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On Species Preservation and Non-Cooperative Exploiters*

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ABSTRACT

Game-theoretic models of fisheries typically consider cases where some players harvest a single common fish stock. However, these types of models do not capture many real-world mixed fisheries, where species can be biologically independent or dependent. The present paper considers cases where several non-cooperative exploiters are involved in mixed fisheries. This paper is targeting the preservation of biodiversity by setting up a two-species model with the aim of exploring the conditions under which both species can survive exploitation under non-cooperative management. The model starts out as a two-species model without biological dependency and is then modified to also include biological dependency. We contribute to the literature by analytically finding the maximum number of players that can preserve both species while satisfying the model's conditions. For visualization purposes, we simulate a two-species model with different kinds of interrelationships.

Keywords: Species preservation; bioeconomic modeling; two-species fisheries; non-cooperative game.

JEL Code: C70; Q22; Q28.

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INTRODUCTION

Game-theoretic models of fisheries typically consider cases where some limited number of countries harvest a single common fish stock. However, in the case of real-world fisheries, countries do often exploit several stocks simultaneously in mixed fisheries, where the stocks may or may not be biologically dependent. This paper seeks to analyze the species' preservation with the aim of avoiding the extinction of the species when non-cooperative exploiters harvest in two-species fisheries. The importance of this economic competition problem has been discussed by May *et al.* (1979).

Representing an early contribution to the literature on bioeconomic extinction is Clark (1973). He shows that even in the socially optimal case, the extinction of one of the species is possible. Hannesson (1983) presents a general multi-species model with interdependent fish species and studies the optimal exploitation of two-species predator–prey fisheries. He examines methods of achieving optimal exploitation in a Lotka-Volterra type of model with costless harvesting and the impact on the optimal exploitation of increasing the discount rate. Mesterton-Gibbons (1988) investigates the optimal policy in a theoretical setting for combining the harvesting of predators and prey.

There is also some literature related to metapopulation models (Potts and Vincent, 2008). These models, however, typically include only one harvested species. As a result, the literature concentrates on comparing privately and socially optimal outcomes, ignoring the effects of economic competition.

Bhattacharya and Begum (1996) study different two-species systems with independent and interactions among species. They define the thresholds for the cost per unit of effort for existence of bionomic or open access equilibrium but do not include the economic competition problem that this paper focus on.

Fischer and Mirman (1996) have studied strategic interaction in two-species fisheries using a theoretical model, whereas Sumaila (1997) has studied the case of Barents Sea fisheries. Many of these authors have investigated the optimal policies corresponding to the joint action by the exploiters of the two species. From the traditional game theoretical analysis of single-species fisheries, we know that full cooperation may be hard to achieve due to free-rider incentives (Kronbak and Lindroos, 2007). Fischer and Mirman (1992, 1996) and Levhari and Mirman (1980) do analyze the decisions of agents in cooperative and non-cooperative frameworks in a two-species model, but they limit themselves to the analysis of the case of two agents. We therefore find a lack in the literature studying the other branch of the game-theoretical behavior, namely, the non-cooperative or the Nash equilibrium for many players, in a two-species setting.

The present paper is the first to consider the number of agents that can be sustained in a non-cooperative equilibrium without driving one stock to extinction. We seek to answer questions such as: what are the driving forces for species extinction in a two-species model with biological dependency? The opposite effect of the tragedy of the commons is the increased usefulness of a resource as the result of many individuals using it. This effect is often referred to as the comedy of the commons (Rose, 1986). Does comedy of the commons occur, and when, in two-species fisheries? Finally, most importantly, what are the consequences for the ecosystem from non-cooperative behavior?

Our modeling approach is to consider two sets of two species; first, we consider biologically independent species, and later, we consider biologically dependent species. The case with biologically independent species is determined as a point of reference. We seek the static optimal harvesting effort in both cases and apply this as a baseline. In both cases, we gradually increase the number of agents until we face the conditions promoting optimal exploitation for a limited number of symmetric competitive exploiters with non-selective harvesting technology. We relate the optimal competitive effort levels to the species' biotechnical productivity and contribute to the literature by finding conditions for the stability and exploitation of stocks in a two-species model with biologically dependent species where it is no longer sufficient to apply biotechnical productivity. Our methodology allows us to relate the number of competitive exploiters to the extinction of the species. Note that our approach is similar to the Fischer–Mirman model (1992, 1996), as we analyze the effects of different forms of biological interactions. However, the economic part of the model is very different. The Fischer–Mirman models' objective function is ignoring key economic parameters such as fishing costs. Moreover, our model concentrates on the non-selectivity of fishing gear and a continuum of players.

In the following section we introduce the model by identifying a single stock and several exploiters. In the section "Two independent stocks", we have a two-species fishery with countries exploiting these biologically independent species. In the section "Two biologically dependent stocks", we set up the model with two-species fishery with countries exploiting biologically dependent species. In the section "Visualizations", we illustrate the analytical results of the previous section. Finally future research issues are discussed and conclusions are given.

BASIC ONE-STOCK MODEL

Consider a game between n agents harvesting a common natural resource, x (Mesterton-Gibbons, 2000). Assume the equilibrium use of the fish stock over time by these agents $\frac{dx}{dt} = F(x) - \sum_{i=1}^{n} h_i = 0$, where the growth function is explicitly formulated as logistic growth, $F(x) = Rx(1 - x/K)$. R is the intrinsic growth rate of fish, and K is the carrying capacity of the single stock in the ecosystem. The production function is assumed to be bi-linear in effort, E and stock, $h_i = qE_ix, i = \{1, 2, 3, \ldots, n\}$, where q is the catchability coefficient. It follows, then, that the equilibrium fish stock is given as $x = \frac{K}{R}(R - q)\Sigma_{i=1}^{n} E_i$, where the equilibrium stock decreases linearly with total effort. If players adapt a traditional non-cooperative Nash game approach when determining their effort, this corresponds to common-pool exploitation, or restricted open access, as the exploiters only consider finding a strategy from which no player has a unilateral incentive to deviate from (Mesterton-Gibbons, 1993). The result is kind of a restricted tragedy of the commons (Hardin, 1968) with overexploitation and partly dissipation of rents, as players only consider their own incentives and not the possible joint outcome.

If extinction of the species should occur, the biomass should be lower than some threshold. With a logistic growth function, there is no positive threshold, and the critical depensation is zero. It would then be the case that extinction occurs when the total effort exceeds the biotechnical productivity, R/q. However, in the one-species case, even with the number of players approaching infinity, the total effort is less than equal to the biotechnical productivity.

TWO INDEPENDENT STOCKS

To examine the consequences of more players exploiting two biologically independent stocks, we start out by defining and solving for the sole-owner solution, and the number of players is then increased to n.

