

Tipping points of the ocean oxygen: A dynamical systems perspectiveAmer Alsulami¹ and Sergei Petrovskii^{2,3,*}¹*Department of Mathematics, Turabah University College, Taif University, Taif 21944, Saudi Arabia*²*School of Computing and Mathematical Sciences, University of Leicester, Leicester LE1 7RH, United Kingdom*³*Peoples Friendship University of Russia (RUDN University), 6 Miklukho-Maklaya St, Moscow 117198, Russian Federation*

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Global biochemical cycles of greenhouse gases have received a lot of attention over the past few decades because of their effect on climate and environment. Surprisingly, the turnover of oxygen received considerably less attention in spite of its truly existential importance: Apparently, any significant perturbation to the oxygen cycle may cause serious threat to humans as well as all animal species. Moreover, there is growing empirical as well as theoretical evidence that global warming can perturb the oxygen cycle considerably. In this Perspective, we discuss how this problem can be addressed using a dynamical systems framework. We argue that an insightful approach can consider a family of conceptual mathematical model that couples oxygen dynamics to vegetation (in particular, phytoplankton) and that produces oxygen as a by-product of its primary production and to the state of the global Earth climate. We show that the suggested approach predicts tipping points resulting in oxygen depletion and ocean anoxia as a response to a change in some environmental parameters. This Perspective leads to insights that help to address important issues largely overlooked in the literature and also suggests directions for future research.

DOI: [10.1103/w5c6-wnv8](https://doi.org/10.1103/w5c6-wnv8)**I. INTRODUCTION**

Understanding of the state and dynamics of vital resources and elements that maintain Earth habitable has been a major focus in studies on the global climate change since the mid-2000s. It led to the emergence of two important concepts (see Fig. 1) allowing for addressing the corresponding issues in a systematic way. The concept of planetary boundaries [1–3] identified several crucial factors and resources [Fig. 1(a)] where exceeding a certain threshold can pose a significant threat to humanity. The concept of Earth's climate tipping elements [4] distinguished several key subsystems [Fig. 1(b)] where crossing a tripping threshold in one of them may trigger tipping in other subsystems (elements), hence ultimately leading to large-scale irreversible changes in the environment globally [5].

Surprisingly, in all those highly influential studies, one crucial resource of truly vital importance to humans and animals has been largely overlooked—and that is oxygen. Meanwhile, availability of oxygen, in particular dissolved oxygen in the oceans, has indeed been a focus of a somewhat different line of research where considerable empirical evidence has been collected showing that the amount of dissolved oxygen exhibits a clear tendency to decrease over the past several decades [6–9]. Moreover, there is some empirical evidence that the amount of oxygen in the atmosphere is also decreasing

[10,11]. The rate of decrease is relatively slowly at present but there are warnings that it may accelerate, potentially leading to tipping [12]—a fast and virtually irreversible transition to an alternative, low oxygen state. We further mention here that the bistability of the global oxygen stock (i.e., the coexistence of a low-oxygen and high-oxygen steady states) have been demonstrated in earlier studies [13–15], so that such transition might indeed be possible. It is a problem of existential importance to identify the factors, processes and mechanisms that can be responsible for those signs of deoxygenation as well as to estimate the possible scales at which this phenomenon may occur. Correspondingly, it is the overarching goal of this Perspective.

Constitutive processes in terrestrial and aquatic systems, in particularly those that determine biochemical fluxes, are significantly different in many respects. There have been attempts to combine them into a global wholistic Earth system [16]; however, our aim in this paper is much more modest. Here we mostly focus on the dynamics of dissolved oxygen in the ocean, although we do believe, for the reasons that we discuss below, that our analysis and findings are likely to have implications for the Earth oxygen stock as a whole. Indeed, it is a well-established fact that a considerable part (estimated as 50–80%) of the current total atmospheric oxygen budget has been produced in the ocean in phytoplankton photosynthesis [17,18]. Should the phytoplankton photosynthesis be disrupted, arguably, it is only a matter of time before the onset of the global anoxia affecting not only oceanic but also terrestrial ecosystems. Whether such catastrophe can really happen in the future remains hypothetical but it did happen in past, as a few of the most severe mass extinctions in the Earth history were caused by the global anoxia [19,20].

The decrease of oxygen in the ocean is usually attributed to the fact that its solubility decreases with an increase in

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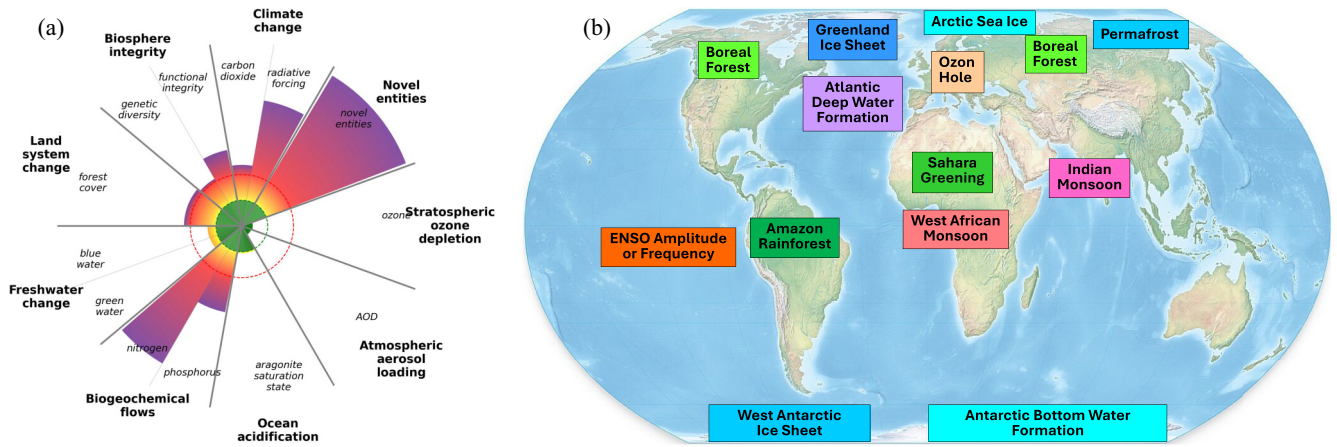


FIG. 1. (a) Overview of the state of the Earth critical resources (adapted from Ref. [3]). (b) Tipping elements of the Earth climate system (redrawn based on Ref. [4]). Tipping in one element can cause a cascade of tipping in other elements.

water temperature. However, it is straightforward to see that the change in solubility by itself is unlikely to cause serious problems to marine fauna. Indeed, an increase in the water temperature from 7°C to 40°C will decrease the solubility about twice, bringing it down to about 6 mg/l [21], while the hypoxic threshold (below which stressful oxygen deficiency occurs) is commonly defined as $2\text{--}3\text{ mg/l}$. Thus, we argue that, on top of the decreased solubility, there must be some other overlooked processes that are ultimately responsible for anoxia.

Similarly to many other biogeochemical fluxes [22,23], the global dynamics of oxygen is essentially a cycle [24,25]; see Fig. 2. Remarkably, oxygen is consumed in many processes but produced only in one: photosynthesis. The rate of net oxygen production depends on environmental factors; in particular, the importance of the presence of sunlight and some minimum concentrations of carbon dioxide are well recognized. The role of the ambient temperature is somewhat less

clear. Meanwhile, there is empirical evidence that the rate of net oxygen production decreases with the water temperature [26,27] and for some phytoplankton species may even become negative when the temperature becomes sufficiently high [28]. Moreover, other common environmental factors are likely to play a role, too, e.g., water turbidity may affect the rate of photosynthesis through changing the sunlight availability at water depths below the immediate subsurface layer.

In this Perspective, we briefly summarize the state of the art in understanding the global oxygen dynamics with a focus on the dissolved oxygen in the ocean. We suggest that the decrease in oxygen solubility occurring with an increase in water temperature, which is usually considered to be the main process that controls the oxygen abundance in the ocean, is not sufficient to predict the response of ocean oxygen to the climate change. Using a paradigmatic toy model (Sec. II), we demonstrate how further progress in the understanding—in particular, to identify possible tipping points in the oxygen cycle that have been previously overlooked—can be achieved using dynamical systems approach (Sec. III). We arrive at some nontrivial, counterintuitive conclusions about the role of different factors in possible scenarios of ocean anoxia catastrophe and suggest an outlook for future research.

