



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



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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. 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 difference between the replicator dynamics and the logit formulation of the best-response dynamics. This fundamental difference results in a different number of equilibria. We show that the replicator equation is a limit case of the best-response model, when agents are assumed to behave with 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 both cases may differ substantially. The replicator dynamics makes the amplitude of 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 assumed in the model. When analyzing social-ecological models, the choice of a socioeconomic dynamics is often little justified but our results show that it may have dramatic impacts on the coupled human-environment system.

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1. Introduction

To account for mutual feedbacks between ecological systems and socioeconomic systems, several articles have proposed social-ecological models. The ecological model typically represents the level of one or multiple resources using population dynamics, whereas the socioeconomic model accounts for some human behaviour influencing the environment, often 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, 2009; Iwasa et al., 2010), grasslands (Lee et al., 2015), forests and land use (Satake and Iwasa, 2006; Satake et al., 2007; Satake et al., 2007; Henderson et al., 2013; Lee et al., 2015) and some other, sometimes general, ecological contexts (Ibáñez et al., 2004; Tavoni et al., 2012; Iwasa and Lee, 2013; Lade et al., 2013; Sugiarto et al., 2015; Bauch et al., 2016).

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; Carpenter, 2003). By contrast, the formulation used to model human behaviour, often with the replicator dynamics (Tavoni et al., 2012; Lade et al., 2013; Bauch et al., 2016) or the logit best-response dynamics (Satake and Iwasa, 2006; Satake et al., 2007; 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 only a few dozen subjects playing a simple game over usually ten rounds in a few hours

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(e.g. Dannenberg et al., 2015). As a consequence, there exist only very few experiments that seem to give clear support for one of the behavioural models, namely for the logit best-response formulation (Lim and Neary, 2016; Mäs and Nax, 2016).

In the modelling literature in ecology and elsewhere, there seems to be little awareness about the implicit assumptions and impact of choosing the replicator over the logit best-response dynamics 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 may remain out of reach for many researchers. Their mathematical formulation as well as the absence of a common terminology could prevent other scientific branches from becoming 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 dynamics, and Hofbauer et al. (2009) proved that both dynamics could be understood as smoothed or perturbed versions of a general fictitious play process. To our knowledge, the consequences of such links in a coupled social-ecological model have not been described. More generally, interpretations of these relationships 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 article, 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. Building upon work by Suzuki and Iwasa (2009) and Iwasa et al. (2010), we previously coupled a lake eutrophication ecological part with a socioeconomic part using the logit best-response dynamics (Sun and Hilker, 2020). We will refer to this model as the best-response model (BRM). In the present article, we compare this previously studied model with another version using the same ecological part but a different socioeconomic part. In this new version, we use the replicator dynamics instead of the best-response dynamics. We will refer to this model as the replicator dynamics model (RDM). Both versions have exactly the same ecological part, but they differ in the socioeconomic part. While the BRM has been studied before (Sun and Hilker, 2020), the RDM and its analysis are novel. The focus of this paper, however, is on the comparison between the BRM and RDM. 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 article 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 models, 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. 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 of 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.

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 (2009) and Sun and Hilker (2020). 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 or at a low level. 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, 2009; Iwasa et al., 2010; Sun and Hilker, 2020) for the BRM – have already been used in a number of social-ecological models.

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. The rate of change of P is given by

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

This assumes a linear global outflow rate (outflow and sedimentation of pollutants leaving the surface waters) with parameter α . 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). In the model by Carpenter et al. (1999), the anthropogenic discharge A of pollutants into the water is a constant.

From a game theoretical point of view, the anthropogenic discharge of pollutants can be represented as a choice between two strategies. A human agent may go on releasing a high amount of pollution at rate π_D (defection) or restrict their release to a lower rate $\pi_D - \delta_p$ (cooperation). δ_p corresponds to a reduction in pollutant discharge ($0 < \delta_p \leq \pi_D$). 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:

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

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. Similarly, *defection* refers to a less environment-friendly behaviour by which an agent discharges a higher amount of pollutants into the lake.

