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

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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 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 low level (cooperation). It is known that feedbacks between the interacting lake pollution and human behaviour can give rise to complex dynamics with multiple stable states and oscillations. Here, we analyze the impact of all model parameters on the shape of the nullclines. S-shaped nullclines are a condition for complex dynamics to occur. Moreover, we find that agents decreasing their pollution discharge into the lake is not necessarily the most effective way to reduce the pollution level in the lake. This is due to coexisting counterintuitive stable equilibria where the lake is in a clear state despite a high level of pollution discharge. We analyze the complex dynamics of the system and describe in detail Hopf, saddle-node, homoclinic and Bogdanov-Takens bifurcations. 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. Apart from the direct perturbation of an ecological variable, we identify three ways a management strategy can influence the social-ecological system: it can change the location, the resilience and the existence of stable equilibria.

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 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*[1] 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; 2009b), for harvested wildlife and fish populations (Bieg et al., 2017;

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[1] Throughout this article, terms appearing in italics when used for the first time are defined in Table 1.

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Table 1
Glossary of terms used in this paper. 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 *defection* and *cooperation*.
attractor	Stable equilibrium or oscillations attracting neighbouring states within the basin of attraction.
cooperation	Individual behaviour of *agents*, resulting here in a lower pollution discharge.
coupling parameter	Mathematical *parameter* whose interpretation links the two *subsystems*.
defection	Individual behaviour of *agents*, 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 $P_1 < P_2$. It is socially more desirable if and only if $F_1 > F_2$.
multistability	Coexistence of several *attractors*, 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 *state variables P* and *F*.
resilience /resistance	Size of the basin of attraction of a given *attractor*. Theoretical ecologists use *resistance* (Grimm and Wissel, 1997) or *ecological resilience* (Holling, 1973; 1996; Van Nes and Scheffer, 2007), whereas social scientists refer to *resilience*.
state variable	Continuous variable representing the state of a *subsystem*. 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, *cooperation* or *defection*, that is individual behaviours.
subequilibrium	Equilibrium for one *subsystem*. 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 *state variable* is fixed.

Fryxell et al., 2010) 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; Schwinning and Parsons, 1999; Westoby et al., 1989), 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., 2017; 2014), 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 can display fast transitions between two alternative stable states due to the anthropogenic 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. The alternative stable states are 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; 2009b) has extended this ecological model by adding a socioeconomic part. It consists in the logit best-response dynamics of evolutionary game theory (Iwasa et al., 2007; Satake and Iwasa, 2006; Satake et al., 2007a; 2007b), which is able to represent the bistability in the collective choice that humans make regarding whether or not to pollute, 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 of which up to four can be stable, as well as cases with sustained oscillations. They investigate which parameters promote this complexity by heuristically comparing the shape of nullclines for particular parameter values. 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 whole model in continuous rather than discrete time. This allows us to build on the well-established theory of differential equations. By contrast, Suzuki and Iwasa (2009b) use a discrete-time formulation. Here, we follow Iwasa et al. (2010) in using a continuous-time reformulation. Since the explicit time lag incorporated within discrete-time models can typically lead to more complex dynamics than in continuous-time models, we may expect that some of the qualitative dynamis in the discrete-time model may be due to explicit time lags, but we do not find any indication in this direction. 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 article 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

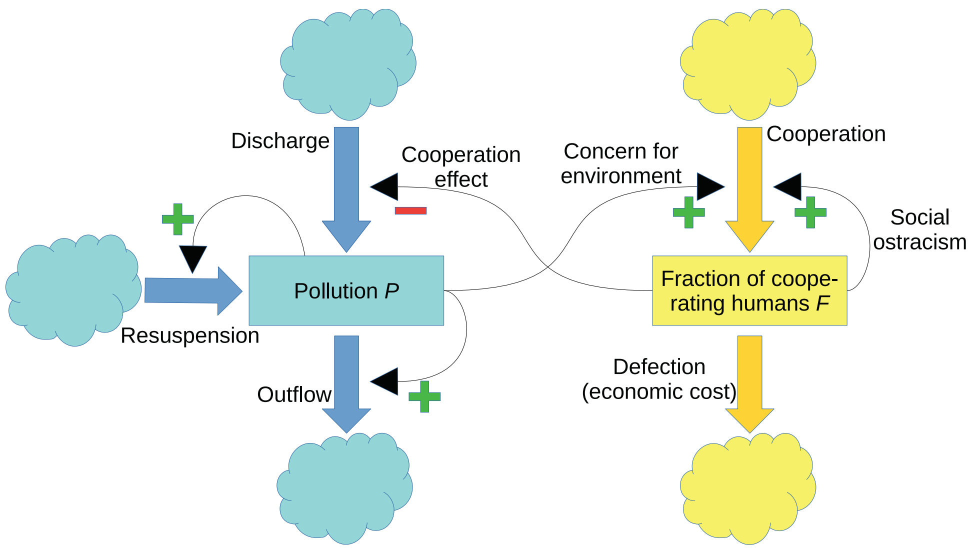

Fig. 1. Schematic representation of the coupled social-ecological model. The ecological subsystem is shown on the left, in blue, and the socioeconomic subsystem on the right, in yellow. Thick arrows show fluxes or pseudo-fluxes between compartments, whereas thin arrows represent the influence of a compartment 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the water, because some other coexisting, counterintuitive stable 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).

2. Model

In this section, we describe our mathematical model. It comprises two interconnected subsystems: an ecological part and a socioeconomic part (Fig. 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 article, the term "cooperation", which comes from game theory, does not refer to a social interaction, but rather to an environment-friendly behaviour (Table 1).

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 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 α. 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, developped 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 $0 \leq \delta_p \leq p_D$. δ_p is the reduction observed in the discharge when switching from defection to cooperation: it is a cooperation effect. 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.

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 (Iwasa et al., 2010; Suzuki and Iwasa, 2009b), relative to the ecological subsystem. The more conservative the agents in keeping and not switching their strategy, the lower s (Satake and Iwasa, 2006). f can be interpreted as the transition rate of 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 β. β can be interpreted as the agents' rationality: if β is very large, then all agents immediately choose the best option according to ΔU.

The variable ΔU 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, ΔU 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 ΔU:

- the baseline $(-\upsilon)$ 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 κ: 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 ξ accounting for the strength of the agents' conformist tendency: the more cooperators there are, the more people tend to cooperate.

