingston, P. A., Mangel, M., McAllister, M. K., Pope, J. and
649 Sainsbury, K. J., 2004. Ecosystem-Based Fishery Management. *Science*,
650 305: 346-347.
- 651 Plagányi et al., 2014. Multispecies fisheries management and conservation:
652 tactical applications using models of intermediate complexity. *Fish and*
653 *Fisheries*, 15, 1: 1-22.
- 654 Quaas, M. and Requate, T., 2013. Sushi or fish fingers? Seafood diversity,
655 collapsing fish stocks, and multi-species fishery management. *The Scan-*
656 *dinavian Journal of Economics*, 115(2): 381-422.
- 657 Rose, K. A. *et al.*, 2010. End-To-End Models for the Analysis of Marine
658 Ecosystems: Challenges, Issues, and Next Steps. *Marine and Coastal Fish-*
659 *eries*, 2, 1, 115–130.
- 660 Wiszniewska-Matyszek A., 2002. Discrete Time Dynamic Games with Con-
661 tinuum of Players I: Decomposable Games, *International Game Theory*
662 *Review*, 4, 331-342.
- 663 Sanchirico, J. N., Smith, M. D. and Lipton, D. W., 2008. An empirical ap-
664 proach to ecosystem-based management. *Ecological Economics*, 64: 586-
665 596.
- 666 Wiszniewska-Matyszek A., 2002. Discrete Time Dynamic Games with Con-
667 tinuum of Players I: Decomposable Games, *International Game Theory*
668 *Review*, 4, 331-342.

669 **Appendix A. Proofs**

670 *Appendix A.1. Proof of Proposition 1*

671 The resolution of the model follows the method proposed by Long (2010)
 672 (see Section 3.1.3 ‘Some technical notes on feedback strategies in fishery
 673 problems’, p 82-84).

674 First set the vector $y(t) = \log(x(t)') = (\log(x_1), \dots, \log(x_m))'$. Taking
 675 the logarithm of ecosystem dynamics (2) controlled by the harvesting rate
 676 $F = (F_1, \dots, F_m)'$ gives the linear dynamics written in matrix form

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

677 where we use the notation $M = (I + S)'$ as defined in equation (8). Using
 678 the change of variable from $x(t)$ to $y(t)$, Bellman equation corresponding to
 679 the non-cooperative optimization problem (5) can be written as follows

$$V_i(y) = \max_{F_i} \{a'(y + \log(F_i)) + \rho V_i(\log(G((1 - F_i - F_{-i})x)))\}.$$

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

$$V_i(y) = \max_{F_i} (a' \log(F_i) + a'y + \rho V_i(r + M' \log(1 - F_i - F_{-i}) + M'y)).$$

Following Long (2010) or Fischer & Mirman (1992), we now prove that the
 value function (assumed to be unique⁹) takes a log-linear form namely it is
 a linear combination of logarithms y in the sense that

$$V_i(y) = v + w'y$$

682 where v and w are vectors of size $(m \times 1)$. We determine the coefficients v
 683 and w by applying the Bellman principle. The Bellman equation for every
 684 agents i becomes

⁹Regarding uniqueness, we have not find out clear proof in the literature. However as
 mentioned in (Fischer & Mirman, 1992), in view of the log-linear nature of the objective
 and dynamics, it seems unlikely that another functional form can serve as a value function.
 This belief is also derived from the functional form of the value function for finite horizon
 versions of this problem. Finally, our belief in the uniqueness of the solution is bolstered by
 the fact that given this log-linear form, there is a unique solution satisfying the functional
 equations.

$$V_i(y) = \max_{F_i} \left(\begin{array}{l} a'y + a' \log(F_i) + \rho v \\ + \rho w' \left(r + M' \log(1 - F_i - F_{-i}) + M'y \right) \end{array} \right).$$

685 First order optimality conditions give for every species j

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

686 We deduce that users are identical in the sense that $F_{ij} = F_j$ for every i .

687 Thus $F_{(-i)j} = (n-1)F_{ij}$ and we obtain

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

688 The aggregate non-cooperative harvesting rate is

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

689 as required. The scarcity constraint $F_j^{nc} \leq 1$ is satisfied because of assump-
690 tion $\rho(Mw)_j > 0$.