II. OCEAN OXYGEN AS A DYNAMICAL SYSTEM

There are different ways to build a model to investigate a complex ecological system theoretically. The most commonly used one is often referred to as a “box model” or “compartment model” where a multidimensional ecosystem is mapped onto a toy system that consists of just a few elements or species (“compartments,” e.g., see Fig. 3), hence only takes into account the main building blocks (and the interactions between them) of a much more complex real-world system [29]. Justification of this approach (also known as coarse-graining [30]) is partly provided by the fact that the focus of the study is often on the ecosystem function rather than individual species, so that the large number of species can be combined into a relatively small number of functional groups. In particular, in the studies on marine ecosystems such approach has been used widely (and proved to be meaningful) by grouping different

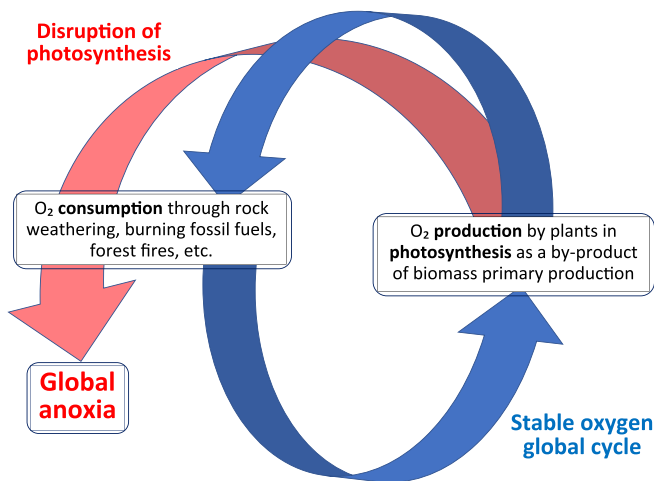


FIG. 2. A sketch of the global oxygen cycle. Note that oxygen is consumed in many different biogeochemical processes but only produced in one process, i.e., in photosynthesis, which is the essential element of plants primary production. Disruption of photosynthesis can break the oxygen cycle potentially leading to ocean anoxia.

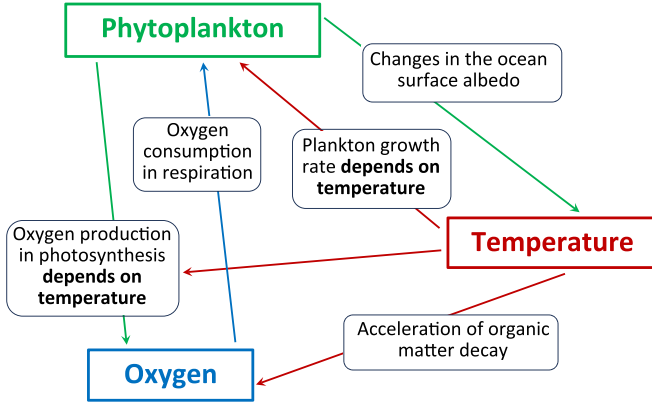


FIG. 3. Block chart of the oxygen-phytoplankton-temperature system visualizing the main variables (as in the colored rectangular boxes) and processes (boxes with rounded corners) that are explicitly taken into account by the conceptual model (1)–(3) of ocean oxygen cycle. Arrows visualize either the coupling between different variables or the effect of water temperature on the processes involved.

phytoplankton species into just “phytoplankton” and different zooplankton species into just “zooplankton” [31].

There is no unique or universal recipe as to how many functional groups (and/or other ecosystem elements, e.g., dissolved nutrients, etc.) should be included into the model and the choice is normally made based on the focus of a particular study [32]. Oxygen is widely regarded as one of the most important indicators of the marine ecosystem health [33]; however, surprisingly, until only recently models of marine ecosystems tended to leave it almost entirely out of scope. A dynamical system approach to study the evolution of oxygen in the ocean using conceptual low-dimensional plankton-oxygen models was introduced in Ref. [34] and then was extended and further developed in later studies. The baseline model can be as simple as consisting of just two elements (the dissolved oxygen itself and phytoplankton as its producer); its advanced modifications can include other factors such as zooplankton (that consumes phytoplankton and hence can control oxygen production through a top-down control) [34,35], explicit space and self-organized pattern formation [34,35], different scenarios of global warming [35], the effects of stochasticity and noise [36], the effect of multiple timescales [37], etc.

Remarkably, while models of different complexity have somewhat different properties, all the variants of the oxygen dynamical system lead to one common prediction: A sufficiently large increase in the water temperature will result in a tipping point leading to ocean anoxia. Correspondingly, a more advanced oxygen dynamical system should also take into account the global energy budget [38]. Here we consider that approach in some more details. Namely, we consider a conceptual nonspatial model consisting of just three environmental variables (see Fig. 3), i.e., the spatially average Earth surface temperature T (in our case, the ocean surface temperature, which we use as a proxy for the water temperature in the subsurface photic layer where most of the photosynthetic activity takes place), the average phytoplankton density u , and the average concentration of dissolved oxygen c . These three

variables are coupled together into a dynamical system by multiple biological, geochemical, and geophysical processes; see Fig. 3. In particular, oxygen is produced by plants (i.e., phytoplankton and algae) through the process of photosynthesis in daytime using sunlight as the source of energy. However, during the night, plants consume oxygen in respiration as is needed for their metabolism. The difference between the production during the day and consumption during the night is called the net oxygen production, which can be quantified by its rate, say, A , and it is known to depend on the ambient temperature [26–28]. The maximum per capita phytoplankton growth rate (say, B) is known to also depend on the temperature.

In its turn, the temperature is determined by the energy balance, i.e., by the difference between the incoming energy brought in with the sunlight falling on the Earth surface. The corresponding system of equations can be written as

$$\frac{dc}{dt} = \frac{A(T)u}{c + c_0} - \frac{\delta uc}{c + c_2} - mc, \quad (1)$$

$$\frac{du}{dt} = \left(\frac{cB(T)}{c + c_1} - \gamma u \right) u - \sigma u, \quad (2)$$

$$\frac{dT}{dt} = \frac{1}{\lambda} (-aT^4 + b[1 - S(u)]). \quad (3)$$

Here the last term in Eq. (1) effectively describes oxygen consumption in other processes not included into the model explicitly.

The subsystem given by Eqs. (1)–(2) is a baseline model of oxygen-phytoplankton dynamics [34,35], here being extended by its coupling to the energy balance. Equation (3) is known in the literature as the Budyko-Sellers equation. The first term in the right-hand side of Eq. (3) describes the energy outgoing to the space due to the thermal radiation (essentially, the Stefan-Boltzmann law). The second term in the right-hand side quantifies the amount of energy captured by the Earth surface (ocean surface in our case). Here S is the surface albedo which is known to decrease in the presence of phytoplankton [39,40]. Precise form of dependence $S(u)$ is unknown; here we consider the following parametrization:

$$S(u) = (s_1 - s_0)e^{-\alpha_1 u} + s_0, \quad (4)$$

(cf. Ref. [41]), where coefficients s_0 , s_1 , and α_1 are parameters, s_1 being the albedo of a clear water and s_0 the high-density limit; $s_1 > s_0$.

The net oxygen production rate is known to be a function of temperature [28,42–45], i.e., $A(T)$. Evidence available from the literature [46,47] suggests the existence of an optimal temperature (say, T_1) where the growth rate and the primary production (and hence the oxygen production) reaches their maximal values. Since the precise dependence is unknown, we consider $A(T)$ to be dome shaped (unimodal) and use the following generic parametrization:

$$A(T) = A_0 \exp \left(-\frac{(T - T_1)^2}{q^2} \right), \quad (5)$$

where A_0 and q are parameters, A_0 being the maximum oxygen production rate, and q quantifying the strength of the temperature dependence.