2.2. Socioeconomic subsystem

For the socioeconomic subsystem, the state variable is the fraction F of cooperators among the human population, which takes values between 0 and 1. For both the replicator formulation and the best-response formulation, we consider a common term ΔU , which can be interpreted equivalently as the incentive to cooperate or as the cost of defection. ΔU 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 agents collectively tend to become cooperators, whereas the incentive to defect is stronger when ΔU is negative. As in Sun and Hilker (2020), 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;
- social ostracism is represented by a linear term in F with parameter ξ accounting for the strength of their conformist tendency: the more cooperators there are, the more people tend to cooperate;
- 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 managing the lake.

Suzuki and Iwasa (2009) argued for considering those factors but assumed a bilinear formulation for ΔU . The interpretation of this bilinear term is difficult and, in general, the functional form of the utility function may involve complex phenomena across multiple scales (Voors et al., 2011; Gurney et al., 2016). However, for simplicity, we assume linear terms for the utility function in this article. This simplified formulation allows us to gain more insights into generic phenomena and is mathematically more tractable (Sun and Hilker, 2020).

The formulation of the socioeconomic subsystem with the replicator dynamics in the RDM is:

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

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 (2009), Suzuki and Iwasa (2009), Iwasa et al. (2010), Sun and Hilker (2020):

$$\frac{dF}{dt} = s \left(\frac{1}{1 + e^{-\beta \Delta U}} - F \right). \quad (2)$$

The mathematical formulation implies that there is always a fraction of the human population changing their strategy. Parameter β represents the agents' rationality. When β is close to 0, agents ready to change their strategy choose almost randomly between the two strategies. When β is large, agents ready to change their strategy tend to follow the more advantageous option according to the sign of ΔU . When $\beta \rightarrow +\infty$, every agent ready to change their strategy switches without error to the best option according to the sign of ΔU . Note that increasing parameters of the utility function (v, ξ, κ) is equivalent to increasing parameter β : we can interpret an increase of the cooperating cost, agents' conformism and ecological concern as an increase in the agents' rationality.

In this best-response formulation, it has been shown (Sun and Hilker, 2020) that parameter s , representing the speed of the social dynamics (Suzuki and Iwasa, 2009), has no influence on the existence or on the location of equilibria; therefore, we will restrict our analysis to the case where $s = 1$.

We do not present any new result concerning the BRM alone, which we previously analysed (Sun and Hilker, 2020). However,

all results regarding the RDM and the comparison between the BRM and the RDM are new.

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. The choice to represent the socioeconomic system by either the replicator dynamics or the best-response dynamics is equivalent to assuming different limit cases. This is not an indifferent or neutral choice: it may potentially change the output of a model. So, it is of paramount importance that not only modellers but also policy makers acknowledge this fundamental difference as a key modelling choice.

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 stay with the same strategy. This fits the idea, already formulated by Aristotle (1973), that humans are naturally social beings.

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

To sum up, the two models fundamentally disagree on the evolution of a pure strategy, whether 100% of a behaviour makes the socioeconomic situation stationary or not. This has been described as the best-response dynamics being innovative (Hofbauer and Sigmund, 2003, p. 494). Indeed, if unanimity of all agents prevents any change of strategy, then the socioeconomic system can be interpreted as non-innovative. On the contrary, if unanimity is not stable, it means that some individual innovation at the agent level happens to prevent stationarity, introducing a new strategy, thus breaking unanimity and making the system innovative.

3. Results

In this section, we compare the two versions of the model: the RDM and the BRM. We start with the impact 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.

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 of the stability of possible equilibria 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 this subsection.

In the BRM, it has been previously shown that the system can have up to nine equilibria arranged as a 3×3 array in the phase plane, with up to four stable equilibria (Sun and Hilker, 2020). The RDM has the same P -nullcline for the ecological system. However, the replicator Eq. (1) is more tractable in a mathematical analysis than the logit best-response Eq. (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 A) 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. 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.