691 The vector w is obtained by identification with the form of the value
692 function $V(y) = v + w'y$. We obtain¹⁰

$$a' + \rho w' M' = w',$$

693 or equivalently $w = (I - \rho M)^{-1} a$ as required.

694 *Appendix A.2. Proof of Proposition 5*

695 In the cooperative case, we know from Proposition 2 that

$$F_j^c = \frac{a_j}{a_j + \rho(Mw)_j}. \tag{A.2}$$

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

$$F_j^c < 1, \forall j$$

696 Assume now for a moment that $\lim_{n \rightarrow +\infty} x_j^c(1) = 0$. From Gompertz dy-
697 namics (1), this implies that

¹⁰The computation of the term v^{nc} is omitted.

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

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

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

701 *Appendix A.3. Proof of Proposition 7*

702 By taking the logarithm of the exploited dynamics (2) at the steady state
703 $x_j(t+1) = x_j(t) = x_{*j}$, we obtain

$$\log(x_{*j}) = \log(x_{*j} - h_j) + r_j + \sum_k s_{jk} \log(x_{*k} - h_k)$$

704 Since $h_j = F_j x_j$ it yields

$$\begin{aligned} \log(x_{*j}) &= \log((1 - F_j) x_{*j}) + r_j + \sum_k s_{jk} \log((1 - F_k) x_{*k}) \\ 0 &= \log(1 - F_j) + r_j + \sum_k s_{jk} \log(1 - F_k) + \sum_k s_{jk} \log x_{*k} \end{aligned}$$

705 In matrix form, it gives

$$\begin{aligned} 0 &= (I + S) \log(1 - F) + r + S \log(x_*) \\ -S \log(x_*) &= (I + S) \log(1 - F) + r \end{aligned}$$

706 where the notation $\log(x)$ means the vector of logarithms by species namely
707 $(\log(x))_j = \log(x_j)$. Assuming that S is invertible, this reads:

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

708 with $L = r + M' \log(1 - F)$. The comparison between species states in the
709 cooperative x_*^c and non-cooperative x_*^{nc} cases yields

$$\log(x_*^c) - \log(x_*^{nc}) = -S^{-1}(L^c - L^{nc}) = -(I + S^{-1}) \log\left(\frac{1 - F^c}{1 - F^{nc}}\right).$$

710 We deduce that

$$\begin{aligned}
\frac{\text{ER}(x_*^c)}{\text{ER}(x_*^{nc})} &= \frac{\exp(-(1, \dots, 1) \cdot (I + S^{-1})^{-1} \log(x_*^c))}{\exp(-(1, \dots, 1) \cdot (I + S^{-1})^{-1} \log(x_*^{nc}))} \\
&= \exp(-(1, \dots, 1) \cdot (I + S^{-1})^{-1} (\log(x_*^c) - \log(x_*^{nc}))) \\
&= \exp\left((1, \dots, 1) \cdot \log\left(\frac{1 - F^c}{1 - F^{nc}}\right)\right).
\end{aligned}$$

711 Since for every species $\frac{1 - F^c}{1 - F^{nc}} \geq 1$, we conclude with

$$\frac{\text{ER}(x_*^c)}{\text{ER}(x_*^{nc})} \geq 1$$

712 *Appendix A.4. Proof of Proposition 8*

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

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

715 Taking the logarithm formulation of equation (2), we can derive by iter-
716 ation that

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

717 We deduce that

$$\text{ECOS}(x^{nc}(t)) - \text{ECOS}(x^c(t)) = w' \sum_{s=1}^t M'^s (\log(1 - F^{nc}) - \log(1 - F^c))$$

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

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

720 The assumption of Proposition 8 guarantees that vector $M^s w$ is positive for
721 every species j and every time s . Moreover, from Proposition 3 related to the
722 gain from cooperation for catch rates, the difference $\log(1 - F^{nc}) - \log(1 - F^c)$
723 is always non-positive for every species j .

