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**Mathematical models of  
social-ecological systems  
Coupling human behavioural  
and environmental dynamics**

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*To the Pomoû.*



“Et depuis tant de siècles nous ne savons pas grand-chose là-dessus.”

Proust.



# Abstract

There is an increasing concern for the impact of humans on the environment. Traditionally, ecological models consider human influence as a constant or linearly varying parameter, whereas socioeconomic models and frameworks tend to oversimplify the ecological system. But tackling complex environmental challenges faced by our societies requires interdisciplinary approaches due to the intricate feedbacks between the socioeconomic and ecological systems involved. Thus, models of social-ecological systems couple an ecological system with a socioeconomic system to investigate their interaction in the integrated dynamical system.

We define this coupling formally and apply the social-ecological approach to three ecological cases. Indeed, we focus on eutrophication in shallow freshwater lakes, which is a well-known system showing bistability between a clear water state and a turbid polluted state. We also study a model accounting for an aquifer (water stock) and a model accounting for a biotic population exhibiting bistability through an Allee effect.

The socioeconomic dynamics is driven by the incentive that agents feel to act in a desirable or undesirable way. This incentive can be represented by a difference in utility, or in payoff, between two strategies that each agent can adopt: agents can cooperate and act in an environment-friendly way, or they can defect and act in an ecologically undesirable way. The agents' motivation includes such factors as the economic cost of their choice, the concern they feel for the environment and conformism to the collective attitude of the human group. Thus, the incentive to cooperate responds to the state of the ecological system and to the agents' collective opinion, and this response can be linear, nonlinear and monotonic, or non-monotonic. When investigating the mathematical form of this response, we find that monotonic nonlinear responses may result in additional equilibria, cycles and basins of attraction compared to the linear case. Non-monotonic responses, such as resignation effects, may produce much more complicated nullclines such as a closed nullcline and weaken our ability to anticipate the dynamics of a social-ecological system.

Regarding the modelling of the socioeconomic subsystem, the replicator dynamics and the logit best-response dynamics are widely used mathematical formulations from evolutionary game theory. There seems to be little awareness about the impact of choosing one or the other. The replicator dynamics assumes that the socioeconomic subsystem is stationary when all agents adopt the same behaviour, whereas the best-response dynamics assumes that this situation is not stationary. The repli-

cator dynamics has formal game theoretical foundations, whereas best-response dynamics comes from psychology. Recent experiments found that the best-response dynamics explains empirical data better. We find that the two dynamics can produce a different number of equilibria as well as differences in their stability. The replicator dynamics is a limit case of the logit best-response dynamics when agents have an infinite rationality.

We show that even generic social-ecological models can show multistability. In many cases, multistability allows for counterintuitive equilibria to emerge, where ecological desirability and socioeconomic desirability are not correlated. This makes generic management recommendations difficult to find and several policies with and without socioeconomic impact should be considered.

Even in cases where there is a unique equilibrium, it can lose stability and give rise to sustained oscillations. We can interpret these oscillations in a way similar to the cycles found in classical predator-prey systems. In the lake pollution social-ecological model for instance, the agents' defection increases the lake pollution, which makes agents feel concerned and convince the majority to cooperate. Then, the ecological concern decreases because the lake is not polluted and the incentive to cooperate plummets, so that it becomes more advantageous for the agents to defect again. We show that the oscillations obtained when using the replicator dynamics tend to produce a make-or-break dynamics, where a random perturbation could shift the system to either full cooperation or full defection depending on its timing along the cycle.

Management measures may shift the location of the social-ecological system at equilibrium, but also make attractors appear or disappear in the phase plane or change the resilience of stable steady states. The resilience of equilibria relates to basins of attraction and is especially important in the face of potential regime shifts. Sources of uncertainty that should be taken into account for the management of social-ecological systems include multistability and the possibility of counterintuitive equilibria, the wide range of possible policy measures with or without socioeconomic interventions, and the behaviour of human collectives involved, which may be described by different dynamics. Yet, uncertainty coming from the collective behaviour of agents is mitigated if they do not give up or rely on the other agents' efforts, which allows modelling to better inform decision makers.

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# 1 Introduction

## 1.1 Modelling social-ecological systems

The past decade has seen an increasing concern for the impact of humans on their environment (Galvani et al., 2016; Mourelatou and European Environment Agency, 2018), resulting notably in movements emerging from the civil society. The fact that the political world is finally starting to consider environmental problems as a top priority illustrates the unprecedented impact of this global tendency. For instance, the President of the newly approved European Commission Ursula von der Leyen talks about a *European Green Deal*. This significantly extends one of ten priorities of the previous European Commission (2014-2019), which was much more restrictive: “a resilient energy union with a forward-looking climate change policy” (European Commission, 2015, p. 6).

Scientists have investigated the interplay between humans and ecological systems for a longer time, but the social-ecological trend is still fairly recent in the modelling field (Colding and Barthel, 2019). Traditional ecological models consider human influence as a constant or linearly varying parameter (*e.g.* Clark, 2007), but instead human behaviour should be considered a dynamical system in itself, responding to management strategies in a potentially non-linear way. For instance, a tax increasing linearly in time might not decrease the frequency of an undesirable behaviour in a linear way. On the other hand, many traditional socioeconomic models and frameworks tend to oversimplify the ecological system (*e.g.* Pearce, 1990; Proops and Safonov, 2004).

Social-ecological models represent human behaviour as a dynamical variable interacting with the ecological dynamics. Thus, in the past fifteen years, several articles have proposed social-ecological models, which couple an ecological system with a socioeconomic system. Social-ecological models have been applied to diverse ecological contexts such as fisheries and other harvested, biological populations (Fryxell et al., 2010; Lee and Iwasa, 2014; Bieg et al., 2017), lakes (Iwasa et al., 2007; Suzuki and Iwasa, 2009; Iwasa et al., 2010), grasslands (Lee et al., 2015a), farmlands (Figueiredo and Pereira, 2011), forests (Satake and Iwasa, 2006; Satake et al., 2007a,b; Henderson et al., 2013; Lee et al., 2015b), groundwater (Ibáñez et al., 2004; Tavoni et al., 2012; Lade et al., 2013) and in the more general context of a theoretical common pool resource (Noailly et al., 2003; Iwasa and Lee, 2013; Sugiarto et al., 2015, 2017).

The study of coupled social-ecological models consists in considering the socioeconomic system and the ecological system as parallel, interacting complex adaptive subsystems within an integrated system (Levin, 2006). This framework allows us to investigate linkages and feedbacks in the coupled system (Colding and Barthel, 2019) and provides options for a management of the ecological system through socioeconomic actions (*e.g.* Suzuki and Iwasa, 2009). And indeed, tackling complex environmental challenges faced by our societies requires interdisciplinary approaches due to the intricate feedbacks between the socioeconomic and ecological components involved (Baumgärtner et al., 2008; Schlüter et al., 2011; Tavoni and Levin, 2014). Difficulties along the way include but are not limited to differences in terminology and in methodology, as well as the coupled social-ecological system being particularly complex since each subsystem brings its own complexity plus additional complexity due to their interaction.

## 1.2 Multistability and non-linearity: features of complexity

The ecological models used in coupled human-environment systems can most of the time be discussed, criticized and improved by considering empirical data. For instance, models of eutrophication in shallow freshwater lakes are strongly supported by experiments, making them reliable, sometimes predictive, and well-accepted (Scheffer, 1998). Building on this knowledge, some social-ecological studies with an economic approach have relied heavily on the assumption that optimal measures could and should be uniquely defined (Kiseleva and Wagener, 2010; Tavoni et al., 2012; Lade et al., 2013).

But many ecological systems show alternative stable states (May, 1977), for instance survival and extinction in living populations such as in coral reefs (Mumby et al., 2007), good and poor condition of a grazing system (Noy-Meir, 1975; Westoby et al., 1989; Schwinning and Parsons, 1999), or oligotrophic (clear water) and eutrophic states (turbid green water) in lakes (Scheffer, 1998). Similarly, socioeconomic systems can also show alternative stable states. Examples can be found between the rich and poor status of an agent in the problem of poverty trap (Ngonghala et al., 2014, 2017), or in the degree of adoption or non-adoption of a new mindset or behaviour at the population level in social learning or when considering social norms (Nyborg et al., 2016).

The study of coupled social-ecological systems where no subsystem shows features of complexity is relatively straightforward. Notably, when each subsystem is monostable, we can expect the coupled system to tend towards the attractor of both subsystems at the same time, formally leading to their intersection. In the present

thesis however, we consider the case where both *subsystems*, the ecological as well as the socioeconomic one, can show bistability. We focus on cases where both are bistable because we expect the dynamics of the coupled human-environment system to be particularly complex in those cases. For that reason, we focus on a well understood ecological system, namely shallow freshwater lakes, which is well-known for displaying bistability (Scheffer, 1998).

Additionally, the fact that human behavioural responses are often not linear provides another important feature of complexity. Human behavioural responses may be intrinsically non-linear as in the case of a bistability, but also because of their collective nature. Such non-linearities in the way humans' incentive to act on their environment changes may be of paramount importance in the field of social-ecological modelling. In this field, such non-linearities have been considered (*e.g.* Tavoni et al., 2012), but we are not aware of investigations of different kinds and levels of non-linearities, especially in the ecological context of lake eutrophication. The set of mathematical terms corresponding to human behavioural responses are often not explicitly interpreted as the incentive that agents have to influence the ecological system.

In the case of lake eutrophication, cooperation consists in having a low discharge of pollution whereas defection consists in having a high discharge of pollution. The choice between the two strategies may depend on various social and economic factors, such as their cost, social conformism or the implementation of management policies. This dependency may be linear, or more complex, with abrupt or non-monotonic variations. Indeed, if the ecological system's state worsens to the point where the situation seems desperate, humans may end up feeling that their efforts cannot have anymore influence. This in turns decreases their incentive to cooperate and results in a giving-up behaviour. Similarly, if we expect cooperation to improve the incentive to cooperate in general, we may also think that, in the situation where most agents already act in an environment-friendly way, at least some individuals can think of relying on the others' collective behaviour and allow themselves to defect more easily. This means that the incentive to cooperate may start decreasing once a certain level of cooperation is achieved in the population.

### 1.3 Evolutionary game theory in social-ecological modelling

Contrary to the ecological component of coupled human-environment systems, the mathematical formulations used to model the human behaviour are usually not explicitly justified. Most mathematical models of a social-ecological system represent the socioeconomic part with an evolutionary game theoretic approach. Indeed, evo-

lutionary game theory provides a unified framework to account for the dynamics of individual decisions at a population level. Yet, abstract tools developed by game theory often cannot be applied as such to the study of social-ecological systems because they do not find an intuitive empirical interpretation: game theory imposes a steep learning curve for quite little empirical reward. As a consequence, many researchers interested in the empirical interpretation of social-ecological dynamics may not be familiar with the origins and with the implications of specific socioeconomic dynamics formulations.

The replicator dynamics and the logit best-response dynamics are the most widely used dynamics proposed by evolutionary theory which are used to describe the evolution of the collective choice of individuals between different strategies at a population level. Despite a growing body of empirical data (*e.g.* Hoffman et al., 2015), experiments on humans' behaviour usually do not allow for quantification of the adoption of a strategy over large populations during a long enough time since the experiments typically involve a few dozen subjects playing a simple game over ten rounds in a few hours (*e.g.* Dannenberg et al., 2015). As a consequence, experiments give little support to game theoretical dynamics. However, in the mathematical social-ecological literature, other approaches are a less common. They are often tailored to the specific socioeconomic and ecological context and rely on various approaches such as more complex game theoretical methods or optimal control (Mähler et al., 2003; Ibáñez et al., 2004; Kossioris et al., 2008), or on statistical physics and/or network models (Hutchinson and Waser, 2007; Fryxell et al., 2010; Wang et al., 2015; Bieg et al., 2017).

There seems to be little awareness about the impact of picking a specific mathematical formulation for a socioeconomic dynamics in the modelling literature. This is a major issue because conclusions derived from models using a given specific formulation may well depend on the way humans are assumed to behave. As to the replicator and the logit best-response dynamics for instance, the game theoretical literature has described very abstract links (Hopkins, 1999; Hofbauer et al., 2009) which have been little discussed by modellers. Thus, the consequences of these theoretical links in a coupled social-ecological model have not been described. More generally, interpretations beyond the mathematical result have not been discussed and it is of paramount importance to raise the awareness of the concepts and assumptions underlying these dynamics.

## 1.4 Outline

The present thesis comprises five main chapters. The first chapter considers a mathematical model for a water stock managed as a common pool resource based on Tavoni et al. (2012) and introduces the concept of *coupling* between the subsystems of a

social-ecological system. Particular definitions of the coupling previously suggested that the coupling could introduce complexity features which were absent from the isolated ecological subsystem (Lade et al., 2013). We discuss this idea by proposing a straightforward way to unequivocally define the coupling between subsystems in a social-ecological model.

The second chapter introduces the social-ecological model for lake eutrophication in shallow freshwater lakes that forms the basis for the thesis. Focusing on questions of multistability, it challenges the intuition that decreasing pollutant discharge should be the best way to decrease lake pollution. It also challenges the conceptual expectation that generic management recommendations should be possible. It concludes that several policies with and without socioeconomic intervention should be considered.

The third chapter focuses on the socioeconomic part of social-ecological models and compares the two most widely used mathematical formulations, the replicator dynamics and the best-response dynamics, which both originate from evolutionary game theory. To that aim, we compare the modelling outcomes of two social-ecological models for lake pollution dynamics which differ only in their socioeconomic component. This difference results in a different number of equilibria as well as differences in their stability. Analyzing the nullclines in the two cases illustrates the fact that having human agents behave more and more rationally makes the best-response dynamics approach the replicator dynamics, so that the coupled models get closer and closer. We note that oscillations found in the two models may not be similar. In particular, the replicator dynamics tends to allow the system to oscillate between states with either almost full defection (undesirable social behaviour) or almost full cooperation (desirable social behaviour). The system then spends extended periods of time in states where random perturbations could shift it to full cooperation or full defection, making the final outcome depend dramatically on the perturbation's timing, what we describe with the term *make-or-break dynamics*.

The fourth chapter consists in a review of the replicator dynamics and of the logit best-response dynamics in the socioeconomic modelling of social-ecological systems. It aims at providing an overview of evolutionary game theoretical dynamics in mathematical social-ecological models and at discussing their theoretical and their empirical justification as well as the reasons to choose a specific formulation.

The fifth chapter focuses on the mathematical formulation of the incentive that human agents have to act in an environment-friendly way in the socioeconomic dynamics of social-ecological systems. In the previous chapters, the incentive to have a cooperating behaviour is always assumed to be linear. This chapter introduces non-linearity. We consider two cases, one where the response is still monotonic but not linear anymore and one where the response is not monotonic, having an increasing then a decreasing part.

Finally, we gather and summarize our results and discuss overall modelling and management implications to arrive at perspectives for research in the modelling of social-ecological systems.

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# 2 Coupling social and ecological models of the exploitation of monostable and bistable ecological resources

## Abstract

We consider two mathematical social-ecological models for the exploitation of an ecological resource by a population of human agents who can choose to exploit the resource either on a low level (cooperation) or on a high level (defection). The first model accounts for the exploitation of an aquifer (water stock) where the ecological component is monostable. We obtain intuitive analytical stability conditions for equilibria. The system cannot be stationary if the water stock dries up. The socioeconomic subsystem imposes that full defection can be stable only if the water level is high, and conversely that full cooperation can be stable only if the water level is low. The second model integrates the same socioeconomic component with a bistable ecological subsystem accounting for a harvested biological population with a strong Allee effect. In this second model, both the ecological and the socioeconomic subsystem can be bistable in isolation. The dynamical coupling between the two subsystems tends to decrease the ecological Allee threshold and to increase the ecological component at the persistence equilibrium when cooperation increases. Similarly, the coupling tends to increase the threshold level of cooperation between equilibria with full cooperation and full defection when the resource level increases. We propose a formal definition of this coupling and prove that a fully linear integrated system cannot exhibit multistability, thus rejecting previous potentially misleading statements in the literature. We review and interpret standard stability results for generalized coupled environment-socioeconomic systems.

## 2.1 Introduction

This chapter aims at introducing a number of theoretical notions and questions relating to mathematical models of social-ecological systems. Following Tavoni et al.

(2012), Lade et al. (2013) provide a well-cited example of a social-ecological model using an economic approach to its social component. Ibáñez et al. (2004) previously used the ecological component and were interested in applying an optimal control approach to their ecological model. Tavoni et al. (2012) added a social component and were interested in the effect of the social pressure they had introduced. Lade et al. (2013) used a generalized modelling approach of this social-ecological model to investigate the possibility of regime shifts in social-ecological models.

In this first chapter, we start by presenting their social-ecological model for a water stock managed as a common pool natural resource by a human population. Then, we investigate a variation with a more complex ecological system exhibiting an Allee effect. Finally, we discuss the approach, the results and the conclusion of Tavoni et al. (2012) and Lade et al. (2013) regarding the emergence of a surprising complexity in a coupled social-ecological model compared to the simplicity of each of its components.

## 2.2 Social-ecological water stock model

### 2.2.1 Ecological component

The ecological component of the system describes the dynamics of the state variable  $P$  representing the abundance of a product, a resource harvested from a common pool. It had been developed to account for the dynamics of a water stock, where water is the natural resource exploited and where a constant inflow replenishes the stock (Ibáñez et al., 2004).

Without harvesting, the dynamics of the aquifer follows the following ordinary differential equation:

$$\frac{dP}{dt} = I - d \left( \frac{P}{K} \right)^k, \quad (2.1)$$

where  $I$  represents a constant positive rate for the replenishment of the stock when it is empty. In the original formulation, Ibáñez et al. (2004) impose that  $k \geq 1$ . Tavoni et al. (2012) and Lade et al. (2013) focus on the case  $k = 2$  in their analyses. Should the water level  $P$  increase towards  $K$ , the replenishment rate would be dampened according to dampening parameter  $d$ . Therefore, Ibáñez et al. (2004, p. 2) interpret  $K$  as the “maximum capacity of the aquifer” and Tavoni et al. (2012) and Lade et al. (2013) follow the same interpretation.

However, it is easy to show that the maximum capacity of the unexploited water stock is actually  $P_{max} = K \sqrt[k]{I/d}$ , so that  $K$  is not the maximum capacity of the aquifer but a scaling factor of the actual maximum capacity  $P_{max}$ . That is obvious in the cases where  $k = 1$  or  $k = 2$ , which allow for exact analytical solutions. We consider an initial condition  $P_0 \geq 0$  for the water level at  $t = 0$ . When  $k =$

1, equation (2.1) is a simple linear first order differential equation with solution  $P(t) = P_{max} - (P_{max} - P_0)e^{-td/K}$ . When  $k = 2$ , equation (2.1) becomes a Riccati equation and we can have three cases. If  $P_0 > P_{max}$ , equation (2.1) has no solution. If  $P_0 = P_{max}$ , the unique solution for equation (2.1) is the constant  $P_{max}$  itself. If  $P_0 < P_{max}$ , the unique corresponding solution for equation (2.1) is

$$P(t) = P_{max} \tanh \left[ P_{max}t + \frac{1}{2} \ln \left( \frac{P_{max} + P_0}{P_{max} - P_0} \right) \right],$$

where  $\tanh$  is the hyperbolic tangent:  $\tanh(x) = (e^x - e^{-x})/(e^x + e^{-x})$  for all  $x$ .

If the water stock is exploited, a harvested part is subtracted from the dynamics without harvesting of equation (2.1). The subtracted quantity is assumed to depend proportionally (parameter  $q$ ) on the harvesting effort  $E$  and on the available quantity of water  $P$ :

$$\frac{dP}{dt} = I - d \left( \frac{P}{K} \right)^k - qEP. \quad (2.2)$$

We note that, because of the constant inflow of the natural resource, all states of the system verifying  $P = 0$  are still unstable: in equation (2.2), the absence of resource spontaneously tends to increase the amount of resource as in equation (2.1). This model could be applied to other natural resources, for instance to a biotic natural resource such as a harvested species as long as there is an inflow in the resource. Indeed, a model for a harvested species without any external inflow, due to dispersal for example, should assume that extinction is stable and that no new living individual can appear spontaneously.

### 2.2.2 Social component

We focus on time periods short enough for the number of harvesters to remain constant. Note that in this model, we consider a population composed of agents exploiting the natural resource. The social component of the system is characterized by a unique social state variable: the proportion  $F$  of harvesters who stick to a cooperating strategy  $C$ . Indeed, the social model relies on the idea that each individual chooses between two strategies, cooperation  $C$  or defection  $D$ . In the context of the management of a common stock of water, those two strategies actually represent social behaviours of a cooperative (coordinated) or non-cooperative (individualistic) way to exploit the water stock.

The two strategies relate to the model through a utility function  $U$ . Utility represents an abstract measure of the satisfaction for an individual, so that an individual's behaviour is assumed to maximize  $U$ . Thus, the utility function  $U$  is defined per unit of harvesting population, that is, for an agent. Moreover, it is

assumed to depend exclusively on the adopted strategy: at any point in time, there is the same value  $U_C$  for each cooperator and the same value  $U_D$  for each defector.

Tavoni et al. (2012) introduce the equation for the social component as the *replicator dynamics*. The inspiration for this mathematical formulation of the social component is to be found in a previous article from the field of evolutionary biology (Taylor and Jonker, 1978). Tavoni et al. (2012, p. 156) explain that they choose this formulation to “avoid the complete rationality requirements typical of models of optimization, while retaining (myopic and lagged) convergence towards better outcomes due to the imitation of successful behavior”. Moreover, they write that “such an approach is particularly well-suited to the analysis of the evolution of norm adoptions as it allows us to focus on emergent phenomena without being confined, as is the case for neoclassical analysis, to equilibrium outcomes and representative agents solely described by their optimizing behavior”. This very dense explanation is a summary of the replicator dynamics properties from an economic and from a game-theoretical perspective. Tavoni et al. (2012) and Lade et al. (2013) do not mention the dynamical characteristics of the replicator, but those are relatively simple. Indeed, the varying proportion of cooperators  $F$  is assumed to stop changing (the infinitesimal variation vanishes) in a one-strategy harvester population, so that  $F = 0$  (full defection) and  $F = 1$  (full cooperation) are stationary states for the social component of the model. Additionally, the direction followed by the population’s collective choice between cooperation and defection depends on the difference between  $U_C$  and  $U_D$ :

$$\frac{dF}{dt} = F(1 - F)(U_C - U_D) = F(1 - F)\Delta U. \quad (2.3)$$

We can interpret the difference  $\Delta U$  as the abstract reward, positive or negative, that an individual obtains from choosing cooperation over defection. We can also interpret it in a similar way as the gain one can expect from cooperating, that is as the positive or negative incentive to cooperate.

The key to the social dynamics is the formulation of the utility functions. Tavoni et al. (2012) use two main assumptions to mathematically formulate the utility of cooperators or of defectors. The first assumption is that each strategy corresponds to a different level  $e$  of individual exploitation effort ( $e_C$  or  $e_D$ ), that utility income is proportional to this exploitation effort and that cooperators provide less effort than defectors:  $e_C < e_D$ . The second assumption is that, depending on the fraction  $F$  of cooperators, a supplementary utility cost  $\Omega(F)$  is inflicted to defectors by means of social pressure. This corresponds to a social punishment.

### **Effort functions**

Let  $e_D$  and  $e_C$  denote a positive measure of the effort provided by a defector or a cooperator, respectively, and let  $\delta_e = e_D - e_C \in \mathbb{R}$  be the difference of effort

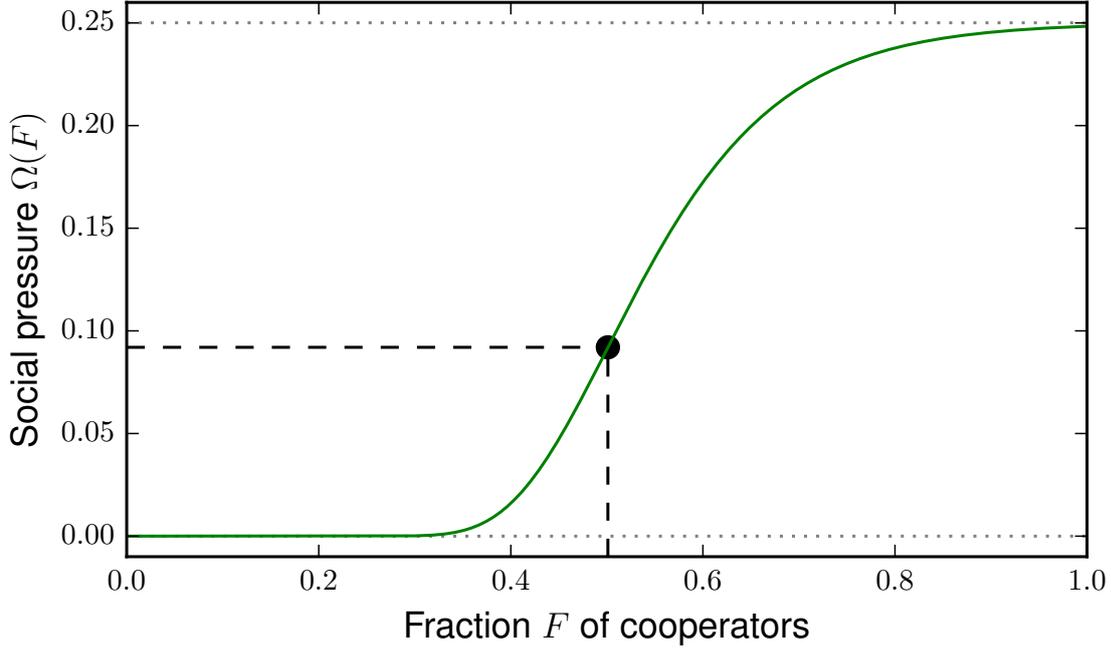


Figure 2.1: Gompertz function  $\Omega$  of the fraction  $F$  of cooperators accounting for the social pressure in the model of a water stock (solid green curve), with the limit values 0 and  $\frac{\delta_e \omega_1}{e_D}$  when defining the function on  $\mathbb{R}$  (dotted grey lines) as well as the inflexion point with  $F = \frac{\ln(\omega_2)}{\omega_3}$  and  $\Omega = \frac{\delta_e \omega_1}{e_D e}$ , showing the asymmetry of the curve. Parameter values:  $e_D = 0.03652$ ,  $\delta_e = 0.02686$ ,  $\omega_1 = 0.34$ ,  $\omega_2 = 150$ ,  $\omega_3 = 10$ .

that cooperators spare individually by following a cooperation strategy. The total harvesting effort  $E$  is the sum of all individual efforts:

$$E = nF e_C + n(1 - F) e_D = n(e_D - \delta_e F) \geq 0, \quad (2.4)$$

where  $n$  is a measure of the agents' population size, for instance the number of individuals. The assumption that cooperators provide less effort than defectors  $e_C < e_D$  means that the total effort is positive.

### Social pressure function $\Omega$

**Definition and assumptions** For the social punishment function  $\Omega$ , Tavoni et al. (2012) and Lade et al. (2013) use a Gompertz function shown in Fig. 2.1:

$$\Omega(F) = \frac{\delta_e}{e_D} \omega_1 \exp(-\omega_2 e^{-\omega_3 F}). \quad (2.5)$$

This mathematical formulation is based on the following assumptions:

- $\Omega(F)$  is proportional to the relative difference in individual effort between defectors and cooperators  $(\frac{\delta_e}{e_D})$ ;
- $\Omega$  is a strictly increasing function of the proportion  $F$  of cooperators, whichever their number  $nF$  is;
- the curve representing  $\Omega$  as a function of  $F$  is sigmoidal: there is a nonlinear increase in social pressure as the fraction of cooperators increases;
- $\Omega$  is asymmetric between  $F = 0$  and  $F = 1$ .

**Discussion of the social pressure function  $\Omega$**  The Gompertz function modelling social pressure as a function of the fraction of cooperators presents two drawbacks. First, as the domain of definition is restricted from  $\mathbb{R}$  to  $[0, 1]$ , its image becomes arbitrary. In particular, it may be argued that a population with no cooperators should induce no social pressure towards cooperation, meaning that  $\Omega(0) = 0$ , which is not the case.

Second, as Fig. 2.1 shows, it is arbitrarily oriented towards the adoption of a behaviour because of its asymmetry: social pressure is assumed to be skewed by the content of the most common decision. Unless some evidence supports this viewpoint, it may be argued that a purely social pressure would equally favour cooperation when the majority cooperates as defection when the majority defects, because social pressure would then depend only on the group effect and not on the specific choice made by the majority of agents. Instead, the choice made by Tavoni et al. (2012) and Lade et al. (2013) implies that social pressure increases more abruptly when departing from full defection and that it decreases more progressively when leaving full cooperation.

### Utility values $U_C$ and $U_D$

Lade et al. (2013) create a link between the effort functions and utility functions with concepts taken from the field of economy. To define a (collective or individual) productivity ratio, they use a Cobb-Douglas production function, which was developed and studied by Cobb and Douglas (1928), and which is widely used in economy and in econometrics to describe the productivity as a function of a capital and of an amount of work:

$$\text{productivity} = \frac{cP^{\alpha_1} E_2^\alpha}{E} = cP^{\alpha_1} E^{\alpha_2-1},$$

where Lade et al. (2013) implicitly assimilate the level of resource  $P$  to a capital and the effort to a kind of work.  $\alpha_1$  and  $\alpha_2$  represent output elasticities ( $\alpha_1 \in ]0, 1[$ ,  $\alpha_2 \in ]0, \alpha_1[$ ).  $c$  is a positive total-factor productivity ( $c > 0$ ).

In addition, the utility functions  $U_C$  and  $U_D$  include a cost  $w$  induced by the (collective or individual) effort, and are supposed to be proportional to the individual effort. The utility function  $U_D$  for a defector also takes into account the social cost  $\Omega(F)$  of choosing the non-cooperative behaviour.

$$\begin{cases} U_C &= e_C (cP^{\alpha_1} E^{\alpha_2-1} - w) \\ U_D &= e_D (cP^{\alpha_1} E^{\alpha_2-1} - w) - \Omega(F) \end{cases} \quad (2.6)$$

From equations (2.4), (2.5) and (2.6), the different layers of the social model are combined in the incentive to cooperate:

$$\Delta U = \delta_e \left[ w - cn^{\alpha_2-1} P^{\alpha_1} (e_D - \delta_e F)^{\alpha_2-1} + \frac{\omega_1}{e_D} \exp(-\omega_2 e^{-\omega_3 F}) \right]. \quad (2.7)$$

### 2.2.3 Integrated water stock model dynamics

#### Coupled model

The integrated system gathers equations (2.2), (2.3) and (2.7):

$$\begin{cases} \frac{dP}{dt} = -\frac{d}{K^k} P^k - qnP(e_D - \delta_e F) + I \\ \frac{dF}{dt} = \delta_e F(1 - F) \\ \left[ w - cn^{\alpha_2-1} P^{\alpha_1} (e_D - \delta_e F)^{\alpha_2-1} + \frac{\omega_1}{e_D} \exp(-\omega_2 e^{-\omega_3 F}) \right] \end{cases} \quad (2.8)$$

The complete system does not appear as such in Tavoni et al. (2012) or Lade et al. (2013), who imply it from the separate equations (2.2) to (2.6) explained at each step of the model derivation. But displaying the complete coupled social-ecological model allows us to realize how complex the model actually is. Note in particular the complexity of the social component, where, additionally,  $\alpha_1$  and  $\alpha_2$  are not integers.

Because of their focus on the socioeconomic system (Tavoni et al., 2012), or on a specific definition of the coupling between the social-ecological system's components and on a generalized modelling approach (Lade et al., 2013), Tavoni et al. (2012) and Lade et al. (2013) have not presented an analysis of the coupled dynamical system's nullclines. The stability analysis presented in the appendix of Tavoni et al. (2012) does not include interpretations beyond the mathematical point of view. In the subsequent sections, we present an analysis of the nullclines and an interpretation of insights obtained from the Jacobian matrix regarding stability.

### Nullclines

The  $P$ -nullcline  $\Delta_P$  has been described for  $k = 2$  by Tavoni et al. (2012, p. 160) but we can derive its equation in the general case:

$$F = \frac{d}{qn\delta_e K^k} P^{k-1} - \frac{I}{qn\delta_e} + \frac{e_D}{\delta_e}, \quad (2.10)$$

which corresponds to a strictly increasing function of  $P$  since  $P$  is positive.

Regarding the  $F$ -nullclines, two are trivial horizontal straight lines ( $F = 0$  and  $F = 1$ ). The third and last one  $\Delta_F$  is more complex:

$$cP^{\alpha_1} = n^{1-\alpha_2} (e_D - \delta_e F)^{1-\alpha_2} \left[ \frac{\omega_1}{e_D} \exp(-\omega_2 e^{-\omega_3 F}) + w \right]. \quad (2.11)$$

As we always have  $\delta_e < e_D$ , equation (2.11) is never satisfied for  $P = 0$ . This means that the social system is not stationary if the water stock is exploited to the point where it dries up. As a consequence, equation (2.11) for  $P > 0$  reduces to:

$$\Delta_F : P = \sqrt[\alpha_1]{\frac{n^{1-\alpha_2} (e_D - \delta_e F)^{1-\alpha_2}}{c} \left[ \frac{\omega_1}{e_D} \exp(-\omega_2 e^{-\omega_3 F}) + w \right]},$$

which means that  $\Delta_F$  is the graphical representation of a function, *i.e.* each value for  $F$  gives a single corresponding value for  $P$  on the non-trivial  $F$ -nullcline. Fig. 2.2 shows that the non-trivial  $F$ -nullcline has two folds. The non-trivial  $F$ -nullcline thus shows three branches. As a consequence,  $\Delta_F$  can intersect with the  $P$ -nullcline three times and the integrated system, including the two trivial  $F$ -nullclines, can have five equilibria.

### Trivial stability of the social part

Here we focus on the Jacobian matrix to study the stability of the system:

$$J_{(P,F)} = \begin{pmatrix} \frac{\partial P'}{\partial P} \Big|_{(P,F)} & \frac{\partial P'}{\partial F} \Big|_{(P,F)} \\ \frac{\partial F'}{\partial P} \Big|_{(P,F)} & \frac{\partial F'}{\partial F} \Big|_{(P,F)} \end{pmatrix}. \quad (2.12)$$

We first note that the term on the top left corner in (2.12) is always negative:

$$\frac{\partial P'}{\partial P} \Big|_{(P,F)} = -\frac{d}{K^k} P^{k-1} - qE < 0.$$

Moreover, the term on the bottom left term in (2.12) is

$$\frac{\partial F'}{\partial P} \Big|_{(P,F)} = -\delta_e c n^{\alpha_2-1} \alpha_1 P^{\alpha_1-1} F (1-F) (e_D - \delta_e F)^{\alpha_2-1}, \quad (2.13)$$

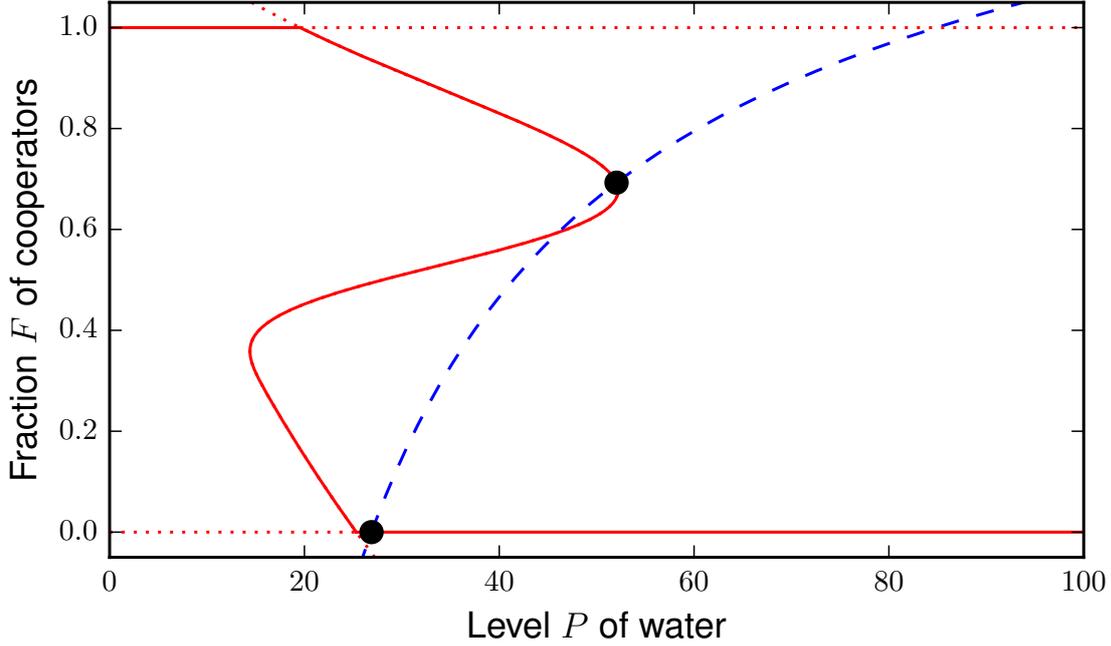


Figure 2.2: Phase plane for the coupled model showing the  $P$ -nullcline (dashed blue) and the  $F$ -nullclines (dotted or solid red), as well as the stable equilibria (filled black circles). Dotted parts of the  $F$ -nullclines cannot be stable. Parameter values:  $I = 50$ ,  $d = 50$ ,  $K = 200$ ,  $k = 2$ ,  $q = 1$ ,  $n = 50$ ,  $e_D = 0.03652$ ,  $\delta_e = 0.02686$ ,  $w = 15$ ,  $c = 10$ ,  $\alpha_1 = 0.2$ ,  $\alpha_2 = 0.6$ ,  $\omega_1 = 0.34$ ,  $\omega_2 = 150$ ,  $\omega_3 = 10$ .  $P_{max} = 200$ .

so that it vanishes whenever  $P = 0$ ,  $F = 0$  or  $F = 1$ . As a consequence, the stability of the system in those cases depends entirely on the term on the bottom right corner of the Jacobian matrix (2.12), because this term is an eigenvalue for (2.12). In the particular cases where  $F = 0$  or  $F = 1$ , the term on the bottom right corner in (2.12) becomes relatively simple, so that we can express a condition for stability.