Thus, all stable equilibria lie on an “edgy” sigmoid set \mathcal{Z} that takes the shape of a mirrored Z (Fig. 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:

$$\left\{ \begin{array}{l} P \leq P_D \\ F = 0 \end{array} \right. \text{ OR } \left\{ \begin{array}{l} P \geq P_C \\ F = 1 \end{array} \right. \text{ OR } \left\{ \begin{array}{l} \Delta U = 0 \\ F \in]0, 1[\end{array} \right.$$

3.2. The replicator dynamics as the limit of the best-response dynamics

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

In Section 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 non-trivial nullcline in the feasible phase

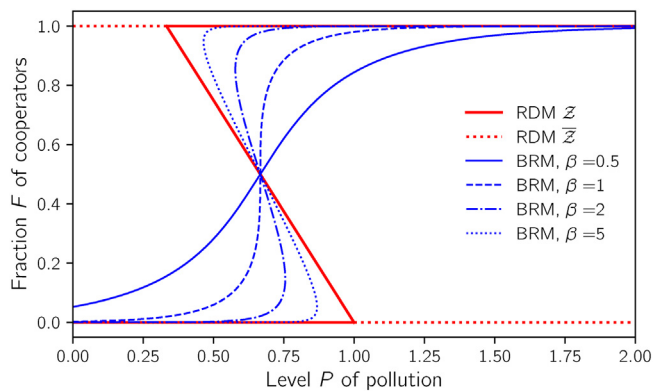


Fig. 1. F -nullcline in the phase plane for the BRM (thin blue curves) with increasing values for the agents’ rationality β . As β increases, the F -nullclines for the BRM converge to the F -nullclines for the RDM (thick red lines), which is independent of β . The RDM F -nullclines are composed of parts on which equilibria must be unstable $\bar{\mathcal{Z}}$ and a potentially stable set (\mathcal{Z}). Parameter values: $\alpha = 0.26$, $r = 0.5$, $q = 2$, $m = 1$, $\pi_D = 0.04$, $\delta_D = 0.0388$, $s = 0.1$, $v = 5$, $\kappa = 5$, $\xi = 4$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

plane. 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. 1, where the F -nullcline of the BRM has an S -shape for many values of β . The larger the agents’ rationality β , the “edgier” the BRM F -nullcline. Ultimately, for $\beta \rightarrow +\infty$, the BRM F -nullcline takes the form of the RDM F -nullcline.

Since β has an interpretation, this provides an intuitive link between the two dynamics and between the two models: when the human agents’ rationality β increases in the BRM, all equilibria tend towards those defined by the replicator F -nullclines. In the general case, our proof (see Appendix B) 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 abstract terms (Hopkins, 1999; Hofbauer et al., 2009), has not been illustrated graphically or exposed in intuitive terms, and is usually not pointed out: in the case where exactly two strategies coexist, the best-response dynamics converges towards the replicator dynamics when the rationality of the agents increases. This means that there is a 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.

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. In this section, we find that the minimum number of equilibria is different between the BRM and the RDM. Then, we show that the two models share the same maximum number of equilibria. Finally, we illustrate the convergence of the number and location of stable equilibria in terms of the agents’ rationality β .

The minimum number is one in the case of the best-response dynamics (Sun and Hilker, 2020). It is two in the case of the replicator dynamics (Appendix C).

The maximum number of equilibria has been shown to be nine in the BRM (Sun and Hilker, 2020). 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 RDM. In both the RDM and the BRM, the equilibria are organized as a 3×3 array in the phase plane, and up to four of them (those on the corners of the square-like array) can be stable.

