

Stability of a planetary climate system with the biosphere species competing for resourcesSergey A. Vakulenko,^{1,2} Ivan Sudakov^{3,*}, Sergei V. Petrovskii^{4,5} and Dmitry Lukichev²¹*Institute for Problems in Mechanical Engineering, Russian Academy of Sciences, St. Petersburg 199178, Russia*²*Faculty of Control Systems and Robotics, ITMO University, Saint Petersburg 197101, Russia*³*Department of Physics, University of Dayton, 300 College Park, SC 111, Dayton, Ohio 45469-2314, USA*⁴*School of Mathematics and Actuarial Science, University of Leicester, Leicester LE1 7RH, United Kingdom*⁵*S. M. Nikol'skii Mathematical Institute, Peoples' Friendship University of Russia (RUDN University), Moscow 117198, Russia*

(Received 8 June 2020; revised 12 November 2020; accepted 6 January 2021; published 1 February 2021)

With the growing number of discovered exoplanets, the Gaia concept finds its second wind. The Gaia concept defines that the biosphere of an inhabited planet regulates a planetary climate through feedback loops such that the planet remains habitable. Crunching the “Gaia” puzzle has been a focus of intense empirical research. Much less attention has been paid to the mathematical realization of this concept. In this paper, we consider the stability of a planetary climate system with the dynamic biosphere by linking a conceptual climate model to a generic population dynamics model with random parameters. We first show that the dynamics of the corresponding coupled system possesses multiple timescales and hence falls into the class of slow-fast dynamics. We then investigate the properties of a general dynamical system to which our model belongs and prove that the feedbacks from the biosphere dynamics cannot break the system’s stability as long as the biodiversity is sufficiently high. That may explain why the climate is apparently stable over long time intervals. Interestingly, our coupled climate-biosphere system can lose its stability if biodiversity decreases; in this case, the evolution of the biosphere under the effect of random factors can lead to a global climate change.

DOI: [10.1103/PhysRevE.103.022202](https://doi.org/10.1103/PhysRevE.103.022202)**I. INTRODUCTION**

An understanding of the mechanisms and scenarios of climate change as well its current and potential effects on ecosystems and biodiversity has been a focus of keen attention and intense research over the last few decades [1–3]. There is a general consensus that climate change will likely have an adverse impact on the ecological systems and population communities resulting in species extinction and a considerable biodiversity loss worldwide.

While the top-down effect of climate on ecosystems is thus well established, relatively little attention has been paid to the possibility of an opposite, bottom-up effect that ecosystems may have on the climate. Mainstream research often tends to consider the ecosystems and population communities as “biological actors on the physical stage” [4], often disregarding possible feedback. Meanwhile, in planetary science, there is the concept of Gaia [5,6] that postulates the biosphere regulates the planetary climate to mitigate it for its own survival. While this hypothesis has been introduced long ago, current research in planetary and earth sciences inspires new applications of this hypothesis. In particular, it has been shown that even if a model exoplanet has significant climate perturbations, then the Gaia concept is still valid [7] (the original Gaia concept is based on a static planetary climate). The possible influence of environmental fluctuations on the evolution of life was considered in Ref. [8]. Coupling between the climate and the biosphere can affect the climate stability through the

existence of climate feedback loops and climate tipping points [9–11]. This supports the Gaia concept but also broadens it compared to its original statement: While showing that the biosphere can indeed affect the climate, it does not necessarily change the climate to provide better conditions for the biosphere to function. The Gaia concept was further developed in Refs. [12,13], where the coupling between the climate and biosphere was studied using the maximum entropy production principle.

Despite the long history of the problem and the large number of papers discussing various aspects of the Gaia hypothesis, relatively little attention has been paid to the specific mechanisms through which the biosphere can make an effect on climate. The few studies that directly addressed this question by means of mathematical modeling used somewhat disputable assumptions or simplistic models. Correspondingly, it remains largely unclear to what extent the population dynamics of species in the biosphere can change the global climate. In this paper, we contribute to the discussion of the Gaia concept by considering a semiquantitative mathematical model of coupled climate-biosphere dynamics. The model explicitly takes into account the well-established empirical observation that the presence of vegetation tends to decrease the planetary albedo [14] and hence can change the global energy balance. We first develop a rigorous mathematical theory that reveals the property of the corresponding class of systems to which our model belongs. By applying the theory to a few particular cases, we then show that both biodiversity and the total biomass can have a significant, albeit different, effect on the state of the climate.

*Corresponding author: isudakov1@udayton.edu

We mention here that modeling physical processes in a climate system often leads to difficult mathematical problems, e.g., involving complicated systems of partial differential equations for biological and chemical processes [2]. There exist climate models with different levels of realism; they can include thousands and even millions of equations, with thousands of parameters to adjust. Usually, one investigates these models by computer simulations [15]. However, it is difficult to estimate the reliability of these computations, since it is connected with a difficult mathematical problem on the structural stability of attractors [16,17]. The theory of the linear response of climate systems to perturbations [18,19] is based on the Ruelle theory of the linear response for dynamical systems that holds on the formal hypothesis that the dynamical system is of the type axiom *A* one. The last fact implies structural stability. However, Smale’s *A*-axiom systems [17] seldom appear in practical applications. The class of structurally stable systems is very narrow; this mainly includes systems with hyperbolic or almost hyperbolic behavior. One can expect, therefore, that the attractors of climate systems are not structurally stable: Their topological structure can change under small perturbations. Correspondingly, they can exhibit complicated bifurcations under small parameter perturbations. Since parameter values are often known with only a poor accuracy, it can make predictions obtained from “realistic” models questionable or even unreliable. The problem is further exacerbated by the uncertainty arising due to, often, insufficient resolution of small-scale processes, as neglecting the variability of the unresolved scales can lead to major errors in the dominant scales [20].

These interesting and important questions are highlighted in detail in a recent review [21] (see also Ref. [22]). An alternative approach to “realistic” models is given by the so-called conceptual climate models. The climate system is a complex system that consists of a large number of coupled subsystems. On a large scale, they include the main agents such as the atmosphere, oceans, the biosphere, etc. Conceptual climate models endeavor to relate the equilibria and the bifurcations of the entire system to the interaction between its parts while describing the subsystems’ states by only a small number of dynamical variables. The effect of “hidden” degrees of freedom (not taken into account explicitly) and the corresponding fluctuations can to some extent be taken into account by including into the model random variables and applying the tools and techniques of random dynamical systems [23].

There are different types of conceptual climate models. Many of them are energy balance models; mathematically, they are defined by an ordinary differential equation describing the energy conservation in the climate system. The most popular model is a *zero-dimensional model* [24] based on the theory of blackbody radiation determining global temperature changes due to the difference in incoming and outgoing solar radiation. This difference may be caused by a change in the control parameters such as the surface albedo, the greenhouse gas emission, and even the solar constant. The system’s equilibria and the ideas on how to find them by the bifurcation theory tools are discussed in Ref. [25].

One question that holds the key to the understanding of long-term climate dynamics is as follows: Why does the

climate stay stable over long time intervals (e.g., hundreds of thousands of years) before experiencing a transition to a different state? To address this question in the context of the Gaia hypothesis [10,11], in this paper we consider a conceptual climate model where the dynamical variables can be decomposed as slow and fast modes. Then for large times the fast mode dynamics is captured by the slow dynamics on a stable slow manifold of a slow-fast system. The slow variables determine a long-term climate evolution under external factors whereas the fast modes may be associated with rapid factors. We mention here that the mode decomposition technique can be used for deterministic as well as stochastic climate models [23].