Indeed, stability may occur with  $F = 0$  only if

$$P \geq P_{stab(F=0)} = \alpha_1 \sqrt{\frac{(ne_D)^{1-\alpha_2}}{c} \left( w + \frac{\omega_1}{e_D} e^{-\omega_2} \right)} > 0. \quad (2.14)$$

As a consequence, the coupled social-ecological system at full defection cannot be stable if the level of the natural resource is too low. In particular, if the water stock dries up and if there are no cooperators, the fraction of cooperators automatically increases because of the social punishment  $\Omega$  added to the constant cost  $w$  of the effort.

Alternatively, stability may occur with  $F = 1$  only if

$$P \leq P_{stab(F=1)} = \sqrt[\alpha_1]{\frac{(ne_C)^{1-\alpha_2}}{c} \left[ w + \frac{\omega_1}{e_D} \exp(-\omega_2 e^{-\omega_3}) \right]}. \quad (2.15)$$

As a consequence, the coupled social-ecological system at full cooperation is stable if the level of the natural resource is sufficiently low. In particular, if the water stock dries up and if there are no defectors, the social punishment  $\Omega$  added to the constant cost  $w$  of the effort prevent the fraction of cooperators from decreasing.

We note that  $P_{stab(F=0)}$  and  $P_{stab(F=1)}$  are precisely the levels of pollution at which the nontrivial  $F$ -nullcline  $\Delta_F$  intersects with the trivial  $F$ -nullclines. That explains why, in Fig. 2.2, the equilibrium with  $F = 1$  is unstable. Thus, there is a subset of the  $F$ -nullclines out of which no equilibrium can be stable. In Fig. 2.2, this is shown by the solid red lines which form a  $Z$ -shaped set in the phase plane.

To this point, we have used the same social-ecological model as Tavoni et al. (2012) and Lade et al. (2013). It becomes obvious that the socioeconomic component can make the coupled model very complex. However, we have focused on an integrated model with a relatively simple ecological subsystem. Indeed, we showed in section 2.2.3 that the  $P$ -nullcline  $\Delta_P$  represented a strictly monotonic function in the phase plane.

## 2.3 Variation with Allee effect in the ecological subsystem

Here, we are interested in considering a more complex ecological component in the social-ecological system. In particular, the social-ecological model from Tavoni et al. (2012) does not display any bistability in its ecological component. To explore this case, we use a widely used representation of a bistable ecological resource. When considering a biotic resource reproducing, a biological population exploited by the human agents, the logistic growth model is a standard formulation. It can be modified to account for a strong Allee effect, or critical depensation, where the population goes extinct if it falls under a fixed threshold. The Allee threshold is the limit below which the population becomes too small to be able to reproduce in a sustainable way.

### 2.3.1 Model with ecological Allee effect

The intrinsic ecological dynamics is based on a logistic growth model with intrinsic growth  $r$ . To include the possibility of an Allee effect, we modify it with a population

threshold  $A < P_{max}$ . In this case, we consider  $P_{max}$  to be a parameter for the carrying capacity of the resource without harvesting.

If we use the same harvesting function as in Tavoni et al. (2012) and Lade et al. (2013), with coefficient  $q$  and a variable harvesting effort  $E$ , we get for the ecological component:

$$\frac{dP}{dt} = rP \left( \frac{P}{A} - 1 \right) \left( 1 - \frac{P}{P_{max}} \right) - qEP.$$

If  $F$  and  $E$  are constant, the last expression is the difference between a cubic function of  $P$  (with roots 0,  $A$  and  $P_{max}$  in increasing order) and a linear term in  $P$  which can be represented by a straight line with equation  $F = qEP$  in the phase plane. Since  $E$  decreases through  $[e_C, e_D]$  as  $F$  increases through  $[0, 1]$ , the more  $F$  increases, the lower the slope of this line gets.

As  $E$  and  $F$  are linked by a linear relation, it doesn't matter for the dynamics whether the social state variable is interpreted as the fraction  $F$  of cooperating people or as the effort  $E$  they impose on the ecological system. If we consider  $F$ , we get:

$$\left\{ \begin{array}{l} \frac{dP}{dt} = rP \left( \frac{P}{A} - 1 \right) \left( 1 - \frac{P}{P_{max}} \right) - qnP(e_D - \delta_e F) \\ \frac{dF}{dt} = \delta_e F(1 - F) \end{array} \right. , \quad (2.16)$$

$$\left[ w - cn^{\alpha_2-1} P^{\alpha_1} (e_D - \delta_e F)^{\alpha_2-1} + \frac{\omega_1}{e_D} \exp(-\omega_2 e^{-\omega_3 F}) \right] \quad (2.9)$$

where the ordinary differential equation (2.9) for the socioeconomic subsystem is the same as previously. Only the ecological subsystem is different, with equation (2.16) replacing equation (2.8) in the coupled system.

### 2.3.2 Model analysis

Since the socioeconomic system remains unchanged, the  $F$ -nullclines also remain unchanged. There is a trivial  $P$ -nullcline  $P = 0$ . Fig. 2.3 illustrates the fact that the nontrivial  $P$ -nullcline  $\Delta_P$  is a parabola defined by

$$F = \frac{r}{qn\delta_e} \frac{P^2}{AP_{max}} - \frac{r}{qn\delta_e} \frac{A + P_{max}}{AP_{max}} P + \frac{r}{qn\delta_e} + \frac{e_D}{\delta_e}.$$

In the Jacobian matrix, we have

$$\frac{\partial P'}{\partial P} \Big|_{(P,F)} = r \left( -\frac{3}{AP_{max}} P^2 + 2 \frac{A + P_{max}}{AP_{max}} P - 1 \right) - qn(e_D - \delta_e F), \quad (2.17)$$

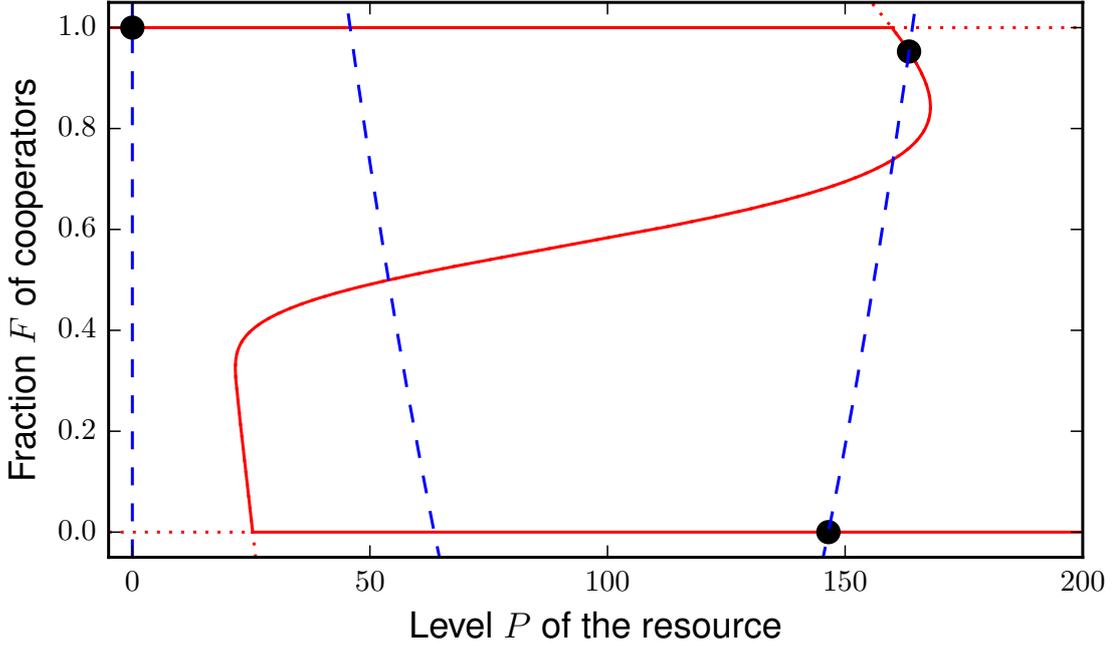


Figure 2.3: Phase plane for a coupled model of an ecological resource with strong Allee effect, showing the  $P$ -nullclines (dashed blue) and the  $F$ -nullclines (dotted or solid red), as well as the stable equilibria (filled black circles). Dotted parts of the  $F$ -nullclines cannot be stable. Parameter values as in Fig. 2.2, except for  $r = 0.5$ ,  $A = 10$ ,  $P_{max} = 200$ ,  $\delta_e = 0.0089$ .

which is always negative on the trivial  $P$ -nullcline as we have seen in the definition of the effort with equation (2.4). Moreover, as we have the same socioeconomic system (2.9) as previously, the term (2.13) on the bottom left part of the Jacobian matrix (2.12) vanishes for  $P = 0$ , for  $F = 0$  and for  $F = 1$ .

Thus, if  $P = 0$ , the term (2.13) on the bottom left part of the Jacobian matrix vanishes and the eigenvalue (2.17) on the top left part of the Jacobian matrix is negative, so that we can express the same conditions of stability (2.14) and (2.15) for  $F = 0$  and  $F = 1$  respectively. For  $F = 0$ , stability condition (2.14) itself imposes that the system cannot be stable unless  $P > 0$ . As a consequence,  $(P = 0, F = 0)$  is always an unstable equilibrium. For  $F = 1$ , stability condition (2.15) is always satisfied on the trivial  $P$ -nullcline  $P = 0$ . As a consequence,  $(P = 0, F = 1)$  is always a stable equilibrium. This state corresponds to full cooperation  $F = 1$  and resource extinction  $P = 0$ . In other words, the situation where all agents cooperate to exploit the resource until it goes extinct is an attractor. It is a counterintuitive equilibrium since agents exploit the resource at a low level  $ne_C$  according to equation (2.4): the low level of exploitation is not sustainable in this case.

Consider a fixed level of cooperation in Fig. 2.3. When starting from  $P = 0$  and increasing  $P$ , the ecological component of the integrated social-ecological system may encounter three stationary states: one at the trivial  $P$ -nullcline and one on each branch of the nontrivial  $P$ -nullcline parabola. This actually describes how the Allee effect of the isolated ecological subsystem is modified by the coupling with the socioeconomic subsystem.

Indeed, the trivial  $P$ -nullcline accounts for the extinction of the resource below the Allee threshold. Thus, it is not surprising that the ecological component is always stable for  $P = 0$ . Then, the left branch of the nontrivial  $P$ -nullcline parabola is the Allee threshold bent by the coupling with the socioeconomic subsystem since its level changes depending on the fraction of cooperators  $F$ . Similarly, the persistence equilibrium for the ecological subsystem in isolation is the right-hand side branch of the parabola. Accordingly, phase plane analyses as in Fig. 2.3 suggest that equilibria occurring on the right-hand side branch may be stable, whereas equilibria occurring on the left branch of the parabola are unstable.

We note that, similarly to the  $Z$ -shaped subset of the  $F$ -nullclines where all stable equilibria must be, the bistable ecological system yields a set of nullclines which has three branches. Across the phase plane, those three branches can be seen as forming a stretched  $S$  corresponding to the bistability of the subsystem being bent by the coupling with the other subsystem.

Fig. 2.4 shows a variety of possible configurations where the nullclines intersect in different ways. Apart from the trivial equilibrium  $(0, 1)$  where agents cooperate and exploit the resource to extinction, which is always stable, simulations show one or two additional stable steady states where the ecological resource is able to persist. The resource being able to persist under exploitation by the agents at equilibrium means that the exploitation is sustainable. The sustainable exploitation of the resource can occur either with a low level of cooperation or with a high level of cooperation. It is surprising that a sustainable exploitation with a low level of cooperation, because the high level of exploitation does not drive the ecological resource to extinction. Therefore, this steady state is a counterintuitive stable equilibrium.

Simulations shown in Fig. 2.4 suggest that a sustainable exploitation with a high level of cooperation achieve a higher level of the resource than a sustainable exploitation with a low level of cooperation. Moreover, remember that the left-hand side branch of the nontrivial  $P$ -nullcline is the Allee threshold for the ecological resource: we also observe that a sustainable exploitation with a high level of cooperation is more distant from the Allee threshold than a sustainable exploitation with a low level of cooperation. Thus, cooperation increases the resilience of the system at equilibrium since random perturbations are less likely to let the system tip passed the Allee threshold and make the resource go extinct.

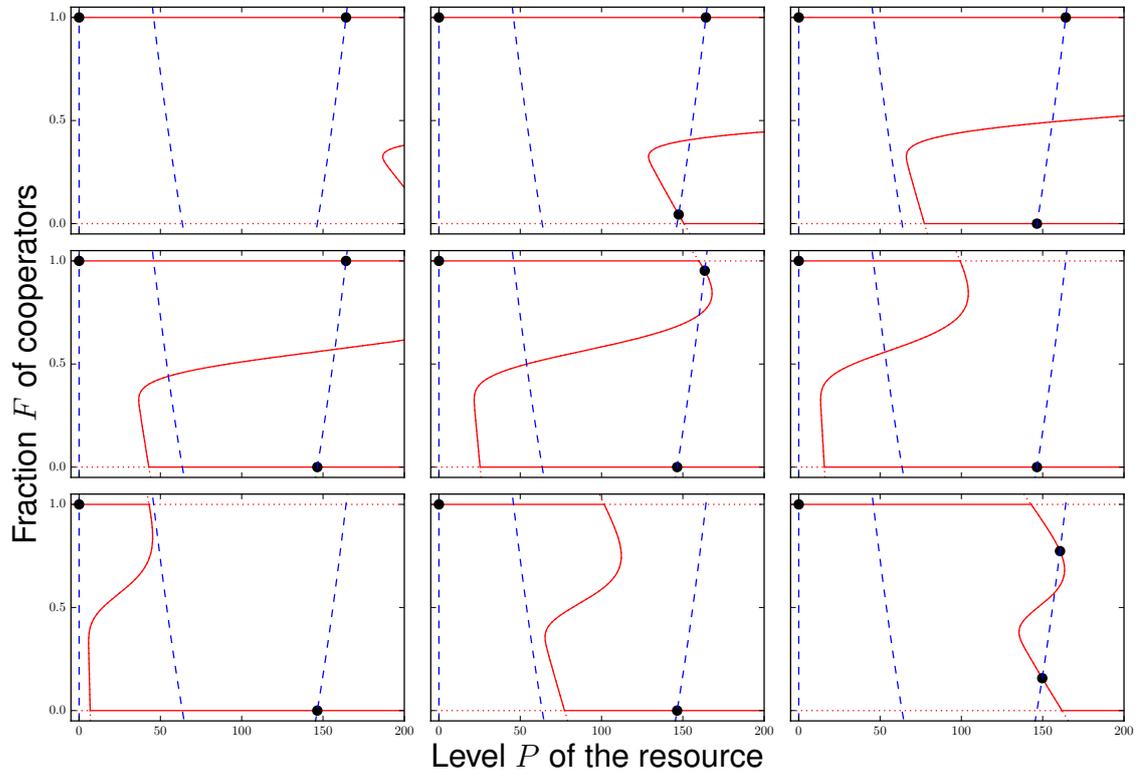


Figure 2.4: *Nine possible configurations of the phase plane for a coupled model of an ecological resource with strong Allee effect, showing the  $P$ -nullclines (dashed blue) and the  $F$ -nullclines (dotted or solid red), as well as the stable equilibria (filled black circles). Dotted parts of the  $F$ -nullclines cannot be stable. Fig. 2.3 is reproduced in the centre. Parameter values as in Fig. 2.3, except for  $c$  and  $\omega_1$ . From top to bottom and on each line from left to right,  $c = 6.5, 7, 8, 9, 10, 11, 13, 8, 6.9$ , and  $\omega_1 = 0.34$  in all panels except for the bottom middle panel ( $\omega_1 = 0.01$ ) and for the bottom left panel ( $\omega_1 = 0.05$ ).*

## 2.4 Emergence of multistability?

A central question regarding the coupling of complex, potentially multistable components into an integrated social-ecological system is whether the coupled system could display multistability from much less complex isolated subsystems. Multistability is a common way to model the possibility of having a regime shift (Scheffer and Carpenter, 2003; Scheffer et al., 2015). Thus, multistability can have dramatic implications in social-ecological systems (Lade et al., 2013) since it goes against linearity and reversibility assumptions that management options often rely on.

Can multistability appear in an integrated social-ecological system coupling subsystems deprived of multistability? This question depends on what we define as being the coupling of an ecological system and a socioeconomic system. Here we discuss an unambiguous way to define this coupling to avoid confusion in interdisciplinary fields, where clear definitions are of special importance.

### 2.4.1 On the emergence of regime shifts

(Lade et al., 2013, p. 360) write: “a central result is that [social-ecological systems] can display regime shifts that are absent from the ecological subsystem in isolation”. This may give the impression that complexity may appear out of the sole coupling of simple subsystems. However, a careful reading makes us notice that the authors did not say anything about the social component. It is obvious that a complex socioeconomic subsystem can bring features of complexity into a coupled system with a simple ecological component.

Similarly, Lade et al. (2013, p. 360) might be misleading when saying that “a non-linear linkage between completely linear social and ecological subsystems, which have no regime shifts of their own, can induce regime shifts in the coupled system”. They provide an equivalent of the following example, which, they report, “removes all non-linearities” (Lade et al., 2013, p. 366):

$$\left\{ \begin{array}{l} \frac{dP}{dt} = c - dP - \text{extraction} \\ \frac{dF}{dt} = \delta_e F(1 - F)[w - \Delta\text{income} + \Omega(F)]. \end{array} \right. \quad (2.18)$$

$$\left\{ \begin{array}{l} \text{extraction} = qPn(e_D - \delta_e F) \\ \Delta\text{income} = cn^{\alpha_2-1}P^{\alpha_1}(e_D - \delta_e F)^{\alpha_2-1} \end{array} \right. \quad (2.19)$$

This corresponds to the model from Tavoni et al. (2012) that we have studied in section 2.2. Lade et al. (2013, p. 366) explain that “the only remaining non-linearities are contained in the linkage *between* the social and ecological subsystems. This linkage is comprised by [...] the amount of resource extracted by the harvesters,

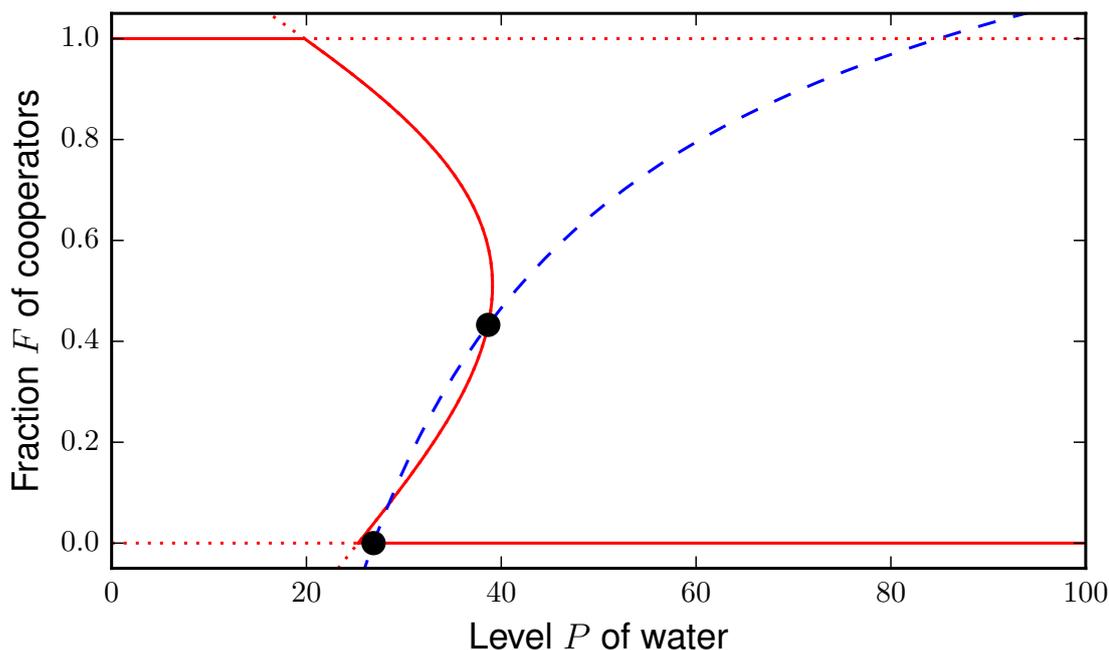


Figure 2.5: *Phase plane for the coupled model of a water stock with a simplified social pressure function  $\Omega_2(F) = \frac{\delta_e \omega_1 F}{e_D}$ , showing that this simplified version still exhibits multistability. The figure shows the  $P$ -nullclines (dashed blue) and the  $F$ -nullclines (dotted or solid red), as well as the stable equilibria (filled black circles). Dotted parts of the  $F$ -nullclines cannot be stable. Parameter values as in Fig. 2.2.*

and the income difference”. Yet, their schematic representation (Lade et al., 2013, fig. 2 p. 363) includes the income difference (2.19) in the social subsystem, *i.e.* the social subsystem is actually *not* deprived from all nonlinearities.

Lade et al. (2013) discuss the importance of the social pressure function  $\Omega$  for the system’s multistability and for its complexity. In fact, the multistable configuration observed in Tavoni et al. (2012) and Lade et al. (2013) does not come from a nonlinear increase in social ostracism given by  $\Omega$  but mainly from the complex dynamics induced by the replicator dynamics of equation (2.3). Indeed, even if the Gompertz function used for  $\Omega$  in our equation (2.5) does make the nontrivial  $F$ -nullcline geometrically more complex in the phase plane, multistability can still be observed in the original model with as simple a function as  $\Omega_2(F) = \frac{\delta_e \omega_1 F}{e_D}$ . This is illustrated in Fig. 2.5, where the coupled system is bistable despite having a linear social pressure function.

Even though the idea of a nonlinear “linkage” being responsible for the overall non-linearity of the system is appealing, there are three arguments against the line

of thoughts presented in Lade et al. (2013). First, equation (2.18) describing the “social subsystem” is not linear in the example provided by Lade et al. (2013). In Fig. 2.5, what has become linear is the way social ostracism is implemented (as  $\omega F$ ). Second, the distinction between what belongs to the “linkage” or not is empirically inappropriate. Indeed, it makes little sense here to say that the extraction of an ecological resource does not belong to its dynamics or that an income difference does not belong to the social dynamics. Third, the theoretical definition of the “linkage” is arbitrary, as shown by the following random equivalent formulation:

$$\begin{cases} P' &= c - dP - qP(e_D + \delta_e F) \\ F' &= \delta_e \text{ linkage } F \\ \text{linkage} &= (1 - F)[w - cn^{\alpha_2-1}P^{\alpha_1}(e_D - \delta_e F)^{\alpha_2-1} + \Omega F] \end{cases},$$

where we define a “linkage” so as to make the socioeconomic subsystem arbitrarily linear. Thus, we need an unambiguous definition of the coupling between the components of a mathematical social-ecological system.

### 2.4.2 Formal definition of subsystems without “linkage”

A non-arbitrary way to refer to a subsystem in a mathematical modelling approach requires that we reduce the mathematical description of the system to the minimum number  $n$  of equations, with  $n \in \mathbb{N}^*$ . For simplicity, we assume that each equation describes the dynamics of a single variable.

Each state variable and its equation can then be associated to a *subsystem*, defined as follows: in a system  $S$  of  $n$  equations describing the dynamics of  $n$  state variables  $x_i$ , the subsystem  $S_i$  is the equation describing the dynamics of the state variable  $x_i$  with all other state variables  $x_j$  fixed, with  $1 \leq i, j \leq n$  and  $i \neq j$ . This is illustrated in Tab. 2.1. In social-ecological models, the definition of the state variable of each component gives an interpretation of whether the corresponding subsystem is a social, socioeconomic or ecological subsystem.

Assuming that the subsystem  $S_i$  has only one variable  $x_i$ , all other state variables of the integrated system  $S$  form a vector  $\vec{x}_i$  of parameters for the subsystem  $S_i$ . Thus, the *coupling* from a subsystem  $S_i$  with variable  $x_i$  to a subsystem  $S_j$  with variable  $x_j$  is the parameterization (map) of  $S_j$  by each possible value of  $x_i$ .

For instance, the social-ecological model for a water stock described by Tavoni et al. (2012) may be reduced to two equations. As  $P$  represents the amount of an ecological resource, the corresponding subsystem ( $\frac{dP}{dt}$ ) can be called *ecological*. The other equation can be written as  $\frac{dF}{dt}$  (fraction of cooperators) or as  $\frac{dE}{dt}$  (level of effort), which can be interpreted as *social*. With this approach, the example given in Lade et al. (2013) includes highly nonlinear components. It is not necessarily a surprise that multistability arises in such a system.

Table 2.1: *Summary on dynamical systems and subsystem under a formal definition of the coupling between subsystems. We denote that function  $f$  is parameterized by a set  $p$  of parameters by  $f^{(p)}$ .*

	System	Subsystem
Symb.	$S$	$S_i$
Var.	$\vec{x} \quad (x_1, \dots, x_n)$	$x_i$
Param.	$p : \begin{cases} \vec{p}_1 & (p_{1,1}, \dots, p_{1,k_1}) \\ \vdots & \vdots \\ \vec{p}_n & (p_{n,1}, \dots, p_{n,k_n}) \end{cases}$	$\begin{cases} \vec{p}_i & (p_{i,1}, \dots, p_{i,k_i}) \\ \vec{x}_i & (x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_n) \end{cases}$
	$\text{dyn } \vec{x} = f^{(p)}(\vec{x})$	
	$\Leftrightarrow$	
Form	$\begin{cases} \text{dyn } x_1 & = f_1^{(\vec{p}_1)}(x_1, \vec{x}_1) \\ \vdots & \vdots \\ \text{dyn } x_n & = f_n^{(\vec{p}_n)}(x_n, \vec{x}_n) \end{cases}$	$\text{dyn } x_i = f_i^{(\vec{p}_i, \vec{x}_i)}(x_i)$

### 2.4.3 Multistability in a fully linear system?

A fully linear system, comprising only linear subsystems responding linearly to all state variables, cannot exhibit multistability. This is also true if one subsystem is linear but does not respond linearly to all state variables. The proof is straightforward.

An equilibrium for the integrated dynamical system  $S$  corresponds to the intersection of subequilibria for all subsystems  $S_i$ . Assuming that all subsystems of a dynamical system are linear with respect to their corresponding state variable, each subsystem must also be defined by a strictly monotonic function  $f_i^{(\vec{p}_i, \vec{x}_i)}$  for this variable. Similarly, each subsystem responding linearly to all other state variables means that any coupling to this subsystem must also be linear and strictly monotonic. It follows that each subsystem has got at most one subequilibrium for each of its parameterizations.

As a conclusion, there can be at most one equilibrium for the whole system, which is the case provided that this equilibrium lies indeed on the relevant domain considered. In particular, there cannot be more than one stable equilibrium. Therefore, multistability is incompatible with a fully linear system. However, it is true that

the coupling we have formally defined can bring multistability in the system even when each subsystem is linear with respect to its own state variable only.

#### 2.4.4 Interpretations of the (de)stabilization of subequilibria

Here, we reconsider and interpret well-known results in dynamical systems (Kot, 2001; Murray, 2002; Edelstein-Keshet, 2005; Allen, 2007). Let us consider a system  $S$  of two subsystems  $S_1$  and  $S_2$  with real variables  $x_1$  and  $x_2$  in continuous time and the Jacobian matrix  $J$  evaluated at an equilibrium  $(x_1^*, x_2^*)$ :

$$S : \begin{cases} \frac{dx_1}{dt} = f_1(x_1, x_2) \\ \frac{dx_2}{dt} = f_2(x_1, x_2) \end{cases} \Rightarrow J_{(x_1^*, x_2^*)} = \begin{pmatrix} \left. \frac{\partial f_1}{\partial x_1} \right|_{(x_1^*, x_2^*)} & \left. \frac{\partial f_1}{\partial x_2} \right|_{(x_1^*, x_2^*)} \\ \left. \frac{\partial f_2}{\partial x_1} \right|_{(x_1^*, x_2^*)} & \left. \frac{\partial f_2}{\partial x_2} \right|_{(x_1^*, x_2^*)} \end{pmatrix}.$$

The equilibrium is stable if the eigenvalues of the Jacobian matrix  $J_{(x_1^*, x_2^*)}$  are negative. The eigenvalues are the solutions  $\lambda_1$  and  $\lambda_2$  of the equation

$$0 = \lambda^2 - \text{tr}(J)\lambda + \det(J), \quad (2.20)$$

where  $\text{tr}(J)$  is the trace of the Jacobian matrix  $J_{(x_1^*, x_2^*)}$  and  $\det(J)$  is its determinant.

The eigenvalues can be both negative only if their mean is negative. This translates directly in the study of equation (2.20) and provides a condition on the trace of the Jacobian matrix:

$$\frac{\partial f_1}{\partial x_1} + \frac{\partial f_2}{\partial x_2} < 0. \quad (2.21)$$

Satisfying condition (2.21) is sufficient when working with real variables, unless the solutions of (2.20) are both real. This happens when the discriminant of this quadratic equation is positive, which is then equivalent to

$$-\left(\frac{\partial f_1}{\partial x_1} - \frac{\partial f_2}{\partial x_2}\right)^2 < 4\frac{\partial f_1}{\partial x_2}\frac{\partial f_2}{\partial x_1}. \quad (2.22)$$

Thus, in the case where condition (2.21) is not sufficient for the equilibrium to be stable, there is an additional condition for stability. Its meaning is the following: provided that condition (2.21) is satisfied, the average of the two eigenvalues is negative, which means that at least one eigenvalue is negative, but the remaining eigenvalue can be negative only if it is sufficiently close to the average. This translates mathematically into a condition on the determinant of the Jacobian matrix  $J_{(x_1^*, x_2^*)}$ :

$$\frac{\partial f_1}{\partial x_2}\frac{\partial f_2}{\partial x_1} \leq \frac{\partial f_1}{\partial x_1}\frac{\partial f_2}{\partial x_2}. \quad (2.23)$$

Now, consider the subequilibria  $x_1^*$  and  $x_2^*$  for each subsystem. We can distinguish three cases depending on the stability of the subequilibria: the case where both subsystems are unstable at  $(x_1^*, x_2^*)$ , the case where one subsystem is unstable and the other is stable, and the case where both subsystems are stable. In mathematical terms, a subsystem  $S_i$  is stable if the derivative of its function with respect to its variable is negative

$$\frac{\partial f_i}{\partial x_i} < 0.$$

### Two unstable subequilibria

Here, we consider that  $(x_1^*, x_2^*)$  is unstable in  $S_1$  and in  $S_2$ . Condition (2.21) cannot be satisfied if the two partial derivatives are positive. Thus, stability cannot appear if all subsystems are unstable at the equilibrium  $(x_1^*, x_2^*)$ . The interpretation is straightforward if we consider the divergence of the system. If condition (2.21) is not satisfied, the trajectory of the system in the phase plane tends to diverge from the equilibrium.

### A stable subequilibrium and an unstable one

Let us assume that, at an equilibrium, we have:

$$\frac{\partial f_1}{\partial x_1} < 0 < \frac{\partial f_2}{\partial x_2},$$

which corresponds to having one unstable subsystem and one stable subsystem at the equilibrium  $(x_1^*, x_2^*)$ . If condition (2.21) is fulfilled, then the case (2.22) prevents condition (2.23) from being satisfied. Therefore, stability can be obtained only if the condition (2.22) is false. This means that a condition for stability is:

$$\left\{ \begin{array}{l} \frac{\partial f_1}{\partial x_1} + \frac{\partial f_2}{\partial x_2} < 0 \\ \left( \frac{\partial f_1}{\partial x_1} - \frac{\partial f_2}{\partial x_2} \right)^2 \leq -4 \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial x_1} \end{array} \right. .$$

In particular, cross-derivatives describing how each subdynamics changes when varying the other variable must be of different signs. This can be interpreted very intuitively since it means that there must be a self-dampening (negative) feedback loop between the two subsystems. This can be opposed to a self-reinforcing (positive) feedback loop, where the interactions between the subsystems are such that an increase in one of the state variables eventually results in a feedback strengthening this increase.

## Two stable subequilibria

Finally, consider the case where both subsystems are stable at  $(x_1^*, x_2^*)$ . Condition (2.21) is always satisfied since the partial derivative for each subsystem is negative. The equilibrium is stable unless the cross-derivatives are not of the same sign. When the cross derivatives on the right side of inequality (2.22) are not of the same sign, this condition (2.22) may be satisfied. Then, condition (2.23) must also be satisfied for the system to be stable.

Intuitively, there is a self-reinforcing feedback loop between the subsystems in the case where the cross-derivatives are of different signs. This self-reinforcing feedback loop destabilizes the system. Yet, the equilibrium can be stable if condition (2.23) is satisfied. Indeed, fulfilling condition (2.23) means that the destabilizing feedback loop produced by the subsystems' interactions is weaker than the combined stability of each isolated subsystem.

## 2.5 Conclusion

In this chapter, we have reproduced and extended the derivation and the analysis of a social-ecological model for a water stock previously developed by Tavoni et al. (2012). We showed that the nullclines reflect how the coupling between the integrated system's components modifies the complexity brought by each subsystem. This appears in the phase plane in that the nullclines adopt the shape of a  $Z$  (with the replicator dynamics in the socioeconomic subsystem) or of an  $S$  (in the ecological subsystem with an Allee effect), which may remind us of a hysteresis in dynamical systems.

Since the ecological subsystem could not display any multistability, we investigated a version of the model with a bistable ecological resource with an Allee effect. We could find a similar  $S$ -shaped nullcline as for the socioeconomic component.

We explored and discussed results presented by Lade et al. (2013) about the coupling between subsystem inside of the integrated system. This lead us to a formal, unambiguous definition of this coupling. Under this definition, it is clear that a linear subsystem cannot be linearly coupled so as to give rise to a multistable, fully linear, integrated system. But it is true that the coupling can introduce multistability in a more general case, even if each subsystem is linear with respect to its own variable.

The complexity of the models we have studied in this chapter does not allow for many analytical results. We may gain more understanding of social-ecological systems in general by working with more generic models of better-understood systems.

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# 3 Analyzing the mutual feedbacks between lake pollution and human behaviour in a mathematical social-ecological model

## Abstract

Does the adoption of environment-oriented actions by individuals necessarily improve the state of an ecosystem in the most effective way? We address this question with the example of eutrophication in shallow lakes. When exposed to fertilizers, such lakes can undergo a critical transition called eutrophication, resulting in a loss of biodiversity and of ecosystem services. We couple a generic model of eutrophication with a best-response model of human behaviour, where agents can choose to pollute the lake at a high level (defection) or at a lower level (cooperation). Feedbacks between the interacting lake pollution and human behaviour can give rise to complex dynamics with multiple stable states and oscillations. We find that when agents decrease their discharge of pollutants into the lake, this is not necessarily the most effective way to reduce the pollution level in the lake because of counterintuitive equilibria where the lake is in a clear state despite a high level of pollution discharge. The complex dynamics with potential multistability and counterintuitive equilibria suggests that generic management recommendations holding for every level of pollution and of cooperation are impossible.

## 3.1 Introduction

In the context of an increasing concern for the impact of humans on their environment (Galvani et al., 2016; Mourelatou and European Environment Agency, 2018), it is often assumed that the adoption of environment-oriented actions will improve the state of the ecological system: harvesting less should preserve a species, our intuition says, fishing less should save a fishery, decreasing our discharge of pollutants should clean the environment. Are we right to think so? The difficult recovery of

Table 3.1: *Glossary of terms used in this chapter. Note that some terms have a particular definition for the system considered here.*

Term	Definition
agent	Human individual able to make a choice, here between <i>defection</i> and <i>cooperation</i> .
attractor	Stable equilibrium or oscillation attracting neighbouring states (the basin of attraction).
cooperation	Individual behaviour of <i>agents</i> , resulting here in a lower pollution discharge.
coupling parameter	Mathematical <i>parameter</i> whose interpretation links the two <i>subsystems</i> .
defection	Individual behaviour of <i>agents</i> , resulting here in a higher pollution discharge.
(un)desirable	State $(P_1, F_1)$ is ecologically more desirable than state $(P_2, F_2)$ if and only if $P_1 \leq P_2$ . It is socially more desirable if and only if $F_1 \geq F_2$ .
hysteresis	Dependence of the state of a system on its history, which is a cause of nonlinearity. Here: situation where a nullcline in the $(P, F)$ - <i>phase plane</i> has the shape of an <i>S</i> .
multistability	Coexistence of several <i>attractors</i> , which implies that different outcomes are possible depending on initial conditions.
parameter	Number which is considered fixed when studying the model dynamics.
phase plane	2D-representation of all of the system's possible states along its two <i>state variables</i> $P$ and $F$ .
resilience /resistance	Size of the basin of attraction of a given <i>attractor</i> . Theoretical ecologists use <i>resistance</i> (Grimm and Wissel, 1997) or <i>ecological resilience</i> (Holling, 1973, 1996; van Nes and Scheffer, 2007), whereas social scientists refer to <i>resilience</i> .
state variable	Continuous variable representing the state of a <i>subsystem</i> . Here, as we consider two unidimensional subsystems, we have two state variables: $P$ for the level of pollution, $F$ for the fraction of cooperators.
strategy	Here, <i>cooperation</i> or <i>defection</i> , that is individual behaviours.
subequilibrium	Equilibrium for one <i>subsystem</i> . It is represented by a nullcline in the phase plane.
substable	A (sub)equilibrium is $P$ -substable if and only if it is stable along the $P$ -axis, assuming that $F$ is fixed.
subsystem	Here, system represented by one of the two ordinary differential equations, assuming that the other <i>state variable</i> is fixed.

the Atlantic northwest cod fishery despite drastic measures reminds us that things may happen differently (Frank et al., 2011).

It is worth noting first how wide the range of possible actions can be. We indeed understand that punctually removing pollutants, banning fishing for a certain period of time and implementing a long-lasting tax or subsidy policy, though all environment-oriented, may have quite different objectives and consequences. Together with socioeconomic policies aiming at influencing the impact humans have on their environment, we will generally refer to such measures as management strategies, in a broad sense (Mäler et al., 2003). How can management strategies actually influence the ecological state?