724 Appendix B. Scilab code for the simulations

Below is the scilab code used for the simulations. Scilab is an open source software for numerical computation available at <http://www.scilab.org/en/download/latest>

```
//The open ecosystem for n_pl players and n_sp species with a gompertz dynamics
clear
n_sp=3;//number of species
n_pl=3// number of player

//Dynamics parameters Simulation 1
r =[-0.0026, 0.0392, 0.0644]' // intrinsic growth rate
S=[-0.0218 0.0005 0.0000; -0.0143 -0.0153 0.0003 ; -0.0003 -0.0085 -0.0161 ] // trophic interactions
// Dynamics parameters Simulation 2
//r=[-0.00002, 0.00018, 0.00027]'
//S=[-0.01902 0.00072 0.00030; -0.01819 -0.01766 0.00054 ; -0.00757 -0.01364 -0.01254 ]

A=(n_sp:-1:1)' // Utility coefficients
rho=0.98
//Computation of optimal harvest rates F
W=inv(eye(n_sp,n_sp)-rho*(eye(n_sp,n_sp)+S))*A
disp('marginal prices', W)
Fmort_nc=n_pl*A./(n_pl*A+rho*(eye(n_sp,n_sp)+S))*W// Non cooperative total fishing mortality vector
Fmort_c=A./(A+rho*(eye(n_sp,n_sp)+S))*W// Cooperative total fishing mortality vector
disp('Mortalities', Fmort_nc,Fmort_c)

function BB=dyn_pop(B) // population dynamics
BB=B.*exp(r + S*log(B))
endfunction

function hnc=optstrategy_nc(B) // Optimal non-cooperative strategy
hnc=Fmort_nc.*B
endfunction

function hc=optstrategy_c(B) // Optimal cooperative strategy
hc=Fmort_c.*B
endfunction

function V=ecosystem(B)
V=W'*log(B)
endfunction

function D=Simpson(B)
D=1-sum((B/sum(B)).^2)
endfunction

// Simulations of catches and biomass nc and c
Horizon=500; // Temporal Horizon
B_init=[0.5 0.5 0.5]'; // initial state 3 species
Bnc=zeros(n_sp,Horizon+1); //init sequence biomass nc
Bc=zeros(n_sp,Horizon+1); //init sequence biomass c
hnc=zeros(Bnc);hc=zeros(Bc); //init sequence catch nc and c
Bnc(:,1)=B_init;
Bc(:,1)=Bnc(:,1);
for t=1:Horizon
    hnc(:,t)=optstrategy_nc(Bnc(:,t));
    Bnc(:,t+1)=dyn_pop(Bnc(:,t)-hnc(:,t));
    Dnc(t)=Simpson(Bnc(:,t))
    hc(:,t)=optstrategy_c(Bc(:,t));
    Bc(:,t+1)=dyn_pop(Bc(:,t)-hc(:,t));
    Dc(t)=Simpson(Bc(:,t))
    Ec(t)=ecosystem(Bc(:,t))
    Enc(t)=ecosystem(Bnc(:,t))
end;
```

```

// plot
years=1:Horizon;
clf(0) // remove past content window 0
for i=1:n_sp
    subplot(2,n_sp,i)
        plot2d(years,[Bnc(i,years)'Bc(i,years)'],[5,2]);//,rect=[0,0,Horizon,3*K(i)];
        xtitle('Species'+string(i), 'time t','state x(t)');
//legends(['non-cooperative';'cooperative'],[5,2],opt="ur");
end

subplot(2,n_sp,n_sp+1)
plot2d(years,[Dnc(years) Dc(years)],[5,2],rect=[0,0,Horizon,1]);
//legends(['non-cooperative';'cooperative'],[5,2],opt="ur");
xtitle('rho = '+string(rho), 'time t','Simpson ');
subplot(2,n_sp,n_sp+2)
legends(['non-cooperative';'cooperative'],[5,2],opt="ur");
subplot(2,n_sp,n_sp+3)
plot2d(years,[Enc(years) Ec(years)]-min(Enc),[5,2]);
xtitle('rho = '+string(rho), 'time t','Ecosystem Value');