For the dependence of the phytoplankton growth rate on the ambient temperature, a few studies showed, based on empirical data, that in a certain temperature range the growth rate is increasing and well approximated by an exponential function $\exp(-\frac{T_0}{T})$ [48,49], which is essentially the Arrhenius law of chemical kinetics considered in the context of metabolic processes [50]. However, it is valid only until the temperature becomes too high. An excessively high temperature will eventually kill organisms, so one should expect that, with a sufficiently large increase in the ambient temperature, the growth rate starts decreasing. Unfortunately, the functional form of such decrease is unknown. Here we assume that it can be described by another exponential function $\exp(-\alpha_2 T)$. Thus, we arrive at the following parametrization:

$$B(T) = b_1 e^{-\frac{T_0}{T}} e^{-\alpha_2 T}, \quad (6)$$

where T_0 and α_2 are the shape parameters determining the sharpness of the peak described by Eq. (6) and the position of its maximum, $T_m = (T_0/\alpha_2)^{1/2}$, and parameter b_1 is the scaling factor for the maximum growth rate $B_{\max} = b_1 \exp(-2\sqrt{T_0\alpha_2})$.

Using appropriate parametrization for other processes involved, see Refs. [34,35,41] for details, the three-component model (1)–(3) of the temperature-phytoplankton-oxygen dynamics can be written in a more specific form:

$$\frac{dc}{dt} = \frac{A_0 u}{c + c_0} \exp\left(-\frac{(T - T_1)^2}{q^2}\right) - \frac{\delta u c}{c + c_2} - mc, \quad (7)$$

$$\frac{du}{dt} = \left(\frac{cb_1}{c + c_1} e^{-\frac{T_0}{T}} e^{-\alpha_2 T} - \gamma u\right)u - \sigma u, \quad (8)$$

$$\frac{dT}{dt} = \frac{1}{\lambda}(-aT^4 + b[1 - (s_1 - s_0)e^{-\alpha_1 u} - s_0]), \quad (9)$$

where all parameters are positive due to their biological or physical meaning.

Note that model (7)–(9) contains a large number of parameters whose values are either unknown or can only be roughly estimated, e.g., see Ref. [37]. Obtaining comprehensive information about the properties of the model (7)–(9) by solving it numerically and varying all the parameters does not seem possible. Instead, we apply a different approach that is commonly used in simulation studies: We only select a few “controlling” parameters with a clear biological or environmental meaning and vary them over a representative range but keep all other parameters fixed at certain values.

What parameters to choose as the “controlling” ones? In this study, we focus on the effect of b_1 , A_0 , s_0 , and s_1 . Our choice is partially justified by the reasons outlined below.

(i) While in our model the dependence of phytoplankton growth rate on the ambient temperature is accounted for explicitly, the effect of all other environmental factors (e.g., humidity, precipitation, salinity, acidity, availability of sunlight, etc.) is taken into account implicitly, described by a single parameter b_1 which quantifies the maximum growth rate. For a given value of b_1 , phytoplankton is in a “thermal equilibrium” with its environment. A change in the environment may break the equilibrium.

(ii) Since the oxygen production in photosynthesis (by phytoplankton) is a central element of our model, using A_0 as a controlling parameter is a natural choice.

(iii) The albedo of the Earth surface plays a central role in determining the Earth thermodynamics [51]. It is also the factor that provides the coupling between the physical (in particular, thermodynamical) aspects of the global climatic system and the biological ones (as is quantified by parameters s_0 and s_1 in our model), because the reflective properties of the ocean surface and hence the radiation balance are changed in the presence of phytoplankton [39,40]. (We mention here that a similar effect was also observed for the land surface [52].) However, how the values of ocean albedo depend on the water properties, in particular on the phytoplankton abundance (as well as the water turbidity more generally), remains unclear.

III. TIPPING POINTS OF THE OXYGEN DYNAMICAL SYSTEM

In order to reveal the properties of the paradigmatic model (7)–(9), in particular its potential to describe transitions between different states of the climate-oxygen-phytoplankton system, we first need to analyze its invariant solutions, in particular the existence and stability of its steady states. Obviously, the steady state values are given by solutions of the following equations:

$$\frac{A_0 u}{c + c_0} \exp\left(-\frac{(T - T_1)^2}{q^2}\right) - \frac{\delta u c}{c + c_2} - mc = 0, \quad (10)$$

$$\left(\frac{cb_1}{c + c_1} e^{-\frac{T_0}{T}} e^{-\alpha_2 T} - \gamma u - \sigma\right)u = 0, \quad (11)$$

$$-aT^4 + b[1 - (s_1 - s_0)e^{-\alpha_1 u} - s_0] = 0. \quad (12)$$

System (10)–(12) is highly nonlinear and in a general case can only be solved numerically. However, one special semitrivial case—namely when $c = 0$ and $u = 0$ (which corresponds to the anoxia and phytoplankton extinction)—can be easily solved resulting in the following boundary steady state $(T^*, 0, 0)$, where

$$T^* = \left(\frac{b(1 - s_1)}{a}\right)^{\frac{1}{4}}, \quad s_1 < 1. \quad (13)$$

In this case, the eigenvalues of the corresponding Jacobian matrix appears to be all negative (see Appendix A). Thus, the semitrivial steady state $(T^*, 0, 0)$ exists and is stable for any feasible parameter values.

Note that the trivial steady state $(0, 0, 0)$ is not a solution of system (10)–(12), which shows that the general properties of the system in agreement with obvious physical constraints.

For a positive steady state (i.e., with $c \neq 0$ and $u \neq 0$), its existence, uniqueness, and stability is not at all obvious. System (10)–(12) cannot be solved analytically. Therefore, instead, Eqs. (10)–(12) are solved numerically with parameter values varying in a broad range. Having performed numerical simulations (see Appendix B for typical parameter values and Appendix C for details of the simulations procedure), we obtain that the system (12)–(10) has at most two positive steady states, (T_1^*, u_1^*, c_1^*) and (T_2^*, u_2^*, c_2^*) . The two positive steady states only exist in a certain parameter range; see Fig. 4. Of those two states, the upper one (black curve) is stable and the lower one (red curve) is unstable (see Appendix A for more