Depending on the specific value for β , the number of stable equilibria can be very different between the two models. This is illustrated in Fig. 2, where, at a low rationality level ($\beta = 0.2$), the BRM shows two stable equilibria whereas the RDM shows four stable equilibria. For lower values of β , the BRM has fewer equilibria than the RDM, and their locations do not coincide with the locations of the RDM equilibria. Since the agents’ rationality β in the BRM relates to how close the model is to the RDM, we observe a convergence in the number of stable equilibria as β increases. When the agents’ rationality β increases, existing equilibria in the BRM converge towards some equilibria in the RDM ($\beta \in [0.2, 0.4]$). Moreover, new stable equilibria appear in the BRM to match the number of stable equilibria in the RDM ($\beta \in [0.8, 1.0]$). For sufficiently large values of β , the number and location of equilibria of the BRM and of the RDM coincide.

As a consequence, the outcome of the models critically depend on the formulation we assume for the socioeconomic system. Indeed, if agents behave in a very rational manner (like in the

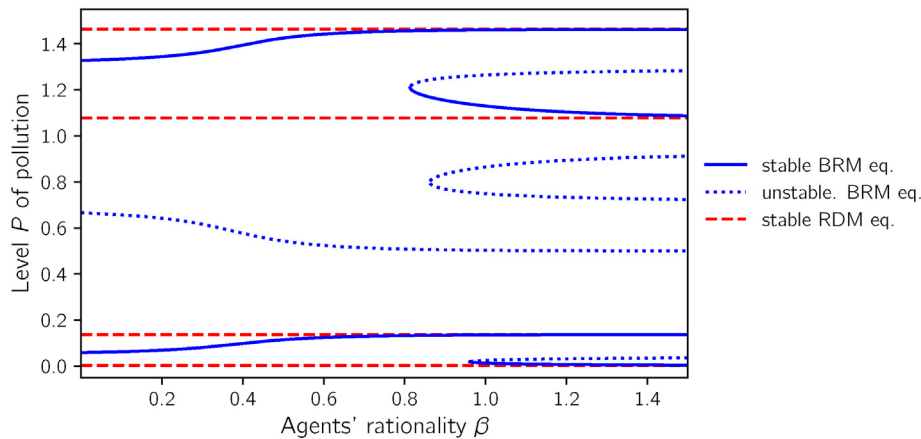


Fig. 2. Bifurcation diagram showing the level P of pollution of the RDM stable equilibria (dashed red) and of the BRM stable (solid blue) and unstable (dotted blue) equilibria for different levels of the agents' rationality β . For simplicity, unstable equilibria in the RDM are not depicted. Parameter values as in Fig. 1, except for $\alpha = 0.4$, $r = 0.8$, $\kappa = 0.25$ and $\xi = 8$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

RDM or in the BRM with a high rationality β), then policy makers may expect multistability. Conversely, if agents do not behave rationally, then policy makers can expect a lower number of stable equilibria. For modellers, the important result is that choosing either the replicator dynamics or the logit best-response dynamics is not neutral: this modelling choice must be justified in terms of the expected rationality of the agents' behaviour. Note that, here, we do not mean a mechanistic or constructive justification, as is often the case in game theory. Rather, we mean a phenomenological justification as to whether policy makers should expect the agents to behave more or less rationally: the fundamental difference exposed in Section 2.3 makes this explanation of the modelling approach necessary.

3.4. Cycles and make-or-break dynamics in the replicator dynamics model

The occurrence of cycles has been described previously in the BRM (Sun and Hilker, 2020). In this section, we focus on the RDM, where we find qualitatively similar sustained oscillations, but which may have significantly different outcomes in the presence of perturbations of the state variables.

Our simulations suggest that sustained oscillations may exist in particular when there is one non-trivial equilibrium (with F in $]0, 1[$) as in Fig. 3, and when this equilibrium loses its stability through a Hopf bifurcation. This is similar to previous reports by Suzuki and Iwasa (2009) and Sun and Hilker (2020) for the BRM. However, limit cycle oscillations can also occur when there is more than one equilibrium, and they can exist in complex multistability or global bifurcation scenarios (Sun and Hilker, 2020). In the RDM, the phase plane then includes two trivial equilibria which happen to be located 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 (Sun and Hilker, 2020):

- 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. 3). The second aspect is that, in the BRM, oscillations occur only when the agents' rationality β is sufficiently large.