```

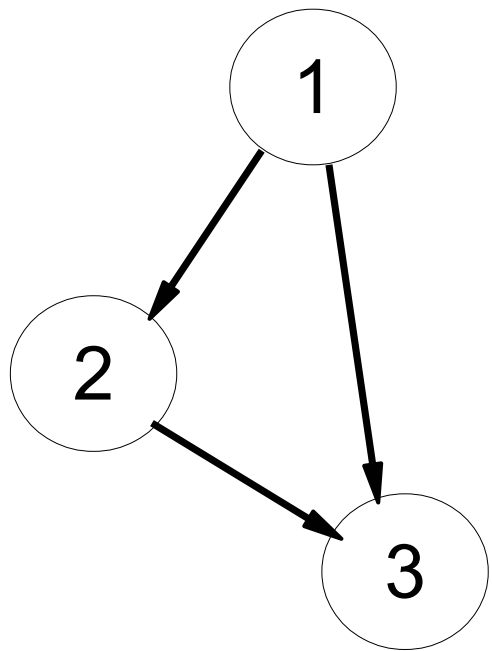


Figure 1: A three-species food web in a configuration of omnivory.

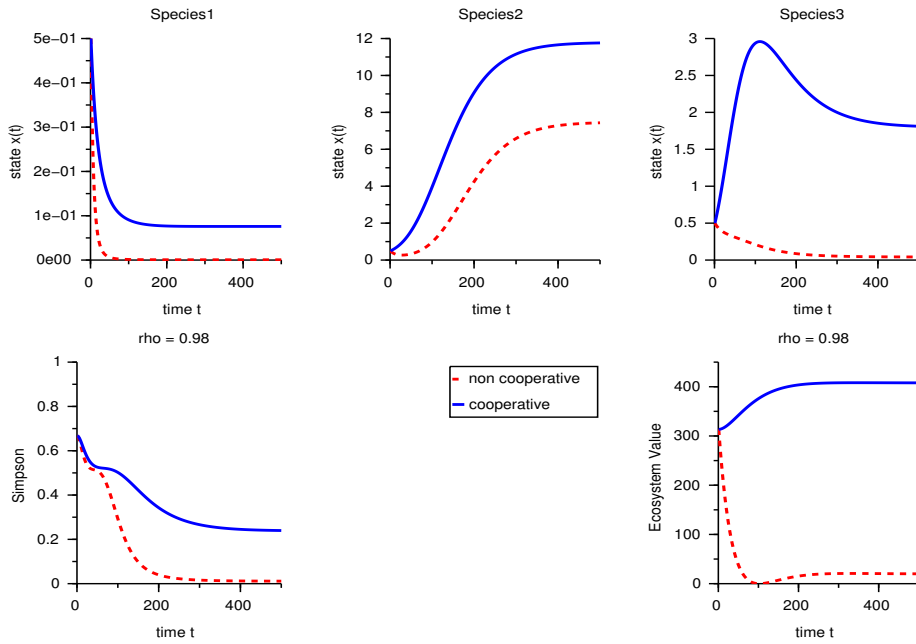


Figure 2: A three-species example with trophic interactions as defined in Section 4.1. In blue (solid line) the cooperative trajectories. In red (dotted line) the non-cooperative trajectories. On the top, stock states $x_j^{nc}(t)$ and $x_j^c(t)$ for the prey (right), the top predator (left) and the mesopredator (center). Cooperation performs better for every species. In particular, both the predator and the prey are jeopardized in the non-cooperative context. At the bottom, the Simpson index and ecosystem index $ECOS(t)$. Thus, cooperation also performs better for these metrics.