The paper is organized as follows. In the next section, we introduce a planetary climate model with a biosphere component that arises from coupling between the conceptual zero-dimensional global energy balance model of climate dynamics and a generic ecosystem dynamics model (a multi-specific population system living on multiple food sources). In Sec. III, we consider a general class of systems to which our model belongs and discuss the stability of those systems. We then show in Sec. IV that, in the case of our climate-biosphere model, the planetary climate remains stable with regard to a variation of the ecosystem model parameters as long as biodiversity is sufficiently large, but it can lose stability (hence potentially resulting in regime shifts and a global climate change) if the number of species is small. A discussion and conclusions can be found in the last section.

II. THE MODEL

The energy balance system is a baseline climate model. It is defined by the following equation [25],

$$\frac{dT}{dt} = \lambda^{-1} \left(-e\sigma T^4 + \frac{\mu_0 I_0}{4} (1 - A) \right), \quad (1)$$

where λ is thermal inertia, T is the averaged surface temperature, t is time, and A is the average albedo of the planet’s surface. On the right-hand side, the first term is the outgoing emission and the second term represents the incoming star’s radiation. Generally, incoming radiation to the planetary surface from a star is modified by a parameter μ_0 to allow for variations in the stellar irradiance per unit area I_0 (the solar constant in the case of the Earth), or for long-term variations of the planetary orbit [26]. On the other side, the outgoing emission depends on the fourth power of temperature, the effective emissivity e , and a Stefan-Boltzmann constant σ .

This model can be coupled with the modeled biosphere’s dynamics as follows. The complete averaged albedo A can depend on the biosphere state. For simplicity, we mostly focus our analysis on a single global ecosystem in which species are competing for several resources. We consider the following classical model,

$$\frac{dx_i}{dt} = x_i[-\mu_i + \phi_i(v) - \gamma_i x_i], \quad i = 1, \dots, m, \quad (2)$$

$$\frac{dv_k}{dt} = D_k(S_k - v_k) - \sum_{i=1}^M b_{ki} x_i \phi_i(v), \quad k = 1, \dots, n \quad (3)$$

(cf. Refs. [27,28]), where $x = (x_1, x_2, \dots, x_n)$ are the species abundances, $m \gg 1$, and $v = (v_1, \dots, v_n)$ the resource concentrations. Here, μ_i are the species mortalities, $D_k > 0$ are resource turnover rates, S_k is the supply of the resource v_k , and ϕ_i is the specific growth rate of species as a function of the availability of the resource (also known as the Michaelis-Menten function). The coefficients $\gamma_i > 0$ define self-limitation effects [29]. We assume that each of the resources v_k , $k = 1, \dots, n$, is consumed by all species so that the fraction of the k th resource in the i th species is positive $b_{ik} > 0$.

We consider general ϕ_j which are bounded, non-negative, and Lipschitz continuous,

$$0 \leq \phi_j(v) \leq C_+, \quad |\phi_j(v) - \phi_j(\tilde{v})| \leq L_j |v - \tilde{v}|, \quad (4)$$

i.e., ϕ_k have a minimal smoothness, and they are bounded and non-negative. The last restriction means that species consume resources.

Moreover, we suppose

$$\phi_k(v) = 0, \quad \text{for all } k, \quad v \in \partial \mathbf{R}_+^m, \quad (5)$$

where $\partial \mathbf{R}_+^m$ denotes the boundary of the hyperoctant $\mathbf{R}_+^m = \{v : v_j \geq 0, \forall j\}$. Moreover, we suppose that

$$\frac{\partial \phi_k(v)}{\partial v_j} \geq 0, \quad \text{for all } k, j, \quad v \in \partial \mathbf{R}_+^m. \quad (6)$$

This assumption means that as the amount of the j th resource increases, all the functions ϕ_l also increase.

Conditions (4) and (5) can be interpreted as a generalization of the well-known von Liebig law, where

$$\phi_k(v) = r_k \min \left\{ \frac{v_1}{K_{k1} + v_1}, \dots, \frac{v_m}{K_{km} + v_m} \right\} \quad (7)$$

(cf. Ref. [27]), where r_k and K_{kj} are positive coefficients, and $k = 1, \dots, M$. The coefficient r_k is the maximal level of the resource consumption rate by the k th species and coefficients K_{ki} , $i = 1, \dots, M$ define the sharpness of the consumption curve $\phi_k(v)$.

A simple way to couple climate subsystem (1) and the modeled biosphere defined by (2) and (3) is to suppose that the resource supply parameters S_k depend on the surface temperature T . Moreover, we can suppose the albedo is a linear function of x_i :

$$A = A(x) = A_0 - m^{-1} \sum_{j=1}^m c_j x_j. \quad (8)$$

Finally, we obtain the following climate-biosphere system,

$$\frac{dx_i}{dt} = x_i[-\mu_i + \phi_i(v) - \gamma_i x_i], \quad i = 1, \dots, m, \quad (9)$$

$$\frac{dv_k}{dt} = D_k(S_k(T) - v_k) - \sum_{i=1}^m b_{ki} x_i \phi_i(v), \quad k = 1, \dots, n, \quad (10)$$

$$\frac{dT}{dt} = \lambda^{-1} \left[-e\sigma T^4 + \frac{\mu_0 I_0}{4} \left(1 - A_0 + m^{-1} \sum_{j=1}^m c_j x_j \right) \right]. \quad (11)$$

As an example, let us consider a model planet where the surface is significantly covered by ice [30] and the ice-albedo feedback is the main regulator of the planetary climate dynamics [31]. Let the area of some region of the planet be S_{arc} , the area occupied by ice be S_{ice} , while the free ice area be S_{free} [32], where $S_{\text{free}} = S_{\text{arc}} - S_{\text{ice}}$. One can suppose that different species coexist in the free ice domain and the averaged albedo of this domain is a linear combination of contributions of different species. Then we obtain

$$A_0 = A_{\text{ice}} S_{\text{ice}} S_{\text{arc}}^{-1}, \quad c_j \propto S_{\text{free}} = S_{\text{arc}} - S_{\text{ice}}, \quad (12)$$

where A_{ice} is the albedo of the ice-covered area. This relation will be useful below.

Suppose that species populations x_i and resources v_k are fast variables, while the temperature T evolves slowly. Such a situation arises if, for example, $\gamma_i \gg 1$ (see Ref. [33]). Then one can show that for large times $t x_i(t) \approx X_i(T)$, where $X_i(T)$ are time-averaged equilibrium species populations for fixed T (see Sec. IV). Then we obtain the following equation:

$$\frac{dT}{dt} = \lambda^{-1} \left[-e\sigma T^4 + \frac{\mu_0 I_0}{4} \left(1 - A_0 + m^{-1} \sum_{j=1}^m c_j X_j(T) \right) \right]. \quad (13)$$

Note that Eq. (13) formally resembles the well-known ice-albedo feedback modification of the zero-dimensional energy balance model [25].