Sole Owner Optimum with Two Species

Consider two biologically independent species x_1 and x_2, each following a logistic growth function. The optimal harvest is determined as a sole owner harvesting the two stocks. It is assumed that there are no possibilities for selectivity; therefore, the same effort reduces both stocks, which is reflected by the identical catchability coefficient for the stocks. The two biologically independent steady-state equilibrium stocks are

$$x_j = K_j - \frac{K_j q E}{R_j}, \quad j = \{1, 2\}, \tag{1}$$

where the sub-script, j, is an indicator for the species. The optimal fishing effort for the sole owner is derived from the following objective function

$$\underset{E}{\text{Max}} \quad p_1 q E x_1 + p_2 q E x_2 - cE, \tag{2}$$

$$\text{s.t. (1).}$$

This corresponds to finding the effort level that maximizes the equilibrium uses of the stocks. Here, p_1 is the market price of fish stock x_1, p_2 is the market price of fish stock x_2, prices are assumed to be exogenously given, and c is the unit cost of effort. Based on the first-order condition (FOC), the optimal fishing effort for a sole owner exploiting two stocks is

$$\hat{E} = \frac{p_1 q K_1 + p_2 q K_2 - c}{\frac{2 p_1 q^2 K_1}{R_1} + \frac{2 p_2 q^2 K_2}{R_2}}. \tag{3}$$

Reinserting $\hat{E}$ into the equilibrium stocks yields the specific steady-state stock levels. Note that in this model, it may be optimal to drive one of the stocks to extinction. This is the case if the optimal effort level exceeds a threshold defined by the biotechnical productivity, $\hat{E} \geq R_j/q, j = \{1, 2\}$ (Clark, 1990). Because the optimal effort is defined by Equation (3), extinction is of particular concern if one of the stocks has a low biotechnical productivity and the cost–price ratio of other species is sufficiently low (Clark, 1990). The optimal effort level is a trade-off between harvesting the different species and their productivity. If the intrinsic growth rate of a species is increased, then the optimal effort level is also increased. The trade-off occurs when there is an increase in the carrying capacity or in the price of one of species. The change in the optimal effort level depends on whether the size of the intrinsic growth rate of the species is larger than the growth rate of the other species (then effort increases) or lower (then optimal effort decreases) (Clark, 1990). With two species, this is relatively simple to test, but with many species, the results are more ambiguous.

The *n*-player Equilibrium with Two Independent Species

Assume there are *n* symmetric countries competing for the harvest of two biologically independent species. Each country maximizes the following profit function subject to the steady state of the logistic growth of the stocks. The interdependency or the economic competition among fishermen is reflected in the equilibrium of growth functions.

$$\max_{E_i} p_1 q E_i x_1 + p_2 q E_i x_2 - cE_i, \quad i = \{1, 2, \ldots, n\} \tag{4}$$
$$\text{s.t. } x_j = \frac{K_j}{R_j}\left(R_j - q\sum_{i=1}^{n} E_i\right), \quad j = \{1, 2\}.$$

From the FOC (Ruseski, 1998), the reaction functions for each country can be derived:

$$E_i = \hat{E} - \sum_{k \neq i} \frac{E_k}{2}, \quad i = \{1, 2, \ldots, n\}, \quad k = \{1, 2, \ldots, n\}. \tag{5}$$

Because we know that the countries are symmetric, we can easily solve for the optimal effort level by each country $E_i = \frac{2}{n+1}\hat{E}$, and the total effort in a Nash equilibrium becomes $E_T = \frac{2n}{n+1}\hat{E}$, and with n approaching infinity, the total fishing effort approaching restricted open access becomes $2\hat{E}$.

The equilibrium stocks are

$$x_j = K_j - \frac{K_j q \frac{2n}{n+1}\hat{E}}{R_j}, \quad j = \{1, 2\}. \tag{6}$$

Equation (6) clearly indicates that one stock might be eliminated if the total effort is too high, which, as Clark (1993) demonstrates, also could happen for a single player. Because total effort depends on the number of non-cooperative exploiters, we can find the critical number of players playing a Nash game, which simply shifts from preserving both species to eliminating one species. Setting Equation (6) equal to zero for each of the species, we find this critical number of players. Clark (1990) demonstrates that it is sufficient to consider the species with the lowest biotechnical productivity, which in this case corresponds to lowest intrinsic growth, as the catchability coefficients are identical. In addition, Clark (1990) shows that this species will only be eliminated if the cost–price ratio for other species in question is sufficiently low. Therefore, for the elimination of one species to occur, we need to find the stock with the lowest biotechnical productivity; call this stock l. This stock will only face elimination if the following condition is satisfied[1]:

$$\frac{c}{p_{j \neq l} q} < K_l \frac{1 - R_{j \neq l}}{R_l} \quad \text{for } j,\ l = \{1, 2\}. \tag{7}$$

Equation (7) is a necessary condition for extinction to occur. If Equation (7) is not satisfied, there is no critical limit on the number of players exploiting the two stocks in terms of preserving the ecosystem, and it must be assumed that this will result in a restricted open-access exploitation of the stocks. If Equation (7) is satisfied, then extinction will occur for the stock with lowest biotechnical productivity when the number of non-cooperative exploiters reaches

$$\hat{n} = \frac{R_l}{2q\hat{E} - R_l}, \quad \text{where } R_l = \min(R_1, R_2). \tag{8}$$

The term $\hat{n}$ is now defined as the limit of non-cooperative exploiters where a shift occurs from preserving to non-preserving biodiversity. For a number of players exceeding $\hat{n}$, not all species in the ecosystem will be sustained, that is, Equation (7) is satisfied such that the species with lowest biotechnical productivity will be extinct. Seemingly, the independency of the stocks implies that it is sufficient to consider the single species independently with regard to the critical number. There is, however, implicit economic interdependence among the species because of the lack of selectivity. This interdependency is reflected in the optimal effort level being dependent on all intrinsic growth rates and carrying capacities for all species in the two-species fishery. Therefore, the optimal effort level $\hat{E}$ is dependent on the carrying capacity and the intrinsic growth rate of all the species in this two-species fishery.

We now proceed towards finding analytical characteristics of the critical number of players under economic competition for biologically dependent species.

TWO BIOLOGICALLY DEPENDENT STOCKS

In many fisheries, not only an economic interdependence between stocks but also a biological interdependency among stocks is present. Biological interdependency may have different structures; It may be predator–prey relationship, such as seals feeding on smaller pelagic fish, it may be a prey–prey relationship, such as, the cod feeding on sprat and the sprat feeding on cod eggs in the Baltic Sea, or it may be symbiosis or mutualism, which has a particular importance in tropical reef environment; representing an example of this are cleaner fish and their mutualism with other species.

[1] This is simply a rewritten version of Clark's two-player condition for a species to be extinct (Clark, 1990, p. 315).