We thus obtain:

$$\Delta U = \underbrace{-\upsilon}_{\substack{\text{economic}\\ \text{baseline}}} + \underbrace{\xi F}_{\substack{\text{social}\\ \text{ostracism}}} + \underbrace{\kappa P}_{\substack{\text{ecological}\\ \text{concern}}}. \tag{1}$$

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

$$\Delta U = -\upsilon + (1 + \xi F)(1 + \kappa P), \tag{2}$$

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 Eq. (1), which is actually a linearization of (2).

2.3. Integrated system and coupling parameters

The integrated model is:

$$\begin{cases} \frac{\mathrm{d}P}{\mathrm{d}t} = -\alpha P + \dfrac{rP^q}{m^q + P^q} + p_D - \delta_p F \\ \frac{\mathrm{d}F}{\mathrm{d}t} = s\left[\dfrac{1}{1 + \mathrm{e}^{-\beta(-\upsilon+\xi F+\kappa P)}} - F\right] \end{cases} \tag{3}$$

All parameters of the model are positive. The parameters in the environmental subsystem describe lake properties except for p_D and δ_p. The parameters in the human subsystem describe the socioeconomic situation. The interpretation of all parameters is summarized in Table 2.

There are exactly two *coupling parameters* linking the two subsystems, namely κ and δ_p:

- the influence of the ecological subsystem on the human subsystem is represented by κ, 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 δ_p, which tells us how different the two strategies are in terms of their discharge levels; we will refer to it as the cooperation effect (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 (κ): 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 ΔU, which introduces an influence of the lake pollution level on the socioeconomic subsystem.

The human subsystem influences the lake pollution through the cooperation effect (δ_p): when there is no difference between cooperators and defectors ($\delta_p = 0$), *i.e.* no impact of cooperation, then the 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.

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. Nevertheless, it is possible to gain insight by studying the nullclines. Nullclines represent *subequilibria* in the phase plane and their intersections are equilibria of the coupled system. We prove in Appendix A.2 that each nullcline either represents a strictly monotonic function (not shown here) or takes the shape of an *S*. In the latter case, we have an S-shaped ecological nullcline (P-nullcline, Fig. 2, top) or an S-shaped socioeconomic nullcline (F-nullcline, Fig. 2, bottom). S-shape configurations allow for complex multistability to emerge, with alternative stable equilibria having different levels of pollution or cooperation.

We prove that there is at least one and at most nine equilibria (Appendix A). In the latter case, the nine nullcline intersections can be schematically ordered as a 3 × 3 array in the (P, F)-plane (Fig. 3). The four equilibria on the corners are stable ones. When there are four stable equilibria, we label them $(P_{lo}, F_{lo})^*$, $(P_{lo}, F_{hi})^*$, $(P_{hi}, F_{lo})^*$ and $(P_{hi}, F_{hi})^*$, where *lo* means a low value of the state variable and *hi* means a

Table 2
Influence of parameters on the condition for nullclines to be S-shaped and potentially exhibit multistability, based on the analysis in Appendix C. For comparison, we provide numerical results reported by Suzuki and Iwasa (2009b) based on a visual analysis of the nullcline for selected parameter values. Parameters given in the upper part influence the ecological nullcline whereas parameters in the lower part of the table influence the socioeconomic nullcline. We report the impact on the existence of S-shaped nullclines as: positive (+), negative (-), none (0) or not reported (./.) A positive (negative) impact means that the nullcline is more (less) likely to be S-shaped if the parameter increases.

Parameter	Interpretation	Impact on the potential for multistability as permitted by S-shaped nullclines	
		this paper	Suzuki and Iwasa (2009b)
p_D	discharge of defectors	0	./.
δ_p	cooperation effect	0	./.
$p_D - \delta_p$	discharge of cooperators	0	./.
α	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	./.
β	rationality of agents	+	./.
υ	economic cost of cooperation	0	+
κ	ecological concern of agents	0	./.
ξ	conformism of agents	+	+

high value of the state variable, relatively to the value of the state variable at other equilibria. We do not assume a necessary correlation between this relative location of stable equilibria and their absolute desirability in social or ecological terms. However, 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 $(P_{hi}, F_{lo})^*$. Indeed, in $(P_{lo}, F_{hi})^*$, the lake is in a relatively clear state and many agents cooperate. On the contrary, in $(P_{hi}, F_{lo})^*$, the lake is polluted and agents defect.

With no coupling ($\delta_p = 0$ and $\kappa = 0$), the subsystems are isolated: their dynamics are independent (see Fig. 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 (threshold). This explains why, among the nine possible equilibria, the stable ones are located at the corners of the 3×3 array. The unstable threshold line also gives a boundary between the basins of attraction of stable equilibria (Fig. 3).

3. Results

In this section, we focus on the coupled system ($\delta_p > 0$ and $\kappa > 0$). We first summarize analytical results concerning the influence of each parameter on the appearance of an S-shape configuration in the nullclines, a condition for the model to allow for complex dynamics (multistability 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.

3.1. S-Shaped nullclines

In the simplest cases, the model has a unique equilibrium (see Appendix A for the proof) which is asymptotically stable. This happens when nullclines represent monotonic functions. From this situation, changes in parameters can give the nullclines an S-shape (see Appendix A for the proof). More complex dynamics emerge when the nullclines are S-shaped and this S-shape is a necessary condition for the nullclines to have new intersections. Thus, S-shaped nullclines are a necessary but not sufficient condition for complex dynamics to occur, such as multistability.

Whether or not the nullclines are S-shaped can be investigated analytically based on their algebraic expression. We provide in Appendix C the analytical condition for each nullcline to be S-shaped. The influence of all parameters on the existence of an S-shaped nullcline is summarized in Table 2.

Four parameters (α, r, m and q) have an impact on the existence of an S-shaped P-nullcline. The other parameters have no influence on the existence of an S-shaped P-nullcline. The S-shape in the ecological nullcline depends only on the lake's properties, not on the influence that humans have on it.

Two parameters (β and ξ) have an impact on the existence of an S-shaped F-nullcline. The other parameters have no influence on the existence of an S-shaped F-nullcline. The S-shape in the socioeconomic nullcline depends only on features of the agents, namely their rationality and their conformism.

Interestingly, coupling parameters have no influence on the existence of S-shaped nullclines. That is, how much pollution defectors or cooperators discharge in the lake (δ_p) cannot make an S-shape configuration appear or disappear. Economic (υ) and ecological (κ) incentives similarly play no role in the appearance of a configuration with S-shaped nullclines.