When the system (9), (10), and (13) is regarded as a model of a particular biosphere, the choice of coefficients c_k is determined by the environmental conditions at a given location and the corresponding species properties. Since we are aiming at building a global model, we want Eqs. (9), (10), and (13) to be applicable to any part of a modeled planet. Thus, we consider the coefficients unspecified. More precisely, we suppose that coefficients c_k are random numbers described by certain probability distributions. We introduce these coefficients randomly assuming the randomness of the biological evolution.

In the upcoming section, we will consider a general class of a slow-fast system with random coefficients, which includes the system (13) as a particular case.

III. A GENERAL CLASS OF SYSTEMS

A. A slow-fast system

In this section, we consider the following class of systems,

$$\frac{dy_i}{dt} = \kappa g_i(y, x), \quad (14)$$

$$\frac{dx_j}{dt} = \sum_{l=1}^p A_{jl} x_l + \kappa_1 F_j(y, x), \quad (15)$$

where $i = 1, \dots, n$, $j = 1, \dots, p$, and

$$F_j(y, x) = \sum_{k=1}^m b_{jk} f_k(y, x).$$

In these equations, the unknown vector-valued function $y(t) = [y_1(t), \dots, y_n(t)]$ consists of slow components, the unknown function $x = (x_1, \dots, x_p)$ determines fast components, κ, κ_1 are small positive parameters, g_i, f_k are given smooth and uniformly bounded functions, b_{jk} are bounded coefficients,

and the square matrix A_{jl} defines a linear operator \mathbf{A} with the spectrum $\sigma(\mathbf{A})$ such that

$$\text{Re } \sigma(\mathbf{A}) < -\delta_0 < 0.$$

Then for sufficiently small $\kappa, \kappa_1 > 0$ the system of equations (14) and (15) has a locally attracting smooth and locally invariant in an open neighborhood U_{κ, κ_1} of $x = 0$ manifold \mathcal{M} defined by

$$x_j = \Phi_j(y, \kappa, \kappa_1) = \kappa_1 \left(\sum_{k=1}^m c_{jk} f_k(y, 0) + \tilde{X}_j(y, \kappa, \kappa_1) \right), \tag{16}$$

where

$$c_{ik} = - \sum_{j=1}^m (A^{-1})_{ij} b_{jk}.$$

Here, A^{-1} stands for a matrix inverse to A and sufficiently smooth functions $\tilde{X}_j(y, \kappa, \kappa_1)$ define small corrections such that

$$|\tilde{X}_j(\cdot, \kappa, \kappa_1)|_{C^1(U_{\kappa, \kappa_1})} \rightarrow 0 \quad (\kappa, \kappa_1 \rightarrow 0). \tag{17}$$

The existence of \mathcal{M} follows from the known results (for example, Refs. [16,34,35]).

As a result, we obtain the following system for slow variables,

$$\frac{dy_i}{dt} = \kappa g_i[y, \Phi(y, \kappa, \kappa_1)], \tag{18}$$

where $\Phi(y, \kappa, \kappa_1) = [\Phi_1(y, \kappa, \kappa_1), \dots, \Phi_p(y, \kappa, \kappa_1)]$.

For consideration of the systems with random parameters we need to use arguments from dynamical system theory and the Hoeffding inequality, one of the concentration inequalities.

Recall the basic concept of structural stability introduced by Andronov and Pontryagin in 1937 [36]. Consider a smooth vector field F on a compact domain \mathbb{D}^n of \mathbb{R}^n with a smooth boundary (or on a compact smooth manifold M of dimension n). Assume that $F \in C^1(\mathbb{D}^n)$ and consider all ϵ -small perturbations \tilde{F} such that

$$|\tilde{F}|_{C^1(\mathbb{D}^n)} < \epsilon. \tag{19}$$

Consider systems of differential equations $dx/dt = F(x)$ and $dx/dt = F(x) + \tilde{F}(x)$ and suppose that they define global semiflows S_F^t and $S_{F+\tilde{F}}^t$ on \mathbb{D}^n . The system $dx/dt = F(x)$ is called structurally stable if there exists an ϵ_0 such that for all positive $\epsilon < \epsilon_0$ trajectories of semiflows S_F^t and $S_{F+\tilde{F}}^t$ are orbitally topologically conjugated (there exists a homeomorphism, which maps trajectories of the first system into trajectories of the second one). Roughly speaking, the original system is structurally stable if any sufficiently small C^1 perturbations of that system conserve the topological structure of its trajectories, for example, the equilibrium point stays an equilibrium (maybe slightly shifted with respect to the equilibrium of a nonperturbed system), or the perturbed cycle is again a cycle (maybe slightly deformed and shifted). We denote the structural stability constant of the system $dx/dt = F(x)$ by $\epsilon_0(F)$.

Note that structurally stable dynamics may be, in a sense, “chaotic.” There is a rather wide variation in different

definitions of “chaos.” Chaotic (not periodic and no rest point) hyperbolic sets occur in some model systems [16,36–41].

B. Systems with random parameters

We consider systems (18), which arise, in a natural way, from systems decomposed in slow and fast variables. We will use the following notation. We denote by EX the expectation of a random quantity X , and by $\text{Var } X$ its variance. Moreover, $\text{Pr}[A]$ denotes the probability of a random event A . In this section, we formulate general principles on averaging with respect to the parameters that are applicable to fast-slow climate models.

Consider the following general system of differential equations,

$$\frac{dy_i}{dt} = g_i[y, \Phi(y)], \tag{20}$$

where $i = 1, \dots, n, y(t) = [y_1(t), \dots, y_n(t)]$ is an unknown vector function, and $\Phi = (\Phi_1, \dots, \Phi_p), \Phi_l(y)$ are functions, which will be defined below. Let \mathbb{B}^n be a compact subdomain of \mathbb{R}^n with a smooth boundary $\partial\mathbb{B}^n$. We suppose that $g_i(y, \Phi)$ are smooth functions uniformly bounded as are the first and second derivatives with respect to all variables y, Φ ,

$$|g_i|_{C^2(\mathbb{B}^n \times \mathbb{R}^p)} < C_g, \tag{21}$$

where C_g is a positive constant.

We assume, moreover, that the functions $\Phi_i(y)$ are sums of other functions $f_{ij}(y)$ with random parameters c_{ij} :

$$\Phi_i(y) = m^{-1} \sum_{j=1}^m f_{ij}(y, c_{ij}). \tag{22}$$

For (20) we set the initial data

$$y(0) = y^{(0)}. \tag{23}$$

Let the following assumptions hold:

Assumption 1. Let c_{ij} be independent random quantities such that $Ec_{ij} = \bar{c}$. Moreover, we suppose that almost surely in c_{ij} the functions f_{ij} and their derivatives satisfy

$$\sup_{y \in \mathbb{B}^n} |f_{ij}(y, c_{ij})| < C_f, \tag{24}$$

$$\sup_{y \in \mathbb{B}^n} |D_y^k f_{ij}(y, c_{ij})| < C_{f,k}, \quad k = 1, 2, \tag{25}$$

where positive constants $C_f, C_{f,k}$ are uniform in i, j, m .