3.4.1. Large limit cycle

The limit cycle of the RDM shown in Fig. 3 is very large in the sense that its trajectory stretches over 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, the stable manifold of each 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 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. As a consequence of both the large limit cycle and the long time spent near $F = 0$ or $F = 1$, a random perturbation is 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

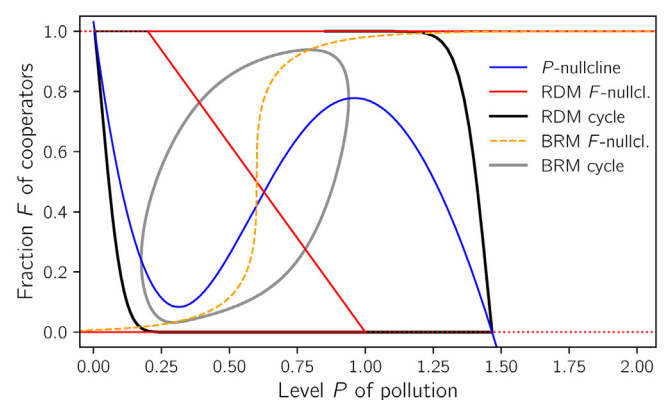


Fig. 3. Example of a large limit cycle in the phase plane (black) in the RDM. The straight red lines indicate the F -nullclines in the RDM. For comparison, the F -nullcline of the BRM is shown as a dashed orange line and the corresponding limit cycle is in grey. The solid blue P -nullcline is common to both models. Parameter values as in Fig. 1, except for $\beta = 1$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

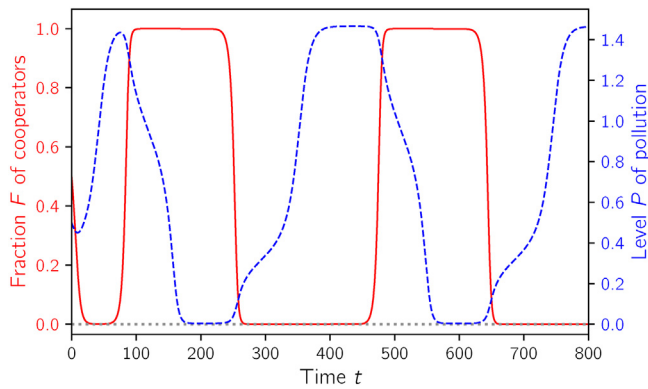


Fig. 4. Time plot of a large limit cycle in the RDM showing the fraction F of cooperators (solid red) and the level P of pollution (dashed blue). Parameter values as in Fig. 1, except for $\xi = 3$. Initial condition: $(P = 0.5, F = 0.5)$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

alternative 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. 5. To express this idea, we suggest to use the term *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.

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

Previous numerical results in the BRM (Sun and Hilker, 2020) suggest that the agents’ rationality β needs to be sufficiently large

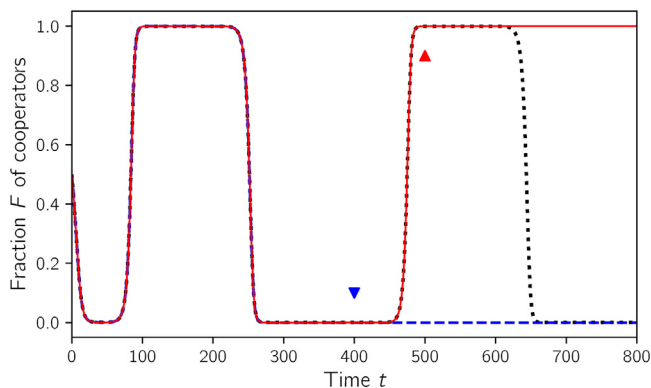


Fig. 5. Time plot of the RDM fraction F of cooperators from the same initial condition but perturbed (triangles) at different times on the large limit cycle, showing the scenario without perturbation (dotted black), a scenario with a perturbation at $t = 400$ (dashed blue) and a scenario with a perturbation at $t = 500$ (solid red). The perturbation consisted in reaching $F = 0$ or $F = 1$ when the system is very close to full defection or full cooperation. Parameter values as in Fig. 4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