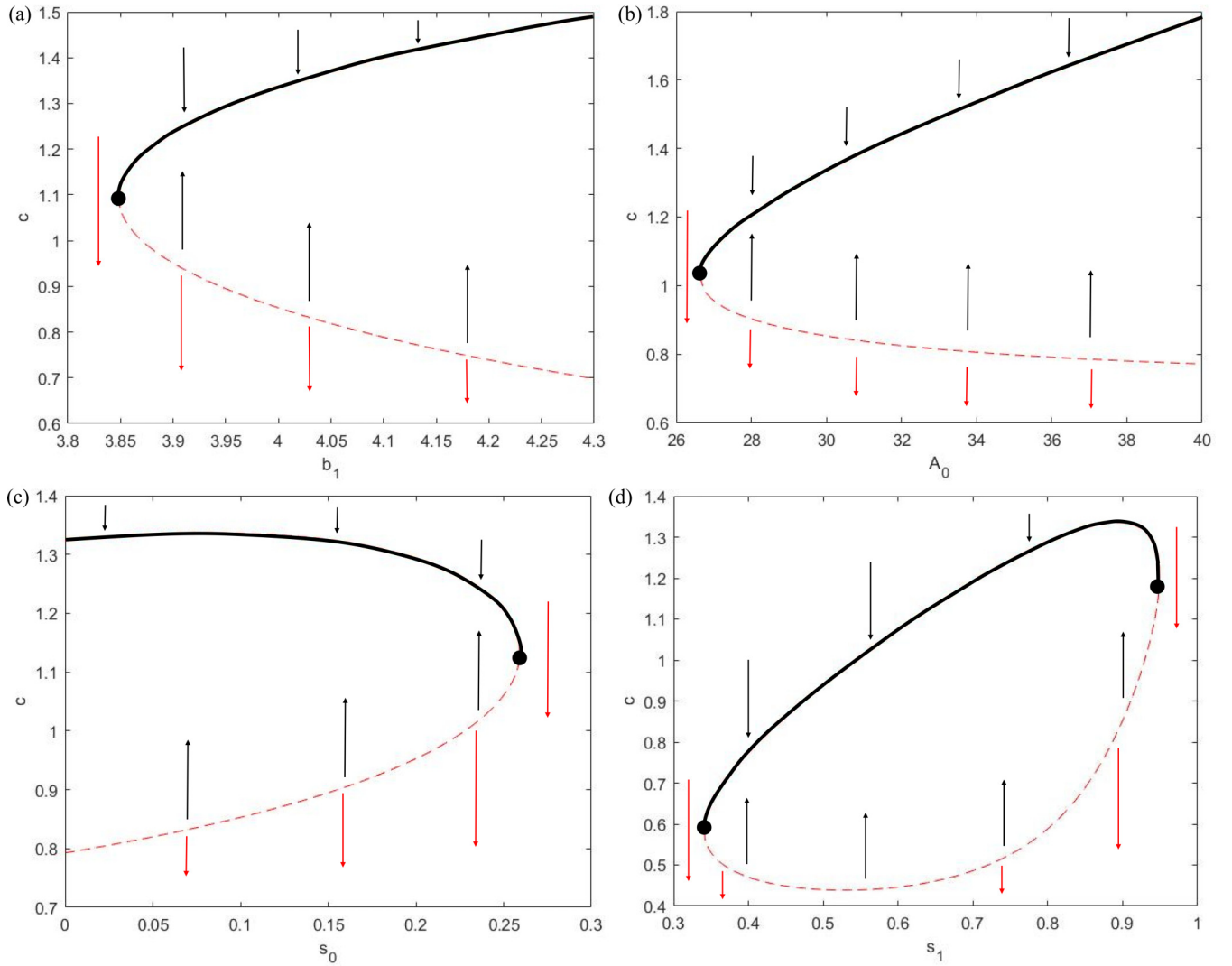


FIG. 4. Bifurcation diagrams. The steady state values of the average oxygen concentration c [obtained by solving system (10)–(12) numerically] are shown as a function of four bifurcation parameters: (a) b_1 , (b) A_0 , (c) s_0 , and (d) s_1 . Other parameter values are given in the text. Solid (black) and dashed (red) curves show the steady and unsteady states, respectively; the large black dots show the tipping points (saddle-node bifurcations) where the two branches merge. The arrows show the direction of the phase flow; black arrows correspond to a “safe” case where the system asymptotically approaches its stable positive case, red arrows correspond to the onset of anoxia when the system asymptotically approaches its semitrivial steady state ($T^*, 0, 0$) (not shown in the figure). Note that all variable and parameters are dimensionless, see Appendix B for details.

details). In the corresponding parameter range, the system therefore is bistable: Depending on the initial conditions, its solution converges to either the upper oxygen-rich steady state (as is symbolically shown by the black arrows in Fig. 4) or to the anoxic state (cf. the red arrows). The unstable steady state (the separatrix between the two phase flows) acts as the boundary between the two basins of attraction. Outside of that range, the only steady state of the system is ($T^*, 0, 0$), i.e., regardless of the initial conditions the system always converges to the anoxic state.

We mention here that, in principle, the three-dimensional dynamical system (7)–(9) can have invariant solutions of other type, e.g., limit cycles or chaotic attractors. However, in our extensive numerical investigation of the system (7)–(9), we did not find any other invariant solutions except for steady states.

Interestingly, the properties of the corresponding bifurcation diagrams are significantly different depending on the choice of the bifurcation parameter (b_1 , A_0 , s_0 , or s_1 , see the end of Sec. II). In the case of b_1 [Fig. 4(a)], the “safe” oxygen-rich steady state only exists if b_1 is sufficiently large, i.e., above a certain threshold (say, b_1^*). This is in good agreement with the biological meaning of parameter b_1 : Since it determines the maximum of phytoplankton growth rate, it seems intuitive to expect that the system is only viable if the growth rate is sufficiently large.

This survival threshold—the value of b_1 where the two branches (the black and red curves) merge and disappear—apparently works as a tipping point (see Fig. 5). As a hypothetical example, consider a situation where the system initially is in its upper steady state for a certain value $b_1^0 > b_1^*$. Consider a decrease in parameter b_1 to a new lower value

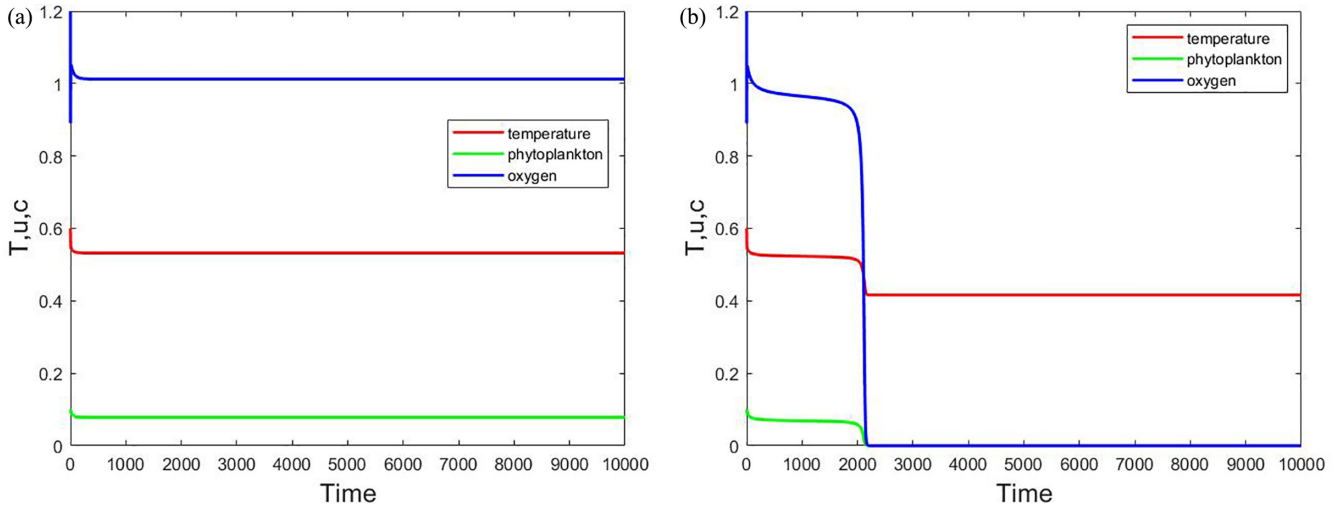


FIG. 5. Response of the system to a change in parameter b_1 . Temperature (red), phytoplankton density (green), and oxygen concentration (blue) versus time obtained as the solution of system (7)–(9) for $b_1^0 = 4$ and (a) $b_1^{\text{new}} = 3.95 > b_1^*$ and (b) $b_1^{\text{new}} = 3.927 < b_1^*$. The initial conditions are $T(0) = 0.6$, $u(0) = 0.1$, $c(0) = 1.2$. Other parameters are given in the text.

(e.g., mimicking a change in the global climatic and environmental conditions). Note that here we focus on the case where the decrease is slow, so that the corresponding change in the properties of the system can be thought of as a sequence of ‘frozen’ systems, with the parameter values for each of the frozen systems being kept constant [53]. Depending on the magnitude of the environmental change, the decrease in b_1 may either bring the system to a new value of the positive stable steady equilibrium if $b_1^{\text{new}} > b_1^*$, so that the system remains in the oxygen-rich state [see Fig. 5(a)] or to the semitrivial anoxic state if b_1^{new} crosses the tipping threshold, $b_1^{\text{new}} < b_1^*$ [see Fig. 5(b)].

Changes in the system properties in response to changes in parameter A_0 are similar to the above. However, in the case where s_0 is used as the bifurcation parameter, see Fig. 4(b), the situation is opposite to the above: The system is only sustainable, i.e., possesses a stable (positive) oxygen-rich state, if s_0 is smaller than a certain threshold value (say, s_0^*). The critical transition (tipping) resulting in ocean anoxia occurs if s_0 increases to a new value $s_0^{\text{new}} > s_0^*$; examples of the corresponding system’s dynamics are shown in Fig. 6.

In case s_1 is used as the bifurcation parameter, see Fig. 4(c), the situation is significantly different. In this case, there are two threshold, s_1^* and s_1^{**} , so that the system possesses a stable oxygen-rich state only if $s_1^* < s_1 < s_1^{**}$. Correspondingly, the tipping resulting in ocean anoxia occurs whenever either of those two threshold is crossed (as a result of some climatic or environmental changes), i.e., if s_1 becomes too small ($s_1^{\text{new}} < s_1^*$) or s_1 becomes too large, then $s_1^{\text{new}} > s_1^{**}$. Examples of the corresponding system’s dynamics are shown in Fig. 7.