Table 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 α), if the resuspension r is large, if the lake is shallow (large q) or if the agents are very responsive to social pressure (large ξ). Our analytical results confirm simulations from Suzuki and Iwasa (2009b) for two parameters (the resuspension rate r and the agents' conformism ξ) and contradict them for one parameter (the cost c of cooperation), which is however not exactly homologous in our two models. Regarding the seven other parameters we have investigated here, no result was previously reported on the existence of S-shaped nullclines.

3.2. Impacts of mutual feedbacks κ and δ_p on equilibria

We have already shown that the coupling parameters have no influence on the existence of S-shaped nullclines, but that they can flatten or stretch them. As a consequence, 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 an equilibrium.

3.2.1. Location of stable equilibria

Varying the strength of each unidirectional feedback may shift the equilibrium point to more desirable levels of pollution and cooperation (Figs. 2 and 4). Indeed, the model's behaviour fits our intuition: considering any stable equilibrium, if cooperators reduce the amount of pollution they release (increased cooperation effect δ_p), the pollution level decreases, and if agents care more about the lake (increased ecological concern κ), then they tend to cooperate more.

However, Fig. 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 among the agents' strategies, the impact of the cooperation effect δ_p is negligible. On the contrary, even modest changes to cooperation effect δ_p change the $(P_{hi}, F_{hi})^*$ equilibrium drastically and can drive a saddle node bifurcation that makes it disappear (Fig. 2, top, $\delta_p = .024$).

3.2.2. Resilience of stable equilibria

The larger a basin of attraction, the more *resistant* to perturbations its *attractor*. The boundaries between basins of attraction are called separatrices. Here (Fig. 4), they correspond to invariant manifolds of unstable equilibria. How those unstable equilibria are affected by mutual feedbacks can already be seen in Fig. 2, where unstable equilibria correspond to non-marked intersections between red and blue sets. Fig. 4 illustrates the effect of increasing feedbacks on the resistance of equilibria in cases with bidirectional coupling. Increasing δ_p shifts unstable equilibria towards higher levels of pollution and increasing κ shifts unstable equilibria towards lower levels of cooperation. This holds for cases with a unidirectional coupling as well as for cases with a bidirectional coupling (see Appendix 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. 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. 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. 4), the same feedbacks make the equilibrium lose resistance to perturbations. Overall, management strategies which consist in increasing the cooperation effect and the ecological concern may end up increasing the resilience of desirable

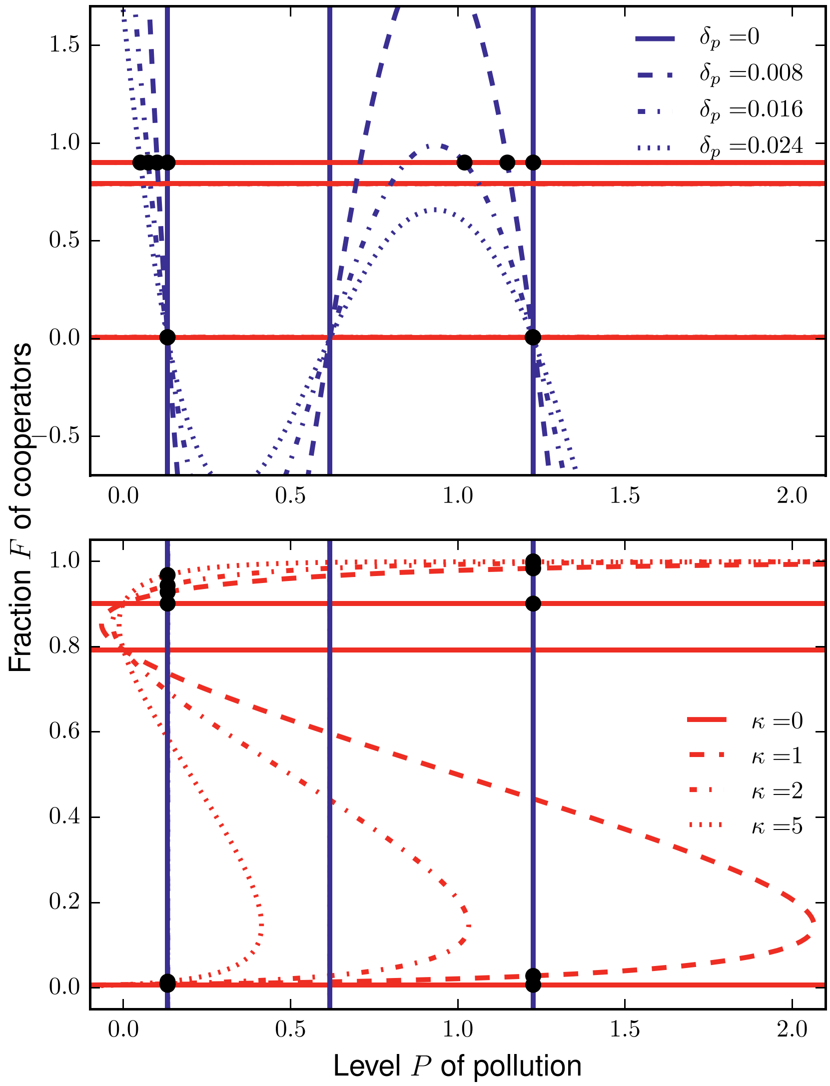

Fig. 2. Phase plane for the model with unidirectional coupling introduced by the cooperation effect δ_p (top) or by the ecological concern κ for the lake (bottom). The vertical P-nullcline (blue) is shown for $\kappa = 0$ and (top) for several values for δ_p. The horizontal F-nullcline (red) is shown for $\delta_p = 0$ and (bottom) for several values for κ. Only stable equilibria are marked (filled circles). Parameter values: $\alpha = 0.4$, $r = 0.75$, $q = 2$, $m = 1$, $p_D = 0.04$, $s = 0.1$, $\beta = 1$, $\upsilon = 5$, $\xi = 8$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