We consider a static game between n agents harvesting two common natural resources. Assume the equilibrium use of the two fish stocks by symmetric countries

$$\frac{dx_1}{dt} = F(x_1, x_2) - \sum_{i=1}^{n} qE_i x_1 = 0 \tag{9a}$$

$$\frac{dx_2}{dt} = G(x_1, x_2) - \sum_{i=1}^{n} qE_i x_2 = 0. \tag{9b}$$

The growth functions include interaction between species and are explicitly formulated as a variation of the competition model originally suggested by Gause (see Clark, 1990 or Brown and Rothry, 1993). These growth functions can be regarded as variations of the traditional logistic growth functions

$$F(x_1, x_2) = R_1 x_1 (1 - x_1/K_1) - \theta_1 x_1 x_2 \tag{10a}$$

$$G(x_1, x_2) = R_2 x_2 (1 - x_2/K_2) - \theta_2 x_1 x_2, \tag{10b}$$

where the parameters $\theta_i, i = \{1, 2\}$, are referred to as the interdependency parameter between species and can be positive or negative constants. If they are both positive, they describe the biological competition between the stocks; if they are both negative, they describe a biological symbiosis between stocks; and finally, if they have different signs, they describe a predator–prey relationship, where the constant with the negative sign represents the predator. In some cases, nature in itself is so favorable that exploitation, in this model, cannot eliminate any of the species. In other cases, nature itself will lead to the elimination of one of the species. In the following, if a stock has a negative effect on the other stock (both thetas are positive), then it is referred to as prey, and, vice versa; if a stock has a positive effect on the other stock (both thetas are negative) it is referred to as prey. Therefore, competition is found in the prey–prey corner, and symbiosis is found in the predator–predator corner.

A main critique of the applied model in Equations (10a) and (10b) is that the growth model applied results in a linear functional response; this means that the consumption per capita increases linearly and predicts the unlimited growth of both species in the case of mutualism. There exist other models for two-species growth and consumption (see Noy-Meir, 1975 for a description of some of these models), but they lack the modeling advantages of the one we suggest. A variation of this type of model is also applied in Hannesson (1983) and in a theoretical paper by Mesterton-Gibbon (1988). Another critique of the Gause model is that the cases of predator–prey systems are known for their structural instability and for yielding limit cycles. There is only a narrow range where the Gause model predicts a stable coexistence equilibrium, which will also be reflected later in our results. In general, it is very difficult to estimate functional forms for interdependent populations (Yodzis, 1994).

It follows from the above model that the following two equations jointly describe the equilibrium fish stocks when n players exploit the stocks, where $E_T = \sum_{i=1}^{n} E_i$ describes the total effort by all exploiters

$$x_1 = \frac{K_1}{R_1}(R_1 - qE_T - \theta_1 x_2) \tag{11a}$$

$$x_2 = \frac{K_2}{R_2}(R_2 - qE_T - \theta_2 x_1). \tag{11b}$$

The two equilibria of the stocks depending on applied effort are defined as

$$x_1 = \frac{K_1(-R_1R_2 + K_2R_2\theta_1 + E_Tq(R_2 - K_2\theta_1))}{-R_1R_2 + K_1K_2\theta_1\theta_2} \tag{12a}$$

$$x_2 = \frac{K_2(-R_1R_2 + K_1R_1\theta_2 + E_Tq(R_1 - K_1\theta_2))}{-R_1R_2 + K_1K_2\theta_1\theta_2}. \tag{12b}$$

Equations (12a) and (12b) demonstrate that in some cases, an increase in the total effort level reduces the equilibrium stocks. Whether an increase in total effort increases or decreases the equilibrium stocks depends on what the biological parameters are in relation to each other. The following exemplifies this for species 1

— If $\text{Sign}[R_2 - K_2\theta_1] \neq \text{Sign}[-R_1R_2 + K_1K_2\theta_1\theta_2]$, which is always the case in a predator–prey model, where species 1 is the predator, but could also occur for competition and mutualism, then we have a case where the equilibrium biomass of species 1 diminishes with an increase in effort.
— If, on the other hand, $\text{Sign}[R_2 - K_2\theta_1] = \text{Sign}[-R_1R_2 + K_1K_2\theta_1\theta_2]$, this could be a predator–prey case, where species 1 is the prey or, in a competition or mutualism model, a case where the equilibrium biomass for species 1 increases with effort. This means that the fishing pressure has less of an impact on the species compared to the ecological pressure due to the biological interdependency.

We can conclude that with biological interdependence among species, an increase in effort in the fishery is by itself not sufficient for determining whether the equilibrium stock will increase or decrease, as the ecological pressure from the interdependence also has an effect.

Two Biological Dependent Stocks with Sole Owner

The sole-owner optimum effort with interacting species is defined by the equilibrium yields (Equations (11a) and (11b)) and then by maximizing the economic benefits from a single effort level. The solution to the problem yields

$$E^* = \frac{\begin{array}{c} c(-R_1R_2 + K_1K_2\theta_1\theta_2) + q(K_2p_2R_1R_2 \\ + K_1(p_1R_1R_2 - K_2p_1R_2\theta_1 - K_2p_2R_1\theta_2)) \end{array}}{2q^2(K_1p_1R_2 + K_2(-K_1p_1\theta_1 + p_2(R_1 - K_1\theta_2)))}. \tag{13}$$

This solution corresponds to the solution in Equation (3) if $\theta_1 = \theta_2 = 0$ but is far more complicated if there is a biological interaction. Whether the optimal effort in a dependent two-species setting is higher or lower than the baseline in (3) depends on the

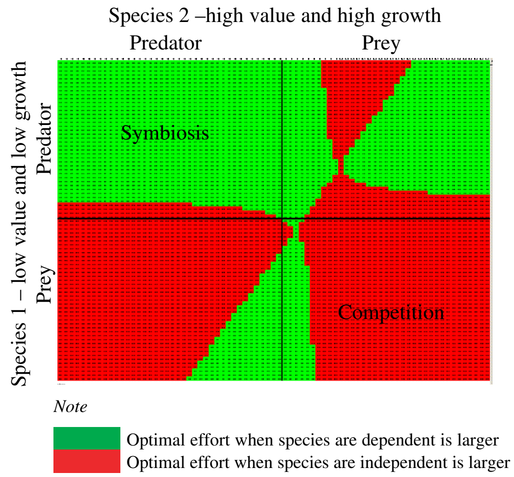

Figure 1. Comparison of optimal effort level for dependent and independent species.

sign of the interdependency between species. For illustrative purposes, we have set up a numerical example comparing the optimal or cooperative effort levels when species are independent and dependent, respectively. This corresponds to comparing Equations (3) and (13). The applied parameter values are described in Appendix A.

Figure 1 is an illustrative example of how effort differs between the cases of biological dependency and independency in the case of two stocks, one with high value and a high intrinsic growth rate and one with low value and a low intrinsic growth rate. The optimal effort in the case of a symbiosis (predator, predator) among species will be larger when species are dependent than when they are independent. This is intuitively clear, as the ecosystem can support a higher harvest due to the mutually beneficial relationship between the two species, and vice versa. In the case of a predator–prey relationship, it is harder to say which optimal effort level is the largest. In these cases, it depends on the relative price and the growth of the two species. In the lower-left corner, the largest optimal effort is found when species are independent. This is the case where the species with the lowest price and the lowest intrinsic growth is prey, which is intuitively clear from the fact that the 'prey-pressure' is not available in the independent case and thus the optimal effort can be higher in this case.