Here, we do not suppose that c_{ij} are normally distributed, so we can consider sufficiently general random c_{ij} with different probability density functions (PDFs). Our assumption is general enough and it allows us to apply the Hoeffding theorem [42]. The two main cases are particularly interesting. The first arises when f_{ij} are linear functions of c_{ij} . In this case we suppose that the PDF of c_{ij} has a bounded support. For example, we can take a bounded Pareto distribution for c_{ij} , but it is not allowed to take the standard Pareto density law. This case occurs in the presented paper, where c_{ij} are variations of albedo. A more interesting case can occur, if, for example, $f_{ij}(y) = y_i/(c_{ij} + y_i)$ with $y_i \geq 0$. Then the support of c_{ij} should lie in $(c_0, +\infty), c_0 > 0$, and here we can take the Pareto distribution. So, it is possible to make averaging

over species parameters for a system with Holling’s functional responses.

Together with system (20) we consider the corresponding averaged system,

$$\frac{d\bar{y}_i}{dt} = \bar{g}_i(y), \tag{26}$$

where

$$\bar{g}_i(y) = g_i(y, \bar{\Phi}_1(y), \dots, \bar{\Phi}_p(y)), \tag{27}$$

where $i = 1, \dots, n$, and $y(t) = [y_1(t), \dots, y_n(t)]$ is an unknown vector function, and $\bar{\Phi}_i(y)$ are averages of functions $\Phi_i(y)$ over the random parameters c_{ij} :

$$\bar{\Phi}_i(y) = m^{-1} \sum_{j=1}^m f_{ij}(y, c_{ij}). \tag{28}$$

We assume that the following conditions hold,

$$\bar{g}(y) \cdot e(y) < 0 \quad \forall y \in \partial\mathbb{B}^n, \tag{29}$$

and

$$g(y, \Phi(y)) \cdot e(y) < 0 \quad \forall y \in \partial\mathbb{B}^n, \tag{30}$$

where $e(y)$ is a normal vector to the boundary $\partial\mathbb{B}^n$ at the point y directed inward on the domain \mathbb{B}^n . For the system (26) we set the same initial data (23). Condition (29) implies that the Cauchy problem (23) and (26) defines a global semiflow on the domain \mathbb{B}^n .

C. Main features of the systems with random parameters

For slow variable systems (18) we prove an averaging theorem assuming that c_{ik} are random independent parameters (see the Appendix). This theorem asserts the attractor of the original system is close to the attractor of the averaged one with a probability Pr_m , which is exponentially close to 1 for large m . So, our main idea is as follows: A relative climate stability results from the effect where a large number of independent factors can mutually cancel each other out. The probability Pr_m satisfies an inequality that involves the number ϵ_0 , which is a measure of stability under perturbations. If $\epsilon_0 > 0$ is small, i.e., the original system is weakly stable and conserves its dynamics only under very small perturbations, then the estimate (A12) from Theorem 1 (see Appendix) makes sense only for large $m > m_0(\epsilon_0)$ [in fact, for bounded m the right-hand side of (A12) is negative].

Moreover, structurally stable systems are seldom found in real applications (if we exclude the cases $n = 1$ and $n = 2$, where they are generic). According to the basic result of Smale [16,41], for dimensions $n > 2$ structurally stable systems are not generic. To overcome this difficulty, we consider an approach which allows us to show that solutions of the original system stay in a small neighborhood of a local attractor of the corresponding averaged system.

The stability of many dynamical regimes can be proved by using Lyapunov functions. Recall that $L(y)$ is a Lyapunov function of a system $dy/dt = g(y)$ in a domain $\mathbb{V} \subset \mathbb{R}^n$ if L is at least C^1 smooth and $L(y(t))$ does not increase along trajectories $y(t)$ of the system:

$$\nabla L(y) \cdot g(y) \leq 0, \quad y \in \mathbb{V}. \tag{31}$$

For example, if y^* is a stable rest point of the system, then one can construct a $L(y)$ close to a quadratic form, which is a Lyapunov function in a small neighborhood \mathbb{V} of y^* and

$$\nabla L(y) \cdot g(y) \leq c|y - y^*|^2, \quad y \in \mathbb{V}, \tag{32}$$

for some $c > 0$.

The next statement (see the Appendix) can be proven for the Lyapunov functions. If the averaged system defined by (26) has a Lyapunov function, then the original system (20) has the same Lyapunov function, a probability Pr_L , which is exponentially close to 1 as m large.

This theorem can be applied to the energy balance system (13) as follows. Suppose that the averaged system is gradient-like [note that (13) enjoys this property]. Let \bar{A} be an attractor of the original system, which consists of stable equilibria. Suppose that all equilibria of the averaged system are hyperbolic. Then there exists a Lyapunov function $L(y)$ such that

$$H_{\bar{g}}(y) = \nabla L(y) \cdot \bar{g}(y) \leq -\epsilon,$$

for all $y \in \mathbb{V}(\bar{A})$ and some $\epsilon > 0$, where $\mathbb{V}(\bar{A})$ is an open subset of the attraction basins of \bar{A} . This subset contains all points y except for small δ neighborhoods of equilibria, where $\delta \rightarrow 0$ as $\epsilon \rightarrow 0$. Then with probability $\text{Pr}_{\delta, \epsilon, m}$ all of the original system also has the same Lyapunov function with analogous properties.

IV. BIFURCATIONS OF THE COUPLED CLIMATE-BIOSPHERE SYSTEM

For slow variable systems (18) we prove averaging theorems (see Theorems 1 and 2 stated in Appendix) assuming that c_{ik} are random independent parameters. In the general case this system is complicated. To simplify the problem, we suppose that the c_i are random independent quantities such that $E c_i = \bar{c}$, and, moreover, we apply the approximation obtained in Refs. [28,43,44]. We assume that the turnovers satisfy $D_k \gg 1$. Then

$$v_k = S_k - \tilde{S}_k, \quad 0 < \tilde{S}_k < \text{const} D^{-1}. \tag{33}$$

We consider two cases: $\gamma_i = O(1)$, when self-limitation is not small, and $\gamma_i = 0$.

A. Systems with self-limitation

Suppose that all species X_j survive and have positive abundances. Then

$$X_j(T) = U_j(T) + O(D^{-1}),$$

$$U_j(T) := \gamma_j^{-1} [\phi_j(S(T)) - \mu_j]_+,$$

where we use the notation $f_+ = \max(f, 0)$. Then Eq. (13) takes the form [we remove the terms the order $O(D^{-1})$]

$$\frac{dT}{dt} = \lambda^{-1} \left[-e\sigma T^4 + \frac{\mu_0 I_0}{4} \left(1 - A_0 + m^{-1} \sum_{j=1}^m c_j U_j(T) \right) \right]. \tag{34}$$

We apply Theorems 1 and 2, with $p = 1$ and

$$\Phi_1 = m^{-1} \sum_{j=1}^m c_j U_j,$$

where c_j are random independent parameters. The averaged system takes the form

$$\frac{dT}{dt} = \lambda^{-1} \left(-e\sigma T^4 + \frac{\mu_0 I_0}{4} [1 - A_0 + CB(T)] \right), \quad (35)$$

where

$$B(T) = m^{-1} \sum_{j=1}^m U_j(T), \quad C = m^{-1} \sum_{i=1}^m E c_i = \bar{c}.$$

The function $B(T)$ is the average biomass per species, and C is the average perturbation of albedo per species.