We mention here that system (7)–(9) was studied through extensive numerical simulations and the bifurcation diagrams shown in Fig. 4 present only a part of the obtained results. Some more results can be found in Appendix C, where in particular we show the bifurcation diagrams for other variables (i.e., u and T) and also check their sensitivity to a change in parameter q which quantifies the strength of the dependence of A on temperature.

In conclusion to this section, we note that in case the change in parameter value crosses the tipping point, the transition of the system to its new (anoxic) steady state does not necessarily happen fast. The system’s dynamics can in fact be very slow (to the extent that it may even give an impression, e.g., to an observer in a real-world system for which our model is a caricature—that the system is around its steady state) over a certain period of time that can be quite long [e.g., see Fig. 7(b)] before the system experiences a fast transition to its actual new asymptotic steady state. This slow system’s dynamics occurs near the values of the system variables that correspond to the steady state for the parameter value just prior the bifurcation. The corresponding dynamics is called a long transient caused by the “ghost attractor” [54,55]. The duration of the transient is the longer the closer is the new value of the parameter to its bifurcation value [56].

IV. CONCLUSIONS AND OUTLOOK

Understanding existential threats that the climate change and/or rampant anthropogenic activities can pose to the humankind and life on Earth more generally has been attracting growing attention recently [57,58]. In particular, considerable progress was made to identify factors, resources and elements that are crucial for maintaining Earth habitable [1,2,4]. Surprisingly, the issues like availability of oxygen (both in the ocean and in the atmosphere) and the stability of the oceanic oxygen cycle have not been included¹ in spite of their literally vital importance, even in spite of the significant empirical evidence of the oxygen decline [6,8]. One of the motivations behind this Perspective is to attract attention to these largely overlooked issues. In particular, we argue that a dynamical systems approach utilizing a hierarchy of simple low-dimensional “conceptual” models of variable complexity can be a powerful theoretical tool to make insights into the

¹Although they were indeed considered, e.g., see the footnote to Table 1 in Ref. [4], they “failed to make the short list” [4].

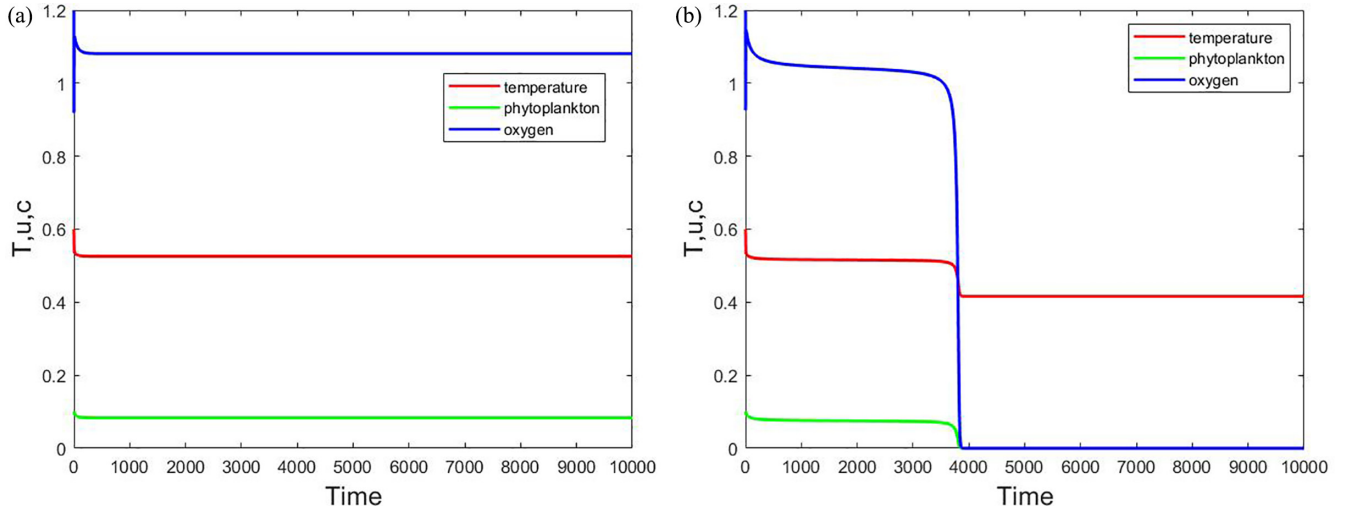


FIG. 6. Response of the system to a change in parameter s_0 . Temperature (red), phytoplankton density (green), and oxygen concentration (blue) versus time obtained as the solution of system (7)–(9) for $s_0^0 = 0.19$ and (a) $s_0^{\text{new}} = 0.2 < s_0^*$ and (b) $s_0^{\text{new}} = 0.227 > s_0^*$. Other parameters and the initial conditions are the same as in Fig. 5.

properties of the ocean oxygen cycle, in particular to reveal possible tipping points and regime shifts. As a paradigmatic example, by considering a three-dimensional “box model” (see Fig. 3) that couples the rate of oxygen production to the global energy budget, we have shown that the oxygen cycle can be fragile with respect to perturbations of some environmental and biological parameters, to the extent that the present oxygen-rich state may disappear hence forcing the system to transition to the anoxic state.

What does this article offer to improve the understanding of bioclimatic systems, in particular the oxygen-phytoplankton-temperature system and the ocean oxygen cycle? The main message from this Perspective is that the “safe” oxygen-rich state is not unconditionally feasible. It exists only for parameter values inside some bounded or semibounded intervals, where interval’s end points work as tipping points. What may be processes or phenomena that could force the system to cross those tipping point (hence pushing it to the anoxic state)? In terms of our dynamical-systems approach, the answer depends on the parameter, as different parameters are related to different processes. For example, b_1 quantifies the general quality of the environment [41]. Should the quality decrease (as a result of processes not explicitly included

into the model), b_1 would decrease, too. For instance, water acidification is known to be a process negatively affecting marine species fitness, hence likely leading to a decrease in b_1 . In case the decrease is sufficiently large, it can lead to system’s tipping [see Fig. 4(a)] and hence to ocean anoxia. A similar chain of arguments apply also to the case where the bifurcation parameter is A_0 .

In the case where the bifurcation parameter is s_1 (the albedo of “pure water,” i.e., in the absence of phytoplankton), the arguments are different and slightly more intricate. If there is no phytoplankton, then biological factors like fitness become irrelevant. However, the albedo of water surface is known to depend on other factor, for instance on water turbidity, with the trend to increase with an increase in turbidity [59]. Thus, it seems possible that water pollution with microparticles (e.g., microplastic) may push the value of s_1 sufficiently high to lead to system tipping and hence to anoxia.

Note that our paradigmatic model has deliberately been made very simple, hence omitting many details and only taking into account the processes and elements that we believe are central to the problem. Therefore, one can ask how our findings may change in a more complicated model. Although at the moment it is a largely open question, here we argue

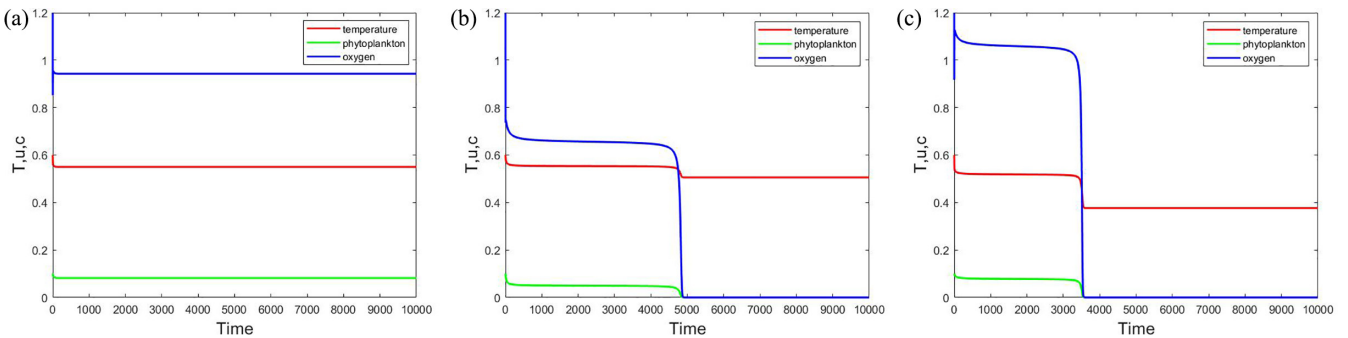


FIG. 7. Response of the system to a change in parameter s_1 . Temperature (red), phytoplankton density (green), and oxygen concentration (blue) versus time obtained as the solution of system (7)–(9) for $s_1^0 = 0.87$ and (a) $s_1^{\text{new}} = 0.86$, where $s_1^* < 0.86 < s_1^{**}$, (b) $s_1^{\text{new}} = 0.7819 < s_1^*$ and (c) $s_1^{\text{new}} = 0.9329 > s_1^{**}$. Other parameters and the initial conditions are the same as in Fig. 5.

that the effect of many missing factors can be implicitly yet efficiently taken into account as noise. Interestingly, using a simplified version of our model (7)–(9), it was shown in a recent study [60] that the presence of noise does not change the model properties dramatically. The main effect of noise appears to be a transformation of the sharp boundary between the two basins of attraction (in the bistable range) into a smooth one, the degree of smoothness depending on the strength of noise [60]. Thus, we presume that our conceptual model (7)–(9) captures some principle properties of the real-world oxygen-phytoplankton-temperature system and hence can be used as a skeleton of (or incorporated to) more complicated and more realistic models.