Two Biologically Dependent Stocks with *n* Players

With n symmetric players, the problem at a first glance looks similar to the case with independent species, as we have $E_i = \frac{2}{n+1}E^*$, but from comparing the optimal effort level when stocks are biologically independent and dependent (Equations (3) and (13)), complex differences appear. The total effort level employed in the industry in a Nash equilibrium is $E_T = \sum_{i=1}^{n} E_i = \frac{2n}{n+1}E^*$.

The steady-state stocks in Nash equilibrium are defined by the following equations

$$x_1 = \frac{K_1\left(-R_1R_2 + K_2R_2\theta_1 + \frac{2n}{n+1}E^*q(R_2 - K_2\theta_1)\right)}{-R_1R_2 + K_1K_2\theta_1\theta_2} \tag{14a}$$

$$x_2 = \frac{K_2\left(-R_1R_2 + K_1R_1\theta_2 + \frac{2n}{n+1}E^*q(R_1 - K_1\theta_2)\right)}{-R_1R_2 + K_1K_2\theta_1\theta_2}. \tag{14b}$$

The critical number of players where one of the stocks is eliminated is defined by setting Equations (14a) or (14b) equal to zero and solving for the critical number of competitive exploiters for each stock, n_j, where $j = \{1, 2\}$. Therefore, n_j represents the knife's edge for eliminating or not eliminating species j. It is, however, not always the case that there is a meaningful interpretation of the critical number of players that eliminates one of the stocks. Because solving this might result in negative n_j or in an n_j where the stock would actually benefit from more players — the comedy of the commons — in principle, $n_j \in [-\infty, \infty]$, but the economic meaningful interval is $n_j \in [0, \mathrm{OA}]$, where OA is an upper limit of players, referred to as an restricted open access. This critical number of players exists if, under traditional open access, one of the species is eliminated and if a natural equilibrium exists. If a critical number of players exists, it is derived according to the following formula for each stock.

$$n_j = \frac{R_jR_w - K_wR_w\theta_j}{2qE^*R_W - R_jR_w - 2E^*K_wq\theta_j + K_wR_w\theta_j}, \quad j, w = \{1, 2\}, \quad w \neq j. \tag{15}$$

Let n^* be the threshold number of non-cooperative players exploiting two biologically dependent species that will no longer be able to sustain both species in the ecosystem.[2] n^* is then the variable we are seeking.

Dealing with biological interaction among species and economic completion among players in some cases results in growing stock sizes with an increasing number of players. Mathematically, this will occur when

$$q\sum_{i=1}^{n} E_i < \theta_j x_w \quad \text{for } \theta_j > 0. \tag{16}$$

When inequality (16) is satisfied, the tragedy of the commons no longer occurs; it is instead a comedy of the commons.

Several conditions are needed to define n^*. These conditions correspond to Equation (7) but are far more complicated due to biological interdependence. The following conditions set up the threshold for the number of competitors that drives one of the two species to the exact level of extinction. These conditions depend solely on the economic

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[2] In the case of the extinction of one species, a new situation arises. The optimal effort levels will change, and other species might show up. This situation is not analyzed further in this paper, as we primarily seek the number of players that exactly avoids extinction.

parameters (price, costs and catchability) and ecological parameters (intrinsic growth rates, carrying capacities and interaction parameters).

— *Both stocks decrease when total effort increases (tragedy of the commons)*
  If $\text{Sign}[R_w - K_w\theta_j] \neq \text{Sign}[-R_1R_2 + K_1K_2\theta_1\theta_2] \quad \forall w, j = \{1, 2\}, \quad w \neq j$
  then $n^* = \max(\min(n_w, n_j), 0)$.
— *Both stocks increase when total effort decreases (comedy of the commons)*

$$\text{If } \text{Sign}[R_w - K_w\theta_j] = \text{Sign}[-R_1R_2 + K_1K_2\theta_1\theta_2] \quad \forall w, j = \{1, 2\}, \quad w \neq j \tag{17}$$

  then $n^* = \text{OA}$ (upper limit of players corresponding to restricted open access, assuming stock levels are positive at this exploitation level).
— *Stock j increases and stock w decreases when total effort increases*
  If $\text{Sign}[R_w - K_w\theta_j] \neq \text{Sign}[-R_1R_2 + K_1K_2\theta_1\theta_2]$ and
  $\text{Sign}[R_j - K_j\theta_w] = \text{Sign}[-R_1R_2 + K_1K_2\theta_1\theta_2] \quad \text{for } w, j = \{1, 2\}, \quad w \neq j$
  then $n^* = \max(n_w, 0)$.

The biological interdependency of the species creates more complexity when determining sustainability of the ecosystem for the species. An additional dimension is added, as the tragedy of the commons does not always occur. The biotechnical productivity is no longer in itself sufficient for finding the critical number. Equations (16) and (17) are an extension of Equations (7) and (8), as they also include the interrelations between the species and thus incorporate advanced biotechnical productivity for a two-species model. If the interrelations are zero ($\theta_j = 0$), Equations (7) and (8) are in themselves sufficient.

The critical number in Equation (15) depends on all the economic parameters through the optimal baseline effort (E^*) in Equation (13). Appendix B analyses the effects on how this optimal baseline effort changes when economic parameters are changed and how the critical number of players changes if the optimal effort level is changed. Based on this analysis, it is difficult to say anything specific on what happens to the critical number, as it depends highly on the balance between the prices, intrinsic growths, the carrying capacities and the interdependency among species. We thus include a visualization example in the following section.

VISUALIZATIONS

To get a better understanding of the analytical results in the previous section, and to elaborate in particular on the case with biological dependency, this section simulates the exploitation of two stocks with biological dependency. The simulations include two stocks with identical carrying capacities. The intrinsic growth rates of the two stocks can be either high or low, and the stocks have different prices. This gives four cases to consider:

Case 1: Both stocks have a low intrinsic growth rate.
Case 2: Both stocks have a high intrinsic growth rate.

Case 3: Low-value stock has a low intrinsic growth rate.
High-value stock has a high intrinsic growth rate.
Case 4: Low-value stock has a high intrinsic growth rate.
High-value stock has a low intrinsic growth rate.

Each case allows for a predator–prey relationship, competition and mutualism, as the interdependency parameter (θ) varies between positive and negative values for both species. The applied parameter values and the natural equilibria are presented in Appendix C.

The results are presented as three-dimensional figures describing the critical numbers of players in a non-cooperative exploitation of two stocks where one of the stocks is eliminated. This number (n^*) derived from Equations (16) and (17) is pictured on one axis and the two interdependence parameters (θ_1 and θ_2) on the other two axes. In the cases where the natural equilibrium itself eliminates one of the stocks, the number of players is always zero.