Such questions address the interplay between humans and an ecological system. They cannot be answered using only traditional ecological models, which consider human influence as a constant or linearly varying *parameter*<sup>1</sup>. Instead, human behaviour should actually be considered a dynamical system in itself, responding to management strategies in a potentially non-linear way, because a tax increasing linearly in time might not decrease the frequency of an undesirable behaviour in a linear way. Similarly, many traditional socioeconomic models and frameworks tend to oversimplify the ecological system. On the contrary, social-ecological models represent human behaviour as a dynamical variable interacting with the ecological dynamics. Examples of social-ecological models have been developed for instance for eutrophication in lakes exposed to fertilizers (Suzuki and Iwasa, 2009a,b), for harvested wildlife and fish populations (Fryxell et al., 2010; Bieg et al., 2017) and for the management of self-refilling water stocks (Lade et al., 2013).

Many ecological systems show alternative stable states (May, 1977), for instance survival and extinction in living populations such as in coral reefs (Mumby et al., 2007), good and poor condition of a grazing system (Noy-Meir, 1975; Westoby et al., 1989; Schwinning and Parsons, 1999), or oligotrophic (clear water) and eutrophic (turbid green water) in lakes (Scheffer, 1998). Socioeconomic systems can also show alternative stable states, for example between the rich and poor status of an agent (poverty trap) (Ngonghala et al., 2014, 2017), or the degree of adoption or non-adoption of a new mindset or behaviour at the population level (social learning) (Nyborg et al., 2016). Here, we consider the case where both *subsystems*, the ecological as well as the socioeconomic one, can show bistability. The dynamics of the coupled human-environment system may therefore be particularly complex. For that reason, we focus on a well understood ecological system, namely shallow freshwater lakes (Scheffer, 1998).

Extensive empirical studies (Scheffer, 1998) have demonstrated that shallow lakes could display fast transitions between two alternative stable states due to the an-

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<sup>1</sup>Throughout this chapter, terms appearing in italics when used for the first time are defined in Table 3.1.

thropogenic discharge of fertilizers. Those two stable states are: on the one hand, the oligotrophic state (clear water, vegetation dominated by macrophytes, high biodiversity and ecosystem services), observed when the pollution level is low; and, on the other hand, the eutrophic state (turbid water, vegetation dominated by microscopic chlorophyllian organisms, low biodiversity and ecosystem services), when the pollution level is high. This bistability is due to positive feedbacks maintaining a low level of pollution when the lake is clean and maintaining a high level of pollution when the lake is already polluted (Scheffer, 1998).

This bistability has been represented by a mathematically simple model (Carpenter et al., 1999). In the past decade, some pioneering work (Suzuki and Iwasa, 2009a,b) has extended this ecological model by adding a socioeconomic part. It consisted in the logit best-response dynamics of evolutionary game theory (Satake and Iwasa, 2006; Iwasa et al., 2007; Satake et al., 2007a,b), which is able to represent the bistability in the collective choice that humans make regarding whether to pollute or not, maintaining a wide-spread polluting behaviour on the population level when the environment-oriented behaviour is rare and maintaining the environment-oriented behaviour when it is already wide-spread on the population level. For their shallow lake social-ecological model, Suzuki and Iwasa (2009b) acknowledge the possibility to observe *multistability* with up to nine simultaneous equilibria, as well as cases with sustained oscillations, and investigate which parameters promote this complexity. Their method consists in producing numerical bifurcation diagrams for particular parameterizations. However, it is not always obvious which mechanisms generate the complex dynamics and are responsible for the occurrence of the various bifurcations, and what they mean from the biological or socioeconomic point of view. Moreover, already small changes in parameter values could lead to bifurcation diagrams that are not only quantitatively, but also qualitatively different.

Here, we reconsider the dynamic interaction in the model from Suzuki and Iwasa (2009b) in order to improve our understanding of underlying mechanisms from an analytical and from a biological perspective. We aim at reviewing multistable cases more systematically. To that end, we reformulate some modelling assumptions that will facilitate a more systematic analysis. First, we formulate the model in continuous rather than discrete time. This allows us to build on the well-established theory of differential equations. Secondly, Suzuki and Iwasa (2009b) assume that the level of pollution released by humans is an intermediate between two extreme strategies called *cooperation* and *defection*. The human population's collective choice depends on the incentive to pollute less, which they formulate as a non-linear function of two arguments: the level of pollution, and the fraction of cooperators. Since the interpretation of this non-linearity is difficult, we consider only linear terms. As a consequence, the whole system becomes more amenable to mathematical analysis. This allows us to investigate the nullclines of the model analytically and graphically

in the phase plane rather than focusing on numerical bifurcation diagrams, which depend more on specific parameterizations of the model. We use numerical simulations in order to explore the basins of attraction for the different equilibria, which can be interpreted in terms of resilience.

This chapter is organized in three parts. First, we develop a social-ecological model for the pollution of a lake by agents who can choose between two levels of pollutant discharge into the lake. Then, we explain the model's complexity. We start from the simplest dynamics where there is no coupling between the ecological part and the socioeconomic part, and then study the consequences of introducing some coupling. A clear understanding of the phase plane allows us to discuss whether the adoption of an environment-friendly behaviour by the agents necessarily leads to an ecologically desirable state. It is true that decreasing the discharge of fertilizers decreases the level of pollution in the water if we focus on a specific equilibrium. Yet, due to feedbacks between the lake subsystem and the socioeconomic subsystem, it is not always true that the higher the cooperation, the lower the pollution in the water, because some other, counterintuitive equilibrium may have an even lower level of pollution despite having less cooperation and a higher discharge of pollutants. Finally, we analytically derive management conclusions and compare them to those discussed by Suzuki and Iwasa (2009b).

## 3.2 Model

In this section, we describe our mathematical model. It comprises two interconnected subsystems: an ecological part and a socioeconomic part (Fig. 3.1). The ecological *state variable* is the level of pollution  $P$  ( $P \geq 0$ ). It represents the amount of pollutants present in the lake, such as the concentration of phosphorus in the surface waters typically. The socioeconomic state variable is the fraction of cooperators  $F$  ( $0 \leq F \leq 1$ ). It represents the frequency of individuals adopting the *cooperation* behaviour among all agents discharging pollutants into the lake.

Note that in this chapter, the term "cooperation", which comes from game theory, does not refer to a social interaction, but rather to an environment-friendly behaviour (Table 3.1).

### 3.2.1 Ecological subsystem

For the ecological dynamics, we use the following model:

$$\frac{dP}{dt} = \underbrace{A}_{\text{anthropogenic discharge of pollution}} - \underbrace{\alpha P}_{\substack{\text{global outflow rate} \\ \text{(outflow and sedimentation)}}} + \underbrace{\frac{rP^q}{m^q + P^q}}_{\text{resuspension}}.$$

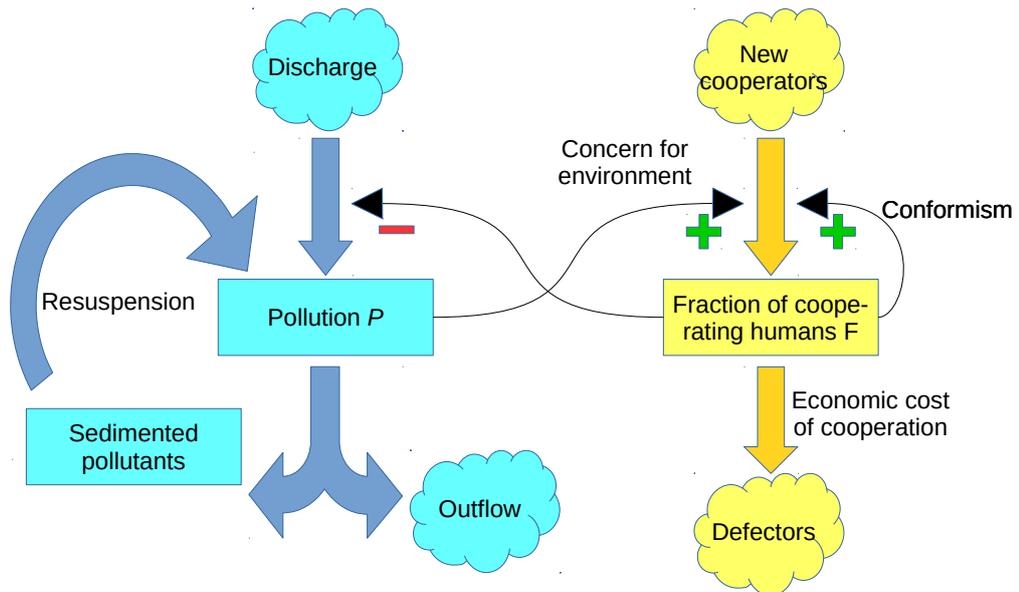


Figure 3.1: Schematic representation of the coupled social-ecological model. The ecological subsystem is shown on the left, in blue, and the socioeconomic subsystem on the right, in yellow. Thick arrows show fluxes or pseudofluxes between compartments, whereas thin arrows represent the influence of a compartment on those fluxes, with a red minus sign or a green plus sign for a negative or positive influence, respectively. The incentive to cooperate is distributed between the economic cost of cooperation, the concern for the environment and the conformism.

$A$  is the amount of pollution (phosphorus) discharged into the lake due to the use of fertilizers in neighbouring agricultural fields. We assume a linear global outflow rate (outflow and sedimentation of pollutants leaving the surface water) with parameter  $\alpha$ . The resuspension term corresponds to the interaction between the water and the sediments, which is stronger in shallow lakes (less than 3 m deep). Its Hill function was primarily used to account for “the sigmoidal decline of vegetation with turbidity” (Scheffer, 1998, p. 270), and also for the pollution resuspension (Carpenter et al., 1999). It corresponds to a sigmoid curve where  $r$  determines the upper bound and  $m$  the half-saturation level. The parameter  $q$  is negatively correlated to the depth of the lake; for our model, we have  $q \geq 2$  (Carpenter et al., 1999). This model, developed by Carpenter et al. (1999), is sufficient to represent the bistability of shallow lakes, but more complicated models accounting for vegetation density, light attenuation or the size of sediments have also been proposed (Scheffer, 1998).

From a game theoretical point of view, the anthropogenic release  $A$  can be represented as a collective choice between two *strategies*. A human *agent* may adopt a high discharge of pollutants  $p_D$  (*defection*) or a lower discharge  $p_D - \delta_p$  (*cooperation*) with  $0 \leq \delta_p \leq p_D$ .  $\delta_p$  is the reduction observed in the discharge when switching from defection to cooperation: it is a cooperation effort. If we consider the entire population, the collective discharge  $A$  depends on the fraction  $F$  of cooperators ( $0 \leq F \leq 1$ ):

$$A = p_D(1 - F) + (p_D - \delta_p)F = p_D - \delta_p F.$$

Here we can see that increasing the fraction  $F$  of cooperators logically decreases the discharge of pollutants into the lake: more agents choose to lower their use of fertilizers.

### 3.2.2 Socioeconomic subsystem

The socioeconomic dynamics is modelled by a logit best response because of its mathematical simplicity. The functional form which can be found in the literature is sometimes a discrete time formulation (for example in Iwasa et al. (2007)). We approximate the continuous time variation  $\frac{dF}{dt}$  of the state variable using the difference between each discrete time step  $\Delta F = F_{t+1} - F_t$  and assuming small time steps  $\Delta t = 1$ :

$$\frac{dF}{dt} \approx \frac{\Delta F}{\Delta t} = s \left( \frac{1}{1 + e^{-\beta \Delta U}} - F \right) = s [f(\Delta U) - F],$$

which yields the same formulation as in Iwasa et al. (2010) and Hofbauer and Sigmund (2003).

The strictly positive parameter  $s$  tunes the speed of the social dynamics and thus the time scale of the subsystem (Suzuki and Iwasa, 2009b). The more conservative

the agents, the lower  $s$  (Satake and Iwasa, 2006).  $f$  can be interpreted as the transition rate of non-conservative defectors to cooperators (Satake and Iwasa, 2006). It has values between 0 and 1 and corresponds to a sigmoid curve whose steepness is determined by parameter  $\beta$ .  $\beta$  can be interpreted as the agents' rationality: if  $\beta$  is very large, then all agents immediately choose the best option according to  $\Delta U$ .

The variable  $\Delta U$  represents the difference in utility between the two strategies: when it is positive, people tend to become cooperators, whereas, when it is negative, the incentive to defect is stronger. Thus,  $\Delta U$  can be interpreted as the incentive to cooperate, or as the cost of defection compared to the cost of choosing cooperation.

We consider three factors affecting the incentive  $\Delta U$ :

- the baseline ( $-v$ ) is assumed to be negative, because it is economically more advantageous for an agent to release high amounts of pollution;
- the agents' ecological concern is represented by a linear term in  $P$  with parameter  $\kappa$ : the more polluted the lake gets, the more people tend to cooperate in decreasing the discharge of pollutants;
- social ostracism is represented by a linear term in  $F$  with parameter  $\xi$  accounting for the strength of the agents' conformist tendency: the more cooperators there are, the more people tend to cooperate.

We thus obtain:

$$\Delta U = \underbrace{-v}_{\text{economic baseline}} + \underbrace{\xi F}_{\text{social ostracism}} + \underbrace{\kappa P}_{\text{ecological concern}}. \quad (3.1)$$

For comparison, Suzuki and Iwasa (2009b) assumed:

$$\Delta U = -v + (1 + \xi F)(1 + \kappa P), \quad (3.2)$$

which additionally includes a bilinear term which depends simultaneously on both the level  $P$  of pollution and on the fraction  $F$  of cooperators. The interpretation of this bilinear term is not always obvious. Moreover, it makes the mathematical analysis more cumbersome. Therefore, we consider the equation (3.1), which is actually a linearization of (3.2).

### 3.2.3 Integrated system and coupling parameters

The integrated model is:

$$\begin{cases} \frac{dP}{dt} = -\alpha P + \frac{rP^q}{m^q + P^q} + p_D - \delta_p F \\ \frac{dF}{dt} = s \left[ \frac{1}{1 + e^{-\beta(-v + \xi F + \kappa P)}} - F \right] \end{cases}.$$

All parameters of the model are positive. The parameters in the environmental subsystem describe lake properties except for  $p_D$  and  $\delta_p$ . The parameters in the human subsystem describe the socioeconomic situation. The interpretation of all parameters is summarized in Table 3.2.

There are exactly two *coupling parameters* linking the two subsystems, namely  $\kappa$  and  $\delta_p$ :

- the influence of the ecological subsystem on the human subsystem is represented by  $\kappa$ , which describes how much the agents care about the level of pollution in the lake; we will refer to it as the ecological concern;
- the influence of the human subsystem on the ecological subsystem is represented by  $\delta_p$ , which tells us how different the two strategies are in terms of their discharge levels; we will refer to it as the cooperation effort (not to be confused with cooperation (level)  $F$ ).

Thus, those two parameters account for mutual feedbacks between the subsystems. The lake pollution subsystem influences the socioeconomic dynamics through the concern humans have for the environment ( $\kappa$ ): if their environmental concern is zero, then the level of pollution observed in the lake does not affect their choice to cooperate or to defect. If  $\kappa > 0$ , the pollution level  $P$  in the lake influences the cost of defection  $\Delta U$ , which introduces an influence of the lake pollution level on the socioeconomic subsystem.

The human subsystem influences the lake pollution through the cooperation effort ( $\delta_p$ ): when there is no difference between cooperators and defectors ( $\delta_p = 0$ ), *i.e.* no impact of cooperation, then agents' collective choice has no influence on the lake pollution dynamics. If  $\delta_p > 0$ , there exists a difference in the discharge of pollutants in defectors ( $p_D$ ) and cooperators ( $p_D - \delta_p$ ), which introduces an influence of cooperation on the lake dynamics.

Setting one or both of the *coupling parameters* to 0 is equivalent to making one or all of the connections vanish between the two subsystems and yields simplified versions of the model.

### 3.2.4 Summary of the equilibria

Equilibria are situations  $(P^*, F^*)$  where the system does not change. They can be asymptotically stable or unstable. In our model, equilibria are nontrivial and algebraically too cumbersome to work with their analytic definition directly: they have no closed-form expression in the general case. It is possible to gain insight by studying the nullclines. They represent *subequilibria* in the phase plane and their intersections are equilibria of the coupled system. Each nullcline either represents a strictly monotonic function (not shown here) or takes the shape of an  $S$ . In the

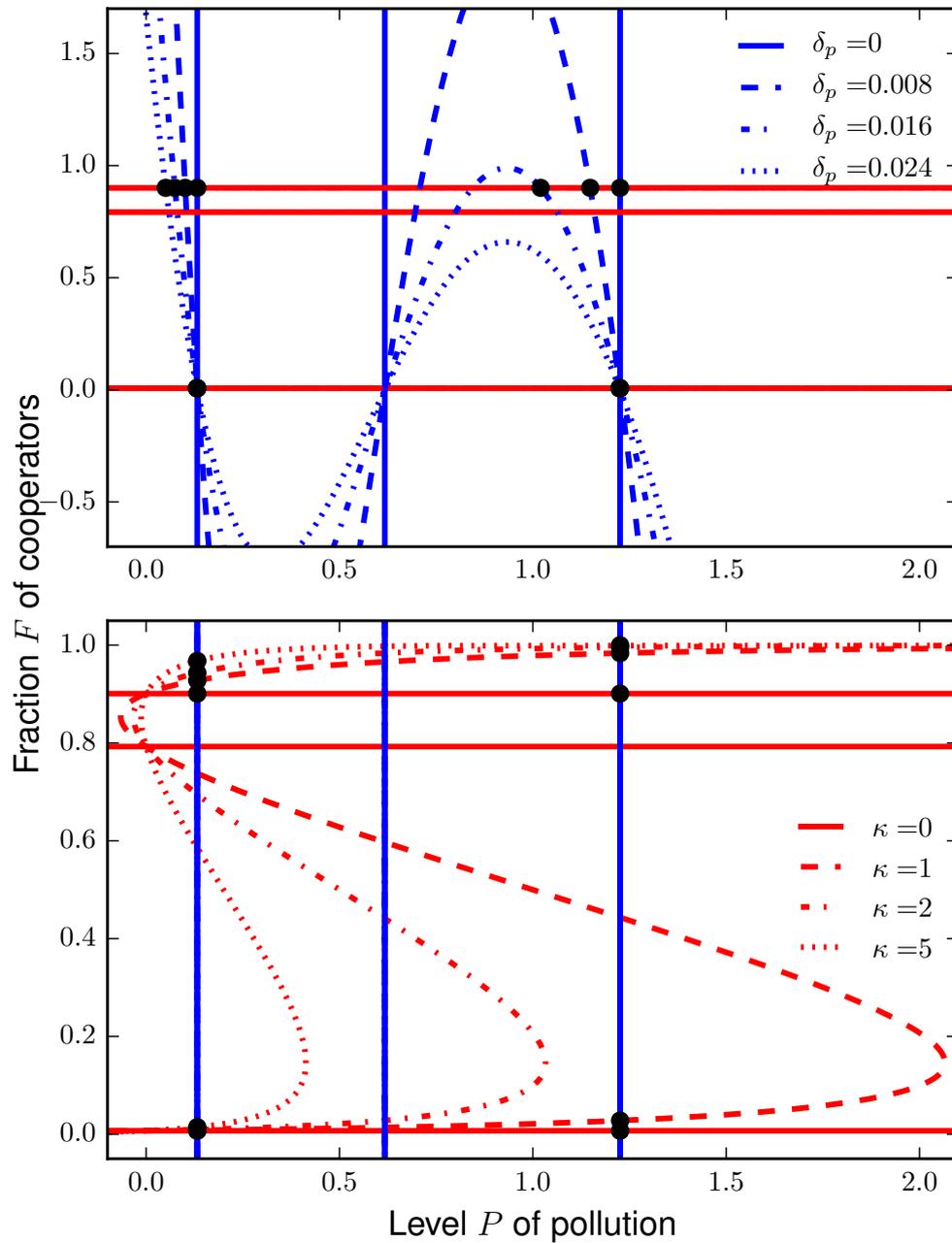


Figure 3.2: Phase plane for the model with unidirectional coupling introduced by the cooperation effort  $\delta_p$  (top) or by the ecological concern  $\kappa$  for the lake (bottom). Top: the vertical  $P$ -nullcline (blue) is shown for  $\kappa = 0$  and several values for  $\delta_p$ . Bottom: the horizontal  $F$ -nullcline (red) is shown for  $\delta_p = 0$  and several values for  $\kappa$ . Only stable equilibria are marked (filled circles). Parameter values:  $\alpha = 0.4$ ,  $r = 0.75$ ,  $q = 2$ ,  $m = 1$ ,  $p_D = 0.04$ ,  $s = 0.1$ ,  $\beta = 1$ ,  $v = 5$ ,  $\xi = 8$ .

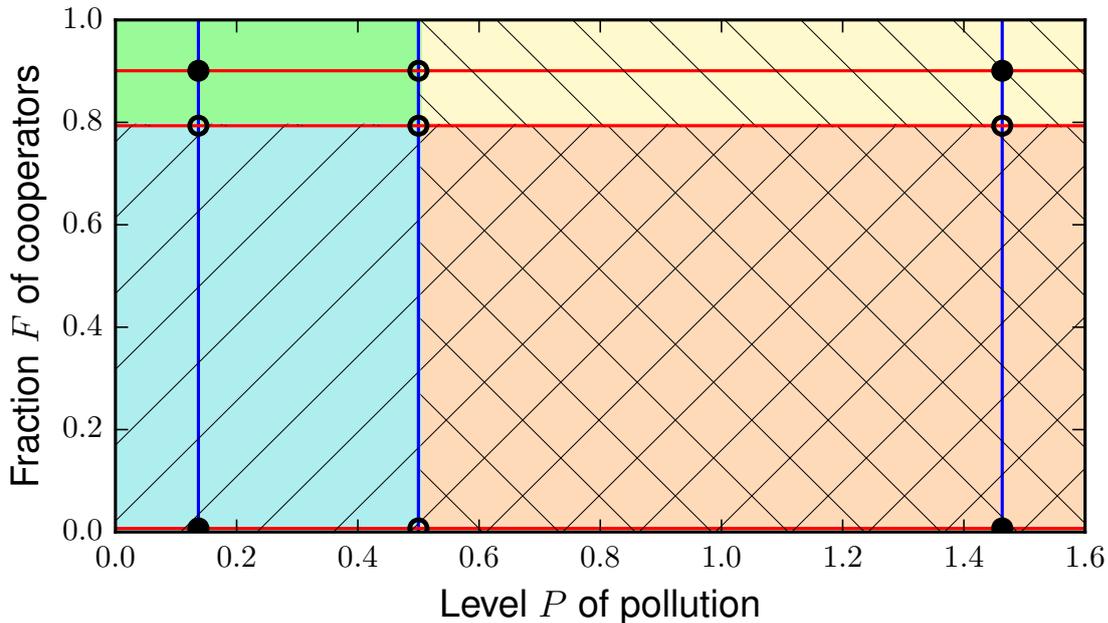


Figure 3.3: *Phase plane for the uncoupled model showing the vertical  $P$ -nullclines (blue) and the horizontal  $F$ -nullclines (red). Filled circles show stable equilibria, and unfilled circles show unstable equilibria. Basins of attraction are indicated by colour and hatching. Parameter values as in Fig. 3.2, except for  $r = 0.8$ ,  $\delta_p = 0$  and  $\kappa = 0$ .*

latter case, we have an ecological *hysteresis* ( $P$ -nullcline, Fig. 3.2, top) or a socioeconomic *hysteresis* ( $F$ -nullcline, Fig. 3.2, bottom). Hysteresis configurations allow for complex multistability to emerge, with alternative stable equilibria having different levels of pollution or cooperation.

We can prove that there is at least one and at most nine equilibria (see Appendix 3.A for details). In the latter case, the nine nullcline intersections can be schematically ordered as a  $3 \times 3$  array in the  $(P, F)$ -plane (Fig. 3.3). The four equilibria on the corners are stable ones:  $(P_{lo}, F_{lo})^*$ ,  $(P_{lo}, F_{hi})^*$ ,  $(P_{hi}, F_{lo})^*$  and  $(P_{hi}, F_{hi})^*$ , where *lo* means *low* and *hi* means *high*, relatively to the other equilibria. The most *desirable* equilibrium state, from both the ecological and social point of view, is  $(P_{lo}, F_{hi})^*$ , and the least desirable equilibrium state is  $(P_{hi}, F_{lo})^*$ .

With no coupling ( $\delta_p = 0$  and  $\kappa = 0$ ), the subsystems are isolated: their dynamics are independent (see Fig. 3.3). Each subsystem can have one, two or three subequilibria, with either one or two *substable* ones. In the  $(P, F)$ -plane, each subequilibrium extends into a straight nullcline for the integrated system. Among the three potential nullclines, the middle one corresponds to an unstable subequilibrium

Table 3.2: *Influence of parameters on the hysteresis (S-shape) of the nullclines, based on the analysis in Appendix 3.C, and compared with numerical results, for selected parameter values, reported by Suzuki and Iwasa (2009b). Parameters given in the upper part influence the ecological hysteresis whereas parameters in the lower part of the table influence the socioeconomic hysteresis. Positive (+), negative (-), variable (+/-), none (0), not reported (./.)*

Parameter	Interpretation	Impact on hysteresis	
		this chapter	Suzuki and Iwasa (2009b)
$p_D$	discharge of defectors	0	+/-
$\delta_p$	cooperation effort	0	./.
$p_D - \delta_p$	discharge of cooperators	0	+/-
$\alpha$	total outflow of pollution	-	./.
$r$	resuspension rate in lake	+	+
$m$	half-saturation in resuspension	-	./.
$q$	shallowness of the lake	+	./.
$s$	speed of human subsystem	0	./.
$\beta$	rationality of agents	+	./.
$v$	economic cost of cooperation	0	+
$\kappa$	ecological concern of agents	0	./.
$\xi$	conformism of agents	+	+

(threshold). This explains why, among the nine possible equilibria, the stable ones are located at the corners of the  $3 \times 3$  square. The unstable threshold line also gives a boundary between the basins of attraction of stable equilibria (Fig. 3.3).

### 3.3 Results

In this section, we focus on the coupled system. We first summarize analytical results concerning the influence of each parameter on the appearance of a hysteresis configuration in the nullclines, a condition for the model to allow for complex dynamics (potential regime shifts or oscillations). Then we explain how mutual feedbacks between the ecological subsystem and the socioeconomic subsystem impact equilibria in three different ways: the location of stable equilibria, the location of unstable equilibria and the sheer existence of equilibria. Finally, we show that counterintuitive equilibria challenge the often assumed correlation between cooperation and ecological improvement.

### 3.3.1 Influence of the coupling on the nullclines: With some coupling, the nullclines can show hysteresis

Setting either  $\delta_p > 0$  or  $\kappa > 0$  introduces a unidirectional coupling from one subsystem to the other and allows us to understand mathematically the effect of the coupling on the shape of the affected nullcline (Fig. 3.2, see Appendix 3.B for more details). The case of a bidirectional coupling ( $\delta_p > 0$  and  $\kappa > 0$ ) will be considered starting from section 3.3.2 onward.

Based on analytical results presented in Appendix 3.C, Table 3.2 shows that, overall, the system is likely to have several stable equilibria if the pollutants tend to remain in the water for a long time (small  $\alpha$ ), if the resuspension  $r$  is large, if the lake is shallow (large  $q$ ) or if the agents are very responsive to social pressure (large  $\xi$ ). Interestingly, coupling parameters, which represent the intensity of mutual feedbacks between subsystems, have no influence on the existence of hystereses. That is, how much pollution defectors or cooperators discharge in the lake cannot make a hysteresis configuration appear or disappear. Hysteresis in the ecological subsystem depends only on the lake's properties, not on the influence that humans have on it. Hysteresis in the socioeconomic subsystem depends only on features of the agents, namely their rationality and their conformism. Economic and ecological incentives play no role in the appearance of a hysteresis configuration.

Table 3.2 shows that our analytical results confirm simulations from Suzuki and Iwasa (2009b) for two parameters (the resuspension rate  $r$  and the agents' conformism  $\xi$ ) and contradict them for the three other parameters they investigated (the pollution discharge  $p_D$ , the cooperation effort  $\delta_p$  and the cost  $c$  of cooperation). Regarding the seven other parameters we have investigated here, no result was previously reported.

### 3.3.2 Impacts of mutual feedbacks $\kappa$ and $\delta_p$ on equilibria

Mutual feedbacks between the subsystems affect stable equilibria by influencing their location, their resistance to perturbations and their existence. In the following, we always assume that the human-lake system approaches equilibrium.

#### Location of stable equilibria

A first type of management policies aims at “improving” the current equilibrium state. In the phase plane, this consists in shifting the equilibrium point to more desirable levels of pollution and cooperation.

Varying the strength of each unidirectional feedback may achieve this goal (Fig. 3.2). Indeed, the model's behaviour fits our intuition: considering any stable equilibrium, if cooperators reduce the amount of pollution they release (increased cooperation

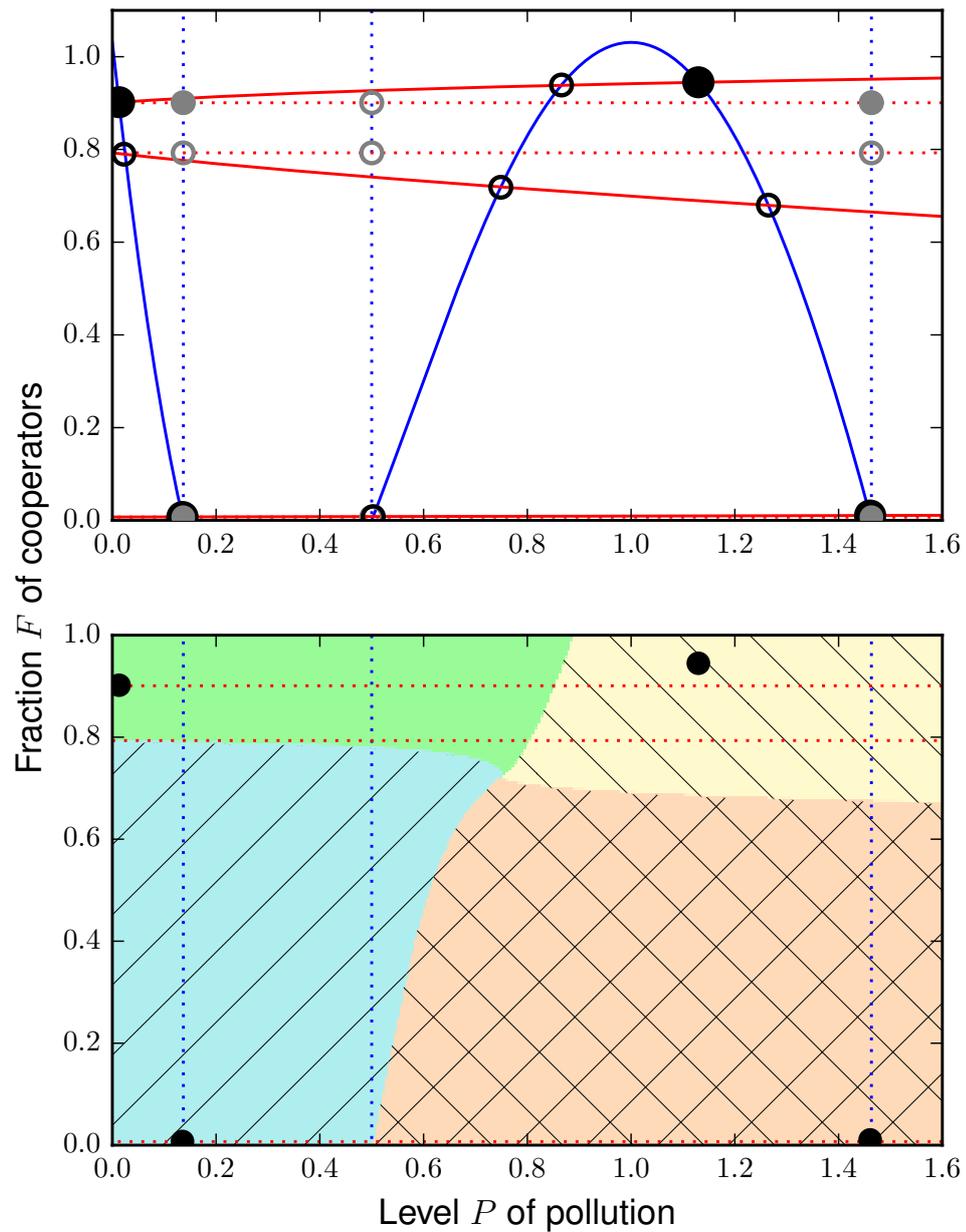


Figure 3.4: Location of equilibria (top) and resilience of the stable equilibria (bottom) in the coupled system. Top:  $P$ -nullclines (blue) and  $F$ -nullclines (red) for the uncoupled system (dotted) and with coupling (solid); the equilibria are marked as grey and black circles, respectively. Bottom: Basins of attractions of the uncoupled system (shown by the middle dotted lines) and with coupling (shown by coloured and/or hatched surfaces). Filled circles show stable equilibria, and unfilled circles show unstable equilibria. Parameter values as in Fig. 3.3, except for  $\delta_p = 0.03988$  and  $\kappa = 0.25$ .

effort  $\delta_p$ ), the pollution level decreases, and if agents care more about the lake (increased ecological concern  $\kappa$ ), then they tend to cooperate more.

However, Fig. 3.2 (top) also illustrates how different in extent this shift can be depending on the level of cooperation: the location of stable equilibria with a low cooperation level in the  $(P, F)$ -plane are almost not affected by the coupling, whereas the location of stable equilibria with a high cooperation level are very affected by the coupling. This is also intuitive: as long as defection is the majority, the impact of the cooperation effort  $\delta_p$  is negligible.

### Location of unstable equilibria (resilience of stable equilibria)

The larger a basin of attraction, the more *resistant* to perturbations its *attractor*. Boundaries between basins of attraction (separatrices) are organized by the location of unstable equilibria. How those unstable equilibria are affected by mutual feedbacks can already be seen in Fig. 3.2, where unstable equilibria correspond to non-marked intersections between red and blue sets. Fig. 3.4 illustrates the effect of increasing feedbacks on the resistance of equilibria in cases with bidirectional coupling. Increasing  $\delta_p$  shifts unstable equilibria towards higher levels of pollution and increasing  $\kappa$  shifts unstable equilibria towards lower levels of cooperation (see Appendix 3.B for details).

The consequences of increased coupling between the subsystems for the resilience of stable equilibria is less intuitive than in the previous section. Assuming we are at an ecologically desirable stable equilibrium (attractors of the blue and green areas in Fig. 3.4), if cooperators reduce the amount of pollution they release, the equilibrium becomes more resistant to perturbations. Assuming we are at a socioeconomically desirable stable equilibrium (attractors of the green and yellow areas in Fig. 3.4), if people care more about the lake, then the equilibrium also becomes more resistant to perturbations. But assuming we are at an undesirable stable equilibrium (attractors of the orange and potentially of the blue or yellow areas in Fig. 3.4), the same feedbacks make the equilibrium lose resistance to perturbations. Overall, management strategies which consist in increasing the cooperation effort and the ecological concern may end up increasing the resilience of desirable equilibria and decreasing the resilience of undesirable equilibria.

A consequence of having alternative basins of attraction is that the level of pollution and the level of cooperation at equilibrium may abruptly change without any change in the parameters. Indeed, a perturbation affecting the lake pollution or the fraction of cooperators can be enough to push the system to a new basin of attraction and trigger a change of the equilibrium approached by the system with all parameters remaining constant (Fig. 3.4, bottom).

Fig. 3.5 shows how the same initial condition can lead to completely different attractors depending on the location of the boundaries between basins of attraction:

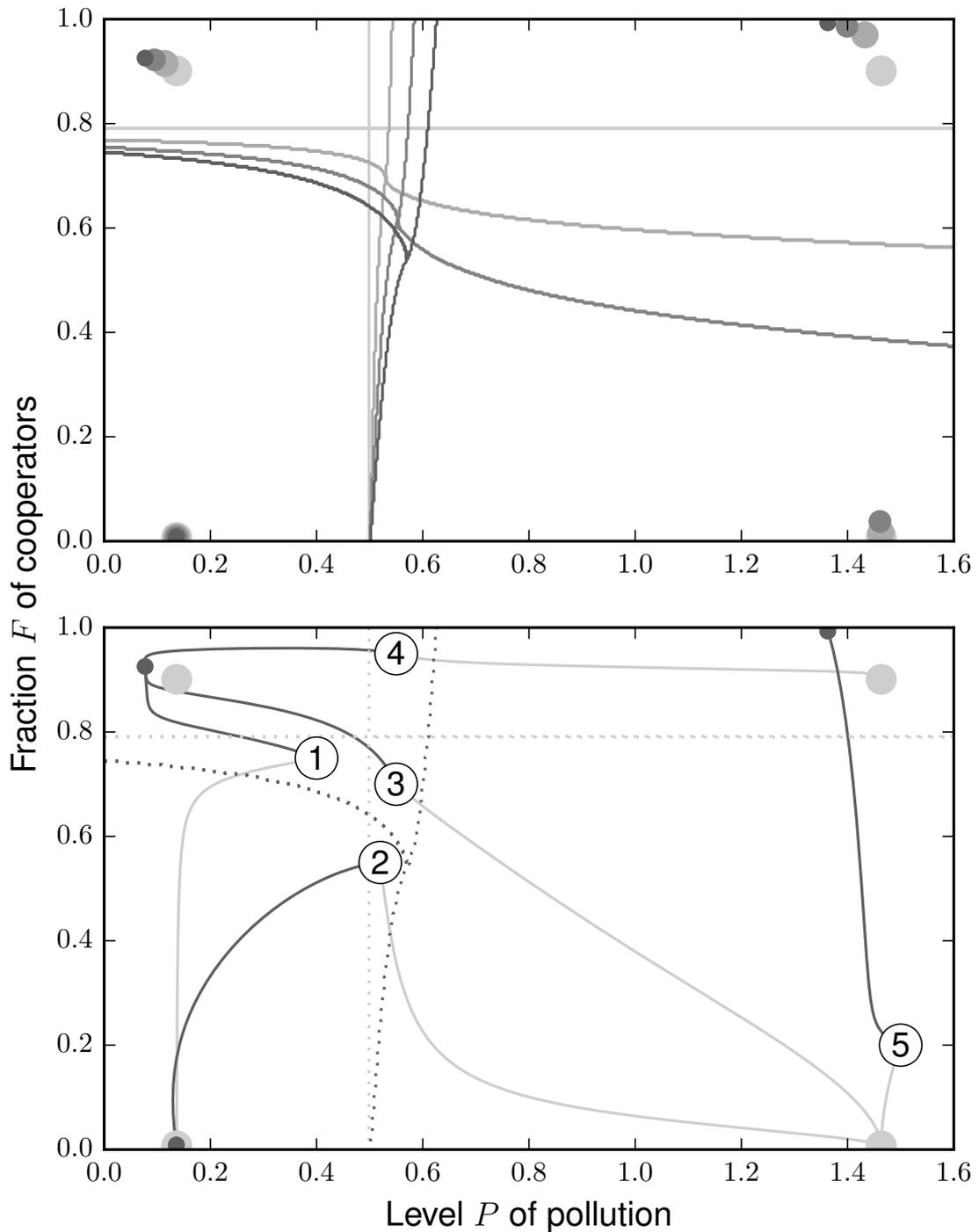


Figure 3.5: *Top: Basins of attraction for the coupled system with an increasing bidirectional coupling. From light to dark grey, the boundaries between basins of attraction as well as the stable equilibria are shown for an increasing coupling, respectively for  $(\delta_p, \kappa) = (0, 0)$ ,  $(0.005, 0.5)$ ,  $(0.01, 1)$  and  $(0.015, 1.5)$ . Bottom: Some trajectories are given for the first and last cases starting from the same initial conditions  $(P_0, F_0)$ , indicated by circled numbers. Parameter values as in Fig. 3.3 except for  $\delta_p$  and  $\kappa$ .*

for instance, the initial condition ③ leads to the undesirable  $(P_{hi}, F_{lo})$ -equilibrium when the coupling is low or to the most desirable  $(P_{lo}, F_{hi})$ -equilibrium instead when the coupling is high.