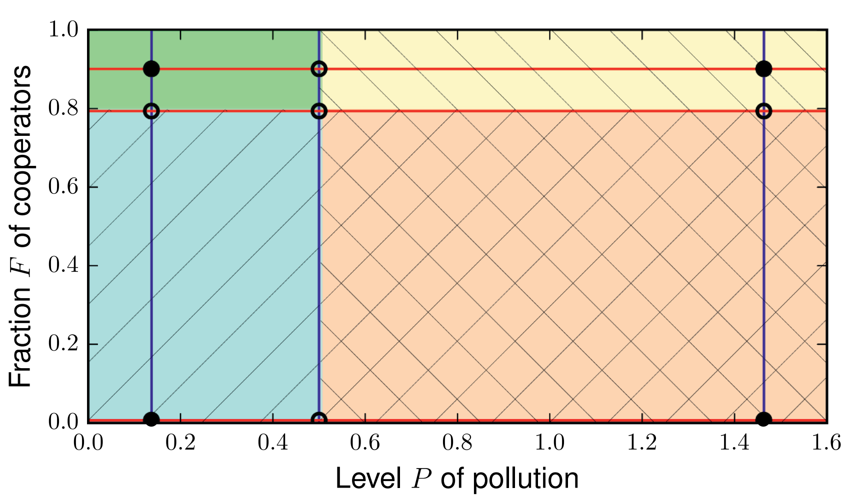

Fig. 3. Phase plane for the uncoupled model showing the vertical P-nullclines (blue) and the horizontal F-nullclines (red). Filled circles show stable equilibria, and unfilled circles show unstable equilibria. Basins of attraction are indicated by colour and hatching. Parameter values as in Fig. 2, except for $r = 0.8$, $\delta_p = 0$ and $\kappa = 0$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

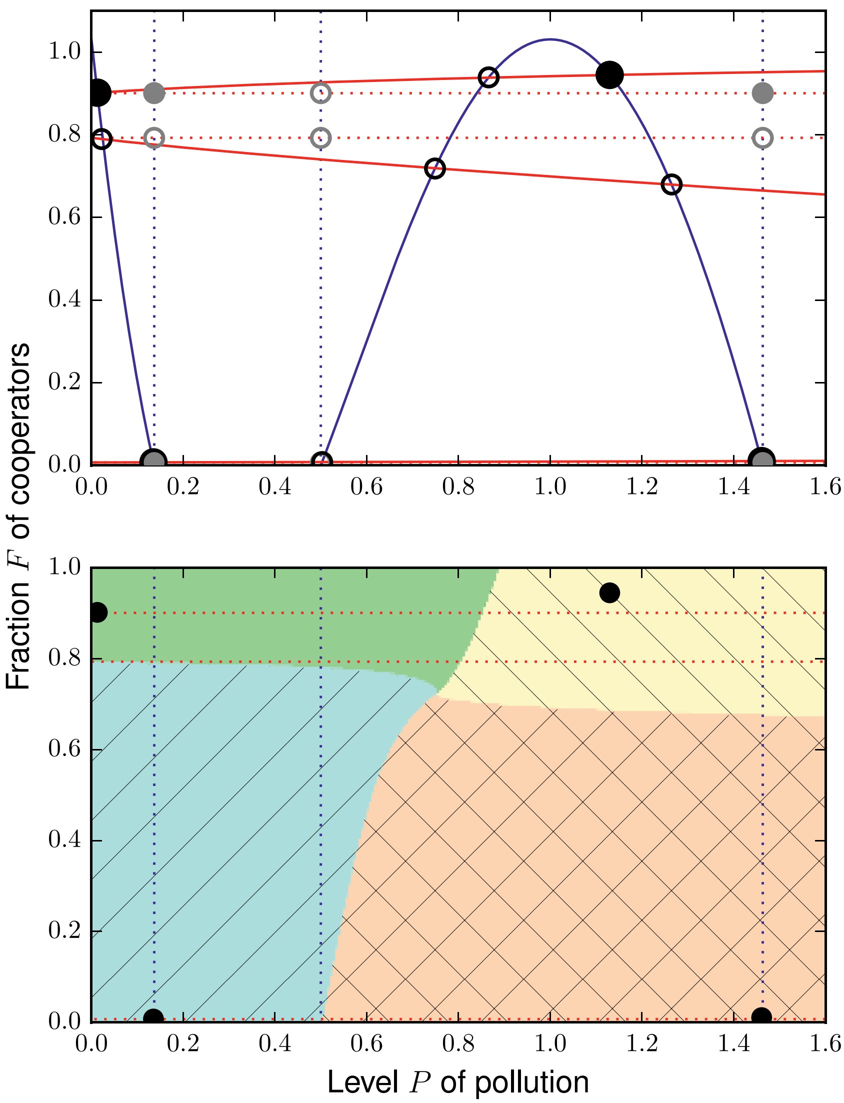

Fig. 4. Location of equilibria (top) and resilience of the stable equilibria (bottom) in the coupled system. Top: *P*-nullclines (blue) and *F*-nullclines (red) for the uncoupled system (dotted) and with coupling (solid); the equilibria are marked as grey and black circles, respectively. Filled circles show stable equilibria, and unfilled circles show unstable equilibria. Bottom: Basins of attractions of the uncoupled system (shown by the middle dotted lines) and with coupling (shown by coloured and/or hatched surfaces). We only show stable equilibria of the coupled system, which are the attractors for each basin of attraction. Parameter values as in Fig. 3, except for $\delta_p = 0.03988$ and $\varkappa = 0.25$. To obtain the basins of attraction, we discretized the phase plane, ran a simulation for each initial condition and coloured each initial condition depending on the equilibrium to which the system converges. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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: 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. 4, bottom).

Fig. 5 shows how the same initial condition can lead to completely different attractors depending on the location of the separatrices when parameter values change: 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.

3.2.3. *Collapse of equilibria*

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 B), illustrated by Fig. 2. When the cooperation effect 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. 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. 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.