The upper plateaus in Figures 3a–d represent the restricted open-access equilibrium, where both species will coexist with the high number of non-cooperative exploiters. For all cases, the symbiosis always leads to an upper plateau, and in these cases, the number of players can result in the comedy of the commons, which would grow to very

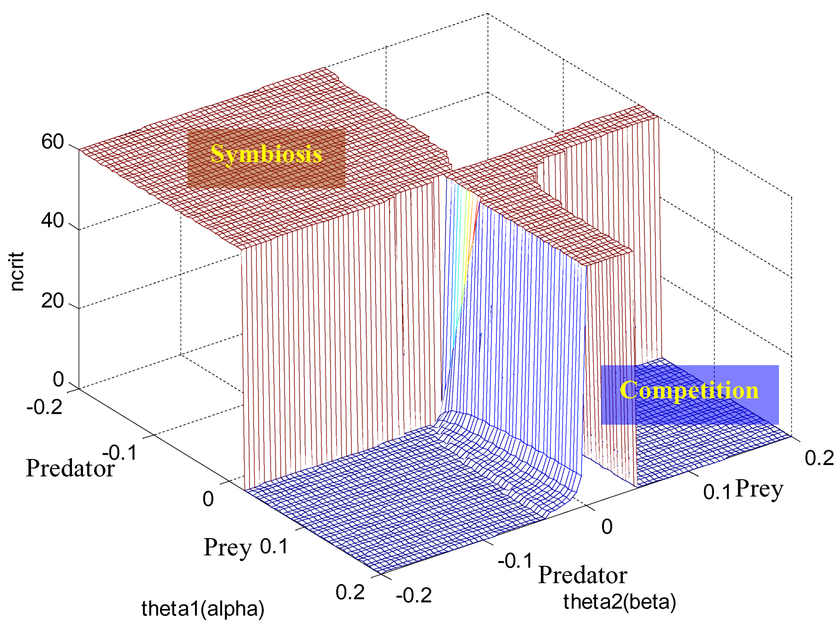

Figure 3a. Critical number of players, where the ecosystem cannot be sustained. Both stocks have low intrinsic growth rates (case 1). *Note*: ncrit is identical to n^* in the theoretical model.

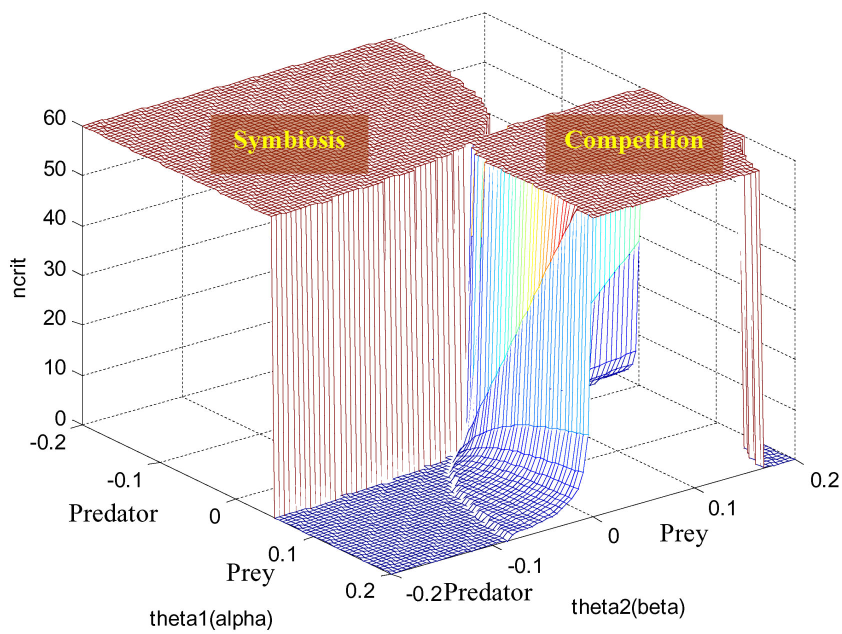

Figure 3b. Critical number of players, where the ecosystem cannot be sustained. Both stocks have a high intrinsic growth rates (case 2). *Note*: ncrit is identical to n^* in the theoretical model.

high number of competitive players in the case of no restricted open access. Figure 3a shows that there are only limited areas where the extinction of species will occur due to the number of players. These areas are concentrated in the predator–prey models and correspond to the areas between the upper (restricted open access) plateaus and the lower (no natural equilibria) plateaus. This is due to the narrow range of the stable coexistence equilibrium in the defined predator–prey model. In these cases, the management of the species, to limit the number of players, becomes of particular importance, as new entrants could result in an extinction of one of the species. For symbiosis among species, it is not surprising that, if the ecosystem can sustain interaction if species are independent ($\theta_1 = \theta_2 = 0$), then a symbiosis can also sustain a restricted open access or even a higher number of players. In the case of competition among species, the ecosystem can to some extent sustain a restricted open access and maybe a higher number of players, but if the competition becomes too large, then the ecosystem will not itself have a natural equilibrium where both stocks coexist.

In Figure 3b, where both stocks have high growth, the overalls conclusions are more or less the same as the conclusions from Figure 3a. There are, however, two main differences between them: first, the case with higher intrinsic growth (Figure 3b) can, in the case of competition, better sustain the restricted open-access situation (the size of the upper plateau in the competition area is larger), and second, in a predator–prey case, higher

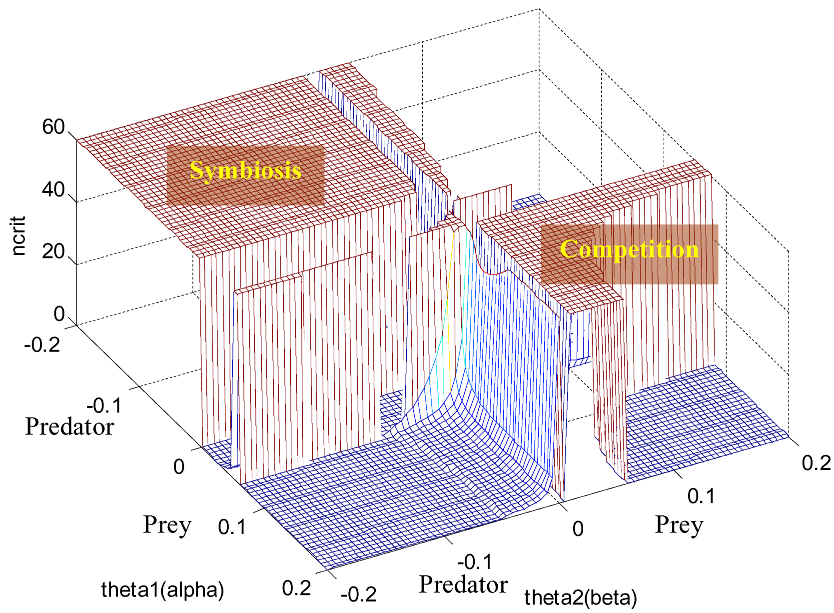

Figure 3c. Critical number of players, where the ecosystem cannot be sustained. Low-value stock has a low intrinsic growth rate. High-value stock has a high intrinsic growth rate (case 3). *Note*: ncrit is identical to n^* in the theoretical model.

predation by the high-valued species can sustain more players in the equilibrium (the rainbow-colored area is prolonged into the predator–prey square). With regard to management, the predator–prey square requires in particular the management of the fishery, as the area with a limited number of players lower than restricted open access is large.