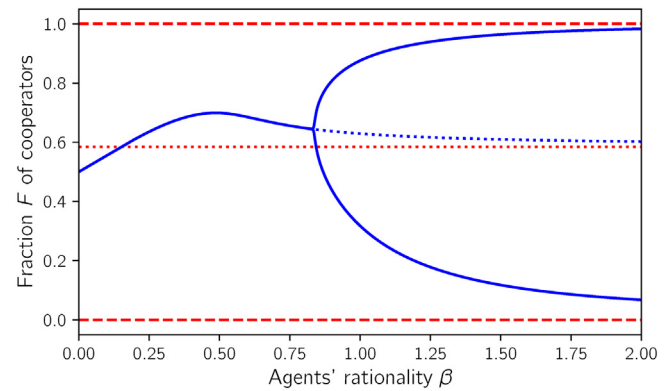


Fig. 6. Bifurcation diagram showing the extrema of the fraction F of cooperators in the asymptotic regime for different levels of the agents’ rationality β in the BRM (solid blue), which overlap when the equilibrium is asymptotically stable. The chosen configuration always displays a unique equilibrium in the BRM (dotted blue) and a single non-trivial equilibrium in the RDM (dashed red), which is unstable. The maximum and minimum of the RDM limit cycle corresponds to the case where $\beta \rightarrow \infty$. Other parameter values as in Fig. 1, except for $\alpha = 0.3$ and $\pi_D = 0.072$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to allow for the nullclines to be S-shaped and for 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. It seems that, under the same parameter values, cycles cannot occur in the BRM if they are absent from the RDM. This is illustrated in Fig. 6, where limit cycles in the BRM appear only for sufficiently large values of the rationality parameter β .

However, two distinct factors play a role in the occurrence of oscillations. The first one, reported here, is the agents’ rationality. The second factor is the location of the equilibrium on each nullcline. Indeed, simulations show that equilibria tend to be unstable on the middle part of the S-shaped nullclines but stable on the outer branches. The two factors cannot be disentangled on the one hand because the agents’ rationality has an impact on the location of the equilibria on each nullcline, and on the other hand because the location of the equilibria on each nullcline depends simultaneously on many parameters. Regarding other factors, the relative speed or different time scales of the ecological and socioeconomic systems has an impact on the occurrence of oscillations, but this impact is not monotonic (Appendix D).

4. Discussion and conclusions

Our results show that conclusions drawn from the study of social-ecological systems can strongly depend on the specific formulation of the socioeconomic subsystem. For example, Fig. 2 shows that the RDM and the BRM exhibit a different number of stable equilibria. Fig. 3 shows that cycles can have different properties in the two models, with the RDM suggesting a make-or-break dynamics that may be absent from the BRM, which may have no limit cycle oscillations at all, as in Fig. 6 for $\beta = 0.1$.

Divergent features between the RDM and the BRM are consequences of the fundamental difference we have described in Section 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 may be more appropriate 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 may be more appropriate 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 noisy systems where variation happens on a random basis. In humans, similar noise could represent deviations from pure flock behaviour. Notably, individuals changing their strategy for a time might not have very strong fitness or utility consequences, which allows for a more exploratory behaviour.