Let all $\phi_i(S)$ be uniformly bounded by a constant a , $\phi_i(S) < a$ for all $i = 1, \dots, m$ and S . Then we find that, with a probability exponentially close to 1, there exists a Lyapunov function defined by

$$L(T) = -\frac{e\sigma T^5}{5} + \frac{\mu_0 I_0}{4} [(1 - A_0)T + CW],$$

where

$$W(T) = \int_0^T B(s) ds.$$

Nondegenerate local minima of this function are steady states (local attractors) of the averaged system, and local extrema are saddle points or repellers of that system. If \bar{c} is small enough, we have only a single local attractor $T = \bar{T}_e$. Our theorems (see the Appendix) imply that the original system then also has (with a probability close to 1) a single local attractor $T = T_e(m)$ and $|T_e(m) - \bar{T}_e| \rightarrow 0$ as $m \rightarrow \infty$.

The situation dramatically changes if the condition $\phi_i < a$ is violated, say, one species dominates or if m is small. Then it is impossible to guarantee that $|T_e(m) - \bar{T}_e| \rightarrow 0$. This means that decreases in biodiversity can produce global climate changes.

To find possible bifurcations, we consider the simplest case when we are dealing with a single resource $v_1 = v$ and the growth functions are identical for all species, $\phi_i(v) = v(K_i + v)^{-1}$. We assume that $S(T) = S_0 + S_1 \Delta(T)$, where the coefficient S_1 defines an influence of temperature on the resource supply and

$$\Delta(T)^2 = \exp \left[-(T - T_0)^2 / 2\sigma_T^2 \right].$$

This means that there exists an optimal temperature T_0 for species growth and a characteristic spread of this temperature σ_T . Then we obtain Eq. (35) with

$$B(T) = m^{-1} \sum_{i=1}^m \frac{S_0 + S_1 \Delta(T)}{\gamma_i [K_i + S_0 + S_1 \Delta(T)]},$$

and the equation for the steady-state temperature takes then the form

$$F(T) = G(T), \quad (36)$$

where

$$F(T) = e\sigma T^4, \quad G(T) = \mu_0 \frac{I_0}{4} [1 - A_0 + CB(T)].$$

Note that for $C > 0$ a biomass B growth diminishes the averaged planetary albedo producing a hotter climate.

Depending on C we have either a single root of (36) or three roots (see Fig. 1); in the latter case, two roots are local attractors and the third root is a saddle point. With the

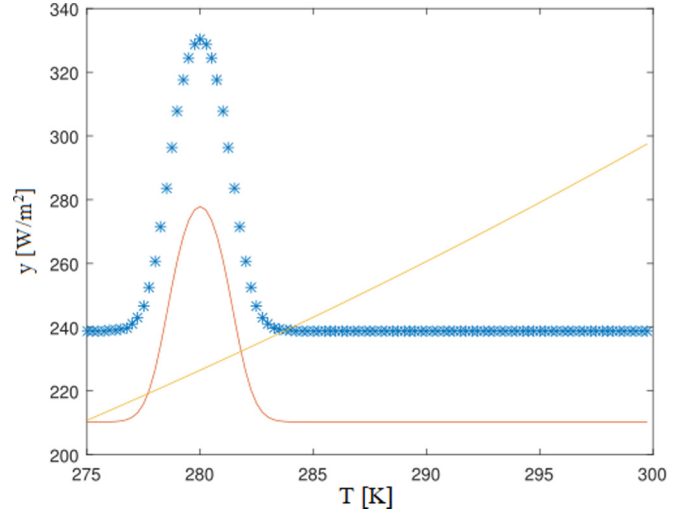


FIG. 1. This plot shows possible bifurcations in a climate-biosphere system. The equilibrium temperature values are given by intersections of curves $y = F(T)$ and $y = G(T)$. For the biosphere, we have $m = 20$ species, where the parameter values are $K_i = 0.1$, $S_0 = 0.1$, $\mu = 0$, $S_1 = 0.2$, $T_0 = 280$ K, and $\sigma_T = 1$. The albedo coefficients c_i are distributed randomly according to normal density $\text{Norm}(E_c, \sigma_c)$, where $E_c = 0.2$, $\sigma_c = 0.03$. We use parameters similar to the Earth's climate system, so we have $\sigma = 5.67 \times 10^{-8} \text{ J s}^{-1} \text{ m}^{-2} \text{ K}^{-4}$, $A_0 = 0.62$, $\mu_0 = 1$, $e = 0.65$, and $I_0/4 = 340 \text{ W m}^{-2}$. The self-limitation parameters $\gamma_i = \gamma$, where $\gamma = 2$. We have a single intersection for $E_c = 0.2$ and the three intersections for $E_c = 0.15$.

growth in C , the lower stable root eventually merges with the unstable one and disappears in a pitchfork bifurcation. We mention here that a similar bifurcation occurs in the ice-albedo feedback problem (see above). A similar bifurcation resulting from the bistability of the system is also found in Ref. [45]. In that paper, another energy balance model is considered, in particular, A_0 depends on temperature T and the cause of bistability is connected with that dependence. Bistability can lead to a transition from a hothouse Earth to snowball Earth and vice versa. In our case the averaged biomass $B(T)$ dependence on surface temperature T is important, and to obtain bifurcations, we should have a $B(T)$ sufficiently sharply increasing in T .

It is interesting to investigate how small the number of species should be to cause these bifurcation effects. Such a sensitivity analysis can be done as follows. Let C_{crit} be a critical value of C in Eq. (35) such that the bifurcation still exists for $C > C_{\text{crit}}$ but it is absent for $C < C_{\text{crit}}$. Let us estimate the probability P_{bif} that the random quantity $X = m^{-1} \sum_{j=1}^m c_j$ is more than C_{crit} . The probability P_{bif} depends on m . For large m the PDF of that quantity is close a normal density, $X \in \text{Norm}(\bar{c}, m^{-1}\sigma_c^2)$, where \bar{c} and σ_c^2 are the expected value and the variance of c_i , respectively. By these arguments we conclude that, if the value P_{bif} is not negligible, then the following condition should be satisfied:

$$m < m_c = \frac{\sigma_c^2}{(\bar{c} - C_{\text{crit}})^2}.$$

For $m < m_c$ fluctuations in random species parameters can essentially influence system dynamics (Fig. 2).

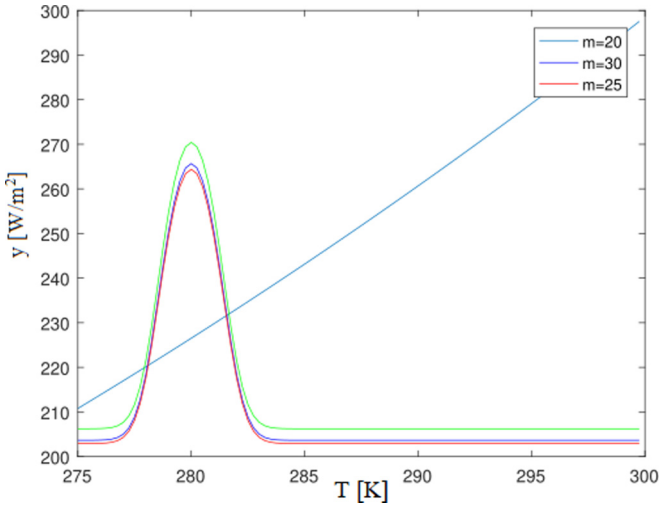


FIG. 2. This plot shows the robustness of the climate-biosphere system with respect to a change of species number. The choice of parameters is the same as in the previous plot, $E_c = 0.2$ and $\gamma = 0.03$. The red, dark blue and green curves show dependences $y = G(T)$ for different species numbers, $m = 20, 25$, and 30 , while the linearlike curve is $y = F(T)$. The temperature T_{eq} that defines a stable climate state is given by the second intersection of curves $F(T)$ and $G(T)$. This intersection weakly depends on m that is consistent with theoretical results. Note that T_{eq} depends on the biodiversity m in a nonmonotone manner while the biomass growth pushes the curve $y = G(T)$ upward, leading to a hotter climate that is consistent with experimental data from Ref. [46].