The cases in Figures 3c and 3d are fairly complicated, with plateaus, peaks and canyons appearing in many places. This shows that small changes in the parameters of the ecosystem can have a significant economic effect: a system previously able to sustain several fishers may suddenly be able to sustain only a few fishers or none at all; therefore, the management of the species has either to be on a knife edge or to be very constrained based on the uncertainty of biological parameters. However, it is still the case that the symbiotic interaction can sustain even restricted open access, and the same is true for some parameters in the competition square.

Figures 3a–d also illustrate how sensitive the ecosystem is to even small changes in the interaction parameter. This is very relevant, for instance, when considering invasive species or pests or in cases with management of species with great uncertainty about biological parameters. Such species might alter the interaction in the ecosystem, and species that could be exploited by a limited number of cooperative players might now be extinct. If there is great uncertainty about the interrelation of species, it requires the strict management of the fishery under a precautionary approach.

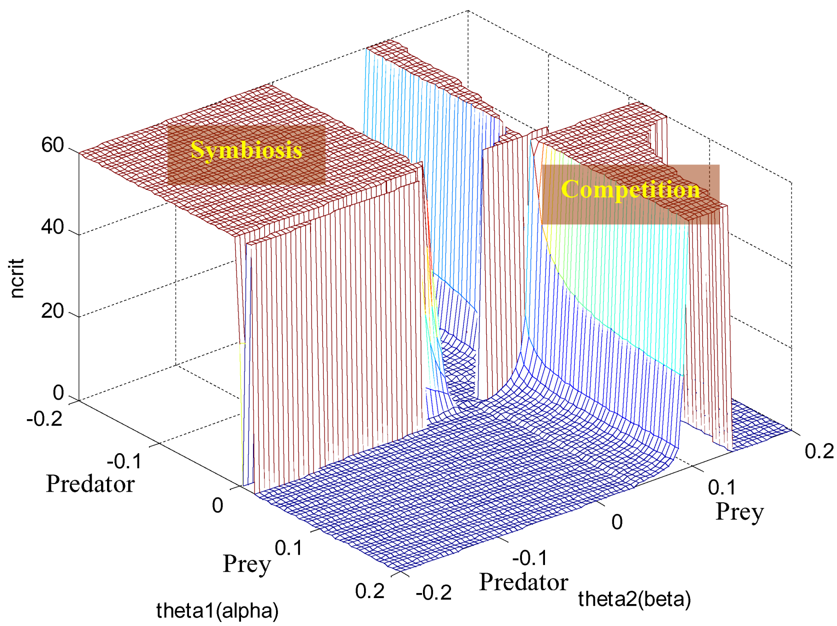

Figure 3d. Critical number of players, where the ecosystem cannot be sustained. Low-value stock has a high intrinsic growth rate. High-value stock has a low intrinsic growth rate (case 4). *Note*: ncrit is identical to n^* in the theoretical model.

DISCUSSION AND CONCLUSION

The paper merges bioeconomic two-species modeling with non-cooperative game theory. We set up an analytical framework for non-cooperative exploiters harvesting biologically dependent and independent two-species in a non-selective manner. In this setup, we have analytically defined the conditions for species preservation when several non-cooperative exploiters harvest two-species fisheries. Our modeling is clearly a very important issue in fisheries economics as many commercial fisheries include more than one species and can indeed be characterized by non-cooperative exploitation.

When species are biologically independent, it is sufficient to consider the biotechnical productivity to find stocks that are in danger of not being preserved. When, on the other hand, species are biologically dependent, it is not straightforward to apply the biotechnical productivity from the independent model. The conditions, for which the stock is in danger of not being preserved, also require including the interdependency parameters. We contribute to the literature with a general definition of the critical number of non-cooperative players to preserve biodiversity in a two-species fishery for all possible sets of interdependency parameters. In our analytical model with biologically dependent species, we have shown that the tragedy of the commons does not apply for some parameters; instead, we have the comedy of the commons, where open access is favorable.

Applying the results from the analytical model, we visualized a two-species fishery with two dependent species. We show that in the cases of symbiosis and competition, open access may not be a problem. Among the lessons to be learned from the visualizations is that it is primarily the low values of interdependency parameters that are the interesting values but that in this parameter range, the model is very sensitive to small changes in those small dependency values. A small change in the interdependency can lead to large changes in the critical number of non-cooperative players. The visualization also demonstrates that management of the fishery is of more importance when growth rates are low than when growth rates are high. Finally, when there is competition among species, a higher intrinsic growth rate tends to extend the range of parameters for which restricted open access is sustained. When we have a critical number of players that is lower than restricted open access, then the management of the fishery is important for the preservation of the species.

In this context, it is important to notice that we set up a simple non-spatial model and in a spatial setting, such as the natural environment, the different patches are likely to have different characteristics, and different species may thus survive in different patches. Our bioeconomic model is a simple approach used to provide a discussion on the biotechnical productivity for a two-species model. The paper attempts to close this gap in the literature, although we are aware of the widespread skepticism of one mathematical model's ability to capture all crucial aspects of even one type of interaction (Begon *et al.*, 1996) and of the limitations of the applied Gause model.

Among areas for further research are simulations of cases where a two-species fishery with biologically independent stocks has a limited number of players that can preserve the species. It is expected that such a simulation example could yield more information about the critical number function for small levels of dependency. The biologically independent case is straightforward for extending to more than two species, but the biologically dependent species requires more considerations for the interactions for the species. We believe that it is a possible research issue, although the analysis might become extremely complicated.

There are also various economic issues left for future research, such as market interactions between two fish species. Further, varying rents or viability of rents with different biological interactions would be an interesting avenue for further studies. In the present model, there is no specific direct interaction between the different players and the different species (such as player one's only targeting one stock and player two's only targeting the other stock). The effect of non-cooperative exploitation is confined to a suboptimally high effort. The case of cooperation versus non-cooperation for players with different target species is an issue for future research.

APPENDIX A

For illustrative purposes in Figure 1, the following parameter values are applied to compare the difference in effort levels with and without ecological dependency.

Table A1. Parameter values applied for visualization.

p_1	p_2	R_{low}	R_{high}	$K_1 = K_2$	c	q	θ_1	θ_2
1	2	0.3	0.9	50	7	0.5	$[-0.2; 0.2]$	$[-0.2; 0.2]$

APPENDIX B: SENSITIVITY ANALYSIS WHEN CHANGING ECONOMIC PARAMETERS

The section "Two biologically dependent stocks" investigates the conditions for the number of non-cooperative players that can preserve the two species in the ecosystem. This appendix conducts a sensitivity analysis on the baseline optimal effort when changes in the economic parameters occur. Further, the impact of the baseline effort on the number of players is analyzed. Together, this results in a sensitivity analysis on the critical number of players when economic parameters are changed.