### Collapse of equilibria and oscillations

Another kind of policy could aim at making undesirable equilibria disappear: knowing that the current situation corresponds to an undesirable equilibrium, making it disappear could ensure that the system leaves this undesirable situation in the hope that it reaches a more desirable one. In the phase plane, this consists in reducing its basin of attraction to the extreme, making it vanish. In modelling terms, this means that the undesirable stable equilibrium collides with an unstable equilibrium in a saddle-node bifurcation where both equilibria disappear.

The geometrical effect of coupling parameters on the nullclines provides an intuitive explanation of the possibility for equilibria to appear or disappear (Appendix 3.B), illustrated by Fig. 3.2. When the cooperation effort is high enough, stable equilibria with a high level of cooperation can only have a clean water state. And when agents are very concerned for the lake water, any stable polluted equilibrium forces them to cooperate.

For example, in the case with the strongest coupling (Fig. 3.5, darkest colours), the undesirable  $(P_{hi}, F_{lo})^*$  equilibrium disappears: the initial condition ⑤ then leads asymptotically to the adoption of cooperation among the population, with the pollution remaining at a similar level.

Fig. 3.2 shows that the stable equilibria which are the most threatened to disappear by increased coupling are the ones with high levels of pollution:  $(P_{hi}, F_{lo})^*$  and  $(P_{hi}, F_{hi})^*$ . This is plausible since the coupling favours lower levels of pollution.

The model can display a configuration with no stable equilibrium (Fig. 3.6, see Appendix 3.D for a more in-depth exploration). In this case, simulations show sustained oscillations similar to those found in Suzuki and Iwasa (2009b). First, at a low level of cooperation, the level of pollution increases. The latter induces an increase in the fraction of cooperators, which in turn decreases the lake pollution. Finally, the low pollution level decreases the incentive to cooperate and the level of cooperation drops and the cycle starts again.

#### 3.3.3 Counterintuitive equilibria

Our model permits the existence of stable, partially desirable equilibria: an ecologically desirable low pollution level fixed point  $(P_{lo}, F_{lo})^*$  without the adoption of the socioeconomically desirable option (low cooperation); or the converse,  $(P_{hi}, F_{hi})^*$ , where the ecological subsystem is in the undesirable state while the socioeconomic subsystem is in a desirable state.

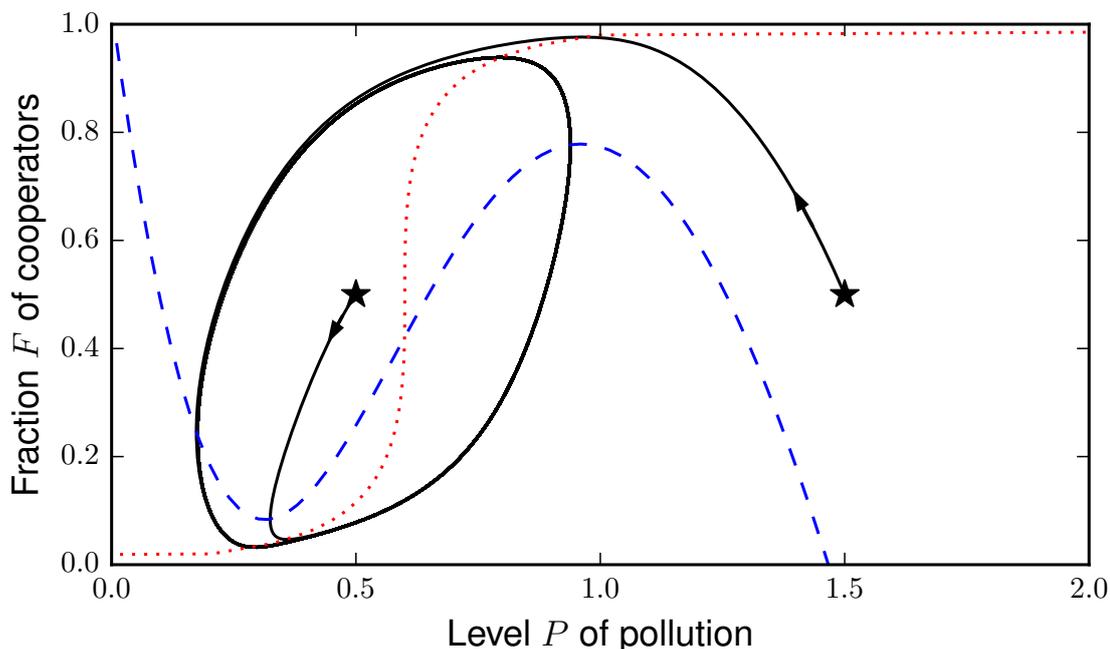


Figure 3.6: *Limit cycle oscillations in the phase plane for the model with bidirectional coupling and no stable equilibrium. The  $P$ -nullcline (dashed blue) and the  $F$ -nullcline (dotted red) are shown as well as two trajectories (solid black) and their initial condition (black stars). Parameter values as in Fig. 3.2 except for  $\alpha = 0.26$ ,  $r = 0.5$ ,  $\delta_p = 0.0388$ ,  $\kappa = 5$  and  $\xi = 4$ .*

Such counterintuitive equilibria are related to lock-in effects due to the bistability of the subsystems. In the case of  $(P_{lo}, F_{lo})^*$ , for instance, the discharge of pollutants is high but the lake system can bear with it, so that the clear water state does not collapse; even if the adoption of cooperation is low, the ecological feedback in the lake preserves the clear water state and makes it resilient against a high discharge of pollutants. In the case of  $(P_{hi}, F_{hi})^*$ , a majority of human agents cooperate, which results in a relatively low discharge, but this environment-friendly effort is not enough for the lake to leave the eutrophic state; indeed, the resuspension of pollutants in the water, acting as an ecological positive feedback, makes the polluted state resilient against increased cooperation.

Consider for instance the most undesirable equilibrium  $(P_{hi}, F_{lo})$  in Fig. 3.4. If it were possible, cleaning the lake (decreasing  $P$ ) would be far more ecologically effective than trying to convince the agents to cooperate (increasing  $F$ ) and actually ending up in  $(P_{hi}, F_{hi})$ . Indeed, the ecological state of  $(P_{lo}, F_{lo})$  is much more desirable than that of  $(P_{hi}, F_{hi})$ , despite its lack of cooperation. This highlights the importance of considering counterintuitive equilibria in a management perspective.

With this result, we answer the question about the correlation between cooperation and the ecological goal since we show that cooperation does improve the ecological state, but the improvement may be negligible and a high level of cooperation does not guarantee a desirable ecological state. Moreover, a low level of cooperation does not always imply an undesirable ecological state.

## 3.4 Discussion

In this section, we interpret our results and compare them with those of Suzuki and Iwasa (2009b). We start with general modelling results, then we discuss implications for management strategies. All of our results focus on equilibrium states; they do not hold for transient dynamics.

### 3.4.1 General modelling results for the coupled system

Here we sum up our findings on the various configurations and dynamics of our model. We discuss first the key factors influencing the number of equilibria existing simultaneously and multistability, then the possibility to observe oscillations.

#### Multistability

Suzuki and Iwasa (2009b) mention the possibility of multistability in their model. Some of their bifurcation diagrams show such a situation, but they do not discuss it further in the perspective of management. Multistability is favoured by a hysteretic configuration. In graphical terms, this corresponds to S-shaped nullclines in the phase plane.

We find analytically the parameters influencing the appearance of a hysteresis for the ecological nullcline and for the socioeconomic nullcline (Appendix 3.C). Key parameters include all lake characteristics influencing the pollutant fluxes on the one hand, and social properties of the agents on the other hand. Notably, all of those parameters characterize internal feedback loops within each subsystem and feedbacks concerning the coupling between the subsystems don't play a role in making a hysteresis appear.

Table 3.2 compares our results with numerical ones obtained by Suzuki and Iwasa (2009b). From the twelve homologous parameters between our models, Suzuki and Iwasa reported the effects of five based on particular bifurcation diagrams. We confirm analytically the same effect of the resuspension rate of pollutants in the lake and the effect of agents' conformism on the appearance of a hysteresis.

We notably show, however, that neither the discharge of pollutants of defectors or of cooperators, nor economic incentives can influence the existence of a hysteresis

configuration in our model. This can also be said of ecological incentives, which were not investigated by Suzuki and Iwasa (2009b). Results in Suzuki and Iwasa (2009b) were based on numerics and were specific for certain parameter values. By contrast, the analytical results presented here are general. The differences that we report may be due to a number of factors. First, Suzuki and Iwasa (2009b) focused on stable equilibria, whereas we investigated the existence of a hysteresis in the nullclines. Secondly, they present and interpret mainly monostable cases in their bifurcation diagrams. As a consequence, they analyze the influence of parameters on a unique stable equilibrium which may be opposed to different equilibria in the multistable case. This explains how they were able to report alternatively positive or negative effects (denoted by “+/-” in Table 3.2) on the long-term level of pollution for two parameters, the discharge of defectors and the discharge of cooperators. Finally, the model formulation of the incentive to cooperate  $\Delta U$  was slightly different in Suzuki and Iwasa (2009b). It included a bilinear term which may play a role in arriving at different conclusions. This can be observed in particular for our parameter  $v$  representing the cost of cooperation, which would correspond to two parameters in Suzuki and Iwasa’s model.

Parameters concerning the lake subsystem mostly depend on ecological characteristics of the lake, except for the difference  $\delta_p$  between the environment-friendly and environment-unfriendly strategies. This is important from a management perspective since properties of the lake may or may not be more difficult to modify compared to the behaviour of the population when the lake is big. For instance, it might be easier to isolate a polluted part in a big lake than to make farmers decrease their discharge of pollutants in neighbouring fields. Among parameters of the socioeconomic subsystem, the social conformism  $\xi$  critically determines the existence of a hysteresis configuration, which favours multistability.

Multistability means that regime shifts may happen under large enough perturbations even with no change in parameters (Scheffer et al., 2001), but multistability is neither generally desirable nor generally undesirable. On the one hand, multistability is desirable because some equilibria can represent more desirable states than when there is only one equilibrium. On the other hand, multistability is undesirable because it introduces the possibility of sudden regime shifts, notably towards more undesirable states.

Interestingly, similar configurations of two  $S$ -shaped nullclines exist in metapopulation models where two bistable patches are coupled by dispersal (Amarasekare, 1998; Vortkamp et al., submitted).

In the general case, we observe that counterintuitive stable equilibria achieving either the ecological aim (low pollution level) or the social objective (dominance of the environment-friendly behaviour), but not both, can exist. The possibility of counterintuitive equilibria may not have been stressed much in the literature, since

it can be obvious from a mathematical modelling point of view. It has indeed been given little attention, even though such counterintuitive attractors were previously found in several social-ecological models (Suzuki and Iwasa, 2009b; Tavoni et al., 2012; Lade et al., 2013).

The fact that even simple models can display such counterintuitive equilibria suggests that they are widespread. This mitigates the assumption that there must be a single absolute optimum for both the ecological subsystem and the socioeconomic subsystem. Thus, counterintuitive equilibria should make us question the assumption that ecology-oriented actions are a condition for an ecological “good” state at a stable equilibrium. This highlights the fact that considering counterintuitive equilibria is essential in a management perspective.

### Unique equilibrium in the phase plane

Suzuki and Iwasa (2009b) observe oscillations for certain parameterizations of their discrete-time model. We confirm the possibility to observe sustained oscillations (Fig. 3.6) in our continuous-time model. Since discrete-time systems often show a tendency for oscillations, our results lend some robustness to oscillations emerging in social-ecological systems. Similarly to Suzuki and Iwasa (2009b), we also observed oscillations only in the case of a unique equilibrium.

From the point of view of ecological modelling, the oscillations are similar to a classical cycling behaviour observed in predator-prey models of population dynamics (Rosenzweig and MacArthur, 1963; Turchin, 2003). The level of cooperation behaves as a predator population and the level of pollution behaves as a prey population. The predator has a negative impact on the prey population whereas the prey has a positive impact on the predator, and similarly the cooperation has a negative impact on the pollution whereas the pollution has a positive impact on the cooperation. As a consequence, the cooperation level follows the level of pollution in the way a predator population follows the fluctuations of the prey population. A similar analogy of social-ecological systems to consumer-resource systems has been drawn for a resource exploitation model (Bieg et al., 2017).

Suzuki and Iwasa (2009b) use simulations to find that the stability of the equilibrium they consider critically depends on the relative speed of the two subsystems. We find that the speed of the socioeconomic subsystem  $s$  influences exclusively the stability (not the location) of the equilibrium. While this might suggest that  $s$  is a key factor on which the stability of the equilibrium depends, it does not exclude that other parameters can also have a critical influence (Appendix 3.D). Thus, contrary to Suzuki and Iwasa’s conclusion, the stability of the unique equilibrium does not specifically depend on the relative speed of the two subsystems.

However, based on our simulations, we draw a link between the loss of stability (the emergence of oscillations) and the location of the equilibrium relative to the

nullclines (Appendix 3.D). In particular, a necessary condition for having oscillations seems to be a hysteretic configuration (S shape) for the nullclines.

### 3.4.2 Management perspectives

The management strategies we have mentioned in the introduction have a mathematical interpretation in the model. The different kinds of management strategies aim at providing a perturbation (punctually modify the level of pollution or the fraction of cooperators, *i.e.* the state variables), at changing parameters to move an equilibrium, or at influencing globally the possible equilibria. In all cases, the impact of management strategies is highly dependent on the current state of the system and on its permanent features (parameters). This is due to mutual feedbacks between the two subsystems, which create a possibility for complex, multistable dynamics to emerge.

In this section, we specifically discuss management perspectives regarding three different aims. The first aim is to induce a critical transition between different equilibria, for instance by decreasing the cost of cooperation by implementing taxes for defectors. This was a major point of Suzuki and Iwasa (2009b). The second aim is to move the current equilibrium towards a more desirable state without any critical transition. This also avoids the uncertainty which may result from a critical transition. An example could consist in removing the pollutants from the water directly. The third aim concerns possible effects of policies on the resilience of the different equilibria, for instance in order to increase the ecological resilience of a desirable equilibrium (Holling, 1996) or to make an undesirable equilibrium disappear.

#### Reaching more desirable states through critical transitions

Generic management recommendations are not possible, because, for instance, the highest level of cooperation possible at equilibrium does not ensure the lowest level of pollution possible (Fig. 3.4). The difficulty of general management recommendations is further reinforced by the possibility for stable equilibria to appear or disappear. This possibility makes it impossible to find a general, monotonous correlation between a single parameter and the location of all stable equilibria the system may be attracted to. The diversity of possible system dynamics does not allow us to derive a generic rule of thumb. Indeed, any management strategy should take into account the current state of the system on the one hand and the range of parameters (structure of the *phase plane*) on the other hand.

In particular, it does not seem reasonable to take actions aiming at undergoing a desirable regime shift without knowing whether such a regime shift is possible. For example, having a high level of pollution and a low level of cooperation (un-

desirable state when measured absolutely) does not necessarily mean that there is multistability and that the current state is the  $(P_{hi}, F_{lo})^*$  equilibrium: it can be that the system is not multistable, or that it is simply in a configuration where changing a parameter does not necessarily give rise to a more desirable equilibrium towards which a critical transition could be attempted.

Using simulations and bifurcation diagrams, Suzuki and Iwasa (2009b) explore specific parameterizations, studying mostly monostable situations, and give management recommendations aiming at triggering a critical transition between different equilibria through a regime shift. Thus, in the general case, we do not find the same results as Suzuki and Iwasa (2009b) concerning the possibility to change the pollution and/or cooperation level of the system at equilibrium in a desirable direction by modifying the ecological concern  $\kappa$  among the human population, its conformist tendency  $\xi$  and/or the baseline cost  $\nu$  of defection. For instance, they conclude that increasing  $\kappa$  does not effectively increase the cooperation  $F$ , but our Fig. 3.5 (initial conditions 1, 3 and 5) suggests that it is actually possible when taking multistable configurations into account.

### Societal and ecological aims without critical transition

Although it is not possible to find a rule-of-thumb concerning all possible equilibria at the same time, it is possible to make management suggestions for systems remaining at the same equilibrium. Suzuki and Iwasa (2009b) have not investigated this possibility. Rather than transitioning to alternative stable states, management strategies could aim at shifting the current equilibrium to a more desirable state.

Our simulations suggest that, for all equilibria and as long as they continue to exist, the pollution is reduced when some agents take strong actions (high cooperation effort  $\delta_p$ ) against it. Additionally, this reduction is substantial only when the cooperation level  $F$  itself is high. To illustrate this point, it can be proved that  $\delta_p$  has no influence on the location of the  $P$ -nullcline when there is no cooperation ( $F = 0$ ). The parameter  $\delta_p$  represents the effort that some agents make in order to improve their impact on the environment.

Moreover, cooperation tends to be increased if the concern for lake pollution ( $\kappa$ ) is high. This can be achieved through education to increase the awareness of the population about its ecological impact. We have assumed a good information system on the state of the lake, but this is correlated with the ecological concern since a high concern for the lake pollution implies good monitoring.

### Managing the resilience

Finally, our findings show that the coupling between the ecological subsystem and the socioeconomic subsystem increases the resistance (Grimm and Wissel, 1997),

also called *resilience* (Holling, 1973, 1996; van Nes and Scheffer, 2007), of desirable equilibria while decreasing that of undesirable equilibria. If we assume that the system is at equilibrium, the adoption of environment-oriented actions among the agents (increase in cooperation  $F$ ) or the action of cleaning the lake (decrease in pollution  $P$ ) are perturbations. Thus, in multistable cases, they challenge the resistance of the current equilibrium by dragging the system towards the basins of attraction of more desirable equilibria.

This provides understanding on how the resistance of undesirable states (polluted water and/or environment-unfriendly behaviour) is diminished by an increasing cooperation effort  $\delta_p$ , or by an increasing ecological concern  $\kappa$ . Those parameters may favour a regime shift towards more desirable states, provided that some other equilibria do indeed offer more desirable states. Such regime shifts have been deemed *noise-induced* (N-tipping) (Ashwin et al., 2012) or *extrinsic* (Seddon et al., 2014) in that they are driven by a perturbation which does not belong to the spontaneous dynamics of the system.

#### 3.4.3 Conclusions

The generality of the model and the intuitive understanding we get from it make it suitable for discussion across disciplines. When communicating with other fields or with decision-makers, modellers should be careful about the way they state: 1) what they consider being desirable, 2) what they consider to be a precise management objective, 3) what changes in the social-ecological system can reasonably be made, 4) what can reasonably be known or predicted.

Regarding the first point, our findings suggest for instance that there is no obvious correlation between environment-friendly actions and reaching an ecologically desirable state. However, we find the expected correlation when considering the relative location of simultaneously possible equilibria.

Regarding the second point, consider the very broad objective of reducing the pollution level. Then, changing the location of the current equilibrium, perturbing the current state to reach another (more desirable) equilibrium, and reducing the resistance of the current undesirable equilibrium until it disappears are three very different, more precise objectives. We understand that, as is the case for the concept of stability (Radchuk et al., 2019), management strategies may simultaneously involve several, independent manners to influence possible equilibria.

Regarding the third point, it is worth noting that such diverse measures as changing the resuspension rate in the lake, removing the pollution, convincing more agents to cooperate or increasing the cooperation effort of those who already cooperate may not be all as feasible.

Regarding the last point, compared to more complex, mechanistic models, our generic model does not allow for precise forecasts. However its genericity makes our

conclusions more general and comparatively robust. In particular, the fact that our model already gives rise to a high complexity suggests that it is not possible to make generic recommendations holding for every situation. Indeed, due to dynamical complexity resulting in a qualitative uncertainty, it is impossible to make simple management recommendations.

## 3.A Number of equilibria

### 3.A.1 Existence of at least one equilibrium

We will prove the following proposition: the system has at least one equilibrium  $(P^*, F^*) \in ]0, +\infty[ \times ]0, 1[$ .

Consider the half-plane  $\mathbb{R}^+ \times \mathbb{R}$  for an extended domain of theoretically possible states  $(P, F)$ . The proof comprises the following steps:

- the  $F$ -nullcline gives a boundary between two subsets  $A$  and  $\bar{A}$  of the half-plane;
- the extended  $P$ -nullcline (with  $F \in \mathbb{R}$ ) gives a connected path between those subsets;
- thus, it must cross the boundary given by the  $F$ -nullcline.

Consider the  $F$ -nullcline in the  $\mathbb{R}^+ \times \mathbb{R}$ -half-plane. If  $\kappa = 0$ , it comprises at least one horizontal line representing a constant map over all possible values for  $P$  in  $\mathbb{R}^+$  to a single value for  $F$  in  $]0, 1[$ . If  $\kappa > 0$ , it represents a continuous function from values of  $F$  in its domain  $\mathcal{D}_F \subset ]0, 1[$  to all possible values for  $P$  in  $\mathbb{R}^+$ .

In any case, it is possible to define a connected subset  $\mathcal{F}$  of the  $F$ -nullcline in the  $(P, F)$ -half-plane extending over all values for  $P$  in  $\mathbb{R}^+$  but restricted to  $\mathcal{D}_F \subset ]0, 1[$  for  $F$ .  $\mathcal{F}$  divides the  $\mathbb{R}^2$ -plane into two complementary connected subsets  $A$  and  $\bar{A}$ , with  $(\mathbb{R}^+ \times ]-\infty, 0]) \subset A$  and  $(\mathbb{R}^+ \times ]1, +\infty[) \subset \bar{A}$ .

Consider the same arguments for the  $P$ -nullcline as for the  $F$ -nullcline. If  $\delta_p = 0$ , it comprises at least one vertical line representing a constant map over all theoretically possible values for  $F$  in  $\mathbb{R}$  to a single value for  $P$  in  $\mathbb{R}^+$ . If  $\delta_p > 0$ , it represents a continuous function  $f$  from values of  $P$  in  $\mathbb{R}^+$  to values of  $F$ . Note in particular that  $f(P = 0) = \frac{p_D}{\delta_p}$ , which is strictly greater than 1 since  $p_D > \delta_p$ , and that:

$$\lim_{P \rightarrow +\infty} f(P) = -\infty.$$

In any case, it is possible to define a connected subset  $\mathcal{P}$  of the  $P$ -nullcline with  $\mathcal{P} \cap A \neq \emptyset$  and  $\mathcal{P} \cap \bar{A} \neq \emptyset$ .

As  $\mathcal{P}$  joins points in  $A$  and in  $\bar{A}$  and is connected, it crosses the boundary  $\mathcal{F}$ , which is a subset of the  $F$ -nullcline. Thus,  $\mathcal{P} \cap \mathcal{F} \neq \emptyset$  and the intersection between the  $P$ -nullcline and the  $F$ -nullcline is non-empty: there exists at least one equilibrium.

### 3.A.2 Maximum number of equilibria

In the  $(P, F)$ -phase plane, the  $P$ -nullcline is the graph of a continuous function  $F_{P'=0}$  of  $P$ :

$$F = F_{P'=0}(P) = \frac{1}{\delta_p} \left( p_D - \alpha P + \frac{rP^q}{m^q + P^q} \right), \quad (3.3)$$

and the  $F$ -nullcline is the graph of a continuous function  $P_{F'=0}$  of  $F$ :

$$P = P_{F'=0}(F) = \frac{1}{\kappa} \left[ \frac{1}{\beta} \ln \left( \frac{F}{1-F} \right) - \xi F + v \right]. \quad (3.4)$$

It is easy to prove that the second derivative of those functions vanishes at most once if  $P$  is positive and  $F$  comprised between 0 and 1. As a consequence, on the same domains, their first derivative can vanish at most twice. Having at most two extrema in our domain of interest, the nullclines of the coupled system cannot be more complex than  $S$ -shaped curves, with a maximum of three strictly monotonic branches. As such two  $S$ -shaped curves extending in perpendicular directions cannot cross more than nine times, the maximum number of equilibria is nine.

## 3.B Impact of coupling on the shape of the nullclines

The coupling between the two subsystems of the model influences the shape of the nullclines in a similar way: the more coupled the two subsystems, the more  $S$ -shaped the nullclines. The first two subsections describe this coupling extensively from a mathematical point of view for each subsystem. The third subsection interprets this mathematical influence.

### 3.B.1 Impact on the coupling on the $P$ -nullcline

Equation 3.3 describing the  $P$ -nullcline shows that increasing  $\delta_p$  flattens the  $S$ -shaped curve on the  $P$ -axis (Fig. 3.2 p. 42, top). Thus, the introduction of some coupling explains the transition from three vertical lines when  $\delta_p = 0$  to the  $S$ -shaped curve when  $\delta_p > 0$ : the curve is stretched apart at first, then squeezes on the horizontal axis in the  $(P, F)$ -plane. The middle branch of the  $S$ -shaped curve corresponds to the unstable threshold line of the subsystem with  $\delta_p = 0$ .

For a constant value for  $F$ , the first and third branches of the S-shaped curve move upwards in the  $(P, F)$ -plane as  $\delta_p$  increases, which pushes the stable equilibria to lower levels of pollution. The middle branch gets higher, which pushes the corresponding unstable equilibria down to higher levels of pollution, which suggests that the basin of attraction of the high pollution states become smaller and that of the low pollution states become larger. That is, the high pollution states lose resistance to perturbations whereas the low pollution (ecologically desirable) states become more resistant.

### 3.B.2 Impact on the coupling on the $F$ -nullcline

The equation of the  $F$ -nullcline 3.4 shows that increasing  $\kappa$  flattens the S-shaped curve on the  $F$ -axis (Fig. 3.2 p. 42, bottom). Introducing some coupling triggers the change from three horizontal lines ( $\kappa = 0$ ) to an S-shaped curve. In the  $(P, F)$ -plane, the branches of this S-shaped curve are almost horizontal when  $\kappa \approx 0$  but get closer and closer to the curve of the unit step function as  $\kappa$  increases. The middle branch of the S-shaped curve corresponds to the unstable threshold line of the subsystem with  $\kappa = 0$ .

For a constant value for  $P$ , the first and third branches of the S-shaped curve move upwards in the  $(P, F)$ -plane as  $\kappa$  increases, which pushes the stable equilibria to higher levels of cooperation. The middle branch gets lower, which pushes the corresponding unstable equilibria down to lower levels of cooperation, which suggests that the basin of attraction of the low cooperation states become smaller and that of the high cooperation states become larger. That is, the high defection states lose resistance to perturbations whereas the high cooperation (socially desirable) states become more resistant.

### 3.B.3 Interpretation of the impact of the coupling on the nullclines

Overall, the way the unstable equilibria are shifted by the coupling allows us to anticipate what simulations confirm: the unstable equilibria, and in particular the organizing center  $(P_{mid}, F_{mid})$  of the phase plane, are shifted in the opposite direction, with respect to the stable equilibria, namely towards higher levels of pollution and lower levels of cooperation. As a consequence, the basins of attraction of equilibria with low levels of pollution and high levels of cooperation are extended (Fig. 3.4 p. 46, bottom). Thus, we observe that the introduction of the coupling also increases the resistance of such equilibria in the sense that larger perturbations would be needed to depart from them (compare the basins of attraction of the equilibria in Fig. 3.4 p. 46).

Finally, if we consider the most complex situation with nine equilibria, as each unidirectional coupling increases, the  $S$ -shaped curves are squeezed so much on the axes that some of their crossings disappear. Indeed, when  $\delta_p$  reaches very high levels, the  $(P_{hi}, F_{hi})^*$  equilibrium disappears: the bifurcation corresponds to the collision between the  $(P_{hi}, F_{hi})^*$  stable equilibrium and the  $(P_{mid}, F_{hi})$  unstable equilibrium (Fig. 3.2 p. 42, top, finely dotted nullcline). In that case, the initial conditions which would have approached the  $(P_{hi}, F_{hi})^*$  equilibrium now go to the  $(P_{lo}, F_{hi})^*$  stable equilibrium. The same might then happen, for even higher levels of  $\delta_p$ , for the  $(P_{hi}, F_{lo})^*$  stable equilibrium. However, the  $(P_{lo}, F_{hi})^*$  equilibrium is not at risk of disappearing (Appendix 3.C.1).

Similarly, when  $\kappa$  reaches a very high level, the undesirable equilibrium,  $(P_{hi}, F_{lo})^*$ , disappears in a saddle-node bifurcation with the  $(P_{hi}, F_{mid})$  unstable equilibrium. The same would then happen, for even higher levels of  $\delta_p$ , for the  $(P_{lo}, F_{lo})^*$  stable equilibrium.

### 3.C Hysteresis configuration

Here, we summarize which parameters influence the existence, the amplitude and the location of a hysteresis configuration. A hysteresis configuration corresponds to an S-shaped (connected) extended nullcline in the  $\mathbb{R}^+ \times \mathbb{R}$ -half-plane. In non-trivial cases where there is some coupling between the two subsystems:

- the  $P$ -nullcline gives a hysteresis configuration if it does not represent a bijection from the domain of  $P$  to that of  $F$ ;
- the  $F$ -nullcline gives a hysteresis configuration if it does not represent a bijection from the domain of  $F$  to that of  $P$ .

#### 3.C.1 $P$ -nullcline

The  $P$ -nullcline corresponds to equation 3.3. It is possible to analytically derive the condition for the existence of a hysteresis configuration for the  $P$ -nullcline; it is the following:

$$\frac{r}{\alpha m} > \frac{4q}{q^2 - 1} \left( \frac{q - 1}{q + 1} \right)^{1/q}.$$

This is a generalization of the result obtained by (Mäler et al., 2003) for  $q = 2$ . It means that  $r$ ,  $\alpha$  and  $m$  favour the hysteretic configuration. As we assume that  $q \geq 2$ , the term on the right-hand side is strictly decreasing when  $q$  increases: a larger value for  $q$  also favours a hysteretic configuration. Since  $q$  represents the shallowness of the lake, this result is consistent with the bistability observed in shallow lakes (Carpenter et al., 1999).

### 3.C.2 $F$ -nullcline

The  $F$ -nullcline corresponds to equation 3.4. It is also possible to analytically derive the condition for the existence of a hysteresis configuration for the  $F$ -nullcline:

$$4 < \beta\xi.$$

It means that  $\beta$  and  $\xi$  favour the hysteretic configuration.

The interval of bistability on the  $P$ -axis (the interval of values for  $P$  for which the  $F$ -nullcline gives several corresponding values for  $F$ ) also becomes longer under the influence of  $\beta$  and  $\xi$  exclusively. And, in the  $(P, F)$ -plane, the  $F$ -nullcline has a symmetry center:

$$H_F \left( \frac{1}{\kappa} \left[ v - \frac{\xi}{2} \right], \frac{1}{2} \right).$$

## 3.D Oscillations

Here, we investigate the cases where we observe sustained oscillations. Suzuki and Iwasa (2009b) find parameterizations for which no stable equilibrium exists and where the system shows oscillations. Our continuous-time model also shows such oscillations (Fig. 3.6 p. 50). We heuristically observe this behaviour in some situations where:

- one nullcline shows a hysteresis configuration, with a middle branch corresponding to the unstable branch in the uncoupled system;
- the shape of the other nullcline is also hysteretic or close to fulfilling the hysteresis condition (Appendix 3.C);
- there is exactly one fixed point in the  $(P, F)$ -plane, *i.e.* the number of fixed points is at its minimum (Appendix 3.A.1);
- the fixed point happens to be on a specific part of the nullclines: the middle branch of each S-shaped curve or nearly S-shaped curve (which corresponds to the unstable line when the subsystems are uncoupled).

In such cases, the only equilibrium can be unstable: simulations suggest a supercritical Hopf bifurcation creating a stable limit cycle. The oscillations follow the same direction as reported by Suzuki and Iwasa (2009b).

As Suzuki and Iwasa (2009b), we find through simulations that the stability of the only existing equilibrium depends on  $s$  and  $\alpha$ . When writing the expression for the Jacobian, we can see however that the stability depends on all parameters. Indeed,

the Jacobian matrix of the system evaluated at any equilibrium point  $(P^*, F^*)$  in  $\mathbb{R}^+ \times ]0, 1[$  (excluding states which cannot be equilibria) can be written as:

$$J_{(P^*, F^*)} = \begin{pmatrix} \frac{qm^q}{rP^{*q+1}}(\alpha P^* - p_D + \delta_p F^*)^2 - \alpha & -\delta_p \\ s\beta\kappa F^*(1 - F^*) & s\beta\xi F^*(1 - F^*) - s \end{pmatrix}.$$

Parameter  $s$  is indeed particular, but this specificity is due to the fact that, contrary to the other parameters,  $s$  does not affect the location of the equilibrium, since it has got no influence on the nullclines (it is obvious from their equations in Appendix 3.A.2). It means that the relative speed of the subsystems does not affect the long-term behaviour of the integrated system. Therefore, varying  $s$  can be used to display configurations where the equilibrium is stable or unstable while remaining at the same location. Parameter  $s$  does not influence the stability more than other parameters, but it influences only the stability.

## References

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# 4 Comparison between best-response dynamics and replicator dynamics in a social-ecological model of lake eutrophication

## Abstract

Social-ecological models are often used to investigate the mutual interactions between an ecological system and human behaviour at a collective level. The social system is widely represented either by the replicator dynamics or by the best-response dynamics. Previous analyses found that the two formulations are mathematically could be obtained mathematically from one another. We investigate the consequences of choosing one or the other with the example of a social-ecological model for eutrophication in shallow lakes, where the anthropogenic discharge of pollutants into the water is determined by a behavioural model using the replicator or a best-response dynamics. We discuss a fundamental contradiction between the replicator dynamics and the logit formulation of the best-response dynamics. This fundamental contradiction results in a different number of equilibria in the phase plane. Graphical nullcline analysis reveals that the replicator equation is a limit case of the best-response model in which agents are assumed to behave with an infinite rationality. If agents act less rationally in the model using the best-response dynamics, the correspondence with the model using the replicator dynamics decreases. Finally, we show that sustained oscillations observed in the phase plane in the two cases may differ substantially. The replicator dynamics makes the limit cycle become larger and makes the system come closer to full cooperation or full defection. Thus, the dynamics along the limit cycle imply a different risk for the system to be pushed by a perturbation into a desirable or an undesirable outcome depending on the socioeconomic dynamics we use. When analyzing social-ecological models, the choice of a socioeconomic dynamics is often little justified but may have dramatic impacts on the results obtained.

## 4.1 Introduction

In the past fifteen years, several articles (Ibáñez et al., 2004; Satake and Iwasa, 2006; Satake et al., 2007a,b; Iwasa et al., 2007; Suzuki and Iwasa, 2009a,b; Iwasa et al., 2010; Fryxell et al., 2010; Tavoni et al., 2012; Iwasa and Lee, 2013; Lade et al., 2013; Lee and Iwasa, 2014; Lee et al., 2015a,b; Sugiarto et al., 2015; Bieg et al., 2017) have proposed social-ecological models, coupling an ecological system with a socioeconomic system. The ecological model typically represents the level of a resource using population dynamics, whereas the socioeconomic model accounts for some human behaviour influencing the environment, using evolutionary game theory. Coupled social-ecological models have been widely used to study fisheries or other harvested populations (Fryxell et al., 2010; Lee and Iwasa, 2014; Bieg et al., 2017), lakes (Iwasa et al., 2007; Suzuki and Iwasa, 2009a; Iwasa et al., 2010), grasslands (Lee et al., 2015a), forests (Satake and Iwasa, 2006; Satake et al., 2007a,b; Lee et al., 2015b) and some other ecological contexts (Ibáñez et al., 2004; Tavoni et al., 2012; Iwasa and Lee, 2013; Lade et al., 2013; Sugiarto et al., 2015).

The ecological models used in these coupled human-environment systems can most of the times be discussed, criticized and improved by considering empirical and especially experimental data. For instance, models of eutrophication in shallow freshwater lakes are strongly supported by experiments, making them reliable, sometimes predictive, and quite consensual (Scheffer, 1998). By contrast, the formulation used to model the human behaviour, often with the replicator dynamics (Tavoni et al., 2012; Lade et al., 2013) or the logit best-response dynamics (Satake and Iwasa, 2006; Satake et al., 2007a; Iwasa et al., 2010), is usually not explicitly justified. Both the replicator and the logit best-response dynamics come from evolutionary game theory and describe the evolution of the collective choice of individuals between different strategies at a population level, in our case a population of human agents. Despite a growing body of empirical data (*e.g.* Hoffman et al., 2015), experiments on humans' behaviour do not allow for quantification of the adoption of a strategy over large populations during a long enough time since the experiments typically involve a few dozen subjects playing a simple game over ten rounds in a few hours (*e.g.* Dannenberg et al., 2015). As a consequence, experiments do not give clear support either for the replicator or for the logit best-response formulation.