While we strongly believe that the dynamical systems approach is illuminating, there are many open questions that need to be addressed using more advanced models. For instance, the energy balance equation should be made spatially explicit (cf. Ref. [61]), as the flux of the solar energy obviously depends on the latitude. Also, phytoplankton can affect climate in a few different ways. Changing the albedo of the ocean surface is only one of them; another one is its effect on the cloud formation [62,63] where the latter has the opposite effect as more clouds reflect more light. Finally, we note that ecological processes—in our case, the dynamics of the oxygen-phytoplankton subsystem (7) and (8)—often occur on a faster timescale compared to the global climate process [as represented by the energy balance equation (9)]. In our model (7)–(9), the values of the oxygen concentration and the phytoplankton density can be regarded as averaged over a certain time window (e.g., one year, in order to avoid short-term fluctuations) hence making the timescales compatible. However, a more rigorous approach should address model (7)–(9) as a slow-fast system (cf. Ref. [37]). This will become a focus of future research.

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DATA AVAILABILITY

There are no publicly available research data or software supporting this manuscript. Requests for further information or data should be sent to the authors.

APPENDIX A: STABILITY OF THE STEADY STATES

The Jacobian matrix of the system (7)–(9) is calculated as

$$J = \begin{pmatrix} \Gamma & H & 0 \\ \Theta & \Lambda & K \\ \varpi & \varrho & \tau \end{pmatrix}, \quad (\text{A1})$$

where

$$\begin{aligned} \Gamma &= -\frac{4T^3 a}{\lambda}, \\ H &= -\frac{\alpha_1 b e^{-\alpha_1 u} (s_0 - s_1)}{\lambda}, \\ \Theta &= -u \left[\frac{\alpha_2 b_1 c e^{-T \alpha_2} e^{-\frac{T_0}{T}}}{c + c_1} - \frac{T_0 b_1 c e^{-T \alpha_2} e^{-\frac{T_0}{T}}}{T^2 (c + c_1)} \right], \\ \Lambda &= \frac{b_1 e^{-\frac{T_0}{T}} e^{-\alpha_2 T} c}{c + c_1} - 2u - \sigma, \\ K &= u \left[\frac{b_1 e^{-\frac{T_0}{T}} e^{-\alpha_2 T}}{c + c_1} - \frac{b_1 e^{-\frac{T_0}{T}} e^{-\alpha_2 T} c}{(c + c_1)^2} \right], \\ \varpi &= -\frac{A_0 e^{-\frac{(T-T_1)^2}{q^2}} (2T - 2T_1) u}{q^2 (c + 1)}, \\ \varrho &= \frac{A_0 e^{-\frac{(T-T_1)^2}{q^2}}}{c + 1} - \frac{\delta c}{c + c_2}, \\ \tau &= \frac{\delta c u}{(c + c_2)^2} - \frac{\delta u}{c + c_2} - \frac{A_0 e^{-\frac{(T-T_1)^2}{q^2}} u}{(c + 1)^2} - 1, \end{aligned}$$

where c , u , and T are the steady state values of the system (7)–(9), as defined by Eqs. (10)–(12).

Correspondingly, the eigenvalues μ of the Jacobian matrix for the positive (coexistence) steady states are the solutions of the following characteristic equation:

$$(\Gamma - \mu)[(\Lambda - \mu)(\tau - \mu) - K\varrho] - H[\Theta(\tau - \mu) - K\varpi] = 0. \quad (\text{A2})$$

For a positive steady state, Eq. (A2) is a cubic equation in a general form. Although it can in principle be solved analytically, e.g., by Cardano method, the formulas for its solutions are rather complicated and hence not very instructive. Alternatively, it can be solved numerically. The results show that, when the two positive solutions exist, the upper one is always stable (a node) and the lower one is always unstable (a saddle).

For the semitrivial steady state $(T^*, 0, 0)$, where T^* is given by (13) in the main text, Eq. (A2) factorizes and the eigenvalues are readily found analytically:

$$\mu_1 = -\frac{4T^{*3} a}{\lambda}, \quad \mu_2 = -\sigma, \quad \mu_3 = -1. \quad (\text{A3})$$

Thus, the semitrivial steady state $(T^*, 0, 0)$ exists and is stable for all feasible (positive) parameter values.

APPENDIX B: VARIABLES, PARAMETERS, AND UNITS

Since system (7)–(9) can only be solved numerically, it is convenient to transform it to a dimensionless form [64]. The original system contains many parameters. The number of parameters can be decreased if we choose dimensionless values for the system variables T , c , u , and t . Namely, let us consider $\hat{T} = T/T_0$, $\hat{c} = c/c_0$, $\hat{u} = \gamma u/m$, and $\hat{t} = tm$. Having