Optimal Effort and Price of Species

If the price of species increases, then the change in the optimal baseline effort and thereby also the effort level of non-cooperative players will look like

$$\frac{\partial E^*}{\partial p_1} = \frac{K_1(cR_2 + K_2(p_2 q(R_1 - R_2) - c\theta_1))(R_1 R_2 - K_1 K_2 \theta_1 \theta_2)}{2q^2(K_1 p_1 R_2 + K_2(-K_1 p_1 \theta_1 + p_2(R_1 - K_1\theta_2)))^2}, \tag{A.1a}$$

$$\frac{\partial E^*}{\partial p_2} = \frac{K_1(cR_1 + K_1(p_1 q(R_2 - R_1) - c\theta_2))(R_1 R_2 - K_1 K_2 \theta_1 \theta_2)}{2q^2(K_2 p_2 R_1 + K_1(-K_2 p_2 \theta_2 + p_1(R_2 - K_2\theta_1)))^2}. \tag{A.1b}$$

To find the effects on the optimal effort level in the case of an increase in the price of one species, it is necessary to determine whether (A.1a) and (A.1b) are positive or negative.

Although it is clear that the denominator, $2q^2(K_2p_2R_1 + K_1(-K_2p_2\theta_2 + p_1(R_2 - K_2\theta_1)))^2$, will always be positive because of the second power, the nominator, $K_1(cR_2 + K_2(p_2q(R_1 - R_2) - c\theta_1))(R_1R_2 - K_1K_2\theta_1\theta_2)$, is more ambiguous. The following focuses on the sign of the nominator.

If $\text{Sign}[cR_2 + K_2(p_2q(R_1 - R_2) - c\theta_1)] = \text{Sign}[R_1R_2 - K_1K_2\theta_1\theta_2]$, then an increase in price increases effort.

In the case of a predator–prey model, θ_1 and θ_2 will have different signs, and the last term will thus be positive.

A sufficient but not necessary assumption for the effort level to increase as a result of a price change for one of the species is then that the growth of the species that experiences the price change is larger than the growth of the other species. For a price change for species 1, this will look like $R_1 > R_2$ and that $p_2q(R_1 - R_2) \geq c\theta_1$. This is more likely to be true if the intrinsic growth of species 1 is high relative to species 2 and if species 1 is the predator ($\theta_1 < 0$). It is thus seen that an increase in the effort level requires a balance between the value of the two species, their intrinsic growths and their interdependency.

Optimal Effort and Cost of Harvesting

If the cost of harvesting is changed, then the effort is changed, according to the following:

$$\frac{\partial E^*}{\partial c} = \frac{-R_1 R_2 + K_1 K_2 \theta_1 \theta_2}{2q^2(K_1 p_1 R_2 + K_2(-K_1 p_1 \theta_1 + p_2(R_1 - K_1\theta_2)))}. \tag{A.2}$$

One would expect this to be negative, such that the effort is decreased if the cost of harvesting is increased, ceteris paribus. However, for this to be true, either $R_1R_2 > K_1K_2\theta_1\theta_2$ or $K_1p_1R_2 < K_2(-K_1p_1\theta_1 + p_2(R_1 - K_1\theta_2))$ has to be satisfied.

Conclusion on Changes in Effort When Economic Parameters are Changed

It is difficult to say anything concrete on what happens to the optimal effort level if the economic parameters change. It is a balance between the prices, the intrinsic growths, the carrying capacities and the interdependency among species. However, it can be concluded that economic parameters will, except in rare cases, change the optimal effort level for the sole owner and thereby also for the *n*-players.

Critical Number of Players and Effort Level

We know from the above analysis that changes in economic parameters make E^* change and that this is true without changing other parameters in the critical number of players. Changes in optimal effort can therefore be interpreted as an effect of economic parameter changes.

If the optimal effort level in the sole owner case increases, then the number of players needed to sustain biodiversity changes according to the following:

$$\frac{\partial n^*}{\partial E^*} = \frac{2q(R_2 - K_2\theta_1)(-R_1R_2 + K_2R_2\theta_1)}{(-R_1R_2 + 2E^*q(R_2 - K_2\theta_1) + K_2R_2\theta_2)^2}, \quad \text{(Species 1)} \tag{A.3a}$$

$$\frac{\partial n^*}{\partial E^*} = \frac{2q(R_1 - K_1\theta_2)(-R_1R_2 + K_1R_1\theta_2)}{(-R_1R_2 + 2E^*q(R_1 - K_1\theta_2) + K_1R_1\theta_1)^2}. \quad \text{(Species 2)} \tag{A.3b}$$

The denominators in Equations (A.3a) and (A.3b) positive, but in order to discuss the sign of the nominator, we divide into different subcategories of interdependency.

If $\theta_1, \theta_2 < 0$ (*symbiosis*): the nominators in Equations (A.3a) and (A.3b) are negative, and the critical number of players will decrease if the optimal effort level is increased.

If $\theta_1, \theta_2 > 0$ (*competition*): then the number of players will decrease only if $R_2 < K_2\theta_1$ and $R_1 < K_2\theta_1$ or $R_2 > K_2\theta_1$ and $R_1 > K_2\theta_1$ if species 1 is binding for the critical number or $R_1 < K_1\theta_2$ and $R_2 < K_1\theta_2$ or $R_1 > K_1\theta_2$ and $R_2 > K_1\theta_2$ if species 2 is binding for the critical number.

This can be interpreted as follows: the intrinsic growth rates of both species have to be either sufficiently large or sufficiently small; otherwise, the non-cooperative behavior in the model will drive the stocks to extinction.s

If $\theta_1 < 0$ (*predator*) *and* $\theta_2 > 0$ (*prey*) (*or* $\theta_2 < 0$ (*predator*) *and* $\theta_1 > 0$ (*prey*)) (*predator-prey model*): if the predator sets the limits for the critical number of players, then an increase in the optimal effort level will further decrease the critical number of players.

If, on the other hand, the prey sets the limit for the critical number of players, then this number will only decrease if $R_1 < K_1\theta_2$ and $R_2 < K_1\theta_2$ or vice versa. This means that the increase in effort is only critical if the intrinsic growths of the two species are low.

That is, if the intrinsic growth rate of the prey is small, then the intrinsic growth of the prey must also be small, and vice versa, if the number of players should increase with the optimal effort level.

APPENDIX C

The applied parameters for the visualization in Section 5 are represented in Table C1.

We have defined an upper limit of players, which we refer to as restricted open access (OA) and an upper limit for the stock, a maximum stock size (MS). This is purely for illustrative purposes, as some conditions are so favorable that we have a case of the comedy of the commons, or a case with symbiosis, where stocks will jointly grow unlimited, which is a known limitation of the Gause model.

The natural equilibria for different interdependency among species are simulated to identify where the two species can coexist. If the species cannot coexist, it is not relevant to search for the number of exploiters where one species is extinct. Figure C1 illustrates the patterns for the natural equilibrium for both species with a low intrinsic growth rate (Case 1) as a function of interdependency among species. Figure C2 illustrates the natural equilibria for two stocks, both with a high intrinsic growth rate (Case 2), and Figure C3 shows the natural equilibria for two stocks with a low and high intrinsic growth rate, respectively (Cases 3 and 4). The stocks are symmetric; therefore, (low, high) is equivalent to (high, low) for the natural equilibria. The model illustrated in the "Visualization" sections also includes economic parameters, and because the species are valued differently, (low, high) and (high, low) are no longer equivalent.