In the modelling literature in ecology and elsewhere, there seems to be little awareness about the impact of choosing the replicator over the logit-best-response or vice-versa. This is a major issue, since conclusions derived from such models may depend on the way humans are assumed to behave. Conceptual links between the replicator and the logit best-response have been described in the game theoretical literature (Hopkins, 1999; Hofbauer et al., 2009), but they are highly abstract and remain out of reach for many researchers. Their mathematical formulation as well as the absence of a common terminology prevent other scientific branches from

getting aware of those links, especially in economics, ecology and social sciences. Indeed, Hopkins (1999) proved that the best-response dynamics can be understood as a perturbed version of a generalized replicator, and Hofbauer et al. (2009) proved that, in most cases, the replicator dynamics is a better and better approximation of a best response as time passes within the system. To our knowledge, the consequences of such links in a coupled social-ecological model have not been described. More generally, interpretations beyond the mathematical result have not been discussed.

Here, we investigate the meaning of this formal link between the replicator and a best-response dynamics by addressing the following question: “How does the choice of a socioeconomic model impact the coupled social-ecological dynamics?” Throughout the chapter, we refer to the socioeconomic system as the *replicator dynamics* or as the *logit best-response dynamics*, whereas we refer to the coupled social-ecological systems as *models*. We illustrate and discuss the differences and the similarities of the replicator and the logit best-response dynamics. We reconsider the social-ecological model of eutrophication in shallow lakes from Chapter 3 and compare two versions. Both versions have exactly the same ecological part, but they differ in the socioeconomic part, with one version using the replicator dynamics (replicator dynamics model RDM) and the other version using the logit best-response dynamics (best-response model BRM). We find that the RDM and the BRM can yield very different model outcomes in terms of the number and the stability of equilibria or in the shape of the limit cycle. Yet, an analysis of the phase plane shows a strong analogy between them: the nullclines of the RDM give the limit case of the nullclines of the BRM when the human agents’ rationality tends towards infinity.

This chapter is structured as follows. First, we derive the two similar social-ecological models for lake eutrophication. We explain and interpret a fundamental difference between the two, concerning the stability of situations where all agents choose the same strategy. Then, we find that this fundamental difference has direct consequences on the possible number of equilibria in the phase plane. We illustrate how the replicator dynamics can be considered as giving the limit of the best-response dynamics under certain conditions. And we describe oscillations and the subsequent make-or-break dynamics with the RDM, which has not been described before. Finally, we discuss the fact that failing to keep in mind implicit assumptions about the socioeconomic dynamics chosen might have dramatic consequences on the robustness of conclusions obtained from studying social-ecological models.

## 4.2 Models

In this section, we derive two dynamic social-ecological models. Both share the same ecological subsystem which describes lake pollution dynamics and is the same as in (Carpenter et al., 1999; Suzuki and Iwasa, 2009a, and Chapter 3). The two models

differ in the human subsystem, which describes the dynamics of the collective choice of human agents choosing between two strategies, namely to pollute the lake at a high level  $p_D$  or at a low level  $p_D - \delta_p$ . The two different formulations we consider for the socioeconomic subsystem—the replicator dynamics (Tavoni et al., 2012; Lade et al., 2013) for the RDM and the logit best-response dynamics (Suzuki and Iwasa, 2009a, and Chapter 3) for the BRM—have already been used in social-ecological models.

### 4.2.1 Ecological subsystem

We use the model developed by Carpenter et al. (1999) which can account for the bistability observed in shallow lakes. The state variable representing the ecological subsystem is the level of pollution  $P$  ( $P \geq 0$ ). It represents the amount of pollutants present in the lake, such as the concentration of phosphorus in the surface waters typically.

$$\frac{dP}{dt} = \underbrace{A}_{\substack{\text{anthropogenic discharge} \\ \text{of pollutants}}} - \underbrace{\alpha P}_{\substack{\text{global outflow rate} \\ \text{(outflow and sedimentation)}}} + \underbrace{\frac{rP^q}{m^q + P^q}}_{\text{recycling}}.$$

We assume a linear global outflow rate (outflow and sedimentation of pollutants leaving the surface waters) with parameter  $\alpha$ . The recycling term corresponds to the resuspension of pollutants from the sediments into the water, which is stronger in shallow lakes (less than 3 m deep). It corresponds to a sigmoid curve where  $r$  determines the upper bound and  $m$  the half-saturation level of pollutant density. The parameter  $q$  is negatively correlated to the depth of the lake; for our models we have  $q \geq 2$  (Carpenter et al., 1999).

From a game theoretical point of view, the anthropogenic discharge of pollutants can be represented as a choice ranging between two strategies. A human agent may go on releasing a high amount of pollution  $p_D$  (defection) or restrict their release to a lower level  $p_D - \delta_p$ . If we consider the entire population, the pollution release is the result of a collective choice characterized by the fraction  $F$  of cooperators in the population and the fraction  $1 - F$  of defectors in the population:

$$A = p_D(1 - F) + (p_D - \delta_p)F.$$

Note that in this chapter, the term *cooperation*, which comes from game theory, does not refer to a social interaction, but rather to an environment-friendly behaviour. Similarly, *defection* refers to a less environment-friendly behaviour by which an agent discharges a higher amount of pollutants into the lake.

### 4.2.2 Socioeconomic subsystem

For the socioeconomic subsystem, the state variable is the fraction  $F$  of cooperators among the human population, between 0 and 1. For both the replicator formulation and the best-response formulation, we consider a common term  $\Delta U$ , which can be interpreted equivalently as the incentive to cooperate or as the cost of defection.  $\Delta U$  represents the positive or negative difference in utility between the two strategies: when it is positive, cooperation is of benefit to each individual agent and people collectively tend to become cooperators, whereas the incentive to defect is stronger when  $\Delta U$  is negative. As in Chapter 3, we consider three terms for this incentive:

$$\Delta U = \underbrace{-v}_{\text{economic baseline}} + \underbrace{\xi F}_{\text{social ostracism}} + \underbrace{\kappa P}_{\text{ecological concern}},$$

where:

- the baseline ( $-v$ ) is assumed to be negative, because it is economically easier for an agent to release high amounts of pollution;
- the agents' ecological concern is represented by a linear term in  $P$  with parameter  $\kappa$ : the more polluted the lake gets, the more people tend to cooperate in better managing the lake;
- social ostracism is represented by a linear term in  $F$  with parameter  $\xi$  accounting for the strength of their conformist tendency: the more cooperators there are, the more people tend to cooperate.

The formulation of the socioeconomic subsystem with the replicator dynamics in the RDM is (Hofbauer and Sigmund, 2003; Tavoni et al., 2012; Lade et al., 2013):

$$\frac{dF}{dt} = F(1 - F)\Delta U. \quad (4.1)$$

Derivations of this formulation (Hofbauer and Sigmund, 2003; Tavoni et al., 2012) rely on the idea that agents are fully rational and always choose the option which is the more advantageous for them.

On the other hand, the logit best-response dynamics in the BRM is (Suzuki and Iwasa, 2009a; Iwasa et al., 2010, and Chapter 3):

$$\frac{dF}{dt} = s \left( \frac{1}{1 + e^{-\beta \Delta U}} - F \right). \quad (4.2)$$

Parameter  $\beta$  represents the agents' rationality. When  $\beta$  is close to 0, agents ready to change their mind chooses almost randomly between the two strategies. When

$\beta$  is large, agents changing their mind tend to follow the more advantageous option according to the sign of  $\Delta U$ . When  $\beta \rightarrow +\infty$ , every agent changing their mind switches without error to the best option following the sign of  $\Delta U$ . In this best-response formulation, it has been shown (Chapter 3) that parameter  $s$ , representing the speed of the social dynamics (Suzuki and Iwasa, 2009b), had no influence on the existence or on the location of equilibria; therefore, we will restrict our analysis to the case where  $s = 1$ .

### 4.2.3 Fundamental difference

The replicator dynamics assumes that full defection ( $F = 0$ ) and full cooperation ( $F = 1$ ) are equilibria of the isolated socioeconomic subsystem, whereas the logit best-response assumes that full defection and full cooperation cannot be equilibria of the isolated socioeconomic subsystem. Thus, a fundamental difference between the two dynamics and between the two models is about the stationarity of pure strategies, *i.e.* cases where all agents adopt the same strategy.

Choosing the replicator dynamics means that we assume a strong conformism of each agent to the group, because the adoption of one strategy by the whole human population convinces each agent to keep with the same strategy. This fits the idea, already formulated by Aristotle and Ross (1973, 1.1253a), that humans are naturally social beings.

Choosing the logit best-response, on the contrary, means that we assume that at least some agents always diverge from the main opinion since a fraction of the human population always change their strategy. This can be compared to a non-zero mutation rate.

To sum up, the two models fundamentally disagree on the evolution a pure strategy, whether 100% of a behaviour makes the socioeconomic situation stationary or not.

## 4.3 Results

In this section, we compare the two versions of the model: the RDM and the BRM. We start by the consequence of the socioeconomic dynamics on the number of equilibria. Then, we explain how the replicator dynamics and the logit-best response dynamics are related in their nullcline structure. Finally, we describe the possibility, to observe sustained oscillations in the two models.

### 4.3.1 Location of stable equilibria

Here, we present analytical results on the location of stable equilibria. We briefly summarize previous results concerning the BRM before giving new results regarding the RDM. In particular, the RDM allows for an intuitive interpretation in terms of critical pollution thresholds for full cooperation or for full defection. This is the mathematical basis for all of our other results.

In the BRM, the location of equilibria has previously been described (Chapter 3): in the most complex case, the two nullclines each have the shape of an  $S$  and give nine equilibria arranged as a  $3 \times 3$  array in the  $(P, F)$  phase plane, with up to four stable equilibria, namely those on the corners.

The RDM has the same nullcline for the ecological system. However, the replicator equation (4.1) is more tractable in a mathematical analysis than the logit best-response equation (4.2) of the BRM. This allows for an easier analytical study of the location of stable equilibria and is key for our results. In particular, the  $F$ -nullclines in the RDM are:

- the trivial nullcline  $F = 0$  (full defection);
- the trivial nullcline  $F = 1$  (full cooperation);
- the non-trivial nullcline  $\Delta U = 0$  (no socioeconomic advantage of changing strategies), which is a straight line in the phase plane with equation  $F = (v - \kappa P)/\xi$ .

The analytical simplicity of the RDM allows for the definition of a subset  $\mathcal{Z}$  of the  $F$ -nullclines where all stable equilibria must be. Indeed, by studying the eigenvalues of the Jacobian matrix at any equilibrium  $(P^*, F^*)$ , we find (Appendix 4.B) that:

- no equilibrium with  $F^* = 0$  can be stable if  $P^* > P_D = \frac{v}{\kappa}$ ;
- no equilibrium with  $F^* = 1$  can be stable if  $P^* < P_C = \frac{v-\xi}{\kappa}$ .

That is, there are two critical pollution levels  $P_C$  and  $P_D$  with  $P_C < P_D$ . We can distinguish two cases. First, for pollution levels above the larger critical value  $P_D$ , no equilibrium with with full defection can be stable. Second, for pollution levels below the lower critical value  $P_C$ , no equilibrium with with full cooperation can be stable. On the one hand, there exists a critical pollution level  $P_D$  above which no equilibrium with full defection can be stable. This is because the high level of pollution would then force some agents into cooperating. On the other hand, there exists a critical pollution level  $P_C$  below which no equilibrium can be stable with full cooperation. This is because the low level of pollution would then allow some agents to defect.

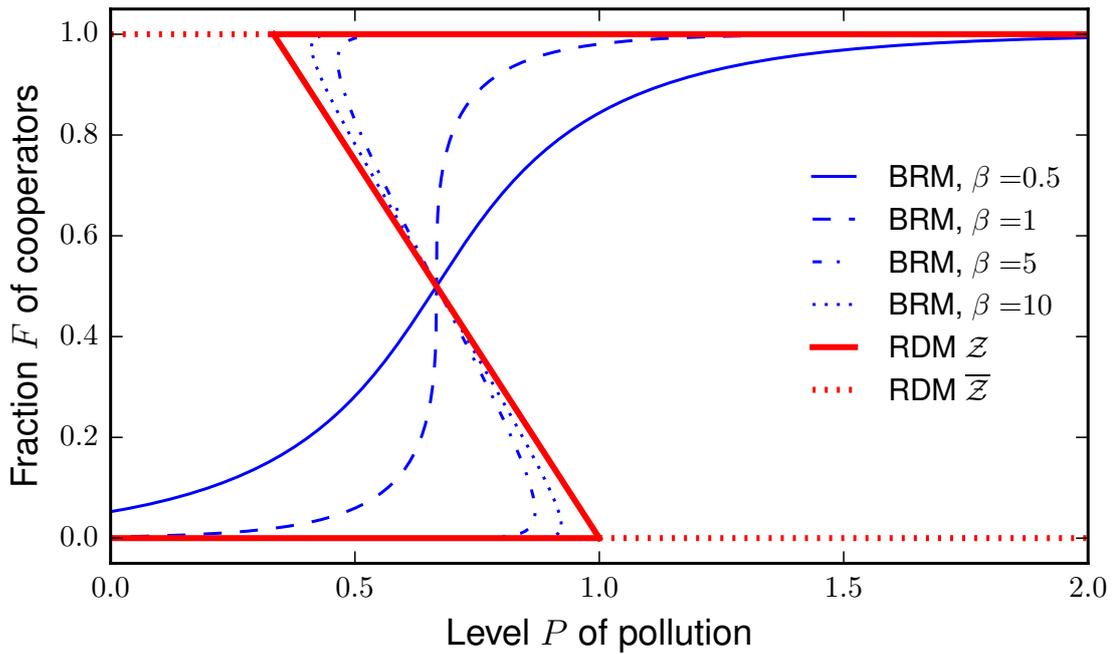


Figure 4.1:  $F$ -nullclines in the phase plane for the RDM (thick red lines) and for the BRM (thin blue curves) with increasing values for the agents' rationality  $\beta$ . The RDM  $F$ -nullclines include parts which must be unstable  $\overline{\mathcal{Z}}$  and a potentially stable set  $\mathcal{Z}$ . Parameter values:  $\alpha = 0.26$ ,  $r = 0.5$ ,  $q = 2$ ,  $m = 1$ ,  $p_D = 0.04$ ,  $\delta_p = 0.0388$ ,  $s = 0.1$ ,  $v = 5$ ,  $\kappa = 5$ ,  $\xi = 4$ .

Thus, all stable equilibria lie on the edgy sigmoid set  $\mathcal{Z}$  that takes the shape of a mirrored  $Z$  (Fig. 4.1, red solid line). The set  $\mathcal{Z}$  is defined by all points of coordinates  $(P, F)$  with  $P \geq 0$  satisfying at least one of the following criteria:

$$\left\{ \begin{array}{l} P \leq \frac{v}{\kappa} \\ F = 0 \end{array} \right. \text{ or } \left\{ \begin{array}{l} P \geq \frac{v-\xi}{\kappa} \\ F = 1 \end{array} \right. \text{ or } \left\{ \begin{array}{l} \Delta U = 0 \\ F \in ]0, 1[ \end{array} \right. .$$

### 4.3.2 The replicator dynamics as the limit of the best-response dynamics

In this section, we summarize a link between the two dynamics and thus between our two models. Proof and details can be found in Appendix 4.C.

In section 4.3.1, we have shown that all stable equilibria of the RDM must be on a certain subset  $\mathcal{Z}$  of the nullclines for the socioeconomic subsystem. This subset  $\mathcal{Z}$  comprises parts of the trivial nullclines as well as the full non-trivial nullcline. We find that this subset  $\mathcal{Z}$  is the limit of the  $F$ -nullcline of the BRM when  $\beta \rightarrow +\infty$ . This is illustrated in Fig. 4.1, where the  $F$ -nullcline of the BRM has an  $S$ -shape for many values of  $\beta$ . The larger the agents' rationality  $\beta$ , the edgier the BRM  $F$ -nullcline. Ultimately, for  $\beta \rightarrow +\infty$ , the BRM  $F$ -nullcline takes the form of the mirrored  $Z$ -shaped RDM  $F$ -nullcline.

Since  $\beta$  has an interpretation, this provides an intuitive link between the two dynamics and between the two models: when the human agents' rationality  $\beta$  increases in the BRM, all stable equilibria tend towards those defined by the replicator  $F$ -nullclines. In the general case, our proof (see Appendix 4.C) holds for all non-trivial values of  $F$ , i.e. strictly between 0 and 1.

To our knowledge, such a remarkable link between the replicator dynamics and the best response dynamics, although it has been formally studied in highly abstract terms (Hopkins, 1999; Hofbauer et al., 2009), has not been illustrated graphically or exposed in intuitive terms, and is not usually pointed out: in the case where exactly two strategies coexist, the best response dynamics tends towards the replicator dynamics when the rationality of the agents increases. This means that there is a smooth transition between the two dynamics and between the two models depending on the reliability of the agents' instantaneous choice for their more advantageous option between cooperation and defection at any time.

### 4.3.3 Number of equilibria

The two models are bidimensional social-ecological systems of lake pollution using the same ecological part. The socioeconomic part is the only difference, which has a direct impact on the number of equilibria that the coupled system can have.

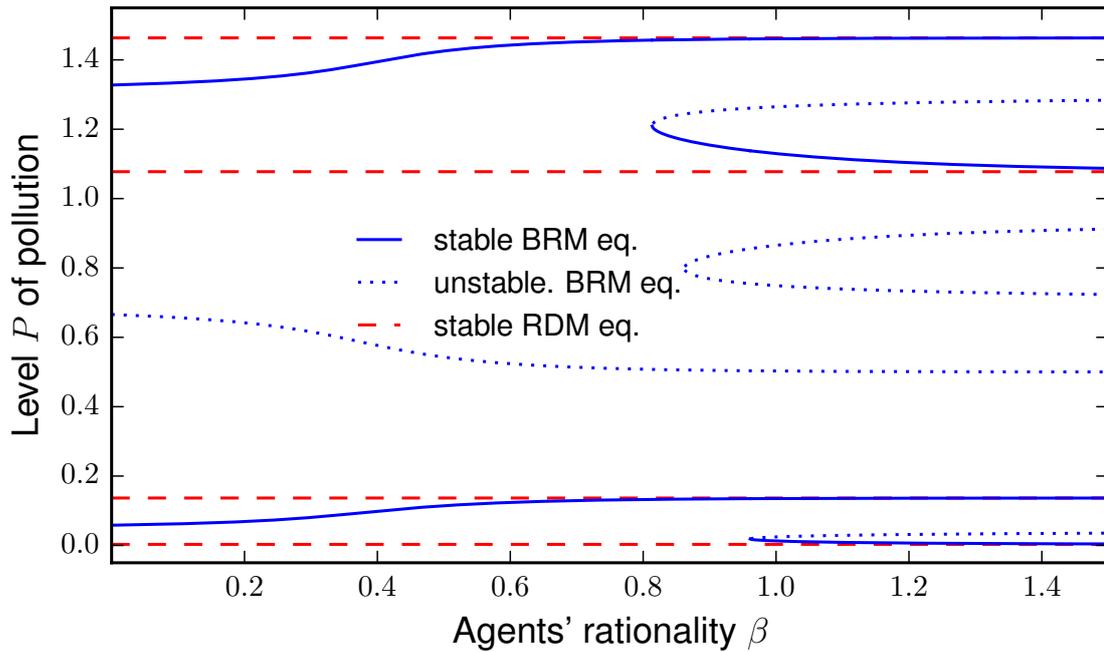


Figure 4.2: *Bifurcation diagram showing the level  $P$  of pollution of the RDM stable equilibria (dashed red) and in the BRM stable (solid blue) and unstable (dotted blue) equilibria for different levels of the agents' rationality  $\beta$ . For simplicity, unstable equilibria in the RDM are not depicted. Parameter values as in Fig. 4.1, except for  $\alpha = 0.4$ ,  $r = 0.8$ ,  $\kappa = 0.25$  and  $\xi = 8$ .*

The minimum number is one in the case of the best response dynamics (Chapter 3). It is two in the case of the replicator dynamics (Appendix 4.A). Our simulations show that the smallest number of stable equilibria in both cases is zero. In those particular situations, the two models give rise to sustained oscillations.

The maximum number of equilibria has been shown to be nine in the BRM (Chapter 3). In the most complex configuration of the RDM, the  $P$ -nullcline has got the shape of an  $S$  with roughly vertical branches in the  $(P, F)$ -phase plane, and the  $Z$ -shape of the  $F$ -nullcline consists of three roughly horizontal lines in the  $(P, F)$ -phase plane. As a consequence, the maximum number of equilibria in the phase plane is also nine with the replicator. In both the RDM and the BRM, the equilibria are organized as  $3 \times 3$  square in the phase plane, and our simulations suggest that up to four of them (those on the corners of the square) can be stable.

Since the agents' rationality  $\beta$  in the BRM relates to how close the model is to the RDM, we observe a convergence in the number of stable equilibria as  $\beta$  increases. Depending on the specific value for  $\beta$ , the number of stable equilibria can be very different between the two models. This is illustrated in Fig. 4.2.

#### 4.3.4 Cycles and make-or-break dynamics in the replicator dynamics model

Cycles have been described previously in the BRM (Chapter 3). In this section, we focus on the RDM, where we find qualitatively similar sustained oscillations.

Our simulations suggest that this happens when there is only one non-trivial equilibrium (with  $F$  in  $]0, 1[$ ) as in Fig. 4.3, and when this equilibrium loses its stability through a Hopf bifurcation. This is similar to previous reports by Suzuki and Iwasa (2009a) and in Chapter 3 for the BRM. In the RDM, the phase plane then includes two trivial equilibria which happen to be out of the potentially stable subset  $\mathcal{Z}$  in addition to the non-trivial equilibrium.

The oscillations can be explained in a similar way as those observed in the BRM (Chapter 3):

- with little cooperation, the level of pollution increases;
- higher levels of pollution let the cooperating strategy spread among the agents;
- the increase in cooperation ends up decreasing the level of pollution;
- lower levels of pollution favour the spread of defection.

In the following, we will investigate two aspects of the oscillations in some more detail. The first aspect is that the limit cycle in the RDM can be very large (Fig. 4.3). The second aspect is that, in the BRM, oscillations occur only when the agents' rationality  $\beta$  is sufficiently large.

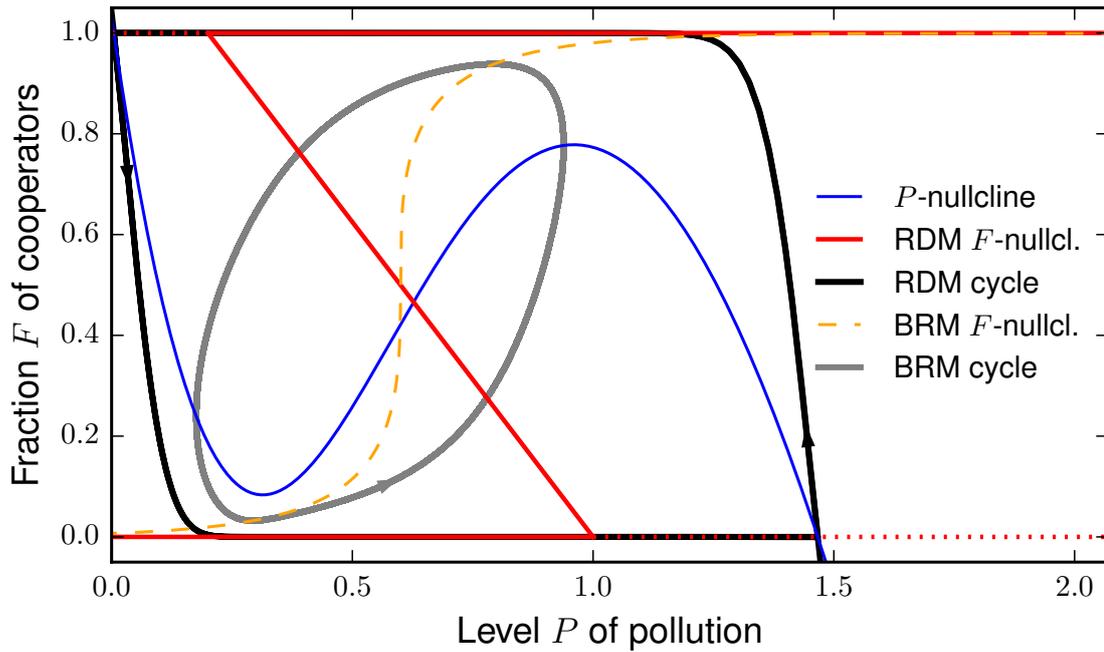


Figure 4.3: *Example of a large limit cycle in the phase plane (black) in the RDM. The straight red lines indicate the  $F$ -nullclines in the RDM. For comparison, the  $F$ -nullcline of the BRM is shown as a dashed orange line and the corresponding limit cycle is in grey. The solid blue  $P$ -nullcline is common to both models. Parameter values as in Fig. 4.1, except for  $\beta = 1$ .*

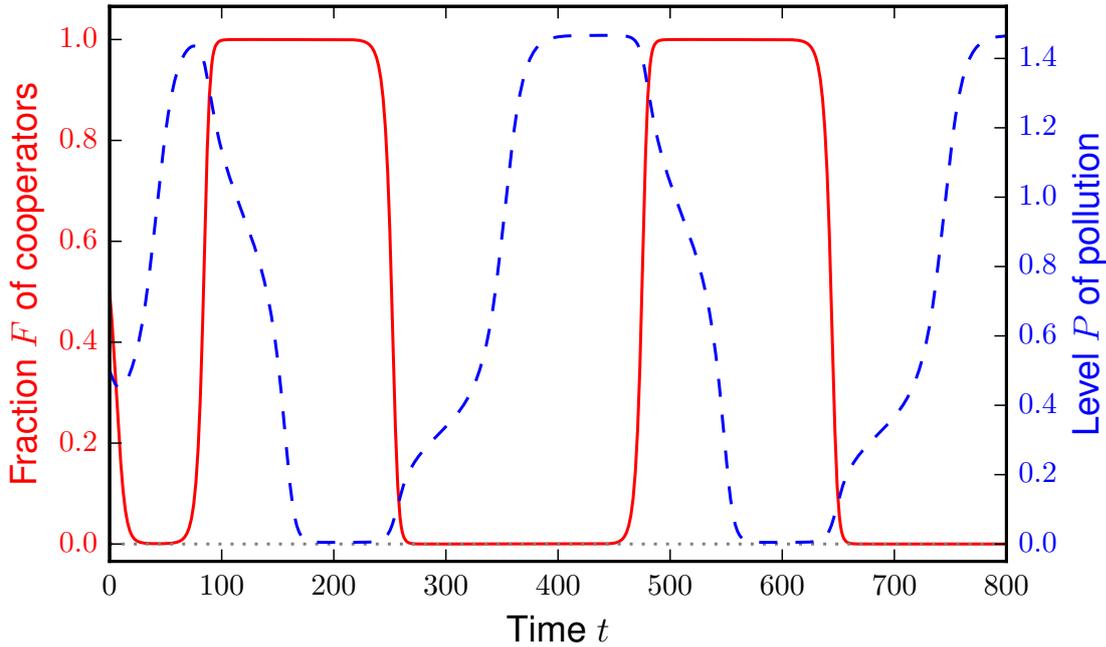


Figure 4.4: *Time plot of a large limit cycle in the RDM showing the fraction  $F$  of cooperators (solid red) and the level  $P$  of cooperation (dashed blue). Parameter values as in Fig. 4.1, except for  $\beta = 1$  and  $\xi = 3$ . Initial condition:  $(P = 0.5, F = 0.5)$ .*

### Large limit cycle

The limit cycle of the RDM shown in Fig. 4.3 is very large in the sense that its trajectory stretches out almost the entire range of possible values between  $F = 0$  and  $F = 1$ . The limit cycle almost looks like a heteroclinic cycle between the two unstable trivial equilibria with  $F^* = 0$  and  $F^* = 1$ . However, our computations suggest that the stable manifold of one of those two unstable equilibria does not meet the other unstable equilibrium.

Thus, the system periodically gets very close to full cooperation or to full defection. While cycling, the system may additionally remain for long periods of time in such a state, where the probability is high that a random perturbation may make the system actually enter full cooperation or full defection. This is illustrated in Fig. 4.4: as a consequence of both the large limit cycle and the long time spent near  $F = 0$  or  $F = 1$ , a random perturbation is more likely to make the system shift to the adoption of a single strategy by the whole population. As the socioeconomic subsystem becomes stable when being in a single strategy state ( $F = 0$  or  $F = 1$ ), the system would remain at this equilibrium unless another perturbation reintroduces the alternative

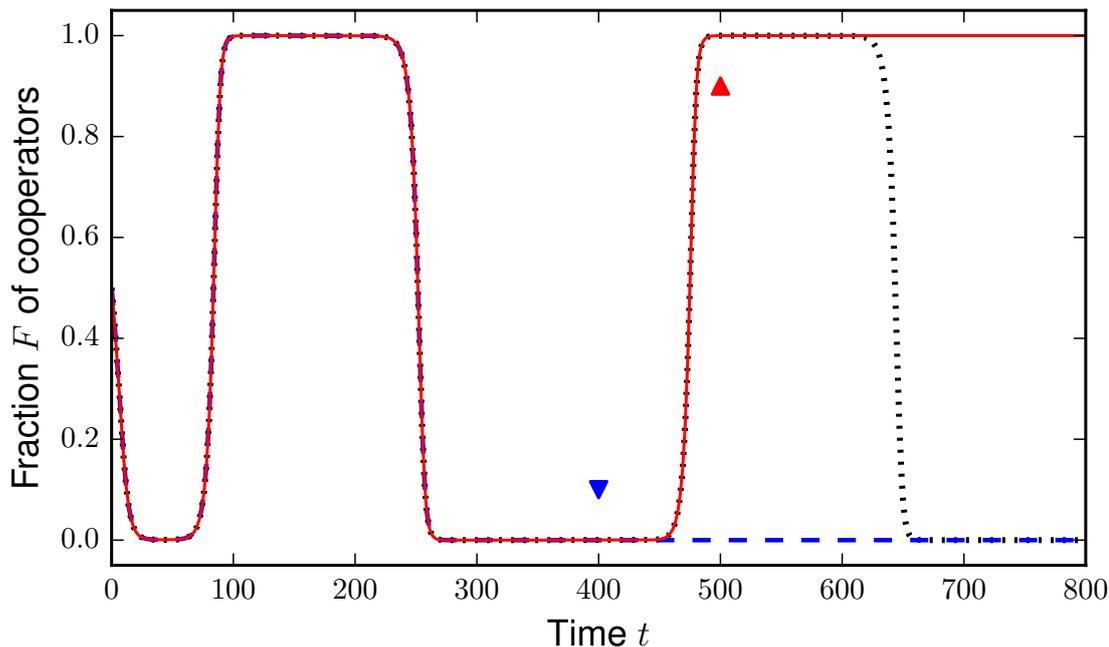


Figure 4.5: *Time plot of the RDM fraction  $F$  of cooperators from the same initial condition but perturbed (triangles) at different times on the large limit cycle, showing the scenario without perturbation (dotted black), a scenario with a perturbation at  $t = 400$  (dashed blue) and a scenario with a perturbation at  $t = 500$  (solid red). Parameter values as in Fig. 4.4.*

strategy among the agents. This trivial equilibrium may be a desirable one (low pollution, full cooperation) or an undesirable one (high pollution, full defection).

A perturbation close to full defection could trigger a complete adoption of the defecting strategy and prevent any switch to a less polluted ecological state. On the contrary, a perturbation near full cooperation could prevent the loss of the cooperating behaviour among the population and keep the pollution level low. This suggests that the specific part of the cycle where a perturbation occurs may dramatically change the final outcome of the transient behaviour. This is shown in Fig. 4.5. To express this idea, we suggest to talk about a make-or-break dynamics, characterized by dramatic success or failure outcomes with no intermediate option in between (Analytis et al., 2019). By make-or-break dynamics, we mean that the same deterministic system can undergo a dramatically desirable (“make”) or dramatically undesirable (“break”) shift towards either full cooperation or full defection based solely on the part of the cycle where a perturbation happens.

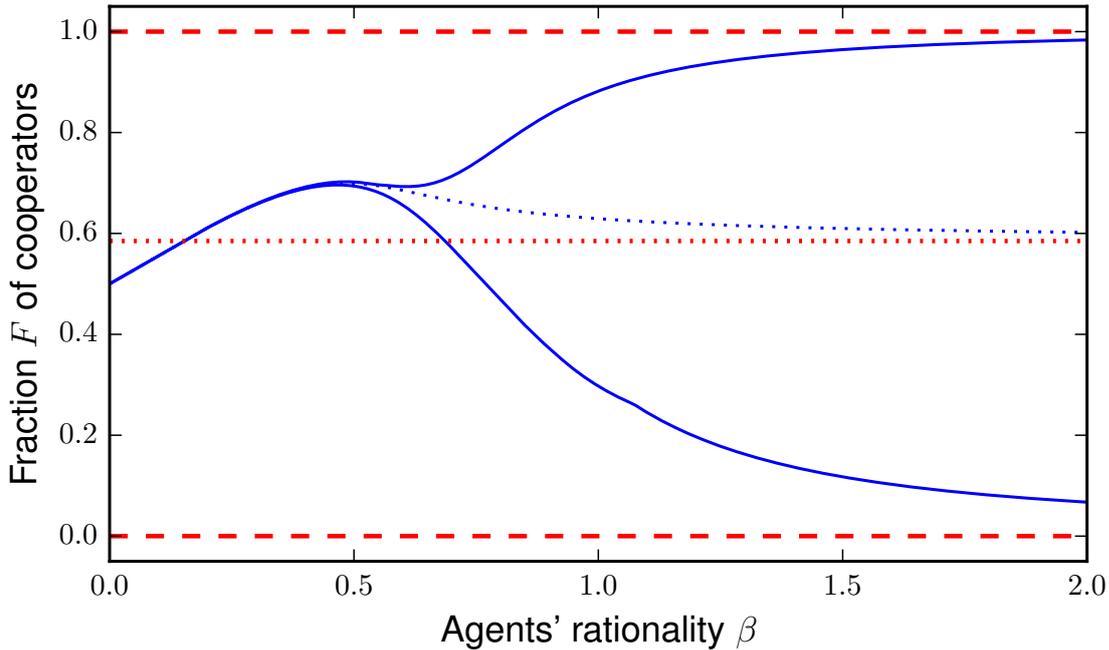


Figure 4.6: *Bifurcation diagram showing the extrema of the fraction  $F$  of cooperators in the asymptotic regime for different levels of the agents' rationality  $\beta$  in the BRM, showing The maximum and the minimum for  $F$  of the BRM cycle (solid blue). The chosen configuration always displays a unique equilibrium in the BRM (dotted blue) and a single non-trivial equilibrium in the RDM (dotted red). The curves overlap when the equilibrium is asymptotically stable. The limit cycle of the RDM corresponds to the case where  $\beta \rightarrow \infty$ . Other parameter values as in Fig. 4.1, except for  $\alpha = 0.3$  and  $p_D = 0.0072$ .*

### Oscillations in the best-response dynamics model are associated with large rationality

Previous results in the BRM (Chapter 3) show that the agents' rationality  $\beta$  needs to be sufficiently large to allow for a hysteresis and oscillations to occur. Because of the link we have described between the two socioeconomic dynamics, this means that cycles may appear in the BRM only if it is close enough to the replicator dynamics. This is shown in Fig. 4.6, where limit cycles in the BRM appear only for sufficiently large values of the rationality parameter  $\beta$ .

However, two distinct factors play a role in the occurrence of oscillations. The first one, reported here, is the agents' rationality. The second factor, reported in Chapter 3, is the location of the equilibrium on each nullcline. Indeed, simulations

showed that equilibria tended to be unstable on the middle part of the  $S$ -shaped nullclines but stable on the outer branches. For instance, in the left part of Fig. 4.6, there are no oscillations: the rationality  $\beta$  is low and the unique equilibrium happens to fall on an outer branch of the  $S$ -shaped nullcline for the lake subsystem. The two factors cannot be disentangled because configurations in which their separate impact could be assessed involve saddle-node bifurcations where new attractors emerge.

## 4.4 Discussion and conclusions

Our results suggest that conclusions drawn from the study of social-ecological systems may depend on the specific formulation of the socioeconomic subsystem. For example, Fig. 4.2 shows that the RDM and the BRM may suggest a different number of stable equilibria. Fig. 4.3 shows that cycles can have a different aspect in the two models, with the RDM suggesting a make-or-break dynamics that is absent from the BRM. This relies in the first place on the assumption that both models agree that there are oscillations, which is not always the case, as Fig 4.6 shows.

All differences between the RDM and the BRM are consequences of the fundamental difference we have described in Section 4.2.3: the former assumes that extreme strategies (here, full defection or full cooperation) are stationary, the latter assumes that extreme strategies are not stationary. Therefore, the replicator dynamics should be used when having evidence of strong social conformism, where agents tend to follow mass movements. Examples may include social learning or any kind of social behaviour. On the contrary, the logit best-response dynamics with a low rationality for agents should be used if there is evidence that group behaviours cannot impair individual innovation from the agents, which tend to act independently. Examples include biological mutations and similar systems where variation happens on a constant random basis.

The advantage of the logit best-response dynamics, though, is that the parameter representing the agents' rationality allows for the investigation of different levels. These various levels of rationality correspond to various distances from the replicator dynamics. The higher the rationality, the closer we are from the replicator dynamics, the more we assume that individual agents are influenced by group behaviours. The lower the rationality, the farther we are from the replicator dynamics, the more we assume that individual agents act independently. This is an interpretation we can give to the mathematical link described by Hopkins (1999) and Hofbauer et al. (2009) about the relationship between the two dynamics.

In the case where no formulation of the socioeconomic subsystem is better supported by some empirical data or theoretical, mechanistic account, it would be ideal to check which conclusions hold for several formulations. This corresponds to our case, since no evidence tells us either that polluting agents tend to follow the ma-

jority blindly, nor that they constantly and independently innovate towards other levels of pollutant discharge. It is difficult to anticipate which of our conclusions hold for different socioeconomic systems and which depend on the particular system we assume if we do not check different formulations. Thus, uncertainty about the way the socioeconomic subsystem behaves potential threatens to the robustness of results involving the study of such a socioeconomic system. Therefore, if comparing different socioeconomic dynamics is not possible or too cumbersome, we should keep in mind that the often implicit assumptions on the behaviour of the socioeconomic system might be a weak point for any of the observed result.