The advantage of the logit best-response dynamics, though, is that the parameter representing the agents' rationality allows for the investigation of different levels of rationality. At the cost of this additional parameter, the logit best-response dynamics offers more "flexibility". Indeed, the higher the rationality, the closer we are to the replicator dynamics, the more we assume that individual agents are influenced by group behaviour. 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 suggested by Hopkins (1999) and Hofbauer et al. (2009) about the relationship between the two dynamics. Hopkins (1999) showed that the best-response dynamics is a perturbed version of a generalized replicator dynamics. Hofbauer et al. (2009) proved that when the best-response dynamics has a global attractor, then the time average of the average strategy given by the replicator dynamics has the same attractor. Depending on the aim of the modelling approach, it may be more advantageous either to cover a broader range of situations and use the logit best-response equation, or to have a parsimonious model with fewer parameters and use the replicator equation.

The replicator dynamics may seem more capable of representing some biological systems with mutation-like variations. Indeed, we could expect some homogenization of the agents' strategies like in the case of a strong selection pressure. However, what determines an optimal strategy in the replicator dynamics is that this strategy is unanimously adopted: it is a social effect. The replicator dynamics makes a strategy become optimal if it is unanimous, whereas a strong selection pressure makes a strategy unanimous if it is optimal. The two phenomena match only in the case where social adoption of a strategy plays an important role in determining the individual agent's resulting fitness. In our models, this corresponds a strong social conformism, due to ostracism for instance. Without clues of such strong social effects however, we should not expect the replicator dynamics to represent any biological system better than the best-response dynamics. As a general rule, the best response dynamics can be seen as more apt to represent noisy systems. Agents do not know the exact level of pollution, nor the consequences of their action. These could be modelled as a noise in the system, where some agents change their behaviour because none of them have perfect information on the ecological system.

In the case where no formulation of the socioeconomic subsystem is better supported by some empirical data or theoretical, mechanistic account than the other, it would be recommendable to investigate more than one formulation of the socioeconomic model and to check which results are robust against the model choice. This corresponds to our case, since no evidence tells us either that polluting agents tend to follow the majority 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 dynamics potentially threatens 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 dynamics of the socioeconomic system might lead to results that are specific for these assumptions and might lead to very different results when using a different socioeconomic model.

Declaration of Competing Interest

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.

CRediT authorship contribution statement

T. Anthony Sun: Visualization, Writing - original draft, Writing - review & editing. **Frank M. Hilker:** Supervision, Writing - review & editing.

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Appendix A. Jacobian matrix in the replicator dynamics model

Here, we consider the RDM. The replicator dynamics of Eq. (1) implies that the socioeconomic system in isolation would be at equilibrium when we have either full defection ($F = 0$) or full cooperation ($F = 1$).

For the coupled social-ecological system, we can study the stability of equilibria using the Jacobian matrix evaluated at the said equilibria. Indeed, the stability of an equilibrium depends on the sign of the Jacobian matrix's eigenvalues.

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 λ_F of the Jacobian matrix evaluated at this point:

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

For an equilibrium to be stable, no eigenvalue of the Jacobian matrix should be positive. Thus, if $F = 0$ or if $F = 1$, we have simple restrictions on the possible value of P for equilibria to be stable since it depends on the sign of λ_F . Indeed, if $F^* = 0$, any equilibrium with $P^* > P_D = \frac{v}{\kappa}$ must be unstable. Similarly, if $F^* = 1$, any equilibrium with $P^* < P_C = \frac{v - \xi}{\kappa}$ must be unstable.

Appendix B. 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 β 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 S_β be the extended F -nullcline over all real values for P with a particular value for the rationality parameter β in $]0, +\infty[$. It represents P as a function σ of F :

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

We show that for all values of β :

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

The equation of the BRM F -nullcline is (Sun and Hilker, 2020)

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

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

$$P_{BRM,\beta} = \sigma_\beta(F) = \frac{1}{\kappa} \left[\frac{1}{\beta} \ln \left(\frac{1-F}{F} \right) + v - \xi F \right] \quad (3)$$

$$\iff \Delta U_{BRM,\beta} = \frac{1}{\beta} \ln \left(\frac{1-F}{F} \right) \quad (4)$$

From Eq. (3) it is clear (i) that σ_β is actually defined on $[0, 1]$ and continuous for all values of β .