All figures for the natural equilibria look very much alike. In the symbiotic case ($\theta_1, \theta_2 < 0$), both stocks are above their carrying capacities as they both benefit from the existence of the other species. For illustrative purposes, the stock sizes in these cases are

Table C1. Parameter values applied for visualization.

p_1	p_2	R_{low}	R_{high}	$K_1 = K_2$	C	Q	OA	MS	Q_1	Q_2
1	2	0.3	0.9	50	7	0.5	60	60	$[-0.2; 0.2]$	$[-0.2; 0.2]$

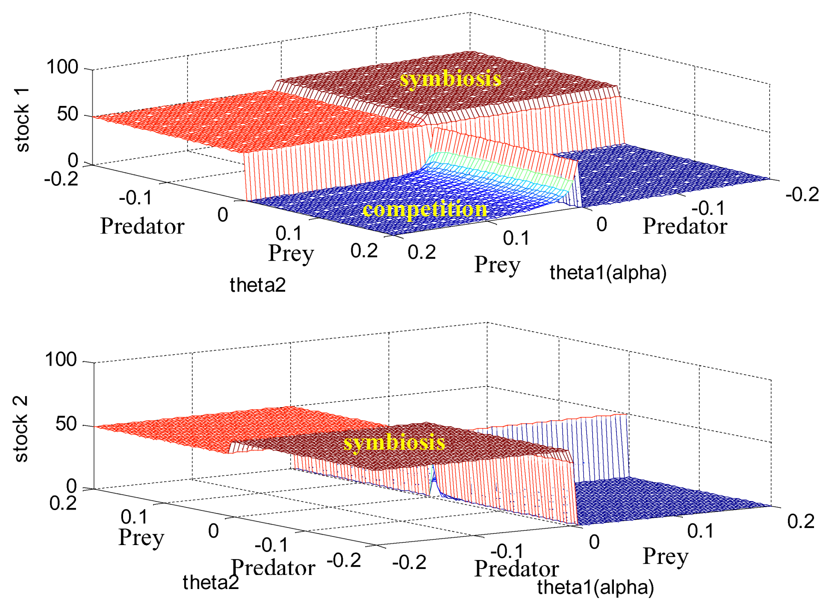

Figure C1. The natural equilibria for two stocks, both with a low intrinsic growth rate (Case 1).

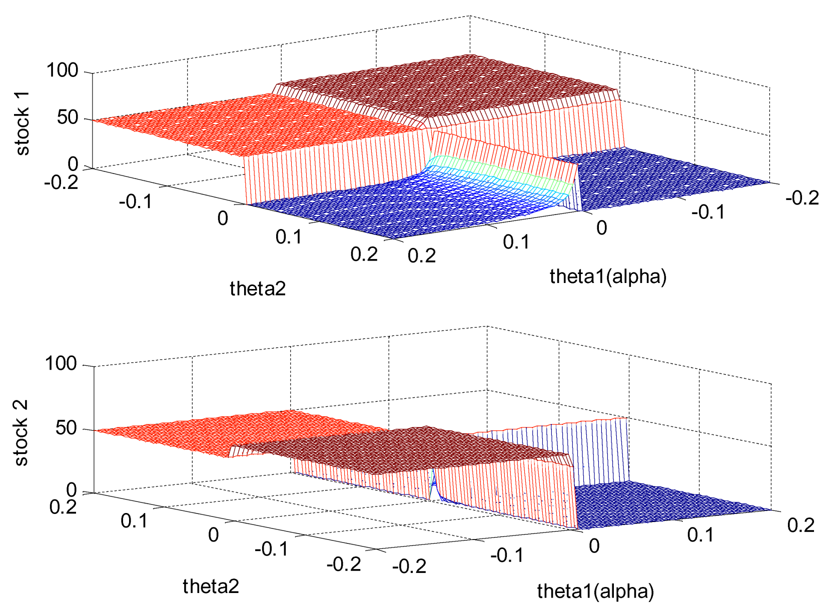

Figure C2. The natural equilibria for two stocks, both with a high intrinsic growth rate (Case 2).

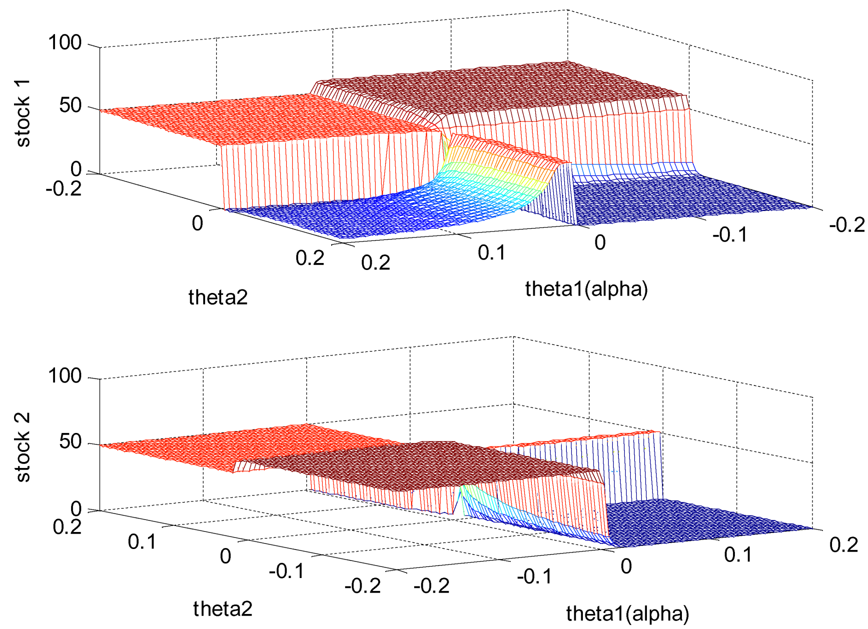

Figure C3. The natural equilibria for two stocks with a low and high intrinsic growth rate, respectively (Cases 3 and 4).

restricted, as the Gause model itself predicts unlimited growth. These upper plateaus when there is a symbiosis (or mutualism) among species are higher than the carrying capacities, due to the upper limit for the maximum stock size (MS), which we forced into being slightly higher than the carrying capacity. The theoretical model itself suggests that the stock could jointly grow to very high stock levels. In the case of predator–prey situations ($\theta_j > 0$ (prey), $\theta_m < 0$ (predator)), the dominant cases in the figures are the cases in which one of the stocks becomes extinct. This is due to the application of the Gause model, which only predicts a narrow range of stable coexistence equilibria. This corresponds to the narrow parameter space at the positive θ-parameter (the prey) close to zero, where both species can coexist. It is due to this narrow range of coexistence in the predator–prey model that the theta parameter is chosen to be within the range $[-0.2; 0.2]$. Finally, the case of competition ($\theta_1, \theta_2 > 0$) is described by decreasing stock levels; an example is where species 1 decreases with increasing θ_1 and species 2 decreases with increasing θ_2.

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