Like for the location of equilibria, we cannot relate the existence or collapse of equilibria to changes in parameters in an easy way. As a consequence, we cannot give any generic conclusion as to the impact of a model parameter on the robustness of equilibria due to the model complexity. Nevertheless, Table 2, insofar as it sums up the analytical conditions for having S-shaped nullclines, suggests which parameters make multistability more likely. This relates to the robustness of equilibria as follows: if at the same time multistability exists and becomes unlikely, then some equilibrium must have a lower and lower

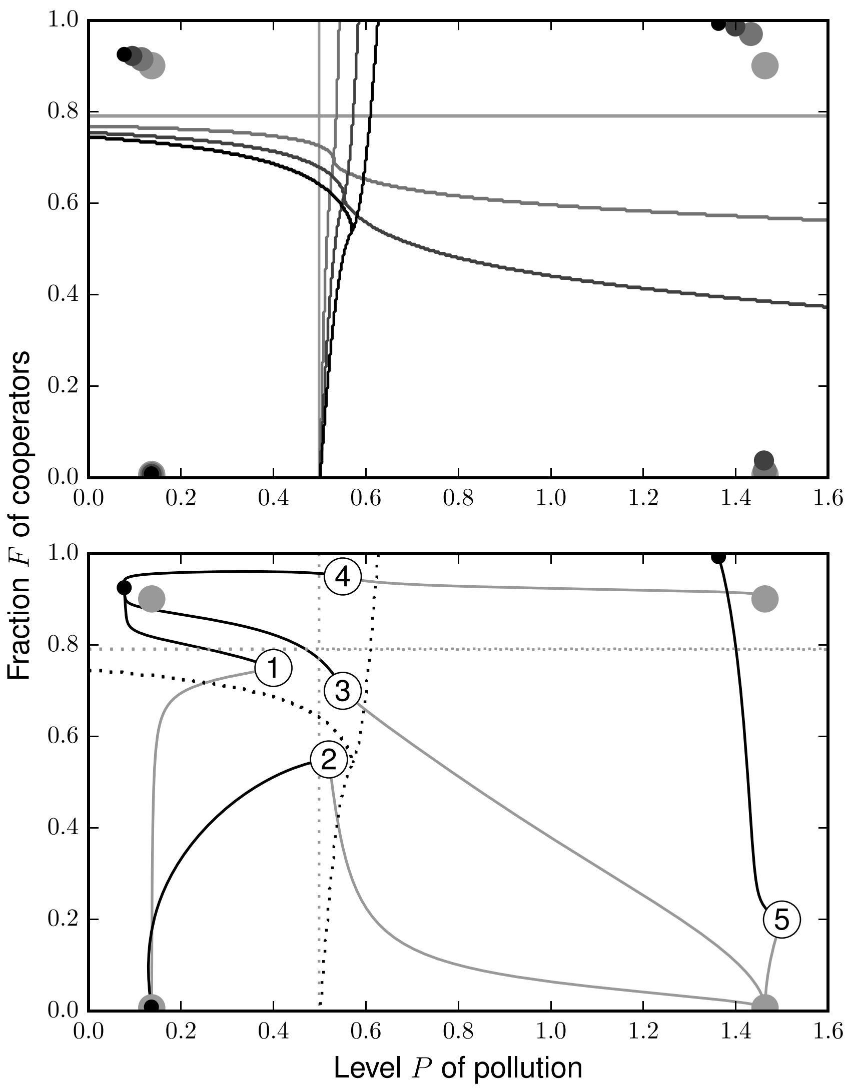

Fig. 5. Top: Basins of attraction for the coupled system with an increasing bidirectional coupling. From light to dark grey, the separatrices as well as the stable equilibria are shown for an increasing coupling, respectively for (δ_p, κ) = (0, 0), (0.005, 0.5), (0.01, 1) and (0.015, 1.5). Bottom: Some trajectories are given for the first case and for the last case, starting from the same initial conditions (P_0, F_0) indicated by circled numbers. Parameter values as in Fig. 3 except for δ_p and κ.

robustness and some equilibrium must become very robust. Thus, assuming a multistable case, a collapse may be more likely to occur if (Table 2) the outflow of pollution increases, if the resuspension rate decreases, if the lake is deeper, if agents are less rational or subject to less conformism.

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.

Such counterintuitive equilibria are related to lock-in effects due to the bistability of the subsystems. We call them "counterintuitive" because their relative location does not fit the expectation that cooperation should lead to a low level of pollution, or that defection should lead to a high level of pollution.

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. 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. Both (P_{lo}, F_{lo}) and (P_{hi}, F_{hi}) are counterintuitive equilibria. 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 even though this may be true in some parameter settings.

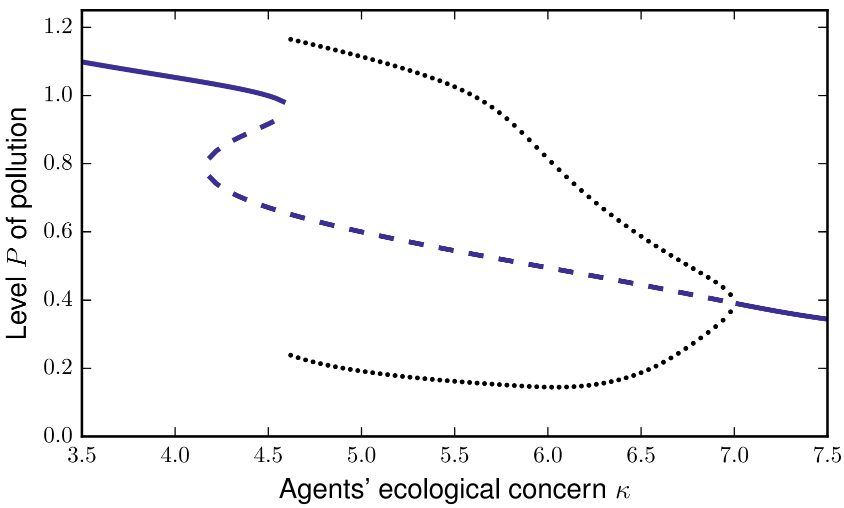

Fig. 6. Bifurcation diagram for the coupled system with varying level of ecological concern κ, showing the level P of pollution for stable equilibria (solid blue), unstable equilibria (dashed blue) and the amplitude of limit cycles (dotted black). There are saddle-node bifurcations at $\kappa \approx 4.1$ and $\kappa \approx 4.6$, a concomitant homoclinic bifurcation at $\kappa \approx 4.6$ and a supercritical Hopf bifurcation at $\kappa \approx 7.0$. Parameter values: $\alpha = 0.26$, $r = 0.515$, $q = 2$, $m = 1$, $p_D = 0.04$, $\delta_p = 0.0388$, $s = 0.1$, $\beta = 1$, $\upsilon = 5$, $\xi = 4$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Oscillations and bifurcations

Up to this point, we have focused on multistable cases with four stable equilibria. Here, we explore other cases through a numerical bifurcation analysis. Indeed, we have already shown that equilibria can disappear (Fig. 5) because of a saddle-node bifurcation, as suggested by Fig. 2. Here, we additionally find that the model can show sustained oscillations and undergo global bifurcations. Complex bifurcation diagrams support the idea that the model is too complex for generic predictions to be valid in all cases.