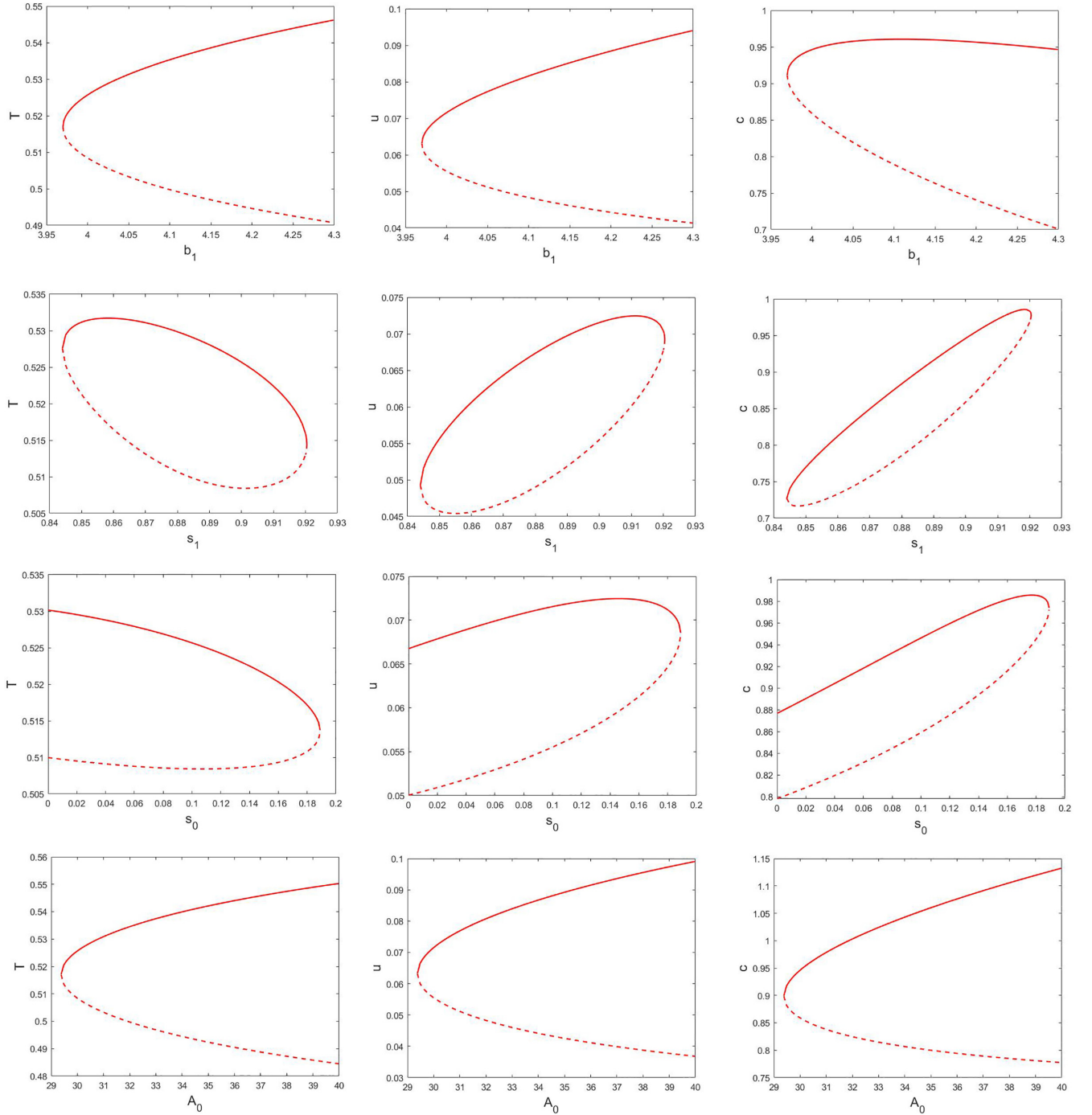


FIG. 8. Bifurcation diagrams for all system variables. Solid and dashed curves show the stable and unstable steady states, respectively. Here $q = 0.075$, other parameter values are the same as in Fig. 4 (see also Appendix B).

performed a simple algebra, it is straightforward to see that the original system (7)–(9) then takes the following form:

$$\begin{aligned} \frac{d\hat{c}}{d\hat{t}} &= \frac{(A_0/mc_0^2)u}{\hat{c}+1} \exp\left(-\frac{(\hat{T}-(T_1/T_0))^2}{(q/T_0)^2}\right) \\ &\quad - \frac{(\delta/mc_0^2)u\hat{c}}{\hat{c}+(c_2/c_0)} - \hat{c}, \end{aligned} \quad (\text{B1})$$

$$\begin{aligned} \frac{d\hat{u}}{d\hat{t}} &= \left[\frac{\hat{c}(b_1/m)}{\hat{c}+(c_1/c_0)} \exp\left(-\frac{1}{\hat{T}}\right) \exp(-(\alpha_2 T_0)\hat{T}) - \hat{u} \right] \hat{u} \\ &\quad - (\sigma/m)\hat{u}, \end{aligned} \quad (\text{B2})$$

$$\begin{aligned} \frac{d\hat{T}}{d\hat{t}} &= \frac{1}{(\lambda m)} (-aT_0^3)\hat{T}^4 + (b/T_0) \\ &\quad \times [1 - (s_1 - s_0) \exp(-(\alpha_1/\gamma)\hat{u}) - s_0]. \end{aligned} \quad (\text{B3})$$

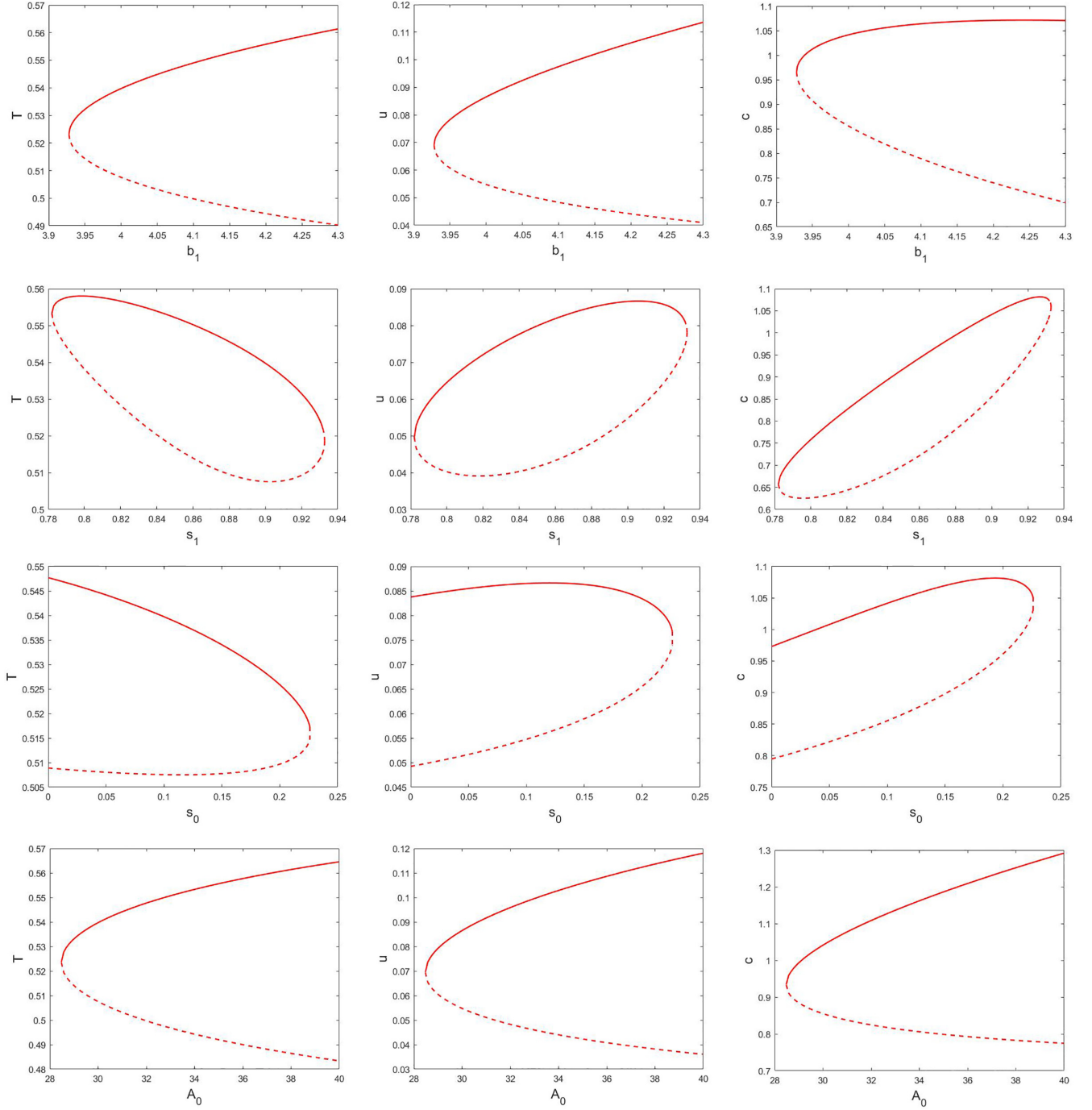


FIG. 9. Bifurcation diagrams for all system variables. Solid and dashed curves show the stable and unstable steady states, respectively. Here $q = 0.1$, other parameter values are the same as in Fig. 8.

The form of the above equations suggests the choice of new (dimensionless) parameters as follows:

$$\hat{A}_0 = A_0/mc_0^2, \quad \hat{T}_1 = T_1/T_0, \quad \hat{q} = q/T_0, \quad (B4)$$

$$\hat{\delta} = \delta/\gamma c_0^2, \quad \hat{c}_2 = c_2/c_0, \quad (B4)$$

$$\hat{b}_1 = b_1/m, \quad \hat{c}_1 = c_1/c_0, \quad \hat{\alpha}_2 = \alpha_2 T_0, \quad (B5)$$

$$\hat{\sigma} = \sigma/m, \quad \hat{\lambda} = \lambda m, \quad (B5)$$

$$\hat{a} = aT_0^3, \quad \hat{b} = b/T_0, \quad \hat{\alpha}_1 = m\alpha_1/\gamma, \quad (B6)$$

so that system [(B1)–(B3)] (now fully dimensionless) can be written in the following more convenient form:

$$\frac{d\hat{c}}{d\hat{t}} = \frac{\hat{A}_0 u}{\hat{c} + 1} \exp\left(-\frac{(\hat{T} - \hat{T}_1)^2}{\hat{q}}\right) - \frac{\hat{\delta} \hat{u} \hat{c}}{\hat{c} + \hat{c}_2} - \hat{c}, \quad (B7)$$

$$\frac{d\hat{u}}{d\hat{t}} = \left[\frac{\hat{c} \hat{b}_1}{\hat{c} + \hat{c}_1} \exp\left(-\frac{1}{\hat{T}}\right) \exp(-\hat{\alpha}_2 \hat{T}) - \hat{u} \right] \hat{u} - \hat{\sigma} \hat{u}, \quad (B8)$$

$$\frac{d\hat{T}}{d\hat{t}} = \frac{1}{\hat{\lambda}} (-\hat{a} \hat{T}^4 + \hat{b} [1 - (s_1 - s_0) \exp(-\hat{\alpha}_1 \hat{u}) - s_0]). \quad (B9)$$