It is interesting to understand how global warming affects the described bifurcation effect. Consider the cold planetary region and relation (12). We observe that a decrease of the area occupied by ice increases the coefficient \bar{c} and decreases A_0 . Thus it reinforces the bifurcation effect and can lead to climate bifurcation.

B. Systems without self-limitation

System (2) and (3) of species competing for resources without self-limitation terms $\gamma_i x_i$ exhibits very interesting properties. In a pioneering work [27] it was shown, by numerical simulations, that three competing species can coexist in a chaotic regime. An analytical proof of the existence of chaos is obtained in Ref. [47] for special Lotka-Volterra (LV) systems, which can be derived from our system (2) and (3) under the assumption $D_k \gg 1$. Those LV systems have a special structure, namely, they can be interpreted as a system with n resources. Under some assumptions they can support the coexistence of $m \gg n$ species. Given an n , by adjusting the LV system parameters one can simulate any prescribed structurally stable dynamics, which can be chaotic or periodic. For example, to simulate the Lorenz dynamics, we take $n = 3$ and $m = 12$ species.

When we couple system (2) and (3) with temperature dynamics, we obtain (9) and (10). That system exhibits new effects. To show it, let us fix the temperature T first. Under the assumption $D_k \gg 1$, we use (33) and then by substituting these formulas into Eqs. (9) and by the Taylor expansion of

$\phi_i(v)$ at S , we have the following weakly perturbed LV system,

$$\frac{dx_i}{dt} = x_i \left(-r_i + \phi_i(S) + \sum_{j=1}^m K_{ij} x_j \right) + O(D^{-2}), \quad (37)$$

where $D = \min D_l$ and

$$K_{ij} = \sum_{l=1}^n A_{il} B_{lj},$$

$$A_{il} = \frac{\partial \phi_i(S)}{\partial S_l}, \quad B_{lj} = b_{lj} D_l^{-1} \phi_j(S).$$

Suppose that

$$-r_i + \phi_i(S) = \sum_{l=1}^n A_{il} \mu_l \quad (38)$$

for some coefficients μ_l . Only under that assumption is the coexistence of many species possible (see Ref. [47]). Then the dynamics of system (37) is determined by some hidden Volterra variables q_i . Species abundances x_i can be expressed via q_i as follows,

$$x_i(t) = x_i(0) \exp \left(- \sum A_{il} q_l(t) \right), \quad (39)$$

while the dynamics of q is governed by

$$\frac{dq_k}{dt} = G_k(q, A, B, m, \mu), \quad k = 1, \dots, n, \quad (40)$$

where

$$G_k(q) = -\mu_k + \sum_{i=1}^m B_{ki} x_i(0) \exp \left(- \sum_{l=1}^n A_{il} q_l(t) \right).$$

In [47] it is shown that $G_k(q)$ can approximate any prescribed functions in a compact domain that implies the existence of complicated dynamics and a chaotic and periodic large time behavior of q .

Suppose now that S depends on the temperature T , and for each T condition (38) is satisfied. From a biological point of view, it is possible only if climate evolves slowly and the parameters of organisms in the population have enough time to adapt so that condition (38) is satisfied. The importance of such a genetic adaptation with respect to climate changes is shown in Ref. [48]. So, if the climate evolves quickly, systems without self-limitations should exhibit mass extinctions.

Let us take into account that now the biomass can explicitly depend on time (since the large time behavior of biomass B may be chaotic or periodic). Then Eq. (35) changes and reads

$$\frac{dT}{dt} = \lambda^{-1} \left(-e\sigma T^4 + \frac{\mu_0 I_0}{4} [1 - A_0 + CB[q[t, T(\cdot)]]] \right), \quad (41)$$

where the biomass per species $B[t, T(\cdot)] = m^{-1} \sum_{i=1}^m x_i[t, T(\cdot)]$ becomes a complicated functional depending on all values of $T(t')$, $0 \leq t' \leq t$. This equation, Eqs. (40) for q , and relations (39) give us a system describing a coupled climate-ecosystem dynamics. Such nonlinear equations with a retarded nonlinearity can exhibit complicated behavior. One can simplify the ecological equations (40) by averaging with respect to random species parameters. For

simplicity, let us consider the case of a single resource S with $\phi_i(S) = a_i S / (K_i + S)$, where a_i, K_i are random parameters subject to the density $\rho(a, K)$ with the support $\mathcal{S} = \{a > 0, K > \delta > 0\}$ and supposing that $x_i(0)$ are also random with the average $\bar{x}(0)$. Then, using our Theorem I from the Appendix, we have the averaged system for q ,

$$\frac{dq}{dt} = -\mu + m\bar{G}(q),$$

where

$$\bar{G}(q) = \frac{\bar{x}(0)}{D} \int_{\mathcal{S}} \frac{aS\rho(a, K)}{K + S} \exp\left(-\frac{aSq}{(K + S)^2}\right) da dK.$$

To simplify the analysis further, let us consider a natural situation, where the dynamics of species is much faster than the temperature dynamics. Then one can make averaging over time t in the equations for $x_i(t)$ in the term $B(t, T)$ that produces the averaging term $\langle B(t, T) \rangle$, where the moving average of f is

$$\langle f(\cdot) \rangle = \tau^{-1} \int_{t-\tau}^t f(s) ds, \tag{42}$$

where $\tau \gg 1$ is a large averaging interval.

We obtain then Eq. (35) with $\langle B[\tau, T(\cdot)] \rangle$ instead of $B(T)$. However, a stochastic (chaotic) dynamics of the averaged biomass $B(t)$ can lead to random transitions between different stable states via an intermediate state (similarly to Ref. [45], where the noise is induced by the solar irradiance).

V. DISCUSSION AND CONCLUSIONS

Understanding the planetary climate dynamics and identification of factors and processes that can affect its stability are important problems, in particular, because of their prominent effect on the biosphere functioning. The climate-biosphere system is an extremely complex system and the corresponding mathematical model, even a relatively simple “conceptual” one, is usually too complicated for a comprehensive analytical study. The possibility of nontrivial model reduction lies in the observation that different processes often go with very different rates, i.e., take place on very different timescales. In particular, many complex systems, including climate models, have slow and fast components. According to classical results [35], large time dynamics of such systems are captured by a dynamics of slow modes on a slow invariant manifold. It is well known that even low-dimensional systems exhibit complex bifurcations that may account for the complexity of the climate dynamics [49–51]. Moreover, such models exhibit multistationarity, i.e., the existence of many stationary states that, according to Ref. [52], provides the climate stability under variations of astronomical factors.