3.4.1. Codimension-one bifurcations

Varying one parameter allows us to draw a one-parameter bifurcation diagram. We take the example of parameter κ for the agents' ecological concern because the corresponding diagram offers interesting results. In Fig. 6, the simplest case of a single equilibrium being stable is shown for $\kappa \gtrapprox 7$. When reducing κ below 7, the stable equilibrium undergoes a supercritical Andronov-Hopf bifurcation, where the only equilibrium loses stability and gives rise to a stable limit cycle. Fig. 6 shows two other types of codimension-one bifurcations. Saddle-node bifurcations occur at $\kappa \approx 4.1$ and $\kappa \approx 4.6$. We can understand them geometrically as in Fig. 2: the flattening or stretching of an S-shaped nullcline lets a pair of a stable and an unstable equilibria appear as new intersections with the other nullcline. For $\kappa \approx 4.6$, Fig. 6 shows a global bifurcation. Simulations suggest that it corresponds to a saddle-node homoclinic bifurcation, where the stable limit cycle collides with the saddle-node point and disappears (Kuznetsov, 2004).

3.4.2. Codimension-two bifurcations

Fig. 7 shows a two-parameter bifurcation diagram in which we vary the ecological concern κ and the resuspension rate in the lake r. We chose these parameters because they impact different subsystems and their variation leads to interesting results. However, it should be kept in mind that the other model parameters also impact the system's dynamics.

In Fig. 7, we can distinguish nine parameter domains with qualitatively different dynamics. They are labelled with letters from A to I. Fig. 8 shows phase portraits for each of these domains in the panel with the corresponding letter.

Consider a low value of the ecological concern, say $\kappa < 3$. If the resuspension rate r is also low (domain F in the lower left part of Fig. 7), there is a unique equilibrium corresponding to an oligotrophic state with low cooperation level (see Fig. 8F). When increasing the resuspension rate, the system undergoes a bifurcation sequence that is well-known from lake eutrophication models. First, the system crosses a saddle-node bifurcation in which a eutrophic state emerges. The system enters parameter domain G, where there is bistability between an oligotrophic and a eutrophic state, both with low levels of cooperation (Fig. 8G). Second, further increasing the resuspension rate, the system crosses another saddle-node bifurcation, in which the oligotrophic state disappears. The system is now in domain D, where all initial conditions approach the eutrophic state. Even though the ecological concern parameter is still low, the fraction of cooperators in this state has increased in comparison to the level in domains G and F, because the lake is more polluted (Fig. 8D).

Fig. 7 shows that the lower branch of the saddle-node bifurcation curves leading to the emergence of the eutrophic state requires larger values of r when the value of κ increases. The same holds true for the upper branch of the saddle-node bifurcation curve leading in which the oligotrophic state disappears and the eutrophic state becomes the only stable stable. Hence, broadly speaking, concern for the environment diminishes the eutrophication due to increased resuspension. At sufficiently large ecological concern, $\kappa \approx 6$, the two saddle-node bifurcation curves meet in a cusp point and disappear.

However, when the resuspension rate is large, approximately $\kappa > 0.51$, even high levels of ecological concern cannot prevent the saddle-node bifurcation sequences leading to bistability and lake eutrophication. This is the reason why there is another bistable domain with a cusp in the upper right part of Fig. 7. In parameter domain C, there is bistability between an oligotrophic and eutrophic state. In both states, the fraction of cooperators is considerably higher compared to the situation in domain G with little ecological concern (compare Fig. 8C with Fig. 8G).

In between the two addedbistable domains, there are parameter regions with a unique equilibrium (domains D, E and F). The corresponding phase portraits in Figs. 8D-F are all for the same value of r but differ in the ecological concern. For low κ the unique equilibrium is eutrophic (Fig. 8D), whereas for high κ the unique equilibrium is oligotrophic (Fig. 8F). For intermediate values of κ, the unique equilibrium is unstable and surrounded by a stable limit cycle (Fig. 8E). The sustained oscillations emerge and disappear in Hopf bifurcations.

The limit cycles in our continuous-time model are similar to the sustained oscillation found in the discrete-time model of Suzuki and Iwasa (2009b): in the phase plane (Fig. 8E), they also follow the counter-clockwise direction. That is, 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.

Limit cycles can also occur in parameter regions within the two bistable domains. As a consequence, there can be bistability between an equilibrium and a limit cycle (domains B and H). In the upper bistable

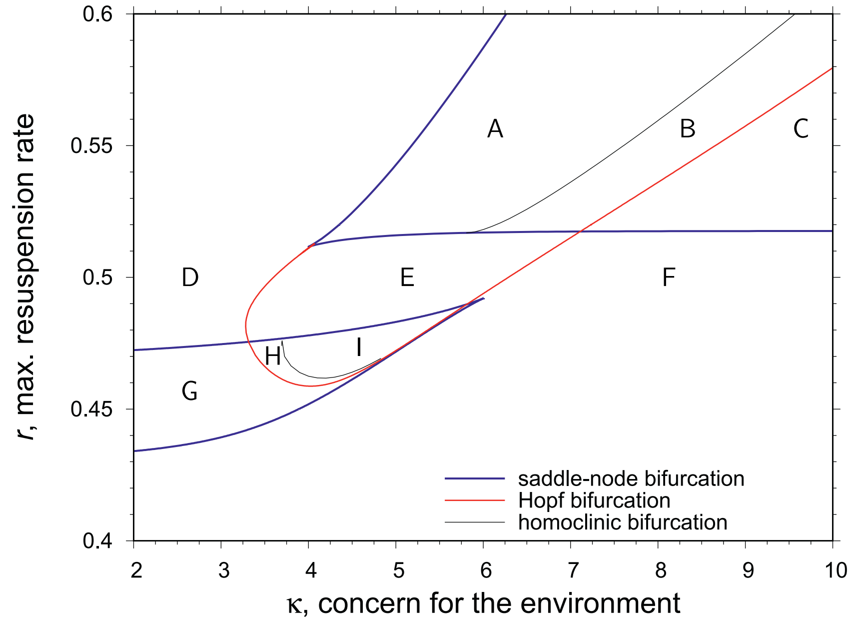

Fig. 7. Two-parameter bifurcation diagram for the coupled system with varying levels of ecological concern κ and resuspension rate r. Letters label parameter domains of qualitatively different dynamics. Parameter values: $\alpha = 0.26$, $q = 2$, $m = 1$, $p_D = 0.04$, $\delta_p = 0.0388$, $s = 0.1$, $\beta = 1$, $\upsilon = 5$, $\xi = 4$.

domain, the limit cycle is around the oligotrophic state and the eutrophic state is stable (Fig. 8B). By contrast, in the lower bistable domain with lower resuspension and lower ecological concern the oligotrophic state is stable and the eutrophic state destabilized towards a limit cycle (Fig. 8H).