Moreover, it makes it obvious (ii) that for all values of β

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

Eq. (4) finally shows (iii) that

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

To conclude, S_β tends asymptotically towards \mathcal{Z}' when β increases, and, as a consequence, the same can be said about their respective restrictions 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 β tends towards infinity.

Appendix C. 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 $\delta_p \neq 0$, then it represents F as a continuous function of P on \mathbb{R}^+ (because $m > 0$ and $q \geq 2$), given by

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

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

Appendix D. Influence of the relative speed s on the oscillations in the logit best-response model

This section is about the asymptotic regime of the logit best-response model using Eq. (2). Previously, we proved that the relative speed s of the socioeconomic system with respect to the ecological system had no effect on the location of the model's equilibria (Sun and Hilker, 2020). Therefore, we decided not to focus on this parameter in the main text. Here, we show that parameter s may impact the stability of an equilibrium and the amplitude of the oscillations that we describe in the main text.

Fig. 7 shows that varying the relative speed parameter s in the BRM has indeed no effect on the location of the equilibrium, but that it can make sustained oscillations appear or disappear. In line with Sun and Hilker (2020), this suggests that s has an impact on the equilibrium's stability. However, the effect of the relative speed s on the occurrence and on the amplitude of the limit cycle is not monotonous. Indeed, at low values of s , when the socioeconomic dynamics is very slow, increasing s increases the size of the cycles until about $s \approx 0.06$. Then, the amplitude of the cycles decreases as s becomes larger. Finally, as soon as the socioeconomic dynamics is fast enough ($s \approx 0.4$) compared to the ecological dynamics, the equilibrium becomes stable and the sustained oscillations disappear.

Turning to the RDM, we can modify it into an sRDM by using the following socioeconomic system instead of Eq. (1):

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

The difference is that we now introduce a relative speed parameter s with the same interpretation as in the BRM. In Fig. 7, the sRDM shows the blue curves, *i.e.* it follows exactly the same

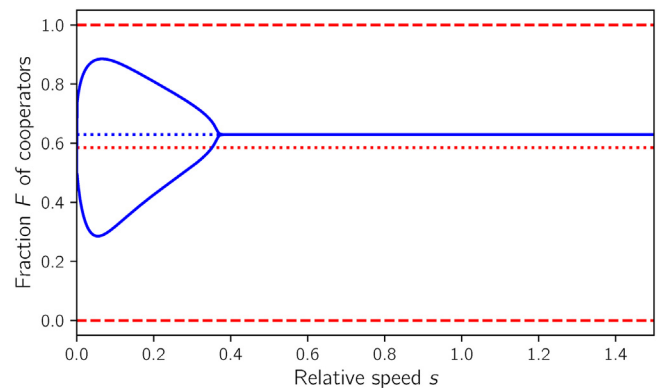


Fig. 7. Bifurcation diagram showing the extrema of the fraction F of cooperators in the asymptotic regime for different levels of the socioeconomic system's relative speed s in the BRM and in the sRDM (solid blue, overlapping), which overlap when the equilibrium is asymptotically stable. The chosen configuration always displays a unique equilibrium in the BRM and in the sRDM (dotted blue, overlapping), and a single non-trivial equilibrium in the RDM (dotted red), which is unstable. The maximum and minimum of the RDM limit cycle are shown in dashed red. Other parameter values as in Fig. 6, except for $\beta = 1$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

asymptotic dynamics as the BRM. As a consequence, the effect of parameter s on the sustained oscillations in the BRM is independent from the formulation of the socioeconomic dynamics.

To conclude, the relative speed s of the two subsystems of the BRM has no simple impact on the model's asymptotic dynamics. This contrasts with the effect of the agents' rationality β , which links the BRM and the RDM in a consistent, monotonous manner.

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