## 4.A Existence of at least two equilibria in the replicator dynamics model

This section proves the following proposition: in the phase plane  $(P, F) \in \mathbb{R}^+ \times [0, 1]$ , the RDM has at least two equilibria  $(P^*, F^*)$ .

Consider the  $F$ -nullclines. They obviously consist of at least two horizontal lines with the equations  $F = 0$  and  $F = 1$ . Thus, it is sufficient for the  $P$ -nullcline to include one point satisfying  $F = 0$  and one point satisfying  $F = 1$  in  $\mathbb{R}^+ \times [0, 1]$  for those points to be equilibria.

Now, consider the  $P$ -nullcline. If  $\delta_p = 0$ , then it consists of at least one vertical line in  $\mathbb{R}^+ \times [0, 1]$  and the proof is trivial. If  $\delta_p \neq 0$ , then it represents  $F$  as a continuous function of  $P$  on  $\mathbb{R}^+$  (because  $m > 0$  and  $q \geq 2$ ), given by

$$F_{P-null}(P) = \frac{1}{\delta_p} \left( p_D - \alpha P + \frac{rP^q}{m^q + P^q} \right).$$

Notice that  $F_{P-null}(0) \geq 1$  since  $p_D \geq \delta_p$  and that

$$\lim_{P \rightarrow \infty} F_{P-null}(P) = -\infty.$$

The intermediate value theorem then tells us that  $F_{P-null}$  must take the values 1 and 0 for  $P$  in  $\mathbb{R}^+$ .

In the phase plane, all points  $(P, F)$  satisfying  $F = 0$  or  $F = 1$  belong to the  $F$ -nullcline. The  $P$ -nullcline has got at least one point satisfying  $F = 0$  and one point satisfying  $F = 1$ . As a consequence, the system has at least two equilibria in the phase plane.

## 4.B Jacobian matrix in the replicator dynamics model

In the RDM, the Jacobian matrix of the system at any point  $(P, F)$  in  $\mathbb{R}^+ \times [0, 1]$  is

$$\begin{pmatrix} \frac{rqm^q P^{q-1}}{(m^q + P^q)^2} - \alpha & -\delta_p \\ \kappa F(1 - F)P & -3\xi F^2 + 2(v - \kappa P + \xi)F + \kappa P - v \end{pmatrix}.$$

In particular, if  $F = 0$  or if  $F = 1$ , we have simple expressions for one of the eigenvalues  $\lambda_F$  of the Jacobian matrix evaluated at this point:

$$\lambda_F = \kappa P - v \quad \text{for } F = 0 \quad \text{and} \quad \lambda_F = v - \kappa P - \xi \quad \text{for } F = 1.$$

## 4.C The replicator dynamics gives the limit of the logit best-response dynamics

Here we show that, when  $\kappa \neq 0$ , the RDM  $F$ -nullclines include the limit of the BRM  $F$ -nullcline when  $\beta$  tends to infinity. As that statement is obviously false in the specific case where  $\kappa = 0$ , we assume that  $\kappa \neq 0$ .

First, consider the RDM. The subset  $\mathcal{Z}$  of the  $F$ -nullclines we define in the main text is restricted to values for  $P$  in  $\mathbb{R}^+$ . Let us consider an extended set  $\mathcal{Z}'$  defined as  $\mathcal{Z}$  but for  $P \in \mathbb{R}$ . It is the union of the three following sets:

$$\begin{aligned} \mathcal{Z}'_0 &= \{(P, 0), P \leq v/\kappa\}, \\ \mathcal{Z}'_1 &= \{(P, 1), P \geq (v - \xi)/\kappa\}, \\ \mathcal{Z}'_{]0,1[} &= \{(P, F) \in \mathbb{R} \times ]0, 1[ : \Delta U = 0\}. \end{aligned}$$

Now consider the BRM and let  $\mathcal{S}_\beta$  be the extended  $F$ -nullcline over all real values for  $P$  with a particular value for the rationality parameter  $\beta$  in  $]0, +\infty[$ . It represents  $P$  as a function  $\sigma$  of  $F$ :

$$\mathcal{S}_\beta = \{(P, F) \in \mathbb{R} \times [0, 1] : P = \sigma_\beta(F)\}.$$

We show that for all values of  $\beta$ :

- (i)  $\sigma_\beta$  is actually defined on  $]0, 1[$  and continuous;
- (ii) the limit of  $\sigma_\beta$  at the endpoints of its domain of definition ensures that  $\mathcal{Z}'_0$  and  $\mathcal{Z}'_1$  are the asymptotic sets for  $\mathcal{S}_\beta$  when  $\beta$  tends towards infinity;
- (iii) on  $]0, 1[$ ,  $\mathcal{Z}'_{]0,1[}$  is the limit of  $\mathcal{S}_\beta$  when  $\beta$  tends towards infinity.

The equation of the BRM  $F$ -nullcline is (Chapter 3)

$$0 = \frac{1}{1 + e^{-\beta\Delta U}} - F.$$

It is possible to reformulate it for all values of  $\beta$  to consider that the  $F$ -nullcline represents either  $P$  or equivalently  $\Delta U$  as a function of  $F$  on  $]0, 1[$

$$P_{BRM,\beta} = \sigma_\beta(F) = \frac{1}{\kappa} \left[ \frac{1}{\beta} \ln \left( \frac{1-F}{F} \right) + v - \xi F \right] \quad (4.3)$$

$$\Leftrightarrow \Delta U_{BRM,\beta} = \frac{1}{\beta} \ln \left( \frac{1-F}{F} \right) \quad (4.4)$$

From equation (4.3) it is clear (i) that  $\sigma_\beta$  is actually defined on  $]0, 1[$  and continuous for all values of  $\beta$ .

Moreover, it makes it obvious (ii) that for all values of  $\beta$

$$\lim_{F \rightarrow 0} P_{BRM,\beta} = \lim_{F \rightarrow 0} \sigma_\beta(F) = -\infty \quad \text{and} \quad \lim_{F \rightarrow 1} P_{BRM,\beta} = \lim_{F \rightarrow 1} \sigma_\beta(F) = +\infty.$$

Equation (4.4) finally shows (iii) that

$$\lim_{\beta \rightarrow +\infty} \mathcal{S}_\beta = \mathcal{Z}'_{]0,1[}.$$

To conclude,  $\mathcal{S}_\beta$  tends asymptotically towards  $\mathcal{Z}'$  when  $\beta$  increases, and, as a consequence, the same can be said about their respective restriction to  $P \in \mathbb{R}^+$ : when  $\kappa \neq 0$ , the subset  $\mathcal{Z}$  of the RDM  $F$ -nullclines is the limit of the BRM  $F$ -nullcline when  $\beta$  tends towards infinity.

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# 5 Behavioural models from evolutionary game theory for social-ecological systems – an overview

## Abstract

Many mathematical models of social-ecological systems base their socioeconomic component on either the replicator dynamics or the logit formulation of the best-response dynamics. Here, we provide an overview of the two dynamics, which both come from evolutionary game theory. The replicator dynamics can be derived with an interpretation in terms of game reward, of economic income or in biological fitness. It can also be derived from the game theoretical concept of imitation. The replicator dynamics plays a central role among evolutionary game dynamics and is well-known. The best-response dynamics is defined formally in game theory but is often approximated by the smooth logit best-response dynamics. This latter formulation has psychophysical foundations and was adopted secondarily in game theory and econometry. The logit best-response dynamics's use for social-ecological systems is relatively recent. Its derivation rely on a probabilistic interpretation where the agents' decision is not deterministic. For modellers, each of the two dynamics rely on key assumptions. Both the replicator dynamics and the logit best-response dynamics assume a total ordering between any agent's choices. The replicator dynamics depends on the average choice among agents. The replicator dynamics assumes that agents exhibit conformism, so that all agents giving up on a strategy is definitive. The logit best-response dynamics assumes that the population of agents is large and that agents exhibit an innovating behaviour. The logit best-response dynamics describes experimental data better than the replicator dynamics. It assumes that agents have imperfect rationality, which is modelled by the stochasticity of their decisions. The logit best-response dynamics tends towards the replicator dynamics when the agents' rationality increases to infinity. In this sense, the replicator dynamics is a particular case of a generalized best-response.

## 5.1 Introduction

A number of recent articles have proposed social-ecological models, which couple an ecological system with a socioeconomic system. Social-ecological models have been applied to as diverse ecological contexts as fisheries and other harvested, biological populations (Fryxell et al., 2010; Lee and Iwasa, 2014; Bieg et al., 2017), lakes (Iwasa et al., 2007; Suzuki and Iwasa, 2009a; Iwasa et al., 2010), grasslands (Lee et al., 2015a), farmlands (Figueiredo and Pereira, 2011), forests (Satake and Iwasa, 2006; Satake et al., 2007a,b; Henderson et al., 2013; Lee et al., 2015b), groundwater (Ibáñez et al., 2004; Tavoni et al., 2012; Lade et al., 2013) and in the more general contexts of a theoretical common pool resource (Noailly et al., 2003; Iwasa and Lee, 2013; Sugiarto et al., 2015, 2017). The socioeconomic model accounts for some human behaviour influencing the environment and usually draws on evolutionary game theory. Indeed, game theory provides a unified framework to account for strategic decisions made by the agents considering their interest and evolutionary game theory similarly provides formal derivations to account for the dynamics of such decisions at a population level.

The discipline of game theory relies on the assumption that individuals make decisions depending exclusively on an abstract situation –the game–, where quantifiable payoffs and expected rewards determine all of the players’ strategic choices. In this context, an agent is an abstract unit of the playing population who makes decisions as a player in the game. Those decisions are driven by the configuration of the game, which is expressed in a quantified manner by payoffs. The unit of the measurable desirability of a specific option for an agent corresponds to the concept of *utility*, an abstract measure of “goodness”. The framework of game theory allows for natural applications in economics of computer science (*e.g.* Shoham, 2008). But because of the abstract nature of this framework, game theory and evolutionary game theory have been applied to broader, various contexts in economics (Friedman, 1986, 1998) and environmental economics (de Zeeuw, 2018), epidemiology and public health (Bauch and Earn, 2004; Bauch and Bhattacharyya, 2012; Bauch et al., 2013; Wang et al., 2015), or evolutionary biology (Taylor and Jonker, 1978; Maynard Smith, 1982; Hammerstein and Selten, 1994). Similarly, these frameworks allow for investigating the dynamics of intertwined environmental problems and social effects (Hauge et al., 2018). In the social-ecological field, other mathematical approaches tend to be more tailored to a specific socioeconomic and ecological context. They rely on agent-based modelling (Grimm et al., 2006), on more complex game theoretical methods or optimal control (Mäler et al., 2003; Ibáñez et al., 2004; Kossioris et al., 2008), or on statistical physics and/or network models (Hutchinson and Waser, 2007; Fryxell et al., 2010; Wang et al., 2015; Bieg et al., 2017).

Many mathematical models of a social-ecological system thus represent the socioeconomic part with an evolutionary game theoretic approach. But evolutionary game

theory proposes several formulations. The most widely used are the replicator dynamics, related to imitation dynamics, and the logit best-response dynamics. However, many researchers interested in the empirical interpretation of social-ecological dynamics may not be familiar with the origin of these formulations and with their implications. This is because (non-evolutionary) game theory imposes a steep learning curve with many specialized concepts and a rich vocabulary for little empirical reward. Abstract formal tools developed by game theory or evolutionary game theory often cannot be applied as such to the study of social-ecological systems, where concepts such as a formalized game and an explicit payoff matrix, or even a Nash equilibrium can be difficult to know empirically. Similarly, attempts to implement a predefined game as an experiment (Cason et al., 2013; Hoffman et al., 2015) often lead to inconclusive results regarding specific mathematical formulations. Indeed, experiments on humans' behaviour do not allow for quantification over large populations during a long time since they typically involve a few dozen students playing a simple game over ten rounds in a few hours (*e.g.* Dannenberg et al., 2015). Theoretical overviews of the main dynamics used to model socioeconomic systems such as Hofbauer and Sigmund (1998), Alós-Ferrer and Netzer (2010), Cressman and Tao (2014) or Castro (2017) may be inaccessible to a part of the scientific community.

This may be a reason why social-ecological articles often give little justification as to the reason why they use either the replicator dynamics or the best-response dynamics (Chapter 4). As the field is growing, it is of paramount importance to raise the awareness of the concepts and of the assumptions underlying these dynamics. Indeed, the replicator dynamics or the best-response dynamics are contradictory regarding the stationarity of extreme cases in which all agents adopt the same behaviour, which can dramatically impact the outcomes of the model (Chapter 4). Therefore, this review aims at providing a non-game-theory-focused introduction into evolutionary game theoretical formulations of the socioeconomic system in mathematical, social-ecological models. We focus on continuous time formulations and do not consider space nor networks.

This review is organized in three main parts. The first part gives an overview of the replicator dynamics. Since the replicator dynamics play a central role in game theory and is well-known, this part is relatively short. The second part focuses on the best-response dynamics and also presents its non-game-theoretical origins. The third part discusses the links and the differences between the two as well as the reasons why to use one or the other.

## 5.2 Replicator and imitation dynamics

Here, we focus on the replicator dynamics. We start by formulating it mathematically and by explaining its derivation as well as its link with imitation dynamics. We

then describe important properties regarding the binary case, where two strategies are considered, and we discuss an alternative derivation of the replicator dynamics in the binary case.

### 5.2.1 Derivation

The replicator dynamics emerges in the general case in evolutionary game theory when considering agents replicating, *i.e.* reproducing asexually while retaining the same strategy, over many generations (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998; Morsky et al., 2016). Considering a strategy  $i$  from the set  $S$  of all strategies, the replicator dynamics can be described by (Hofbauer and Sigmund, 1998; Morsky et al., 2016):

$$\frac{df_i}{dt} = f_i \left( u_i - \sum_{j \in S} f_j u_j \right), \quad (5.1)$$

where  $f_i$  is the frequency of agents with strategy  $i$  in the population and where  $u_i$  is a certain measure of “goodness” for an individual agent adopting strategy  $i$ .

Variations in the mathematical formulation of the replicator dynamics come from the various ways the term  $u_i$  is interpreted. We observe three broad interpretations. First, in game theory, the tendency is to derive the measure of goodness  $u_i$  from the payoff gained when playing strategy  $i$  within the game considered (Hofbauer and Sigmund, 1998; Morsky et al., 2016). Second, in economics, the fitness is taken to be an amount of concrete (money) or more abstract (utility, satisfaction, happiness) wealth agents are assumed to strive for (*e.g.* Tavoni et al., 2012). Third, the interpretation of  $u_i$  as a fitness comes from biological and evolutionary fields and represents a measure of the capacity to survive over several generations (Maynard Smith, 1972).

The Darwinian interpretation of  $u_i$  provides a straightforward derivation of equation (5.1) focusing on the idea of the *evolutionary success* of a particular strategy  $i$  (Hofbauer and Sigmund, 1998, chap. 7). On the one hand, evolutionary success can be defined as the difference between the corresponding fitness and the average fitness in the population. On the other hand, evolutionary success can be taken to be the rate at which strategy  $i$  is collectively adopted by agents, *i.e.* the relative speed at which strategy  $i$  spreads in the population. Equation (5.1) is obtained when equating the two formulations:

$$\text{evolutionary success of } i = \underbrace{\frac{1}{f_i} \frac{df_i}{dt}}_{\text{rate of adoption of strategy } i} = \underbrace{u_i}_{\text{fitness of agents adopting strategy } i} - \underbrace{\sum_{j \in S} f_j u_j}_{\text{average fitness}}. \quad (5.2)$$

The replicator equation can also be interpreted as describing selection in a population of imitators. Imitators are agents playing a game and changing their strategy after each round, to strategies which have given a better payoff (Morsky et al., 2016). Imagining a game between imitators gives rise to an imitation dynamics. The mathematically formalized study of imitation dynamics shows that imitation dynamics are a more general case of the replicator dynamics (Hofbauer and Sigmund, 1998, ch. 8). This is why the term *imitation dynamics* is sometimes assimilated with the formulation of the replicator dynamics (Bauch, 2005; Bauch et al., 2013). To our knowledge, non-replicator imitation dynamics have not been used in social-ecological models.

### 5.2.2 Properties

In the replicator dynamics, Nash equilibria are always fixed points (Morsky et al., 2016). In particular, evolutionarily stable states (ESSs) are always asymptotically stable fixed points (Weibull, 1995; Hofbauer and Sigmund, 1998; Morsky et al., 2016). From equation (5.1), it is obvious that if we have  $f_i = 0$  for a strategy  $i$ , then the dynamics of this strategy becomes stationary. This means that, if the population of agents gives up on a strategy, this is definitive. As a consequence, the adoption by all agents of one strategy is also a stationary state because this is equivalent to the rejection of all other strategies. This can be interpreted as a form of social conformism (Chapter 4).

In the case where only two strategies are considered, it is easy to show that the replicator equation (5.1) simplifies to:

$$\frac{df_i}{dt} = f_i f_j (u_i - u_j) = f_i (1 - f_i) \Delta u, \quad (5.3)$$

where the dynamics relies mainly on the theoretical difference in fitness  $\Delta u$  between the two strategies. In particular, it is sufficient to assume a functional form for  $\Delta u$  to describe the dynamics of the collective strategic choice among agents, without assuming a specific utility function  $u$ .  $\Delta u$  represents the additional reward an agent expects to obtain for choosing strategy  $i$  over strategy  $j$ , *i.e.* it is the incentive, the motivation to choose  $i$  over  $j$ . It has also been referred to as a *differential utility* (Lee and Iwasa, 2014).

Garfinkel et al. (2017, pp. 126–127) derive equation (5.3) in a very intuitive, purely mathematical way. They consider on the one hand the number  $n_i$  of agents adopting a strategy  $i$  and its “reproductive rate”  $r_i$ :

$$\frac{dn_i}{dt} = r_i n_i, \quad (5.4)$$

and on the other hand their frequency  $f_i$ , which represents the adoption of strategy  $i$  among all agents:

$$f_i = \frac{n_i}{\sum_{j \in S} n_j}. \quad (5.5)$$

From equations (5.4) and (5.5), it is not difficult to prove the following:

$$\frac{df_i}{dt} = f_i \left( r_i - \sum_{j \in S} f_j r_j \right). \quad (5.6)$$

Garfinkel et al. (2017) derive equation (5.6) in the case of two strategies. It is then equivalent to:

$$\frac{df_i}{dt} = f_i f_j (r_i - r_j). \quad (5.7)$$

Obviously, equation (5.7) is equivalent to equation (5.3) in the case of two strategies and equation (5.6) is equivalent to equation (5.1) in the general case, if we assimilate the fitness  $u_i$  to the reproductive rate  $r_i$  as in Page and Nowak (2002). However, the key difference is that the reproductive rate  $r_i$  is not the fitness  $u_i$  but rather the evolutionary success of equation (5.2). And Garfinkel et al. (2017) do indeed define  $r_i$  as a function of the different payoffs  $u_i$  in a specific game.

### 5.2.3 Use in social-ecological modelling and underlying assumptions

The replicator dynamics is central in game theory in general as a standard evolutionary game dynamics (Hofbauer and Sigmund, 1998; Page and Nowak, 2002; Benndorf and Martínez-Martínez, 2017). But in social-ecological models, it enjoys a less dominant place since examples with the best-response dynamics are also very present. Without surprise, it has been used by authors from the fields of game theory or of economics.

For instance, Lee et al. (2015b) applied the replicator dynamics to forestry, building on previous work with the best-response dynamics (Satake and Iwasa, 2006; Satake et al., 2007a,b). They considered agents with the two strategies of being honest or being corrupt and concluded that increased education of enforcers, interpreted as more frequent questioning of the agents' honesty, would be effective in combating corruption.

Another example is that of Tavoni et al. (2012), who were interested in a common-pool resource with the dynamics of a stock of water. They use the replicator dynamics to show that sustainability of the common pool resource is promoted by peer pressure and social effects (social stigma, ostracism, reputation).

Social-ecological scientists should keep in mind that the best-response dynamics entails certain assumptions. These assumptions include the following:

1. strategies are totally ordered by their resulting payoffs (utility);
2. the dynamics depends on the average strategy among agents;
3. the Darwinian interpretation of equation (5.2) does not allow for the rejection of a strategy by all agents ( $f_i = 0$ );
4. all agents giving up on a strategy is definitive (conformism).

## 5.3 Best-response dynamics

Here, we focus on the logit best-response dynamics, which is the most widely used formulation of the best-response dynamics. We start by formulating the general best-response. Importantly, the logit formulation has origins outside of game dynamics, therefore, we proceed with a history of its foundations. We then describe important properties regarding the binary case, where two strategies are considered, and we discuss an alternative derivation. Finally, we cover its use in social-ecological modelling.

### 5.3.1 General formulation in game theory

The concept of a best reply (Hofbauer and Sigmund, 1998) or best response (Muñoz Garcia and Toro González, 2016) emerges in game theory in the case where we consider a focal player taking part in a specific game. Given the average strategy profile  $\bar{i}$  played by the other players, the set of best responses are the strategies  $b(\bar{i})$  maximizing the payoff of the focal player (Hofbauer and Sigmund, 1998; Muñoz Garcia and Toro González, 2016). This definition is usually used to introduce the concept of *Nash equilibrium*. Indeed, a Nash equilibrium is a configuration of strategies adopted by players, where no player has any interest in changing their strategy, *i.e.* where all players are already playing a best reply to the other players (Nash, 1950a,b).

However, in the framework of evolutionary game theory, we consider successive rounds of the same game being played repeatedly. The agents are assumed to behave like myopic best repliers, which means that they have bounded rationality: every time, they change their strategy to the best response considering exclusively the current configuration of strategies being adopted and ignoring other past and future configurations (Hofbauer and Sigmund, 1998; Alós-Ferrer and Netzer, 2010). Assuming that each player tends to maximize their payoff, the concept of best reply

leads to a dynamics at the population level, which is the best-response dynamics. Its formal definition was introduced (Hofbauer et al., 2009) in game theory by Gilboa and Matsui (1991).

The best-response dynamics primarily describes the change in the average strategy as being the difference between the best reply to the average strategy and the average strategy itself

$$\frac{d\bar{i}}{dt} = b(\bar{i}) - \bar{i}, \quad (5.8)$$

provided that  $b$  is a function defining a unique best reply, which is usually not difficult (Hofbauer and Sigmund, 2003). Equation (5.8) can also be derived, as in Hofbauer and Sigmund (1998), using the method of *fictitious play*, where, considering a given configuration at generation  $t$  with average strategy  $\bar{i}$  and one new agent entering the game at each time step, each new player would adopt the best reply strategy  $b(\bar{i})$ . Equation (5.8) can also be expressed for the vector  $\mathbf{f}$  of strategy frequencies  $f_i$ :

$$\frac{d\mathbf{f}}{dt} = b(\mathbf{f}) - \mathbf{f}, \quad (5.9)$$

which yields (Hofbauer and Sigmund, 2003) the solution

$$\mathbf{f}(t) = (1 - e^{-t}) b(\mathbf{f}) + e^{-t} \mathbf{f}. \quad (5.10)$$

Equations (5.8), (5.9) and (5.10) impose mathematical constraints, for instance on function  $b$ , which must give a unique and always defined best response, or on the definition of the payoff in the game considered (Hofbauer and Sigmund, 2003). Additionally, they yield a dynamics which is not naturally defined for all time steps  $t$  but rather piecewise (Hofbauer and Sigmund, 2003): the analysis is complicated by abrupt jumps in the game dynamics (Hopkins, 1999).

However, the game-theoretically formal best-response dynamics can be approximated by a smooth dynamics, which can be defined by perturbing the formal best-response by a stochastic element (Hofbauer and Sigmund, 2003), and is therefore sometimes referred to as the *stochastic best response* (Hofbauer and Sigmund, 2003; Miękisz, 2008):

$$\frac{df_i}{dt} = \frac{\exp(\beta u_i)}{\sum_{j \in S} \exp(\beta u_j)} - f_i, \quad (5.11)$$

where  $\beta$  represents the inverse intensity of the stochastic perturbation. Because the formulation in equation (5.11) is related to the logit function used in statistics ( $\text{logit}^{-1}(x) = e^x / (1 + e^x)$ ), it is also called *logit best-response* dynamics.

Equation (5.11) is often not derived mechanistically in econometrics and game theory. Instead, authors prove its mathematical consistency with the formal best-response of equation (5.9) (*e.g.* Fudenberg and Levine, 1998; Hofbauer and Sandholm, 2002; Hofbauer et al., 2009). Nevertheless, following a method suggested in

Hofbauer and Sigmund (1998, p. 94), equation (5.11) was explicitly derived in Suzuki and Iwasa (2009a) for the case where there are two strategies. Thus, the mechanistic derivation of the logit best-response dynamics is closely related to its use in the social-ecological literature and was of less concern to more abstract disciplines. We present Suzuki and Iwasa (2009a)'s derivation in the following as equation (5.18), after the historical and conceptual foundations of the stochasticity of agents' choices. Indeed, the basic idea of this mechanistic derivation is that agents' choices are stochastic and can be described by some probability. From this point of view, the stochasticity parameter  $\beta$  can be interpreted in terms of the agents' rationality.

### 5.3.2 History

Whereas the replicator dynamics has a clear origin in the field of game theory, the logit best-response, although formalized in the fields of game theory, has its origins in mathematical psychology and in psychophysics. Here we present an overview of the history of the concepts leading to the mathematical formulation of the logit best-response dynamics.

#### Psychophysical foundations of pairwise comparisons

Psychophysics scientifically investigates the relation between stimulus and sensation (Gescheider, 1997). From the seminal works of Weber (1834) providing the discipline's foundations, Fechner (1860) inferred that the relation between stimulus and sensation should be logarithmic. Fechner's law was little questioned until experimental evidence showed that a power law fits the data better (Stevens, 1957).

In this context of a search for psychophysical universals, Bradley and Terry (1952), inspired by previous work (Thurstone, 1927), were interested in pairwise comparisons between two options  $i$  and  $j$  and introduced the Bradley-Terry model, previously studied mathematically by Zermelo (1929). This model considers an agent making a pairwise comparison and assumes that the probability that option  $i$  is preferred (perceived as being superior) over option  $j$  can be expressed using a function  $\psi$  as

$$p(i \succ j) = \frac{\psi(i)}{\psi(i) + \psi(j)}. \quad (5.12)$$

Zermelo (1929) interpreted  $\psi$  formally as a probability whereas Bradley and Terry (1952) interpreted  $\psi$  more loosely as a weighing function of options  $i$  and  $j$ . In both cases we have  $\psi(i) \geq 0$  for every  $i$ . The function  $\psi$  describes the link between stimuli, represented by options  $i$  and  $j$ , and their pairwise quantitative perception, represented by the probability  $p(i \succ j)$ .

### Interpretation in econometrics and game theory

Theories of choice modelling have inspired fields outside of psychophysics. They proved especially fertile in domains using an objective measure  $u_i$  of how advantageous choosing a specific option  $i$  could be. This was the case of behavioural economics, marketing, econometrics and game theory, where it is possible to investigate the link between an objective advantage (gains or payoffs  $u_i$ ) and the observed choices  $p(i \succ j)$  made by agents (Corstjens and Gautschi, 1983). This comes from the assumption that economic value provides a general method of measurement extendable to abstract or subjective phenomena such as a desire, since the strength of a wish can be related to the price one would be willing to pay to fulfill it. At first, game theory indeed developed from an economic formulation (von Neumann and Morgenstern, 1944), even though it was then extended into its evolutionary approaches (Maynard Smith, 1972; Maynard Smith and Price, 1973) because of an evolutionary, biological perspective, before inspiring back economics (Osborne, 2004, ch. 13).

When transposed into such frameworks, the function  $\psi$  is thus assumed to weigh the option (strategy)  $i$  and  $j$  according to the corresponding (objective) payoffs  $u_i$  and  $u_j$ . In other words, we have  $\psi(i) = w(u_i)$  for all  $i$ , where  $w$  is a positive weighing function of the payoff  $u_i$ . The probability  $p(i \succ j)$  then describes the probability of choice between strategies  $i$  and  $j$ . It can also be taken to represent the proportion of agents who prefer  $i$  to  $j$  at the population level.

The payoff weighing function  $w$  should be strictly increasing, because we expect that the choice of a strategy giving a higher payoff should be more likely:

$$u_i > u_j \Rightarrow w(u_i) > w(u_j).$$

As a consequence, the weighing functions  $\psi$  and  $w$  can also be interpreted as scaling or ranking functions since they define a total ordering of possible options (Suppes, 1961), which was already the idea and the title in Bradley and Terry (1952).

### Luce's choice axiom

The interpretation of the weighing functions  $\psi$  and  $w$  as defining a total order over possible options makes a generalization to more than two options very intuitive. Luce (1959) subsequently assumed that the probability that option  $i$  is chosen from a set  $S$  of possible options is

$$p_S(i) = \frac{\psi(i)}{\sum_{j \in S} \psi(j)}. \quad (5.13)$$

Equation (5.13) has been referred to as Luce's choice axiom (LCA) (Morgan, 1974; Luce, 1977; Saari, 2005; Luce, 2008) or as the Bradley-Terry-Luce (BTL) model

(Suppes and Zines, 1963). It has commonly been used in theories of choice probability (Fantino and Navarick, 1974) and the interpretation of  $p_S$  as a probability is wide-spread. This has been questioned in the earlier literature though (Luce, 1964) and Luce (2008) has mentioned that his choice axiom does not formally deal with a conditional probability despite looking like one.

The requirements that the weighing function  $w$  should be positive and strictly increasing make an exponential function a natural way to represent the learning dynamics:

$$p_S(i) = \frac{\exp(\beta u_i)}{\sum_{j \in S} \exp(\beta u_j)}. \quad (5.14)$$

Note that the positive parameter  $\beta$  is only related to the base of exponentiation and does not change the dynamics qualitatively. It was not given much importance in the psychophysical literature, but we note that  $\beta = 0$  means that the probability of choosing an option  $i$  does not depend on the associated payoff  $u_i$ , whereas the reward  $u_i$  determines more and more the agent's choice as  $\beta$  increases. Equation (5.14) has provided the “softmax” rule in learning algorithms (Pleskac, 2015; Sutton and Barto, 2018). With  $\beta = 1$ , it has also been referred to as the Bradley-Terry-Luce (BTL) model (Tutz, 1986), as the Luce model (McFadden, 1976) or as the strict utility model (Corstjens and Gautschi, 1983; Tutz, 1986).

The name *strict utility model* comes from the fact that equation (5.14) can also be derived from a random utility model (Block and Marschak, 1959). Random utility models have been associated (Corstjens and Gautschi, 1983; Magnac, 2010) with Thurstone (1927) since the introduction of the concept to economics by Marschak (1960). They were elaborated in psychology to account for the evidence of inconsistencies in behavioural experiments (Manski, 1977). Those inconsistencies suggested that the relation between objective and perceived utility (payoff) is complex and not deterministic. Because of this link, Hofbauer and Sandholm (2002, p. 2268) write that the logit choice function is “the best known example of a choice probability function that can be generated from a random utility model”.

### 5.3.3 Properties

If the logit best-response dynamics converges, then the asymptotic state is a Nash equilibrium (McKelvey and Palfrey, 1995). In equation (5.11), it is obvious that the fraction on the right-hand side must be strictly between 0 and 1. This means that, if all agents adopt the same strategy ( $f_i = 1$ ), then the frequency of this strategy  $f_i$  must decrease. Similarly, if no agent adopts a specific strategy ( $f_i = 0$ ), then the frequency of this strategy  $f_i$  must increase. As a consequence, all possible strategies always end up being again tried out. The adoption or the rejection of one strategy by all agents is never a stationary state in the logit best-response dynamics. This

is why the best-response dynamics is deemed *innovative* (Hofbauer and Sigmund, 2003).

In the case where only two strategies are considered, the exponential formulation of equation (5.14) simplifies to the logit best-response dynamics:

$$p_S(i) = \frac{1}{1 + \exp[\beta(u_j - u_i)]} = \frac{1}{1 + \exp(-\beta\Delta u)} = \text{logit}^{-1}(\beta\Delta u), \quad (5.15)$$

where the dynamics relies mainly on the theoretical difference in fitness between the two strategies. The logit function is widely used in statistics (*e.g.* Cramer, 2003). Notice that this formulation is equivalent to the Bradley-Terry model of equation (5.12) with the exponential as a weighing function  $\psi$ .

Arganda et al. (2012) derive a formula for decision making in animal collectives from Bayes' theorem (Bayes, 1763; Laplace, 1774, p. 623). Assuming that agents make their choice without considering correlations between other agents, Arganda et al. (2012, supplementary information) define the probability for an agent to find that strategy  $i$ , from a set  $S$  of any size, is a "good" choice as

$$p_S(i) = \frac{1}{1 + \exp\left(\ln a_i - \sum_{j \in S} n_j \ln s_j\right)}, \quad (5.16)$$

where the quality of information sources distinguishes between non-social sources  $a_i$  and social sources  $s_j$  and where  $n_j$  is the number of agents adopting strategy  $j$ . Since  $n_j$  is associated with social sources of information,  $n_j$  can be interpreted as the social incentive to adopt strategy  $j$ . If we do not distinguish between social and non-social information sources,  $a_i$  becomes a neutral term ( $a_i = 1$ ). Then, assuming symmetry between the different strategies ( $s_j = s$ ) as in Arganda et al. (2012) yields

$$p_S(i) = \frac{1}{1 + \exp\left(-\ln s \sum_{j \in S} n_j\right)}. \quad (5.17)$$

Equation (5.17) is obviously equivalent to equation (5.15) when there are two strategies. But interestingly, the formulation of a social dynamics provided by equation (5.17) is not equivalent to the best-response dynamics when considering three or more strategies.

### 5.3.4 Use in social-ecological modelling and underlying assumptions

The best-response formulation or variants thereof have been used in a number of articles (Satake and Iwasa, 2006; Iwasa et al., 2007; Satake et al., 2007a,b; Suzuki

and Iwasa, 2009a,b; Iwasa et al., 2010; Figueiredo and Pereira, 2011; Henderson et al., 2013; Iwasa and Lee, 2013; Lee and Iwasa, 2014; Lee et al., 2015a), mainly from Yoh Iwasa's team pioneering work. It is remarkable that the mathematical formulation of the logit best-response was already used by Carpenter et al. (1999) in a social-ecological model relying on agent-based simulations. That article further inspired Suzuki and Iwasa (2009a,b), who were interested in the same ecological context, namely lake eutrophication.

In the meantime, in 2006 and 2007, equation (5.15) is interpreted as describing a transition rate between two states (strategies) in models of binary choice (Satake and Iwasa, 2006; Iwasa et al., 2007; Satake et al., 2007a,b). Later on, a slightly different model in discrete time was developed by Suzuki and Iwasa (2009a,b). Their model relies on the idea that, at each turn, a fraction  $s$  of players may change their strategy while the remaining part  $(1 - s)$  does not. Agents who may change their strategy are assumed to make their choice in a probabilistic way according to equation (5.15), so that the collective dynamics is:

$$f_i(t + 1) = (1 - s)f_i(t) + \frac{s}{1 + \exp(-\beta\Delta u)}. \quad (5.18)$$

Thus, the parameter  $s$  represents the readiness for agents to change their opinion, as opposed to conservatism. Numerical simulations suggested that  $s$  could be a key parameter for the stability of equilibria (Suzuki and Iwasa, 2009b), but analytical investigations in Chapter 3 showed that this parameter had not more effect on the stability of equilibria than any other model parameter. Parameter  $s$  had already been introduced earlier (Satake and Iwasa, 2006; Iwasa et al., 2007).

The major difference between the period before 2008 and the period after 2008 is in the interpretation of equation (5.15). Before 2008, it was interpreted as a transition rate for agents moving between two states. After 2008, through the derivation of equation (5.18), it is interpreted as a probability for an agent to choose between two options (Suzuki and Iwasa, 2009a). The latter interpretation reconnects with the probability interpretation of Luce's choice axiom (Luce, 1964) and with the stochastic perturbation of the formal best-response dynamics defined in game theory (Hofbauer and Sigmund, 2003). Note that the interpretation as a probability to choose a strategy assimilates the frequency with the probability, thus assuming that the population of agents is large. In the interpretation as a probability to choose a strategy, parameter  $\beta$  can be interpreted as the agents' rationality (Chapter 4). Indeed, if  $\beta$  is close to 0, agents make random decisions, with different options being equiprobable. If  $\beta$  increases, the differential utility  $\Delta u$  between two options plays an increasing role in the decision outcome. When  $\beta \rightarrow \infty$ , even the slightest incentive  $\Delta u$  makes all agents choose the more advantageous strategy.

Starting from 2010, mathematical social-ecological models use the logit best-response dynamics in continuous time (Iwasa et al., 2010; Lee and Iwasa, 2014,



and Chapter 3). In continuous time, equation (5.18) yields (Chapter 3):

$$\frac{df_i}{dt} = s \left[ \frac{1}{1 + \exp(-\beta\Delta u)} - f_i \right]. \quad (5.19)$$

Fig. 5.1 summarizes the academic paths which lead the logit best-response into the field of social-ecological modelling. Yoh Iwasa's team inherited the psychological foundations of the logit best-response through two major econometric and game theoretical sources, McKelvey and Palfrey (1995) and Hofbauer and Sigmund (2003). McKelvey and Palfrey (1995) draw from the influential (Manski, 2001) work of Daniel McFadden (McFadden, 1973, 1975, 1976, 1981, 2001). McKelvey and Palfrey (1995) is the major foundation for the logit choice function, sometimes called *conditional* or *multinomial logit* (McFadden, 1975; Hausman and McFadden, 1984; Manski, 2001), or *quantal response*, a term introduced by McFadden (1976) to refer to a *discrete* choice. McKelvey and Palfrey (1995) present the quantal equilibria and the logit equilibrium as an example thereof. In econometrics, the logit best-response dynamics has sometimes (Baron et al., 2002) been postulated (*e.g.* Blume, 1995, 1997; Young, 2001).

More recently, Lee et al. (2015a) have incorporated more game-theoretic insights from another branch of sources. Zhuang et al. (2014) and Alós-Ferrer and Netzer (2010) summarize theoretically many of those sources (Blume, 1993, 1997; Fudenberg and Levine, 1998; Blume, 2003; Hopkins, 2002). Fig. 5.1 shows that many social-ecological articles were authored by people academically related to Yoh Iwasa's seminal work, even though counterexamples can be found (Figueiredo and Pereira, 2011; Henderson et al., 2013).