The Hopf bifurcation curve shown in Fig. 7 seems to tangentially touch the saddle-node bifurcation curve in both the upper and the lower bistable domain. This suggests the existence of Bogdanov-Takens

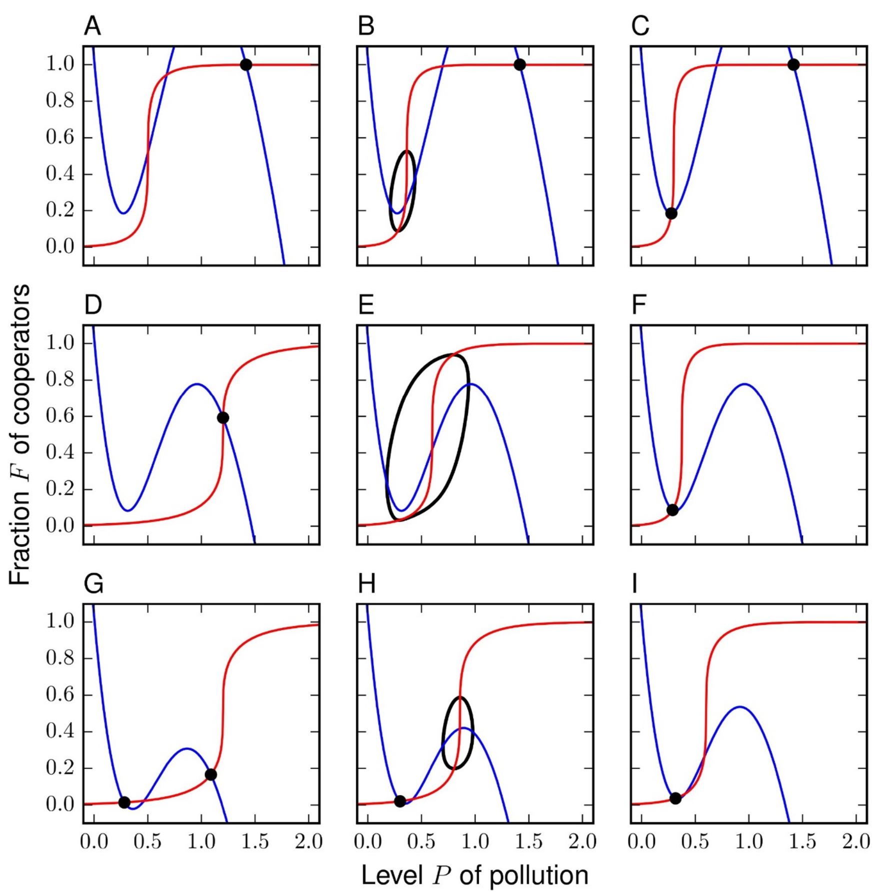

Fig. 8. Phase plane for each lettered domain in Fig. 7, showing the P-nullcline (blue), the F-nullcline (red) and the stable attractors (thick black). Parameter values as in Fig. 7, with, from A to I: (κ, r) = (6, 0.55), (8.25,0.55), (10,0.55), (2.5,0.5), (5,0.5), (8,0.5), (2.5,0.46), (3.5,0.47) and (5,0.48). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bifurcations at those points. Theory predicts that homoclinic bifurcation curves emerge from Bogdanov-Takens points (e.g. Kuznetsov, 2004). Indeed, we found in our numerical simulations homoclinic bifurcations and also what appear to be saddle-node homoclinic (SNH) bifurcations (Kuznetsov, 2004). In the former, limit cycles disappear when colliding with a saddle point and in the latter with a saddle node. In any case, both homoclinic bifurcation types occur only within the two bistable domains because there is neither a saddle node nor a saddle point outside the bistable domains. When the limit cycle disappears in a homolinic or SNH bifurcation, there remain three equilibria, the system loses its bistability and becomes monostable (domains A and I). In the upper bistable domain, only the stable eutrophic state remains when the limit cycle around the oligotrophic state has disappeared (Fig. 8A). In the lower bistable domain, only the stable oligotrophic state remains when the limit cycle around the eutrophic state has disappeared (Fig. 8I).

The SNH bifurcation is also called a saddle-node invariant-circle or a saddle-node infinite-period (SNIPER) bifurcation (e.g. McCormick et al., 1991). This bifurcation type has been used to explain the fission yeast cell cycle (Csikász-Nagy et al., 2006), the appearance of excitable steady states in chemical reactions (Noszticzius et al., 1987) or the propagation of action potential along axon gradients (Ermentrout and Rinzel, 1981). After the SNIPER bifurcation, there are three equilibria, namely a stable node, a saddle point and an unstable focus (cf. Figs. 8A,I). An invariant manifold connecting the unstable focus with the saddle node acts as a separatrix; however, it does not divide basins of attraction (because there is no bistability) but provides a sharp threshold of excitability, also called type II excitability.

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.

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.

4.1.1. 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 configuration where nullclines are S-shaped in the phase plane.

We find analytically the parameters influencing the appearance of an S-shape for the ecological nullcline and for the socioeconomic nullcline (Appendix C). Key parameters include all lake characteristics influencing the pollutant fluxes (α, r, m and q) on the one hand, and social properties of the agents (β and ξ) 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 nullcline become S-shaped.

Table 2 compares our results with heuristic ones obtained by Suzuki and Iwasa (2009b). From the twelve homologous parameters between our models, Suzuki and Iwasa reported the effects of three on the existence of S-shaped nullclines based on the shape of the nullclines under particular parameter values. 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 an S-shaped nullcline. We notably show, however, that neither the discharge of pollutants of defectors or of cooperators, nor economic incentives can influence the existence of a configuration with S-shaped nullclines 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 do not depend on any specific parameter values. The difference that we report may be due to the fact that the model formulation of the incentive to cooperate ΔU 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 υ 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 δ_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 ξ critically determines the existence of a configuration with S-shaped nullclines, 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., 2020).