There is growing evidence that the biosphere can have a variety of feedback loops to the climate and a comprehensive understanding is only possible based on the analysis of a coupled climate-biosphere system. The importance of such coupling is the essential content of the Gaia concept [5,6]. Several specific feedback mechanisms have been investigated. For instance, in the Earth system, the perturbation of the carbon cycle [53], water-vapor [54] cycle, or a disturbance in oxygen production [55] are examples of such feedback, but

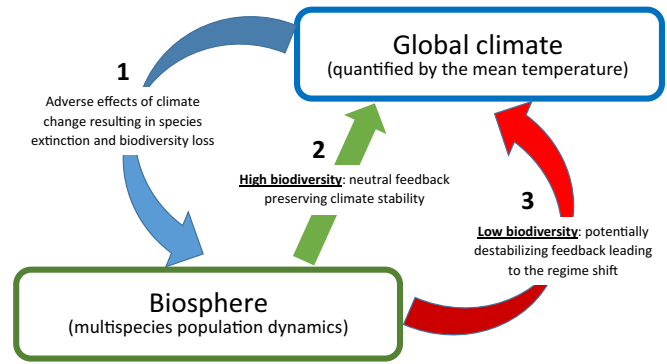


FIG. 3. Schematic summary of the feedbacks in our model of a coupled climate-biosphere system [see Eqs. (9)–(11)]. Arrow 1 shows the potentially destructive effect of the global climate change on the population dynamics and ecosystems functioning. Arrow 2 shows the neutral feedback that the population dynamics has on the global climate in the case of high biodiversity, i.e., a large number of coexisting species. Arrow 3 shows the potentially destabilizing feedback of the population dynamics on the global climate in the case of low biodiversity.

there are many more. In this paper, we focus on the feedback induced by the effect that the biosphere (in particular, vegetation, e.g., see Ref. [14]) can have on the planetary albedo, hence potentially changing the global energy balance. We addressed this issue theoretically by considering a conceptual model of climate-biosphere dynamics arising from the coupling between a global energy balance model and a generic multispecific model of population dynamics. While the zero-dimensional energy balance models have been mostly used to investigate the bistability between hothouse and snowball climates (see Ref. [21] for a review), here we focus on bifurcations within a warm climate induced by an interaction between the climate and biosphere.

In our approach, we assumed that the parameters of fast subsystems are random and mutually independent. Under such assumptions, we prove a general theorem on the connection between attractors of averaged and original systems. If the attractor \bar{A} of the averaged system has a low fractal dimension, then, with a probability close to 1, the attractor of the original system is close to \bar{A} . We mention here that the importance of this result goes beyond the climate dynamics; arguably, it may have a variety of applications in many different fields such as global network systems with unknown parameters, foodwebs, gene networks, etc.

Referring back the Gaia concept, why, however, was the climate system stable over long periods of time in the past? Our study provides a possible answer to this question. Climate stability can be explained by the fact that many independent factors are canceled out. Our findings are summarized in Fig. 3. Thus, our model confirms the Gaia concept in the sense that the stability of the climate system is ensured by high biodiversity. But our analysis also suggests a possibility of positive feedback of the biosphere on climate change. Consider a scenario of a slow change in the energy balance resulting, for instance, in a gradual increase of the mean temperature. It has been shown in many studies that such an increase would eventually result in species extinctions and

biodiversity loss (see arrow 1 in Fig. 3). Our results predict that the exact nature of the feedback loop will depend on the extent of the biodiversity loss. As long as the number of extinctions is not too large, the biodiversity loss will not have any notable feedback on the climate dynamics (arrow 2 in Fig. 3). However, should the biodiversity loss becomes considerable, i.e., the number of surviving species becomes small, the failing biota would increasingly likely have a positive feedback on the climate change, resulting in its destabilization (bifurcation) followed by the transition to another steady state (cf. arrow 3 in Fig. 3). The global climate change resulting from this bifurcation is likely to have a stronger negative effect on the biosphere, hence accelerating extinctions.

This model may be used to reconstruct and project climate change on the ice planets of the Solar System [56,57] and some exoplanets [58,59]. Another possible application of our approach is paleoclimate modeling. For example, in the Cryogenian period, the planet was transformed into so-called “snowball Earth,” where early life survived under the environmental stress [60], and became stable and even diverse [61]. Our model may help to evaluate how biodiversity could contribute to global ice melting in this period.

ACKNOWLEDGMENTS

We are grateful to anonymous referees for useful and interesting remarks. This research is supported by the Swedish Foundation for International Cooperation in Research and Higher Education (STINT), Grant No. IB 2018-7517. I.S. also thanks University of Dayton Research Council Seed Grant, 2019. The publication has been prepared with the support of the “RUDN University Program 5-100” (to S.V.P.). This work was assisted by attendance as a Short-term Visitor at the National Institute for Mathematical and Biological Synthesis, an Institute supported by the National Science Foundation through NSF Award No. DBI-1300426, with additional support from The University of Tennessee, Knoxville. We also would like to thank the Mathematical Biosciences Institute (MBI) at Ohio State University, for helping initiate this research. MBI receives its funding through NSF Grant No. DMS-1440386. I.S. and S.V.P. acknowledge the kind hospitality of Banff International Research Station (BIRS) for Mathematical Innovation and Discovery where they worked on this research.

APPENDIX

In this Appendix, constants c and C_i can depend on system parameters but are uniform in m for large m . Note that we sometimes denote different constants by the same index if it does not lead to confusion. Our proving plan can be outlined as follows. To simplify our statement, we first prove three auxiliary lemmas, and then we state short demonstrations of theorems. The lemmas show the following. Let us choose a point $y^{(k)}$ in a bounded domain of the phase space. Consider the probability that the difference between the original and averaged system at this point is more than a fixed positive number. Our lemmas imply that this probability is exponentially small in the parameter m . Moreover, any bounded domain can be covered by balls centered at such points and

the number of those balls is polynomial in m . Therefore using a sufficient smoothness of averaged and original systems we obtain that the difference between those systems is small with a probability close to 1.

Auxiliary probabilistic estimates. Let us fix some points $y^{(k)} \in \mathbb{B}^n$, where $k = 1, 2, \dots, M$ and M is a positive integer, which will be adjusted later. Let us define the events $\mathcal{A}_{\epsilon,i}(k)$ by

$$\mathcal{A}_{\text{out},\epsilon,i}(k) = \{|\bar{g}_i(y^{(k)}) - g_i(y^{(k)}, \Phi(y^{(k)}))| > \epsilon/4\}, \tag{A1}$$

$$\mathcal{A}_{\epsilon,i}(k) = \text{Not } \mathcal{A}_{\text{out},\epsilon,i}(k), \tag{A2}$$

where $\text{Not } B$ denotes the negation of B and $\bar{g}_i(y)$ are defined by relation (27).

The next auxiliary lemma is elementary but useful.