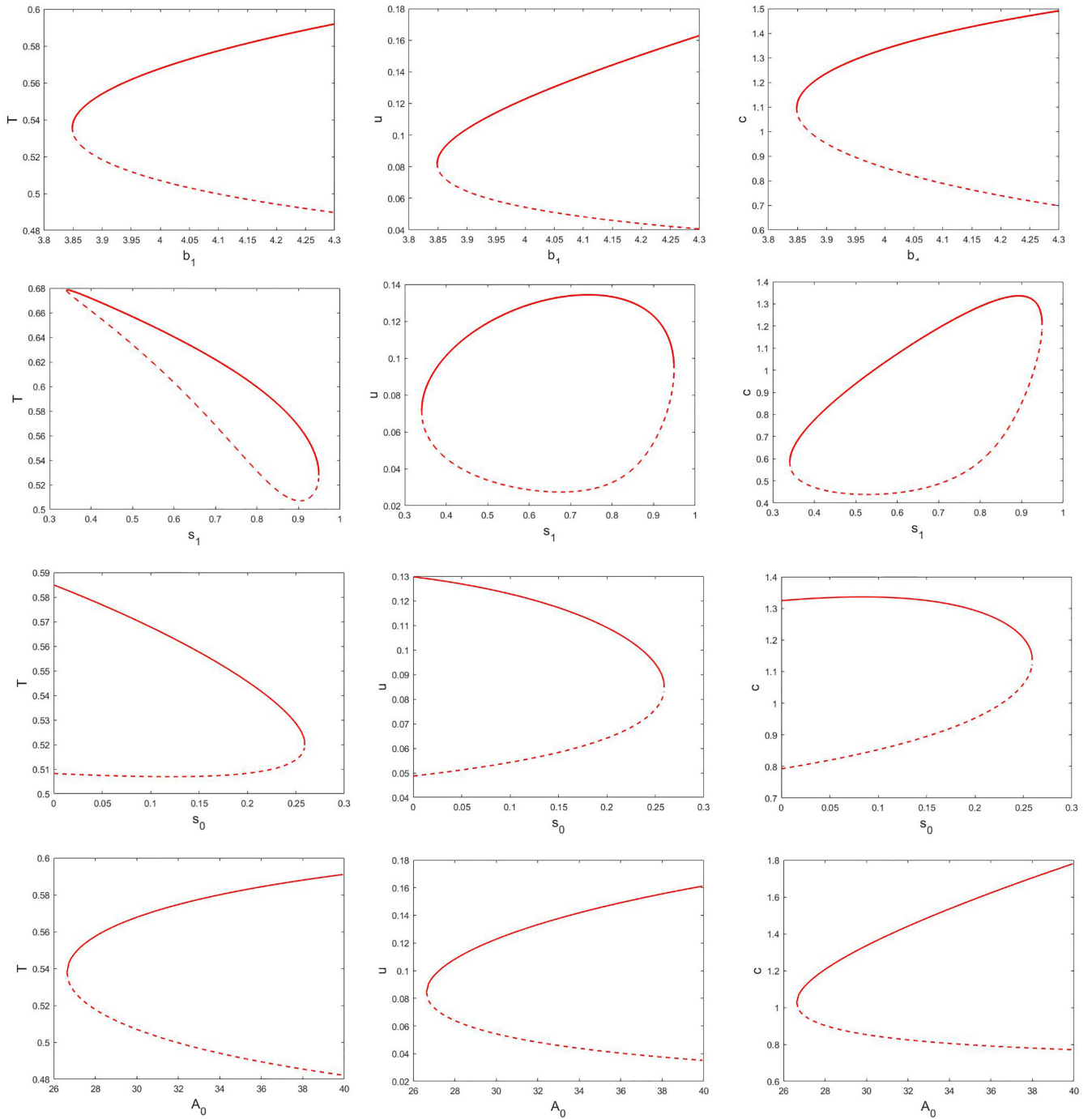


FIG. 10. Bifurcation diagrams for all system variables. Solid and dashed curves show the stable and unstable steady states, respectively. Here $q = 0.2$, other parameter values are the same as in Fig. 8.

Values of the dimensionless parameters used in simulations are given in Table I. Finally, we mention that, in terms of the original (dimensional) system (7)–(9), our choice of dimensionless parameters corresponds to $T_0 = c_0 = m = \gamma = 1$.

With regard to our choice of specific parameter values (as in Table I), we mention that ecological parameters are usually available with a low accuracy (e.g., see Ref. [37] for examples and discussion) or sometimes not available at all. In particular, to the best of our knowledge there are presently no data

about relevant range of values for q and A_0 ; thus, their values used in simulations are hypothetical. Also, there is significant uncertainty with regard to relevant values of s_1 . While the mainstream of oceanographic literature provides its value as 0.1–0.2, there are reasons to believe that the values relevant to phytoplankton primary production (of which oxygen is a by-product) are significantly higher. The albedo of ocean surface varies significantly depending on the solar angle. In its turn, the solar angle varies a lot along with the latitude,

TABLE I. Values of the dimensionless model parameters used in simulations (unless specified differently in the main text). The hats are omitted for the sake of notations simplicity.

Parameter	Meaning	Numerical value
a	Stefan-Boltzmann constant	1
b	Total flux of the incoming solar radiation	0.3
b_1	Scaling factor for the plankton growth rate	4
s_0	Albedo of a heavily polluted water	0.1
s_1	Albedo of the clear water	0.9
T_0	Activation temperature	1
α_1	Coefficient of phytoplankton-albedo coupling	3
α_2	Coefficient of the plankton death rate-temperature coupling	1
λ	Average heat capacity of the surface layer	1
σ	Phytoplankton mortality rate	0.1
m	Oxygen background decay rate	1
c_0	Half-saturation constant	1
c_1	Half-saturation constant	1
c_2	Half-saturation constant	1
γ	Plankton competition coefficient	1
δ	Phytoplankton respiration rate	1
A_0	Maximum oxygen production rate	30
T_1	Optimal oxygen production temperature	0.5
q	Strength of oxygen production temperature dependence	0.2

with the season, and with the time during the day. Especially the first two factors are important to affect the values of albedo relevant to oxygen production:

(i) the ocean primary production (and hence oxygen production as a by-product of the phytoplankton growth) is concentrated in subpolar regions [65] where the solar angle is never too high;

(ii) the rate of primary production in the ocean is usually highest in the spring (sometimes also in the fall) [66] when the solar angle is significantly lower than in summer.

APPENDIX C: DETAILS OF NUMERICAL PROCEDURE AND ADDITIONAL SIMULATION RESULTS

The steady states of the oxygen-phytoplankton-temperature system are the solutions of system (10)–(12). In order to obtain a bifurcation diagram, the bifurcation

parameter—say, p (where according to our choice p can be b_1 or A_0 or s_0 or s_1)—was first discretized with a small step Δp , making a sequence of values, $\{p_0 = p_{\min}, p_1 = p_0 + \Delta p, \dots, p_{n+1} = p_n + \Delta p, \dots, p_N = p_{\max}\}$, over a sufficiently broad interval $[p_{\min}, p_{\max}]$. For each value p_i (where $0 \leq i \leq N$), the system of transcendent algebraic equations (10)–(12) was solved using Matlab function VPASOLVE. We obtained that, for each checked value of the bifurcation parameters, system (10)–(12) has at least one and not more than three solutions. The end points of the subinterval where the system has three solutions have the meaning of bifurcation values.

Below we show an extended set of the bifurcation diagrams (for all three variables, c , u , and T) obtained for a few values of parameter q ; see Figs. 8–10. It is readily seen that our results are generally robust with regard to a change in the parameter value.

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