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 (Lade et al., 2013; Suzuki and Iwasa, 2009b; Tavoni et al., 2012).

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.

4.1.2. Oscillations and bifurcations

Suzuki and Iwasa (2009b) observe oscillations in their discrete-time model for certain parameter values. We confirm the possibility to observe sustained oscillations 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. Contrary to Suzuki and Iwasa (2009b), we also observed oscillations in bistable cases with a stable equilibria.

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), as well as Iwasa et al. (2010), use simulations to find that the stability of the equilibrium they consider critically depends on the relative speed of the two subsystems. This does not refer to any slow-fast dynamics but to the interpretation of model parameter s. We find that the parameter s for the relative speed of the socioeconomic subsystem 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. Thus, contrary to conclusions in Suzuki and Iwasa (2009b) and Iwasa et al. (2010), the stability of the unique equilibrium does not specifically depend on the relative speed of the two subsystems.

Due to the model complexity, there is no simple way to link parameter variations to effects on dynamical regimes. However, Tab. 2 gives the impact of model parameters on the nullclines' S-shape, which is in this model a condition for having multistability. A necessary condition for having oscillations also seems to be a configuration with S-shaped nullclines.

We conducted a partial bifurcation analysis and found that saddle-node bifurcations delimited two bistable domains in two-parameter bifurcation diagrams: region A through C and region G through I in Figs. 7 and 8. Saddle-node homoclinic bifurcations suggest that the Hopf bifurcation letting a limit cycle appear meets the border of each bistable domain at a Bogdanov-Takens bifurcation. We expect the two bistable domains to overlap in situations where we see four stable equilibria. More research is needed to complete the bifurcation analysis for this model.

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 existence of 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 economic 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.

4.2.1. 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. 4). The difficulty of general management recommendations is further reinforced by the possibility for stable equilibria to appear or disappear when parameter values are changed. This possibility makes it impossible to find a general, monotonic 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 (undesirable 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 κ among the human population, its conformist tendency ξ and/or the baseline cost υ of defection. For instance, they conclude that increasing κ does not effectively increase the cooperation F, but our Fig. 5 (initial conditions ①, ③ and ⑤) suggests that it is actually possible when taking multistable configurations into account.

4.2.2. 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 effect δ_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 δ_p has no influence on the location of the P-nullcline when there is no cooperation ($F = 0$). The parameter δ_p represents how much less pollution cooperators discharge in the environment compared to defectors.

Moreover, cooperation tends to be increased if the concern for lake pollution (κ) 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.

4.2.3. 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 effect δ_p, or by an increasing ecological concern κ. 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.

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, (i) changing the location of the current equilibrium, (ii) perturbing the current state to reach another (more desirable) equilibrium, and (iii) 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 effect 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 dynamic 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.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Appendix A. Number of equilibria

A1. Existence of at least one equilibrium

We will prove the following proposition: system (3) 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:

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

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.

A2. Maximum number of equilibria

Here, we show that system (3) has at most nine equilibria.

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

$$F = F_{P'=0}(P) = \frac{1}{\delta_p}\left(p_D - \alpha P + \frac{rP^q}{m^q + P^q}\right), \tag{4}$$

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

$$P = P_{F'=0}(F) = \frac{1}{\kappa}\left[\frac{1}{\beta}\ln\left(\frac{F}{1-F}\right) - \xi F + \upsilon\right]. \tag{5}$$

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.

Appendix 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.

B1. Impact of the cooperation effect on the P-nullcline

Here we investigate how the cooperation effect parameter δ_p influences the nullclines. Actually, it impacts only the P-nullcline. Eq. (4) in Appendix A.2 describing the P-nullcline shows that increasing δ_p flattens the S-shaped curve on the P-axis (Fig. 2, 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 δ_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.

B2. Impact on the coupling on the F-nullcline

Here we investigate how the cooperation effect parameter κ influences the nullclines. Actually, it impacts only the F-nullcline. The equation of the F-nullcline (5) in Appendix A.2 shows that increasing κ flattens the S-shaped curve on the F-axis (Fig. 2, 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 κ 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 κ 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.

B3. 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. 4, 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. 4).

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 δ_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. 2, 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 δ_p, for the $(P_{hi}, F_{lo})^*$ stable equilibrium. However, the $(P_{lo}, F_{hi})^*$ equilibrium is not at risk of disappearing (Appendix C.1).

Similarly, when κ 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 δ_p, for the $(P_{lo}, F_{lo})^*$ stable equilibrium.

Appendix C. Conditions for nullclines to be S-shaped

Here, we summarize which parameters influence the existence, the amplitude and the location of an S-shaped configuration for the nullclines. This configuration corresponds to having 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 is S-shaped if it does not represent a bijection from the domain of P to that of F;
- the F-nullcline is S-shaped if it does not represent a bijection from the domain of F to that of P.

C1. P-nullcline

The P-nullcline corresponds to Eq. (4) in Appendix A.2. By studying the first derivative of function $F_{P'=0}$ in Eq. (4), it is possible to analytically derive the condition for the existence of an S-shape 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), who investigated the particular case where $q = 2$. The condition is more likely to be satisfied when r, α and/or m are large. It means that r, α and m make the S-shape configuration more likely. Moreover, 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 makes it more likely for the condition to be fulfilled. Since q represents the shallowness of the lake, this result is consistent with the bistability observed in shallow lakes (Carpenter et al., 1999). Thus, larger values of parameters r, α, m and q all make it more likely for the P-nullcline to be S-shaped.

C2. F-nullcline

The F-nullcline corresponds to Eq. (5) in Appendix A.2. By studying the first derivative of function $P_{F'=0}$ in Eq. (5), it is also possible to analytically derive the condition for the existence of an S-shape for the F-nullcline:

$$4 < \beta\xi.$$

The condition is more likely to be fulfilled when β and ξ are large. It means that β and ξ favour the S-shape configuration in the F-nullcline.

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 β and ξ exclusively. And, in the (P, F)-plane, the F-nullcline has a symmetry center:

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

Appendix D. Oscillations and relative speed of the subsystems

As Suzuki and Iwasa (2009b) and Iwasa et al. (2010), we find through simulations that the stability of the only existing equilibrium depends on s and α. 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 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.

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