Social-ecological scientists should keep in mind that the best-response dynamics entails many assumptions as a result of its development. These assumptions include the following:

1. strategies are totally ordered by their resulting payoffs;
2. for each agent, the probability  $p_S(i)$  of choosing a strategy  $i$  can be described by a payoff weighing function (existence of  $w$ );
3. the exponential function is a suitable payoff weighing function ( $w = \exp$ );
4. the population of agents is large (the probability  $p_S(i)$  gives the frequency  $f_i$  of adoption of strategy  $i$ );
5. the rejection of one strategy by all agents is not a stationary state (innovation).

## 5.4 Discussion and conclusions

Here, we review the relation between the replicator dynamics and the logit best-response dynamics. We first discuss empirical evidence, then we focus on theoretical links, and finally we compare assumptions on which the two dynamics rely and implications for social-ecological models.

### 5.4.1 Relation with empirical evidence

Empirical investigations have been conducted throughout the history of psychophysics. Yet, better controlled experiments have been allowed by new technologies and behavioural economy is a rapidly growing field. A typical experiment implies to recruit agents (often students) to take part in a predefined game for some real monetary gain. The experiment consists in recording the decisions made by each agent (often on a computer) in order to maximize their payoff. This framework allows for the testing of conjectured game dynamics in the controlled setting of a predefined game. Due to time and financial restrictions on the number of successive rounds of the same game that can be played, it is easier to investigate game theory than evolutionary game theory.

Recent experiments, including those by Lim and Neary (2016) and Mäs and Nax (2016), suggest that the best-response dynamics provides a good fit to experimental data. They specifically explore the best way to model deviations from the standard dynamics in game theory: the replicator dynamics (Benndorf and Martínez-Martínez, 2017). The results presented in Lim and Neary (2016) and in Mäs and Nax (2016) suggest that, in the case of the controlled behavioural economic experiments, the best-response dynamics fits data better than the replicator dynamics. It is still unknown to what extent this result could be generalized to other experimental settings and it is doubtful whether and how it could be verified for less controlled complex decisions in social-ecological systems (Schlüter et al., 2017).

The results of those recent experiments contradict earlier evidence obtained at a time when controlled experiments were more difficult to implement. Indeed, empirical evidence analyzing pooled data from individual subjects had challenged explicitly Luce's choice axiom because of a significant departure from the expected observations (Morgan, 1974). Very early experimental tests of behaviour dynamics had been discussed extensively without any clear conclusion due to the methodological discrepancies between experiments (Luce and Suppes, 1965, pp. 377–401). However, aside from choosing between evolutionary game theoretical dynamics, some basic assumptions common to the game theoretical and behavioural economic approaches remain challenged. For instance, a long-standing discussion point is that mathematical formulation of choice dynamics such as Luce's choice axiom lack robustness regarding multistage choices (Morgan, 1974). This means that the definition of a

unitary choice may be an important weakness. Another example is the experimentally violated expectation that the preference for a probability mixture of two choices should lie between the preference levels of the two choices (Camerer and Ho, 1994).

Critics of the rational modelling of human behaviour through theories of utility in general have been formulated very early on (Allais, 1953). The Allais paradox (Allais, 1953) is a notable example arguing against the axiomatic foundation of expected utility theory and has been confirmed experimentally (Oliver, 2003). Empirical evidence becoming a major concern in economic theory (Machina, 1987; Camerer and Ho, 1994) explains the development of behavioural economics. How the theory of socioeconomic models relates to actual socioeconomic behaviours that can be observed in human groups or structures is still little known.

### 5.4.2 Theoretical links between the replicator dynamics and the logit best-response dynamics

Regarding formal links in game theory, Hopkins (1999) proved that the best-response dynamics could be obtained from a generalized replicator in a game where perturbations are introduced on the game payoffs. Hofbauer et al. (2009) focused on the time average of the average strategy adopted under the replicator dynamics. They proved that if the best-response dynamics has a global attractor, then the time average of the replicator dynamics converges towards the same point.

We previously mentioned that those two approaches are contradictory regarding the stationarity of extreme cases in which all agents adopt the same behaviour (Chapter 4). The replicator dynamics assumes conformism of each agent to the group. Indeed, the adoption of one strategy by the all agents convinces each agent to keep with the same strategy. The logit best-response, on the contrary, assumes that at least some agents always diverge from the main opinion. This has been compared to a non-zero mutation rate (Chapter 4). The replicator dynamics and the best-response dynamics fundamentally disagree on whether the adoption of the same behaviour by the whole population makes the socioeconomic dynamics stationary or not.

The rationality parameter  $\beta$  of the logit best-response dynamics provides an intuitive link with the replicator dynamics. If agents tend to make their decisions randomly,  $\beta$  is close to 0. If all agents immediately choose the best option as soon as they expect even a slight additional payoff compared to other options, then  $\beta$  is large. This is why  $\beta$  can be interpreted as the agents' rationality. We previously showed that equation (5.19) tends towards equation (5.3) as agents become more and more rational  $\beta \rightarrow \infty$  (Chapter 4). Thus, in the case of two strategies, the replicator dynamics can be considered a special case of the logit best-response dynamics where the agents have infinite rationality. Even though the replicator dynamics is

mathematically simple, especially in the two-case strategy with equation (5.3), the advantage of the logit best-response dynamics, is that the parameter representing the agents' rationality  $\beta$  allows for the investigation of different levels of rationality, characterizing the "distance" from the replicator dynamics (Chapter 4). The higher the rationality, the closer we are from the replicator dynamics, the more we assume that the group of agents makes unanimous decisions. The lower the rationality, the farther we are from the replicator dynamics, the more we assume that individual agents act independently and randomly. Thus, in accordance with the experimental evidence we have mentioned in section 5.4.1, we recommend using the logit best-response dynamics by default and keeping in mind that the agents' rationality  $\beta$  is a source of uncertainty.

### 5.4.3 Comparison of assumptions and consequences

Both the replicator dynamics and the best-response dynamics assume that strategies can be totally ordered by an associated abstract measure of utility. Direct implications are challenged by empirical evidence (Camerer and Ho, 1994). The two dynamics are fundamentally contradictory regarding the stationarity of pure strategies. Indeed, the replicator dynamics implies that the full rejection of any strategy by the whole population is stationary, whereas the best-response dynamics imposes revival of all lost strategies.

The replicator dynamics is rooted in a Darwinian interpretation which does not formally extend to cases where a strategy  $i$  is completely rejected ( $f_i = 0$ ). It moreover assumes that the dynamics of the collective choice at the population level depends on the average strategy adopted at all times.

The logit best-response dynamics is rooted in a probabilistic/stochastic interpretation for each agent, which is more realistic than an assumption of determinism. But this probabilistic interpretation also implies that the population is sufficiently large for strategy frequencies to follow their probabilities. Moreover, the logit best-response dynamics assumes that there can be a payoff weighing function and that the exponential function is a suitable choice. The choice of the exponential is not supported by psychophysical evidence (Stevens, 1957).

In spite of abstract mathematical links between the two dynamics (Hopkins, 1999; Hofbauer et al., 2009), choosing the replicator dynamics or the logit best-response dynamics can change the number of stationary states as well as their stability (Chapter 4). As a consequence, we formulated recommendations for choosing between them (Chapter 4): the replicator dynamics seems more appropriate when having evidence of strong social conformism, where agents tend to follow mass movements (social learning or any kind of social behaviour), whereas the logit best-response dynamics seems more appropriate if there is evidence that the group behaviour cannot impair individual innovation from the agents, which tend to act independently

(biological mutations and similar systems where variation happens on a constant random basis). More work should be carried out to explore further implications of the socioeconomic dynamics's functional form on the whole social-ecological model and on management conclusions.

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# 6 Behavioural thresholds and resignation effects in social-ecological models

## Abstract

Social-ecological models are used to investigate the mutual interactions between an ecological system and human behaviour at a collective level. The socioeconomic dynamics relies on the mathematical formulation of the socioeconomic incentive which determines the influence of the human system on the ecological system. This incentive comprises a response to the ecological state of the system as well as a response to its socioeconomic state. We use the example of a social-ecological model for eutrophication in shallow lakes to investigate the consequences of choosing a monotonic or a non-monotonic response in the formulation of this incentive. For a non-monotonic response, we study the case of giving-up behaviours, where reaching a certain level in a state variable causes the socioeconomic incentive to vary in the other direction (to increase if it was decreasing or to decrease if it was increasing). Monotonic formulations are standard and extend the linear case with potentially new equilibria, new attractors and new basins of attraction. A difference between models using a linear response and models using more complex monotonic responses is that the implementation of a threshold may cause the system to remain at the threshold, creating a new attractor. Non-monotonic formulations, however, introduce more substantial changes, where the socioeconomic nullcline can become more complex, such as taking the shape of a closed curve. Moreover, the example of giving-up behaviours suggests that the uncertainties they bring about can impair our ability to anticipate the outcomes of social-ecological models even on a qualitative level. Thus, the undesirable effects of giving-up behaviours are not only direct but they may also prevent us from making informed decisions.

## 6.1 Introduction

Human behavioural responses are often not linear in two ways. First, the response to a stimulus may not grow linearly as the stimulus increases. Physiology offers a

simple example since the existence of sensory thresholds, *e.g.* stimuli under which no sensation occurs, is a well-known fact. This means that, at an individual level, the response to a stimulus may not be linear and could have a threshold or follow a sigmoid curve for instance (Tavoni et al., 2012; Lade et al., 2013). Another example of non-linearities is provided by the literature on tipping points. Second, considering a group of individuals instead of a single agent, the collective response may present a group dynamics. This is illustrated by climate change awareness dynamics, the adoption of innovation in general or by vaccination coverage and media attention in public health and in epidemiology, and boils down to having a social norm (Nyborg et al., 2016) allowing for social tipping points. Such non-linearities are the result of a feedback loop: the adoption of an opinion in the social system influences its own dynamics.

Potential non-linearities of the two types are key in the field of social-ecological modelling. In the past fifteen years, several articles (Ibáñez et al., 2004; Satake and Iwasa, 2006; Satake et al., 2007a,b; Iwasa et al., 2007; Suzuki and Iwasa, 2009a,b; Iwasa et al., 2010; Fryxell et al., 2010; Tavoni et al., 2012; Iwasa and Lee, 2013; Lade et al., 2013; Lee and Iwasa, 2014; Lee et al., 2015a,b; Sugiarto et al., 2015; Bieg et al., 2017) have proposed social-ecological models, coupling an ecological system with a socioeconomic system to study fisheries or other harvested populations (Fryxell et al., 2010; Lee and Iwasa, 2014; Bieg et al., 2017), lakes (Iwasa et al., 2007; Suzuki and Iwasa, 2009a; Iwasa et al., 2010, and Chapters 3 and 4), grasslands (Lee et al., 2015a), forests (Satake and Iwasa, 2006; Satake et al., 2007a,b; Lee et al., 2015b) and some other ecological contexts (Ibáñez et al., 2004; Tavoni et al., 2012; Iwasa and Lee, 2013; Lade et al., 2013; Sugiarto et al., 2015). The ecological model typically represents the level of a resource using population dynamics, whereas the socioeconomic model accounts for some human behaviour influencing the environment, often using evolutionary game theory.

The socioeconomic system accounts for the dynamics of the collective decision made by a population of (human) agents as to their action on the ecological system. The socioeconomic system in turn reacts to the dynamics of the ecological system. The socioeconomic model usually comprises one or several mathematical terms which, taken together, can be interpreted as the incentive for the agents to act in a certain way. For instance, in modelling eutrophication in shallow freshwater lakes in Chapters 3 and 4, we used a term  $\Delta U$  corresponding to the incentive for agents to lower their pollution discharge into a lake. Using economic terminology, this incentive  $\Delta U$  can also be called a *difference in utility*, utility being a theoretical measure of the reward an agent would gain from choosing his strategy, that is, to discharge pollution at a high level or at a low level. In the general case, we refer to the environment-friendly option as *cooperation* and we refer to the less environment-friendly option as *defection*. In the eutrophication example, cooperation consists

in having a low discharge of pollution whereas defection consists in having a high discharge of pollution.

In social-ecological models, the mathematical formulation of the socioeconomic incentive  $\Delta U$  relies on specific assumptions. Indeed, it assumes that the incentive responds to variations in the state variables in a mathematically defined way: the socioeconomic incentive  $\Delta U$  is a function of both the ecological state and the socioeconomic state. To our knowledge, the influence of the socioeconomic incentive's specific mathematical formulation on the model predictions have not been explored. In particular, monotonicity of the incentive's response to the ecological state and to the socioeconomic state is usually assumed. This means that an improvement in the ecological state always leads to either an increase in the incentive or, depending on the model, always leads to a decrease in the incentive. Similarly, an increase in cooperation among the agents is assumed to result in an increase in the incentive to cooperate.

However, our intuition may challenge this assumption that the incentive's response to changes in the state variables is monotonic. We may indeed expect that, if the ecological system's state worsens to the point where the situation seems desperate, humans may end up feeling that their efforts cannot have anymore influence. This in turns decreases their incentive to cooperate and results in a giving-up behaviour. Similarly, if we expect cooperation to improve the incentive to cooperate in general, we may also think that, in the situation where most agents already act in an environment-friendly way, at least some individuals can think of relying on the others' collective behaviour and allow themselves to defect more easily. This means that the incentive to cooperate may start decreasing once a certain level of cooperation is achieved in the population.

Here, we modify the social-ecological model developed in Chapter 4 for eutrophication in shallow freshwater lakes to study the impact of choosing either a monotonic response function or an increasing-decreasing response function for the incentive to cooperate. This article is organized in three parts. First, we derive the social-ecological models. Then, we investigate the phase plane and the dynamics of monotonic response models and of models with a giving-up behaviours. Finally, we discuss the implications of the complexity brought in by the non-monotonic case representing a giving-up behaviour.

## 6.2 Model

In this section, we describe our mathematical models. Each comprises two interconnected subsystems: an ecological part and a socioeconomic part. The ecological state variable is the level of pollution  $P$  (with  $P \geq 0$ ), the socioeconomic state variable is the fraction of cooperators  $F$  (with  $0 \leq F \leq 1$ ). Note that in this article,

the term cooperation, which comes from game theory, does not refer to a social interaction, but rather to an environment-friendly behaviour.

### 6.2.1 Ecological subsystem

For the ecological dynamics, we use the following model:

$$\frac{dP}{dt} = \underbrace{A}_{\substack{\text{anthropogenic discharge} \\ \text{of pollution}}} - \underbrace{\alpha P}_{\substack{\text{global outflow rate} \\ \text{(outflow and sedimentation)}}} + \underbrace{\frac{rP^q}{m^q + P^q}}_{\text{resuspension}}.$$

$A$  is the amount of pollution (phosphorus) discharged in the lake due to the use of fertilizers. We assume a linear global outflow rate (outflow and sedimentation) with parameter  $\alpha$ . The resuspension term corresponds to the interaction between the water and the sediments, which is stronger in shallow lakes (less than 3 m deep). Its Hill function was primarily used to account for “the sigmoidal decline of vegetation with turbidity” (Scheffer, 1998, p. 270), then for the pollution resuspension Carpenter et al. (1999). It corresponds to a sigmoid curve where  $r$  determines the upper bound and  $m$  the half-saturation level. The parameter  $q$  is negatively correlated to the depth of the lake; for our model, we have:  $q \geq 2$  Carpenter et al. (1999). This model, developed by Carpenter Carpenter et al. (1999), is sufficient to represent the bistability of shallow lakes, but mechanistic models accounting for vegetation density, light attenuation or the size of sediments have also been proposed Scheffer (1998).

From a game theoretical point of view, the anthropogenic release  $A$  can be represented as a collective choice between two *strategies*. A human *agent* may adopt a high discharge of pollutants  $p_D$  (*defection*) or a lower discharge  $p_D - \delta_p$  (*cooperation*) with  $0 \leq \delta_p \leq p_D$ .  $\delta_p$  is the reduction observed in the discharge when switching from defection to cooperation: it is a cooperation effort. If we consider the entire population, the collective discharge  $A$  depends on the fraction  $F$  of cooperators ( $0 \leq F \leq 1$ ):

$$A = p_D(1 - F) + (p_D - \delta_p)F = p_D - \delta_p F.$$

### 6.2.2 Socio-economic subsystem

The socio-economic dynamics is modelled by replicator dynamics because of its mathematical simplicity.

$$\frac{dF}{dt} = F(1 - F)\Delta U. \tag{6.1}$$

The variable  $\Delta U$  represents the difference in utility between the two strategies: when it is positive, people tend to become cooperators, whereas, when it is negative,

the incentive to defect is stronger. Thus,  $\Delta U$  can be interpreted as the incentive to cooperate, or as the cost of defection compared to the cost of choosing cooperation.

We consider three processes affecting the incentive  $\Delta U$ :

- the baseline ( $-v$ ) is assumed to be negative, because it is economically more advantageous for an agent to release high amounts of pollution;
- the agents' ecological concern is represented by a response to the level of pollution in the lake  $\kappa(P)$ ;
- social conformism is represented by a response to the fraction of cooperators among agents  $\xi(F)$ .

Thus, we reformulate  $\Delta U$  as:

$$\Delta U = \underbrace{-v}_{\text{economic baseline}} + \underbrace{\kappa(P)}_{\text{ecological concern}} + \underbrace{\xi(F)}_{\text{social conformism}}. \quad (6.2)$$

### 6.2.3 Integrated system and response functions

The integrated model is:

$$\begin{cases} \frac{dP}{dt} = -\alpha P + \frac{rP^q}{m^q + P^q} + p_D - \delta_p F \\ \frac{dF}{dt} = sF(1-F)[-v + \kappa(P) + \xi(F)] \end{cases}.$$

All parameters of the model are positive.

Our study focuses on response functions  $\kappa$  and  $\xi$ . Chapter 4 provided a baseline case where both response functions are linear. They found out that the system could be between two and nine equilibria, and between zero and four stable equilibria. We refer to this model as the linear response model (LRM). Here, we explore two other functional shapes: the first one is a step function, which is a limit case for a monotonic function, while the second one is a Gaussian function, which is a smooth example of an increasing then decreasing function representing a resignation effect.

Including the linear response, we have three options for each of the two response functions  $\kappa$  and  $\xi$  (linear, step, Gaussian), so that we obtain nine models. However we will present only two cases from which, with the LRM, the other cases can be deduced easily. We will refer to the first case as the step response model (SRM). In the SRM, the incentive comprises a step function for the  $P$ -response function ( $\kappa_{SRM}$ ) and a linearly increasing  $F$ -response function ( $\xi(F) = \xi_0 F$ ). This model assumes that there is no giving-up behaviour and that the incentive increases abruptly if a pollution threshold  $P_{thresh}$  is passed or if a cooperation threshold  $F_{thresh}$  is passed.

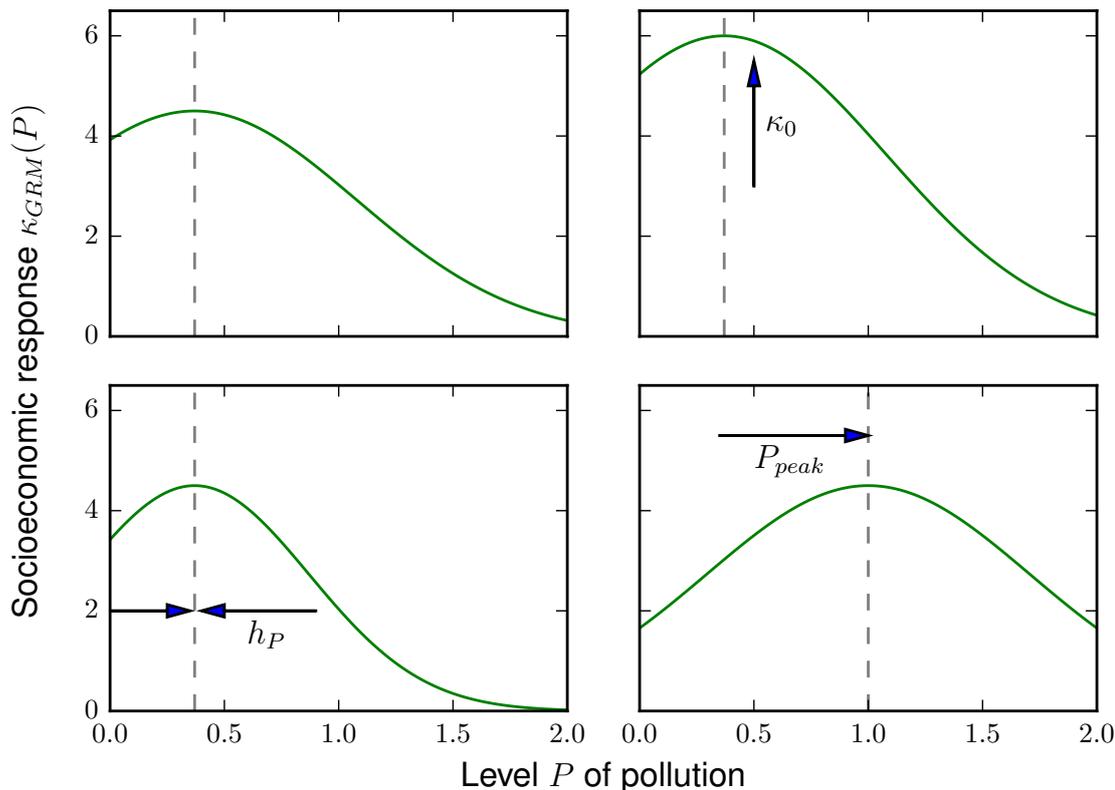


Figure 6.1: Gaussian socioeconomic response  $\kappa_{GRM}(P)$  to the pollution  $P$  observed in the lake. The arrows show the transformation of the curve when a parameter is increased. From the upper left panel with  $\kappa_0 = 4.5$ ,  $h_P = 1$  and  $P_{peak} = 0.37$  (dashed grey line), each other panel displays the influence of one increased parameter:  $\kappa_0 = 6$  (upper right),  $h_P = 2$  (bottom left) or  $P_{peak} = 1$  (bottom right).

We will refer to the second case as the Gaussian response model (GRM). In the CRM, both response functions are Gaussian functions ( $\kappa_{GRM}$  and  $\xi_{GRM}$ ). This model assumes that there is a smooth decrease in the incentive to cooperate passed a peak level  $P_{peak}$  for pollution (giving-up behaviour) and passed a peak fraction  $F_{peak}$  of cooperators (free-riding behaviour).

The functional form  $\kappa_{SRM}$  that we use for the step function in the SRM is as follows (we provide the similar socioeconomic response step function  $\xi_{(SRM)}$  for comparison only):

$$\kappa_{SRM}(P) = \begin{cases} \kappa_{lo} & \text{if } P \leq P_{thresh} \\ \kappa_{hi} & \text{if } P > P_{thresh} \end{cases}, \quad \xi_{(SRM)}(F) = \begin{cases} \xi_{lo} & \text{if } F \leq F_{thresh} \\ \xi_{hi} & \text{if } F > F_{thresh} \end{cases}.$$

The step response to the level of pollution  $\kappa_{SRM}$  means that there exists a threshold  $P_{thresh}$  above which the incentive to cooperate is increased. This could correspond to a tax imposed on users of fertilizers when the lake gets too polluted. Similarly, the step response to the fraction of cooperators  $\xi_{(SRM)}$  means that there exists a threshold  $F_{thresh}$  above which the incentive to cooperate is increased: once cooperation is common enough, it may be accepted as normal and/or normative behaviour so that an excessive discharge of pollution may also be taxed more for example.

Note that the step response function can be approximated by a continuous increasing sigmoid function with a steep increase. We will refer to the approximated SRM, where  $\kappa_{SRM}$  is approximated by a sigmoid function, as the sigmoid response model (SRM'). We will also describe the results obtained with the SRM', but our focus is on the discontinuous formulation of the SRM. Indeed, the interpretation of the threshold in the SRM is intuitive and makes sense in the context of policy making.

The functional forms  $\kappa_{GRM}$  and  $\xi_{GRM}$  that we use for the Gaussian function in the GRM are

$$\begin{aligned}\kappa_{GRM}(P) &= \kappa_0 \exp[-h_P(P - P_{peak})^2], \\ \xi_{GRM}(F) &= \xi_0 \exp[-h_F(F - F_{peak})^2].\end{aligned}\tag{6.3}$$

The Gaussian response  $\kappa_{GRM}$  of the incentive to cooperate to the level of pollution means that an increase in the lake pollution  $P$  results in an increase in the ecological concern up to a certain point  $P_{peak}$ . Passed this point, agents tend more and more to give up because they are discouraged. Fig. 6.1 shows that this socioeconomic response then follows a bell curve. Parameter  $\kappa_0$  influences the height of the curve, parameter  $h$  influences its narrowness and parameter  $P_{peak}$  influences the location of the response's maximum. Similarly, the Gaussian response  $\xi_{GRM}$  to the fraction of cooperators means that having more cooperators produces a group effect motivating other defectors to cooperate up to a certain point  $F_{peak}$ . Passed this point, some agents consider the collective level of cooperation to be sufficient in the population and would drop their cooperating behaviour.

## 6.3 Results

### 6.3.1 Limit case of a monotonic response

In this section, we compare the outcomes of the SRM to the baseline case where the incentive's response to state variable is linear (LRM). We recall that the SRM is the limit case of the SRM' when the sigmoid response in the SRM' becomes steeper.

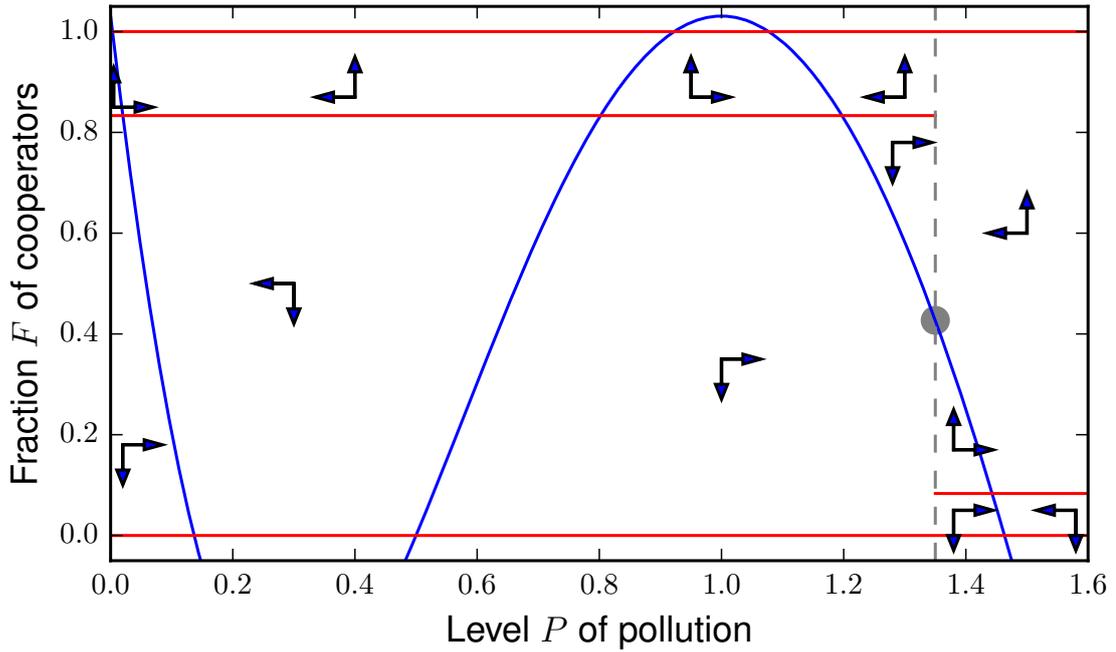


Figure 6.2: Phase plane for the SRM showing the  $P$ -nullcline (blue curve) and the  $F$ -nullclines (red straight lines), with a discontinuity at the threshold (dashed grey line), as well as the direction of the flow (arrows). The intersection between the threshold line and the  $P$ -nullcline is a pseudo-equilibrium (filled grey circle). Parameter values:  $\alpha = 0.4$ ,  $r = 0.8$ ,  $q = 2$ ,  $m = 1$ ,  $p_D = 0.04$ ,  $\delta_p = 0.0388$ ,  $s = 0.1$ ,  $v = 5$ ,  $\kappa = 4.5$ ,  $\xi = 6$ ,  $P_{thresh} = 1.35$ .

### General organization of the phase plane

Fig. 6.2 shows that the nullclines for the socioeconomic system include two trivial lines, one for  $F = 0$  (full defection) and one for  $F = 1$  (full cooperation), as well as two half-lines. The latter correspond to fixed levels of cooperation:  $F_{hi} = (v - \kappa_{lo})/\xi_0$  when  $P$  is below the threshold  $P_{thresh}$ , and  $F_{lo} = (v - \kappa_{hi})/\xi_0$  when  $P$  is larger than the threshold  $P_{thresh}$ , with  $F_{hi} > F_{lo}$ . These two half-lines are states where the incentive to cooperate vanishes, which makes the socioeconomic subsystem stationary because of equation (6.1). In the LRM, those two half-lines are one continuous line (Chapter 4); in the SRM', this continuous line is bent into a sigmoid curve (not shown here); finally, in the limit case of the SRM as in Fig. 6.2, the sigmoid curve becomes discontinuous.

Fig. 6.2 illustrates that  $F_{hi}$  and  $F_{lo}$  represent the boundary between different basins of attractions. When the pollution level  $P$  is below the threshold  $P_{thresh}$ ,

the relevant critical value for the fraction  $F$  of cooperators is  $F_{hi}$ . If the system has a low cooperation level  $F < F_{hi}$ , then the fraction of cooperators decreases. If the system has a high cooperation level  $F > F_{hi}$ , then the fraction of cooperators increases. Similarly, when the pollution level  $P$  is above the threshold  $P_{thresh}$ , the relevant critical value for the fraction  $F$  of cooperators is  $F_{lo}$ . If the system has a low cooperation level  $F < F_{lo}$ , then the fraction of cooperators decreases. If the system has a high cooperation level  $F > F_{lo}$ , then the fraction of cooperators increases.

Thus, Fig. 6.2 reveals a straightforward way to understand which equilibria are stable and which equilibria are unstable. We previously explained for the LRM that the  $P$ -nullcline had the shape of an  $S$  with three branches and that we could expect the outer branches to allow for stable equilibria to occur whereas the middle branch is expected to have unstable states Chapters 2 and 3. The  $F$ -nullclines are organized similarly: the trivial nullclines correspond to the outer branches of a stretched  $S$  and the non-trivial ones correspond to the unstable middle branch. Accordingly, we observe that equilibria on the nontrivial  $F$ -nullclines (the half-lines) are not stable. If  $F_{hi}$  or  $F_{lo}$  is between 0 and 1, then, in the phase plane, the corresponding nontrivial half-line  $F$ -nullcline is between the trivial  $F$ -nullclines. In this case, equilibria on both trivial  $F$ -nullclines can be stable. Otherwise, if  $F_{hi}$  or  $F_{lo}$  is not between 0 and 1, then the corresponding nullcline has no meaning: it occurs out of the phase plane and one of the two trivial  $F$ -nullclines has only unstable states. For instance, consider the left side of the threshold in Fig. 6.2. If  $F_{hi} > 1$ , then the entire half-plane imposes that the fraction of cooperators must decrease and all states with  $F = 1$  are unstable. Conversely, if  $F_{hi} < 0$ , then the entire half-plane imposes that the fraction of cooperators must increase and only states with  $F = 1$  can be stable.

### Pseudo-equilibrium and pseudo-cycles

Compared to the case where response functions are linear, more complex monotonic response functions may result in having additional equilibria. In Fig. 6.2 for instance, the nullclines of the two subsystems have ten intersections, meaning that the system has ten fixed points. In addition to that, we refer to the intersection between the threshold line  $P = P_{thresh}$  and the  $P$ -nullcline as a pseudo-equilibrium. Instead of showing where the socioeconomic subsystem is stationary ( $\frac{dF}{dt} = 0$ ), the middle part of the dashed grey threshold line is the border between domains where the fraction  $F$  of cooperators tends either to decrease strictly (left) or to increase strictly (right). As there is no continuity at the threshold, the incentive to cooperate jumps from negative to positive values without vanishing. Therefore, the pseudo-equilibrium is not formally a stationary point. Note that in the SRM', the pseudo-equilibrium is formally an equilibrium since the non-trivial  $F$ -nullcline is continuous. But in the discontinuous case of the SRM, the  $F$ -nullcline does not pass the pseudo-equilibrium. Simulations show that the pseudo-equilibrium can also be stable (not shown).

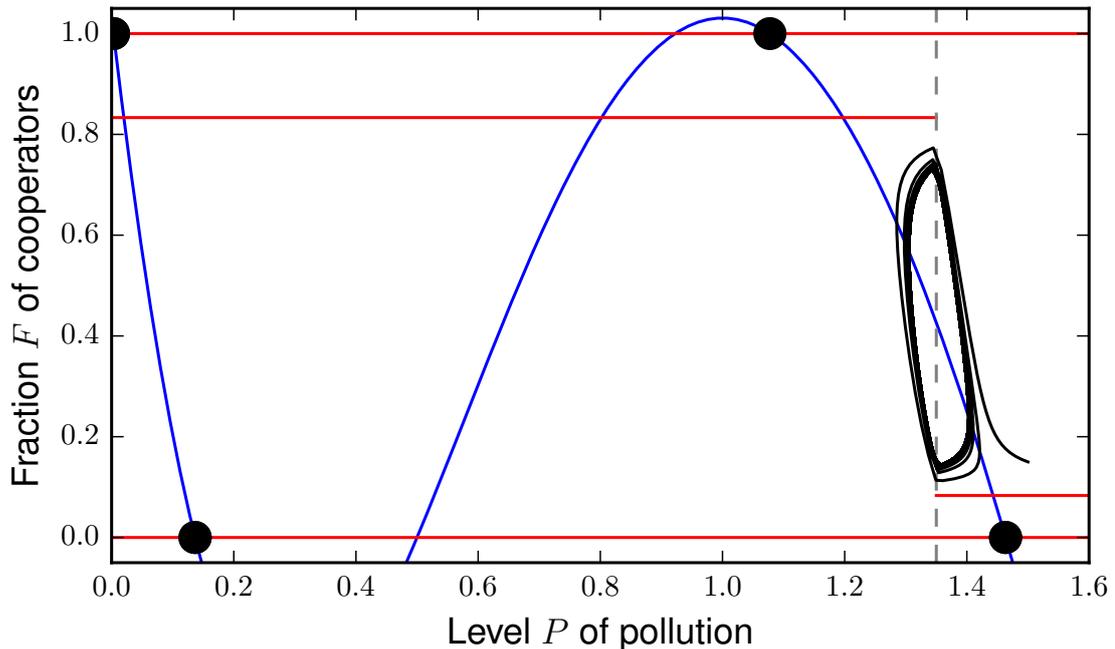


Figure 6.3: Phase plane for the SRM as in Fig. 6.2 showing a trajectory (black curve). Parameter values as in Fig. 6.2. Initial condition:  $(P_0 = 1.5, F_0 = 0.15)$ .

Complex monotonic responses, like the discontinuity in the SRM, may give rise to additional attractors or pseudo-attractors absent from the LRM. This is illustrated in Fig. 6.3, where an additional pseudo-attractor has emerged in the form of sustained oscillations. We refer to it as a pseudo-cycle because we have not formally proven the existence of a limit cycle. In the continuous case of the SRM', this would be a limit cycle around an unstable equilibrium.

There is an intuitive explanation for the pseudo-cycle. We can think of the mathematical threshold  $P_{thresh}$  (dashed grey line) as of the implementation of a tax policy for instance. Above the threshold  $P_{thresh}$ , a tax is imposed on fertilizers, so that the incentive to decrease the use of fertilizers suddenly increases. As a consequence, some initial conditions lead to a situation where the pollution is slightly above the threshold, which makes it advantageous for agents to cooperate. Then the rising cooperation ends up decreasing the pollution level below the threshold, which makes it more advantageous for agents to defect. The drop in the fraction of cooperators then makes the pollution in the lake increase again.

Importantly, this means that a new basin of attraction may emerge. This can be seen in Fig. 6.4, where we find five basins of attraction. Initial conditions leading to the cycle shown in Fig. 6.3 form the white basin of attraction. We can provide

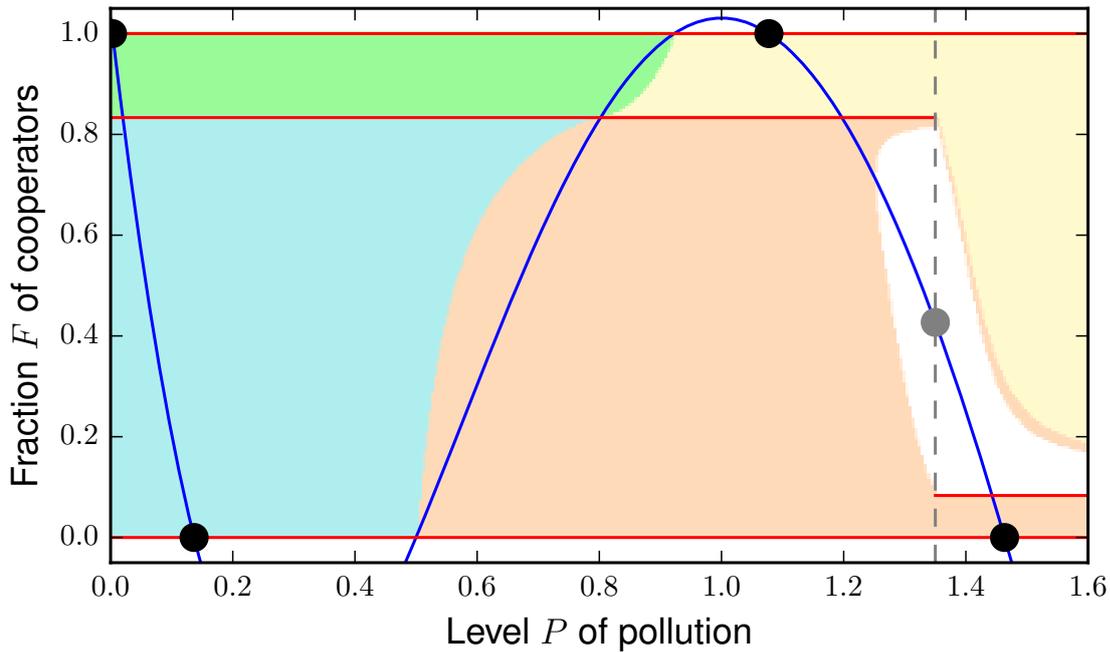


Figure 6.4: Phase plane for the SRM showing the  $P$ -nullclines (solid blue curve), the  $F$ -nullclines (solid red lines), the threshold (dashed grey line) and stable equilibria (black filled circles) as well as the pseudo-equilibrium (grey filled cycle). Basins of attraction are indicated by coloured surfaces. Note that the basin of attraction for the least desirable equilibrium (with high  $P$  and low  $F$ ) surrounds the basin of attraction of the pseudo-cycles. Parameter values as in Fig. 6.2.

an intuitive interpretation of Fig. 6.4. The LRM used to have only the four stable equilibria shown in Fig. 6.2 and in Fig. 6.3. If the system is at the most undesirable equilibrium (highest stable level of pollution and full defection), we could think that a policy implementing a threshold below that level of pollution may be effective in forcing the system into a “better” stable equilibrium. What Fig. 6.3 and Fig. 6.4 show is that, for many initial conditions, this threshold policy would only force agents to pollute just low enough to remain in oscillations around the threshold, but not lower.