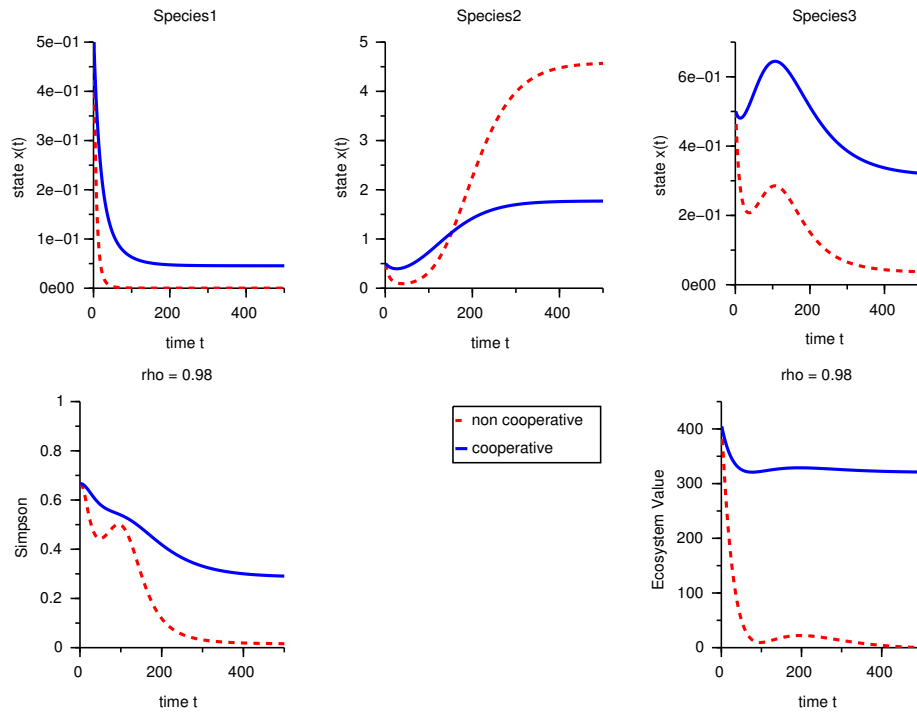


Figure 3: An ecosystem with three species where the gain from cooperation is more ambiguous in terms of biodiversity performance. Parameters are defined in Section 4.2. On the top, in blue (solid line), the cooperative trajectories $x_j^c(t)$ for the prey (right), the top predator (left) and the mesopredator (center). In red (dotted line), the non-cooperative trajectories $x_j^{nc}(t)$. Non-cooperation performs better for meso-predator species. However, at the bottom, the Simpson diversity index and the value of the ecosystem ECOS show better performance with cooperation.

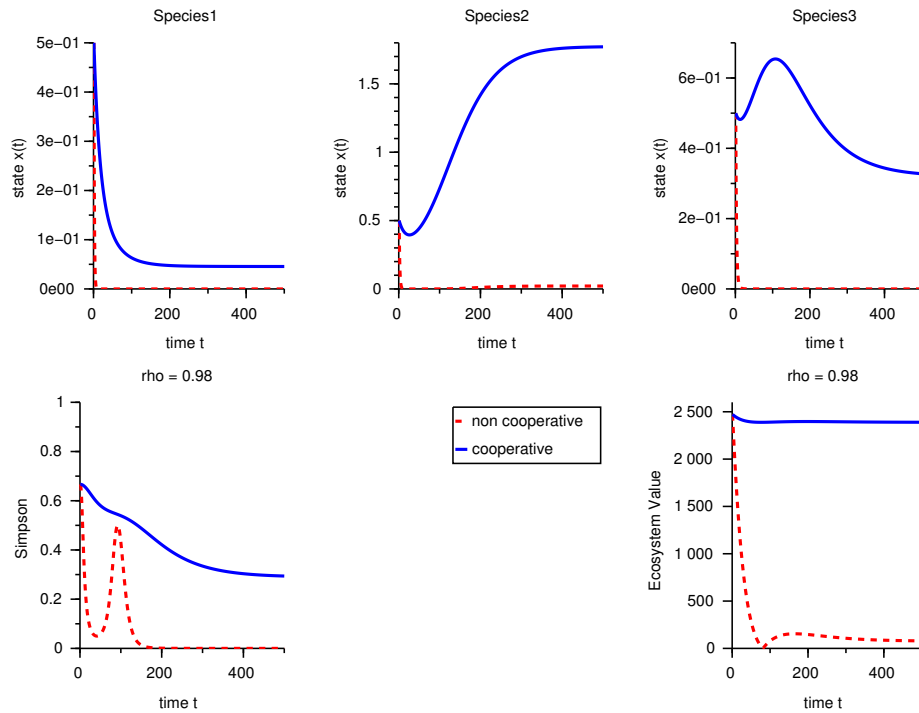


Figure 4: When the number of agents increases to $n = 22$ for the example defined in Section 4.2, the ecosystem performs better with cooperation in terms of biodiversity performance. In blue (solid line), the cooperative trajectories $x_j^c(t)$ for the prey (right), the top predator (left) and the mesopredator (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.