Further simulations (not shown) suggest that both stable pseudo-equilibria and pseudo-cycles occur on the outer branches of the  $S$ -shaped  $P$ -nullcline only. We emphasize that this applies to the outer branch on the right-hand side with large values for  $P$  as well as to the outer branch on the left hand-side with low values for  $P$ . In the latter case, the implementation of a threshold can therefore lock the system in a state with a pollution level just beyond the ecologically desirable equilibrium (with

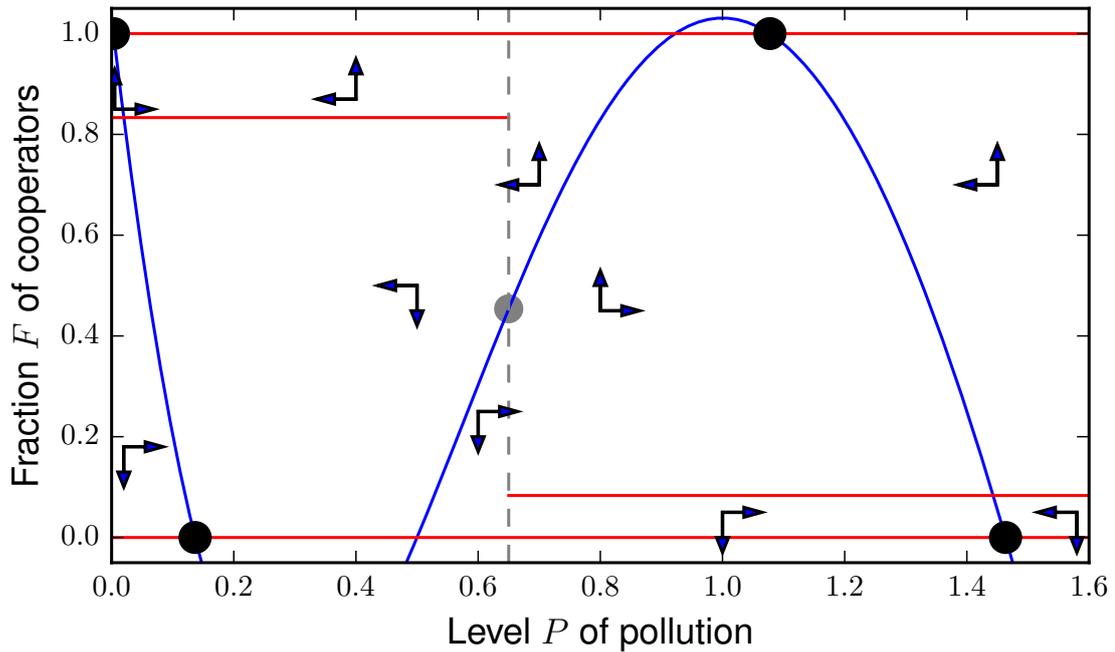


Figure 6.5: Phase plane for the SRM with the threshold (dashed grey line) crossing the  $P$ -nullclines (solid blue curve) on its middle branch, showing the  $F$ -nullclines (solid red lines) and stable equilibria (filled circles), as well as the direction of the flow (arrows). Parameter values as in Fig. 6.2.

low  $P$  and  $F = 0$ ). When the pseudo-equilibrium emerges on the middle branch of the nullcline for the ecological subsystem, it is unstable and does not give rise to a pseudo-cycle. This can be understood geometrically when considering the phase plane as in Fig. 6.5, because the angle between the nullcline and the threshold at their intersection and the directions of the flow make it difficult for the dynamical flow to let a closed trajectory appear.

We can also explain the impossibility to observe a stable pseudo-equilibrium or pseudo-cycles on the middle branch of the nullcline for the ecological subsystem intuitively. The middle branch of the  $S$ -shaped  $P$ -nullcline corresponds to critical values of the pollution level which play the role of a threshold between alternative ecological states: the oligotrophic state where the water is clear and the eutrophic state where it is polluted (Chapter 3). A pseudo-equilibrium occurring in this situation because of the implementation of a threshold is far from all stable ecological states. As a consequence, an initial condition close to this pseudo-equilibrium is attracted by the outer, stable branches of the  $S$ -shaped  $P$ -nullcline. In other words, what seems to determine whether or not the system can remain close to the pseudo-equilibria is the ecological dynamics. When the ecological subsystem imposes its instability on the

coupled system (on the middle branch of the  $P$ -nullcline), the system cannot remain in the same state and is rapidly drawn towards stable steady states. What allows stable pseudo-equilibria and pseudo-cycles on the outer branches of the  $P$ -nullcline is the substability of the ecological subsystem: the coupled system shifts less rapidly in the phase plane and stability is possible. If the pseudo-equilibrium is not stable, the geometrical configuration of flows in the phase plane allow for the integrated system to be caught in a pseudo-cycle.

Stable pseudo-equilibria and pseudo-cycles occur at levels of pollution which are close to stable equilibria but with intermediate values for the cooperation level (Fig. 6.3). In terms of policy making, this suggests that the implementation of a threshold able to force the social-ecological system away from an equilibrium may trap the system around the threshold, but that this cannot happen if the threshold forces the system to move far from equilibria. Thus, vigorous management measures are less likely to retain the system into a minimal-effort stage where agents only do what is necessary. The trajectory shown in Fig. 6.3 would have been impossible if the management threshold had imposed a pollution level lower than 1.0 for example.

### 6.3.2 Non-monotonic response

In this section, we investigate the GRM. In the GRM, the non-trivial nullcline for the socioeconomic subsystem is more complex than in the monotonic cases (LRM, SRM, SRM'). In general, it does not represent a function in the phase plane.

Fig. 6.6 provides an example where the non-trivial  $F$ -nullcline is a closed curve. The dynamical effects of the non-trivial  $F$ -nullcline concern the two equilibria which used to be stable at full cooperation in all previous figures. Indeed, the non-trivial socioeconomic nullcline shifts the most desirable stable equilibrium (lowest pollution, full cooperation) to a significantly lower cooperation level and the equilibrium with a high level of pollution and a high level of cooperation has lost stability.

We refer to the region of the phase plane that is defined by the closed nontrivial  $F$ -nullcline as domain  $\mathcal{D}$ . It is the region where the fraction of cooperator increases. The outcomes of the social-ecological model rely on the interactions between the  $P$ -nullcline and the domain  $\mathcal{D}$ . All uncertainties or unknown characteristics regarding the existence, the location, the shape and the size of the domain  $\mathcal{D}$  impact our ability to anticipate the outcome of management policies using our models.

For example, the domain  $\mathcal{D}$  may be closed like in Fig. 6.6. To our knowledge, closed-curved nullclines have received little attention in the social-ecological literature. This can be explained by the difficulty to find cases where they intuitively make sense beyond their mathematical properties. In our case, to make sense of this closed-curve nullcline, consider equation (6.1). As  $F$  represents the fraction of cooperators in the agents' population, it must be between 0 and 1. This means that,

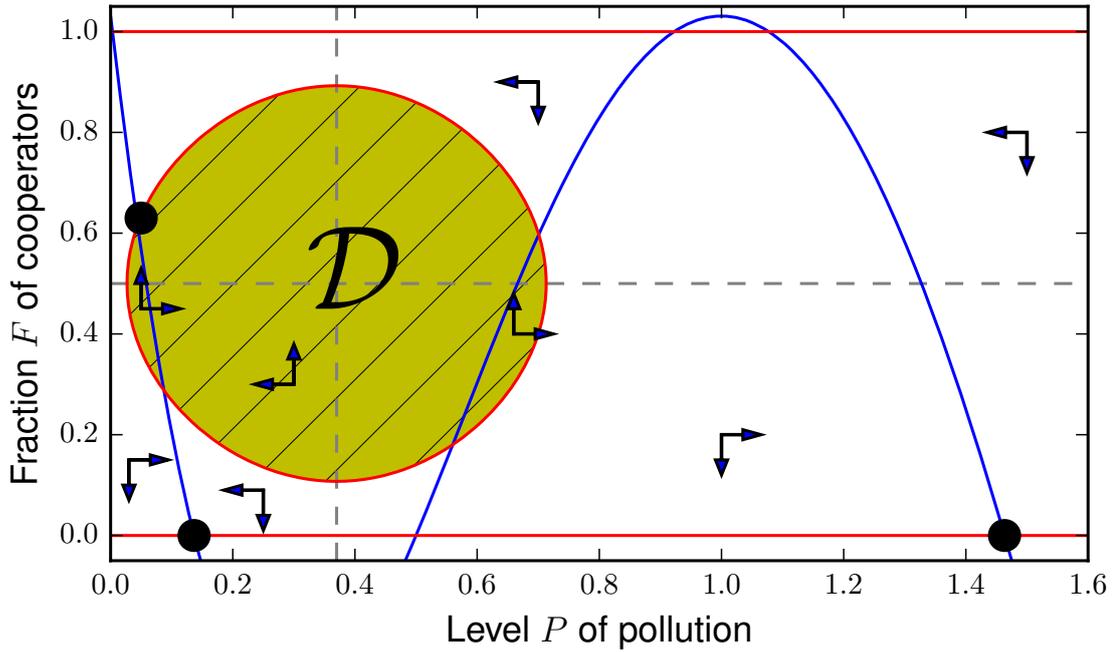


Figure 6.6: Phase plane for the GRM showing the  $P$ -nullcline (blue curve) and the  $F$ -nullclines (red straight lines and closed curve), the direction of the flow (arrows) as well as the stable equilibria (filled black circles). The peak levels  $P_{peak}$  and  $F_{peak}$  are indicated by dashed grey lines and the positive-incentive domain  $\mathcal{D}$  as a hatched surface. Parameter values as in Fig. 6.2 except for:  $v = 7.5$ ,  $\kappa_0 = 4.5$ ,  $\xi_0 = 3.5$ ,  $h_P = 1$ ,  $h_F = 1$ ,  $P_{peak} = 0.37$ ,  $F_{peak} = 0.5$ .

except for the limit cases with full defection or full cooperation, the socioeconomic dynamics is entirely determined by the incentive  $\Delta U$ .

Fig. 6.7 provides an intuitive interpretation of the domain  $\mathcal{D}$ . The domain  $\mathcal{D}$  is the part of the phase plane where the incentive to cooperate  $\Delta U$  is positive, so that cooperation then tends to increase because of equation (6.1). But remember that, in the GRM, the incentive to cooperate  $\Delta U$  defined in equation (6.2) is the sum of a constant and of the two Gaussian functions from equations (6.3),  $\kappa_{GRM}$  and  $\xi_{GRM}$ , varying in  $P$  and in  $F$ , respectively:

$$\Delta U(P, F) = -v + \kappa_0 \exp[-h_P(P - P_{peak})^2] + \xi_0 \exp[-h_F(F - F_{peak})^2]. \quad (6.4)$$

Therefore, as Fig. 6.7 shows, the mathematical formulation for the response functions  $\kappa$  and  $\xi$  within  $\Delta U$  assumes a map of the agent's motivation to cooperate on all possible states of the system.

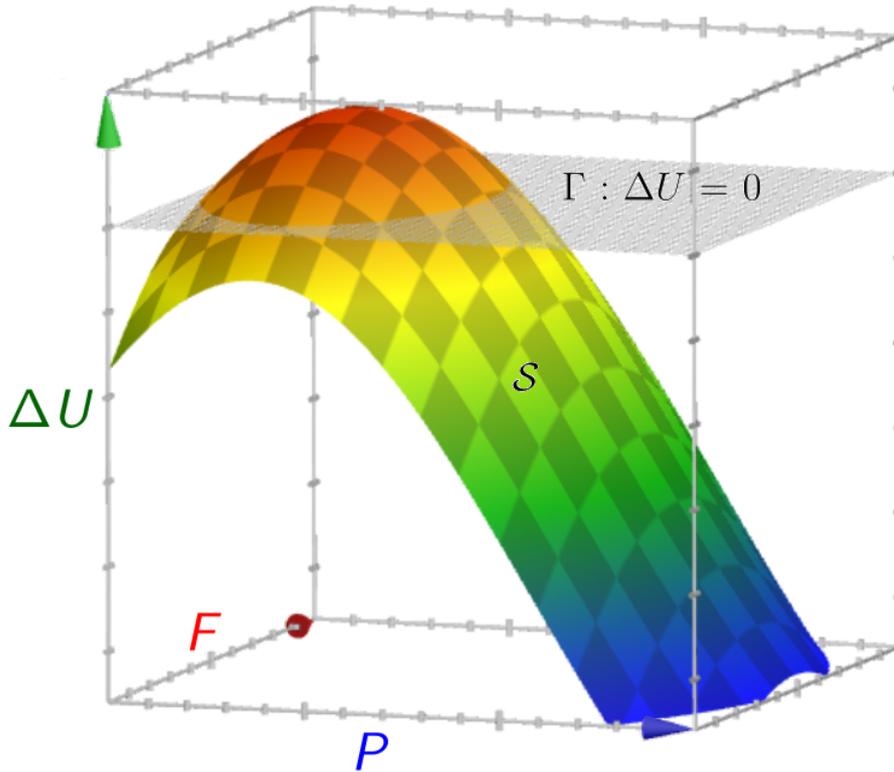


Figure 6.7: Schematic map of the incentive to cooperate  $\Delta U$  over the  $(P, F)$ -phase plane in the GRM, showing the corresponding coloured surface  $\mathcal{S}$  and the plane where the incentive vanishes  $\Gamma : \Delta U = 0$ . The intersection of the incentive surface  $\mathcal{S}$  with the plane  $\Gamma$  is the nontrivial  $F$ -nullcline of the GRM. The part of the phase plane where  $\mathcal{S}$  is above the  $\Gamma$  (where  $\Delta U$  is positive) is the domain  $\mathcal{D}$ .

Since each response function assumes a peak of the incentive for a certain level of the state variables, it makes sense that a domain centered on  $P_{peak}$  and  $F_{peak}$  gathers the highest incentive  $\Delta U$  to cooperate. Among those highest values, some may be positive and define the domain  $\mathcal{D}$ :

$$\mathcal{D} = \{(P, F) \in \mathbb{R}^+ \times [0, 1], \Delta U = -v + \kappa(P) + \xi(F) \geq 0\}.$$

The effect of parameters of the response functions as shown in Fig. 6.1 has direct implications on the domain  $\mathcal{D}$  and on the nontrivial  $F$ -nullcline. For instance, the highest point of the  $\Delta U$  surface in Fig. 6.7, which is the maximum for the value of  $\Delta U(P, F)$ , is  $\Delta U_{max} = \Delta U(P_{peak}, F_{peak}) = -v + \kappa_0 + \xi_0$ . The domain  $\mathcal{D}$  and the nontrivial  $F$ -nullcline exist only if  $\Delta U_{max}$  is positive, that is if the  $\Delta U$  surface in Fig. 6.7 does intersect with the plane where the incentive would vanish. We can see

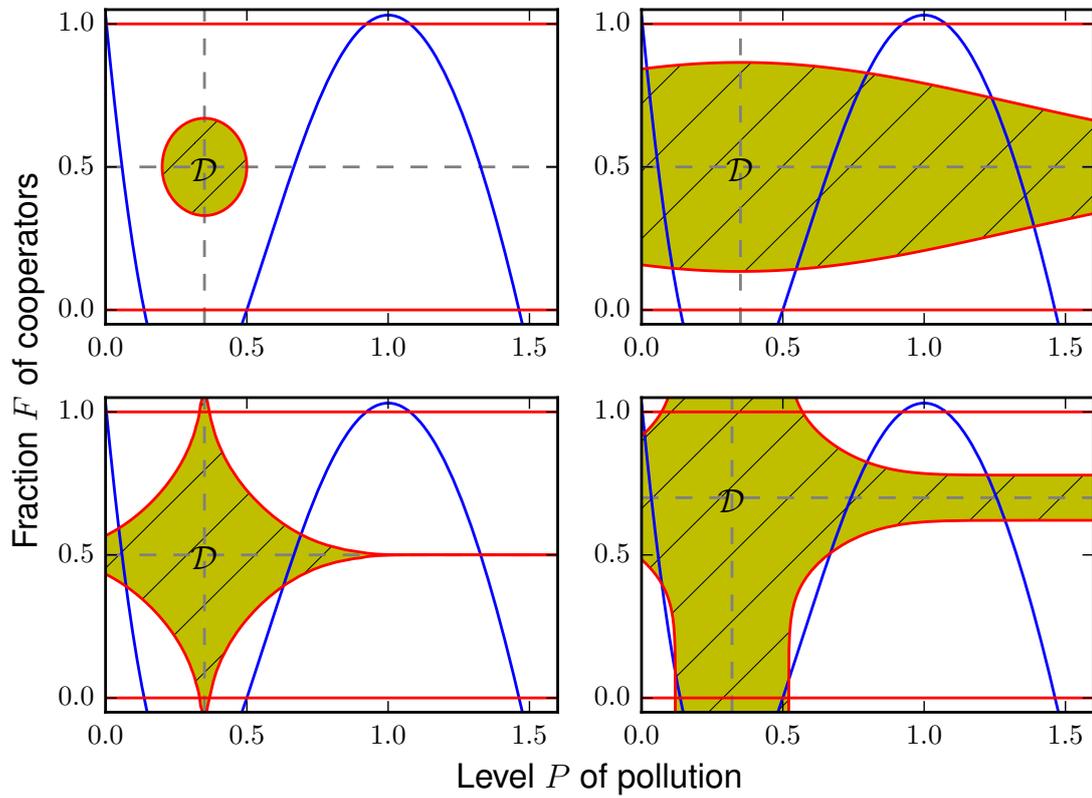


Figure 6.8: Phase planes for the GRM showing the  $P$ -nullcline (blue curve) and different shapes for the  $F$ -nullclines (red straight lines and curves). The peak levels  $P_{peak}$  and  $F_{peak}$  are indicated by dashed grey lines and the positive-incentive domain  $\mathcal{D}$  as a hatched surface. Parameter values as in Fig. 6.6 except, in the top left, top right, bottom left, bottom right order, for  $v = 7.9, 8, 1.5, 1.5$ ;  $\kappa_0 = 4.5, 1, 1.5, 2.2$ ;  $\xi_0 = 3.5, 8, 1.5, 1.7$ ;  $h_P = 1, 1, 20, 9.5$ ;  $h_F = 1, 1, 20, 20$ ;  $P_{thresh} = 0.35, 0.35, 0.35, 0.32$ ;  $F_{thresh} = 0.5, 0.5, 0.5, 0.7$ .

that increasing parameter  $v$  reduces the size of the domain  $\mathcal{D}$  whereas parameters  $\kappa_0$  and  $\xi_0$  tend to extend it. In general, the sheer existence of the domain  $\mathcal{D}$  is not guaranteed because it depends on whether any levels of pollution and of cooperation constitute a sufficient incentive to make the agents cooperate more. Even when the domain  $\mathcal{D}$  exists, its location and/or its size may not allow for the nontrivial  $F$ -nullcline to intersect with the  $P$ -nullcline. This is illustrated in the top left panel of Fig. 6.8.

If, by itself, the maximum  $\kappa_0$  or  $\xi_0$  of the incentive's response to one of the state variables is enough to yield a positive incentive to cooperate, then the peak of the response extends infinitely along the peak line (dashed grey lines in Fig. 6.6 and 6.8). In such a case, the domain  $\mathcal{D}$  becomes open and we do not have a closed nontrivial  $F$ -nullcline. This is illustrated in the top right panel of Fig. 6.8, where the incentive has a high peak response  $\xi_0$  to the fraction of cooperators when it is close to  $F_{peak} = 50\%$  of cooperation among agents. Note that domain  $\mathcal{D}$  then extends across the phase plane horizontally along the peak line  $F = F_{peak}$ . We can also note that it is wider close to the peak of the response to the ecological system  $P = P_{peak}$  because the ecological concern increases even more the incentive to cooperate close to  $P_{peak}$ , as happens in the bottom left panel of Fig. 6.8, where domain  $\mathcal{D}$  is star-shaped. The closed nullcline can open simultaneously because of the incentive's response to both the ecological and the socioeconomic variables, in which case the domain  $\mathcal{D}$  takes the shape of a cross as in the bottom right panel of Fig. 6.8. This gives rise to especially complex cases with up to fourteen equilibria in the last case.

The variety of possible configurations means that there is no straightforward way to predict the number or the location of stable equilibria. If we know the response functions  $\kappa$  and  $\xi$ , we can define the domain  $\mathcal{D}$ , which gives the nontrivial  $F$ -nullcline and allows for accurate anticipation provided that the  $P$ -nullcline is known. However, even small uncertainties on the exact parameterization of the response functions  $\kappa$  and  $\xi$  may lead to a very different configuration of the phase plane. This is due to our primary assumption that the response functions are increasing then decreasing as the state variables increase, which is equivalent to saying that the response of the incentive reaches a peak level. The non-monotonicity of Gaussian response functions does not allow for qualitative predictions unless the location of the peak is known, that is, unless we can distinguish monotonic segments. In other words, behaviours similar to giving up, to resignation or to free-riding, when agents rely on the others' efforts, make anticipation much more difficult than in the case where we can expect a monotonic response.

## 6.4 Discussion

All mathematical social-ecological models are limited by uncertainties on the functional forms they assume. The socioeconomic part can be modelled in different ways (Chapter 4), potentially leading to different outcomes even using the same formulation for the incentive that agents have to influence the ecological system. Here we have shown that, additionally, the monotonicity of the incentive's response to the system itself may dramatically impact our ability to use the model to predict even qualitatively the outcome of policies.

If we expect the response functions to be monotonic, we may wonder whether the socioeconomic system reacts in a linear way, in a more sigmoidal manner or with one or several threshold. Yet, we can infer trends in the model dynamics because of the fundamental expectation that agents feel more concerned when the lake near which they live becomes more polluted. We have shown in Fig. 6.4 that the number of attractors may change, that a cycle could appear as in Fig. 6.3. But we note that the global organization of the phase plane roughly follows the linear case of the LRM studied in Chapter 4. In particular, when considering successively the LRM, the SRM' and the SRM, the stable equilibria tend to be conserved and abrupt changes like when implementing a threshold only result in the system potentially remaining at or around the threshold level.

However, if we expect agents to give up on cooperation when the lake becomes too polluted, or if we expect them to lose motivation once cooperation has become established, new uncertainties come into play. Indeed, predictions become much more difficult unless we can guess where the peak incentive is reached and how high it gets. Such giving-up behaviours may be intuitive regarding the response to the ecological state. Regarding the response to the socioeconomic state, it is similar to the behaviour observed in public health, where vaccination can be difficult to implement so as to reach optimal coverage in the human population. This is due to some individuals relying on the efforts of the majority and discharging their personal responsibility, their incentive as an agent, on the rest of the group.

As a consequence, giving-up behaviour are not only undesirable because of direct effects, on the environment for example, but also because they impair our ability to anticipate and to evaluate what could and should be done in the future.

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# 7 Conclusions

## 7.1 Summary of the results

All main chapters considered mathematical social-ecological models of coupled environmental dynamics and human behaviour dynamics represented by a system of two ordinary differential equations. The ecological context referred to a water stock, to a biotic resource or to lake eutrophication. The socioeconomic subsystem corresponded to either the replicator dynamics or to the logit best-response dynamics. We have investigated linear and nonlinear monotonic cases as well as non-monotonic cases for the response of the agents' incentive to cooperate (adopt a desirable behaviour) to state variables.

Particular definitions of the “linking” between the subsystems of a social-ecological system had suggested that the coupling could introduce complexity features absent from the isolated ecological subsystem (Lade et al., 2013). In Chapter 2, we proposed a straightforward way to unequivocally define the coupling between subsystems in a social-ecological model. With this approach, the coupling can be thought of as being constant in the isolated subsystem. Studying the coupled social-ecological system consists in allowing some constant parameters (the coupling parameters) in each subsystem to vary under the influence of the other subsystems. Under this formal definition, the coupling can introduce multistability in an integrated system comprising subsystems which respond linearly to their own state variable only. It is important to study the nullclines in the phase plane as they can be interpreted intuitively in light of the coupling between the subsystem, which is not the case for direct economic approaches as in Tavoni et al. (2012) or for indirect dynamical approaches such as bifurcation diagrams in Suzuki and Iwasa (2009a).

In chapter 3, a lake pollution model was coupled with a logit best-response dynamics driven by a linear-response incentive for cooperation. This generic coupled model was enough to display counterintuitive equilibria, where the level of pollution remains low despite having no cooperation or where the level of pollution is high despite having cooperation. Counterintuitive equilibria suggest that environmentally desirability and socioeconomic desirability should not be thought of as necessarily associated as could be expected intuitively. For instance, decreasing pollutant discharge is not necessarily the best way to decrease lake pollution.

Multistability allowing for counterintuitive equilibria and oscillations are features of complexity. In the generic model of chapter 3, complexity emerges due to hysteresis in the nullclines. We found model parameters influencing the nullclines' hysteresis analytically. But the model's complexity does not generally allow for generic management recommendations, and we concluded that several policies both with and without socioeconomic intervention had to be considered by decision makers.

In chapter 4, we reconsidered the same model of lake pollution coupled with a best-response socioeconomic dynamics where the incentive to cooperate included linear responses to the state variables, but we compared it to a modified version using the replicator dynamics. As explicit empirical support for specific mathematical models of human behaviour is scarce, it is essential to know the implications of using the replicator or the best-response dynamics. The fundamental difference between the two versions is the assumption of stationarity or non-stationarity of pure strategies (full defection or full cooperation). We found that this fundamental difference could result in a different number of equilibria and in a difference in their stability.

We also found that, in agreement with previous game theoretical studies (Hopkins, 1999; Hofbauer et al., 2009), the model using the best-response dynamics converges towards the model using the replicator when increasing the rationality parameter we denoted by  $\beta$ . Thus, the interpretation of this parameter is key to understand the relation between the two models. Parameter  $\beta$  can be interpreted as the rationality of the agents making a choice in the socioeconomic system, so that  $\beta = 0$  implies a random choice. We found that a best-response dynamics with higher and higher rationality made the coupled model dynamics come closer and closer to the coupled model with replicator dynamics.

Moreover, when using the replicator dynamics, the socioeconomic system is more prone to display an abrupt behaviour in the form of a marked bistability, because of the assumed perfect rationality. Indeed, social conformism then makes it easy for the system to lose stability in intermediate cases where no strong majority emerges in the human population's opinion. As a consequence, the replicator dynamics tends to allow for make-or-break dynamics in the face of oscillations: the system gets very close to full defection or full cooperation, so that alone the timing of a perturbation shifting the population to a pure strategy may determine the final outcome to be either full defection or full cooperation.

In chapter 5, we reviewed the replicator dynamics and the logit best-response dynamics in mathematical social-ecological systems. We found that the replicator dynamics enjoyed a standard status in game theory because of its formal game theoretical foundations, whereas best-response dynamics have their origins in psychophysics and psychology. As a consequence, the replicator dynamics on the one hand leads to analytically simple formulations but does not fit empirical evidence well. On the other hand, the logit best-response dynamics, which is less standard,

is used to accommodate the theory with experimental results. From a modelling point of view, it makes more sense to use the best-response dynamics since it offers different degrees of closeness to the standard replicator approach when varying the rationality parameter of agents. Indeed, the replicator being a limit case of the best-response with an infinite rationality parameter, it can be considered a particular case.

In chapter 6, the lake pollution model is coupled with a replicator socioeconomic subsystem. We varied the way the agents' incentive to follow an environmentally desirable option responds to the environmental state on the one hand and the socioeconomic state on the other hand. Previously, we had assumed that the response was always linear.

We found that monotonic non-linear responses could result in new equilibria, cycles and basins of attraction. Moreover, we considered resignation behaviours as an example of a non-monotonic response, where the response increases then decreases as the stimulus increases. We expected the resulting nullcline to be more complex in general. For example, we found that a giving-up behaviour may produce a closed nullcline. But we also found that additional uncertainties in non-monotonic response formulations could dramatically impair our ability to make predictions.

## 7.2 Evolutionary game theoretical dynamics in social-ecological modelling

Models using the replicator dynamics and models using the logit best-response dynamics disagree because of a fundamental difference: the former assumes that extreme strategies (here, full defection or full cooperation) are stationary, the latter assumes that extreme strategies are not stationary. The replicator dynamics seems more appropriate when having evidence of strong social conformism, where agents tend to follow mass movements (social learning or any kind of social behaviour). The logit best-response dynamics seem more appropriate if there is evidence that group behaviour does not impair individual innovation from the agents, who tend to act independently (biological mutations and similar systems where variation happens on a constant random basis). More work should be carried out to explore further implications of the dynamics chosen on the coupled dynamics of the integrated social-ecological model and on management conclusions. In the case where no formulation of the socioeconomic subsystem is better supported by empirical data or a theoretical, mechanistic account, it would be ideal to check which conclusions hold for several formulations as part of a model-structure sensitivity analysis of the model outcomes.

The logit best-response dynamics has the advantage of allowing for the exploration of various levels of rationality in the agents. It also provides a better fit to empirical data in controlled behavioural economic experiments (Lim and Neary, 2016; Mäs and Nax, 2016). It is still unknown to what extent this result could be generalized to other experimental settings and it is doubtful whether and how it could be verified for less controlled complex decisions in social-ecological systems (Schlüter et al., 2017). More research is needed to link the theory of socioeconomic models to the actual socioeconomic behaviours that can be observed in human groups or structures. Thus, in general, if comparing different socioeconomic dynamics directly is not possible or too cumbersome, we should keep in mind that the often implicit assumptions on the behaviour of the socioeconomic system might be a weakness for the observed result.

### 7.3 Complexity

All mathematical social-ecological models are limited by uncertainty in the functional forms they assume. Nevertheless, we found dramatic differences between cases where monotonicity is assumed and cases where non-monotonicity is expected. If, for example, we expect the response functions to be monotonic, we may wonder whether the socioeconomic system reacts in a linear way, in a more sigmoidal manner or with one or several thresholds. Yet, we can infer trends in the model dynamics because of the fundamental expectation that agents feel more concerned when the lake near which they live becomes more polluted. However, if we expect agents to display a giving-up behaviour, predictions become much more difficult, unless we know the resignation function accurately. Such giving-up behaviour has been observed in public health, where vaccination can be difficult to implement so as to reach optimal coverage in the human population since a part of the population choose to rely on the efforts of the majority (Bauch, 2005). As a consequence, resignation behaviours are not only undesirable because of direct undesirable effects on the environment but also because they impair our ability to anticipate and to evaluate what could or should be done in the future.

With more complex non-linearities as in the case where both the ecological system and the socioeconomic system are bistable, we observe that there can be counterintuitive stable equilibria achieving either the ecological aim (low pollution level) or the social objective (dominance of the environment-friendly behaviour), but not both. The possibility of counterintuitive equilibria may not have been stressed much in the literature, since it can be obvious from a mathematical modelling point of view. The fact that even simple models (*e.g.* Suzuki and Iwasa, 2009b; Tavoni et al., 2012; Lade et al., 2013) can display such counterintuitive equilibria suggests that they are widespread. This also makes predictions more difficult since it mitigates

the assumption that there must be a single absolute optimum for both the ecological subsystem and the socioeconomic subsystem. Thus, counterintuitive equilibria should make us question the assumption that certain ecology-oriented actions are a condition for an ecological “good” state at a stable equilibrium: our findings suggest that there is no obvious correlation between environment-friendly actions and reaching an ecologically desirable state. Therefore, considering counterintuitive equilibria is essential in a management perspective.

## 7.4 Management of social-ecological systems

Coupled social-ecological systems are studied notably for the insights they give about potential management options (Levin et al., 2012; Bauch et al., 2016; Colding and Barthel, 2019). In particular, socioeconomic measures, such as awareness campaigns or the implementation of taxes, subsidies, nudges or other incentives, may be used with the goal of achieving a more desirable ecological state. We should not forget, however, that direct action on the ecological subsystem might be possible and might be more effective than socioeconomically mediated policies to achieve an ecologically desirable state. Policy measures impacting either or both subsystems can impact a social-ecological system in many different ways. Indeed, they can shift stable equilibria towards more or less desirable states, they can change the resilience of stable states, with environment-friendly management measures increasing the resilience of desirable equilibria while decreasing the resilience of undesirable equilibria, and they can make stable states appear or disappear. The broad range of possible policies is due to coupled social-ecological systems being particularly complex in comparison to isolated subsystems. Specifically, multistability may allow for counterintuitive stable states to exist. The outcome of ecological or socioeconomic management measures on the state of the system depends not only on the extent of the measure but also on the current state of the system, and this sensitivity is further enhanced by multistability.

Yet, measures can also aim at enhancing the system’s resilience, which relates to the basins of attractions rather than to the location of the system in the phase plane. Increasing the resilience in a social-ecological system may be used to prevent harmful regime shifts (Crépin et al., 2012). Indeed, social-ecological systems are known to display critical transitions around tipping points, which has many implications (Levin et al., 1998). For instance, the cost of moving to or escaping from a specific equilibrium may be particularly high or particularly low. Moreover, we might be able to use knowledge about a tipping point so as to inform the allocation of resources in order to invest effort in desirable regime shifts or in avoiding or reversing undesirable ones, and in order not to waste effort in preventing an inevitable event.

The complexity of social-ecological systems suggests that it may be more effective to spend resources to study a particular system in order to decrease our uncertainties about the policies' consequences, rather than testing management measures. However, unknowns regarding the socioeconomic subsystem may prevent scientists from making reliable predictions. We have shown indeed that different ways to model the socioeconomic component of a social-ecological system may yield different number of stationary states with a different stability. There are different levels at which expectations can be uncertain: some prediction remains possible even in the face of non-linearities as long as some regularity is retained, such as monotonicity of human behavioural responses to the ecological subsystem and to the socioeconomic subsystem. Yet, actual predictions for human behaviour remain approximate and are restricted to very controlled, artificial situations like behavioural economics or game theory experiments, which suggests that some unknowns will always remain in our theoretical knowledge of a specific social-ecological system (Schlüter et al., 2017).

As a consequence, we must implement policy measures on systems that we can know only partially. Since non-monotonic responses such as giving-up behaviours, resignation effects or the tendency to rely on the others' efforts are particularly bad for the reliability of our expectations about a social-ecological system, it is essential that individuals who can influence the system should learn not to give up and to avoid relying on the others' actions. Thresholds implemented through legal means may help shifting the system away from an undesirable state. Nevertheless there always remains a risk that the social-ecological system then gets trapped around the critical level implemented rather than shifting further to a more desirable state.

### 7.5 Modelling social-ecological systems: perspectives

Social-ecological models constitute a recent, growing interdisciplinary academic field (Schoon and van der Leeuw, 2015; Colding and Barthel, 2019). We have focused on generic mathematical models which may remain accessible to mathematics-inclined scientists on the one hand, who might be familiar with even more mathematical approaches of social-ecological systems such as optimal control (Mäler et al., 2003; Ibáñez et al., 2004; Kossioris et al., 2008), and accessible, on the other hand, to researchers who are more inclined towards social sciences and might be more familiar with social identity or agent-based simulations (Schlüter et al., 2017; DeAngelis, 2018; Railsback and Grimm, 2019; Schlüter et al., 2019). Our contribution has consisted in defining a sound basis from generic and/or well-established ecological

models and from a discussion about different ways to model the socioeconomic component.

This basis may be extended in several ways. Firstly, we have not considered space in our models. The example of lake eutrophication can be much more complex when including space. For instance, continuous space may account for spatial heterogeneity in environmental conditions. Pollution in shallow freshwater lakes takes place at a local or regional level. The spatial organization of the ecological subsystem may be decoupled from the spatial organisation of the socioeconomic subsystem, where decision makers and management institutions as well as group effects among agents are not bound by ecologically relevant lake networks. Discontinuous representations of space include heterogeneous, interconnected patches with a grid-approach (Vortkamp et al., submitted) or with a network approach (Boyd, 2012). Secondly, the social-ecological literature also considers methods for prediction and early warning signals of critical transitions (Bauch et al., 2016; Filatova et al., 2016). Extensions of the models studied in this thesis could contribute to this branch of the literature if for instance agents could respond to early warning signals, that is if knowledge about the likeliness of a regime shift could play a role in their incentive to take action for the environment. Thirdly, the ecological subsystems we have considered were not so complex as to include cycles for instance. It would be interesting to explore further ecological resources and to include stochasticity in the models we have studied.

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# Erklärung über die Eigenständigkeit der erbrachten wissenschaftlichen Leistung

Gemäß §8(2)b) der Promotionsordnung der Fachbereiche Physik, Biologie/Chemie, Mathematik/Informatik der Universität Osnabrück für die Verleihung des Grades Doktorin oder Doktor der Naturwissenschaften (Dr. rer. nat.) erkläre ich hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet.

Bei der Auswahl und Auswertung folgenden Materials haben mir die nachstehend aufgeführten Personen in der jeweils beschriebenen Weise unentgeltlich geholfen:

- Prof. Dr. Frank M. Hilker contributed to the design of the studies, to the development of the models and to the review of the drafts for Chapters 2 to 6.

Weitere Personen waren an der inhaltlichen materiellen Erstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich hierfür nicht die entgeltliche Hilfe von Vermittlungs- beziehungsweise Beratungsdiensten (Promotionsberater oder andere Personen) in Anspruch genommen. Niemand hat von mir unmittelbar oder mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

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