Lemma 1. One has

$$\Pr \left[\prod_{k=1}^M \prod_{i=1}^n \mathcal{A}_{\epsilon,i}(k) \right] \geq 1 - \sum_{k=1}^M \sum_{i=1}^n \Pr [\mathcal{A}_{\text{out},\epsilon,i}(k)].$$

Proof. That lemma can be proved by de Morgan’s rule. ■

Furthermore, we use Chernoff bounds to estimate $\Pr [\mathcal{A}_{\text{out},\epsilon,i}(k)]$. Let $C_{\bar{g},\Phi}$ be a Lipschitz constant of \bar{g} with respect to the variables Φ_1, \dots, Φ_p , i.e., for all $y \in \mathbb{B}^n$ and $i = 1, \dots, n$,

$$|\bar{g}_i(y, \Phi^{(1)}) - \bar{g}_i(y, \Phi^{(2)})| \leq C_{\bar{g},\Phi} |\Phi^{(1)} - \Phi^{(2)}|, \tag{A3}$$

where $|\Phi| = \max_l |\Phi_l|$. This constant $C_{\bar{g},\Phi}$ exists due to assumption (21) to g . Moreover, an analogous estimate holds for derivatives with respect to y :

$$|\nabla_y \bar{g}_i(y, \Phi^{(1)}) - \nabla_y \bar{g}_i(y, \Phi^{(2)})| \leq \tilde{C}_{\bar{g},\Phi} |\Phi^{(1)} - \Phi^{(2)}|. \tag{A4}$$

Lemma 2. One has

$$\Pr [\mathcal{A}_{\text{out},\epsilon,i}(k)] < 2 \exp(-m\epsilon^2/32C_{\bar{g},\Phi}^2 C_f^2),$$

$$\forall i = 1, \dots, n, k = 1, \dots, M.$$

Proof. Our the first step is to estimate the differences $\Phi_i(y^{(k)}) - E\Phi_i(y^{(k)})$. To this end, let us fix indices i and k and introduce X_j by

$$X_j = f_{ji}(y^{(k)}, c_{ij}). \tag{A5}$$

Then

$$\Phi_i(y^{(k)}) = m^{-1} \sum_{j=1}^m X_j. \tag{A6}$$

Assumption 1 on c_{ij} implies that X_j are independent random variables. Moreover, by (24) we have

$$|X_j| \leq C_f. \tag{A7}$$

Let us recall the Hoeffding inequality. Let $X_j, j = 1, \dots, m$ be independent random variables strictly bounded in intervals $[a_j, b_j]$, i.e., almost surely $X_i \in [a_i, b_i]$. Let $\bar{X} = m^{-1} \sum_{j=1}^m X_j$ be the average of those quantities. Then (see Ref. [42])

$$\Pr[|\bar{X} - E\bar{X}| \geq \delta] \leq 2 \exp\left(-\frac{2m\delta^2}{\sum_{j=1}^m (a_i - b_i)^2}\right).$$

Therefore, according to Hoeffding’s inequality for each $\delta > 0$, we obtain

$$\Pr[|\Phi_l(y^{(k)}) - E\Phi_l(y^{(k)})| > \delta] < 2 \exp(-2m\delta^2/C_f^2), \tag{A8}$$

where $l = 1, \dots, p$.

The second step of the proof is as follows. Consider the events

$$\mathcal{B}_{\delta,l,k} = \{|\Phi_l(y^{(k)}) - E\Phi_l(y^{(k)})| < \delta\}.$$

Let $\mathcal{B}_{\delta,k} = \prod_{l=1}^p \mathcal{B}_{\delta,l,k}$ be the product of those events.

Let us take $\delta = \epsilon/4C_{\bar{g},\Phi}^2$. Then, if the event $\mathcal{B}_{\delta,k}$ takes place, we have (because g is a Lipschitz map with the Lipschitz constant $C_{\bar{g},\Phi}$ and by definition of \bar{g}) that

$$|\bar{g}(y^{(k)}) - g(y^{(k)}, \Phi(y^{(k)}))| < \epsilon/4,$$

i.e., the event $\mathcal{A}_{\epsilon,i}(k)$ takes place. Consequently,

$$\Pr[\mathcal{B}_{\delta,k}] \leq \Pr[\mathcal{A}_{\epsilon,i}(k)]$$

that gives

$$\geq \Pr[\mathcal{A}_{\text{out},\epsilon,i}(k)] \leq \Pr[\text{Not } \mathcal{B}_{\delta,k}].$$

The probability $\Pr[\text{Not } \mathcal{B}_{\delta,k}]$ is estimated by (A8), which completes the proof of the lemma. ■

Let us define now the events $\mathcal{A}_{\text{out},\epsilon,i,j}(k)$ and $\mathcal{A}_{\epsilon,i,j}(k)$ by

$$\mathcal{A}_{\text{out},\epsilon,i,j}(k) = \{|g_{ij}(y^{(k)}) - g_{ij}(y^{(k)})| > \epsilon/4n\}, \tag{A9}$$

where

$$\bar{g}_{ij}(y) = \frac{\partial \bar{g}_i(y)}{\partial y_j}, \quad g_{ij}(y) = \frac{\partial g_i(y, \Phi(y))}{\partial y_j},$$

and

$$\mathcal{A}_{\epsilon,i,j}(k) = \text{Not } \mathcal{A}_{\text{out},\epsilon,i}(k). \tag{A10}$$

There holds the following lemma:

Lemma 3. One has

$$\Pr[\mathcal{A}_{\text{out},\epsilon,i,j}(k)] \leq 2 \exp(-mC_0\epsilon^2), \tag{A11}$$

$$\forall i, j = 1, \dots, n, k = 1, \dots, M,$$

where a constant C_0 is uniform in m .

The proof of Lemma 3 repeats the same arguments used in the proof of Lemma 2 so we do not present it.

Demonstrations of Theorems 1 and 2

Theorem 1. Suppose condition (29) holds and that averaged system defined by (26) generates a global dissipative semiflow on the domain \mathbb{B}^n . Moreover, let us assume that the averaged system (26) is structurally stable with a structural stability constant $\epsilon_0(\bar{g})$ and that system has an attractor \bar{A} . Then with probability $\Pr_{\bar{A}}$ the original system (20) also defines a global dissipative semiflow on \mathbb{B}^n , which has an attractor A topologically equivalent to \bar{A} . The probability $\Pr_{\bar{A}}$ satisfies the inequality

$$\Pr_{\bar{A}} > 1 - C_1 n \exp(-C_2 m \epsilon_0^2 - n \ln \epsilon_0), \tag{A12}$$

where C_1, C_2 are positive constants uniform in m .

Proof. We use Lemmas 1–3 and the following construction. The domain \mathbb{B}^n has the dimension n , therefore we can cover it by $N(r\epsilon) \sim (r\epsilon)^{-n}$ balls $\Omega_{\epsilon,k}$ of the radius ϵ centered at some

points $y^{(k)} \in \mathbb{B}^n$. Here, r is a positive constant uniform in ϵ . We denote the union of all those balls by U_ϵ , which is an open neighborhood of \mathbb{B}^n .

Let us consider the perturbation $\tilde{g}(y) = g(y, \Phi(y)) - \bar{g}(y)$ and estimate the C^1 norm of \tilde{g} on U_ϵ . Suppose that all events $\mathcal{A}_{\epsilon,i}(k)$ and $\mathcal{A}_{\epsilon,i,j}(k)$ defined by (A2) and (A10), respectively, take place. Then

$$|\tilde{g}(y^{(k)})| + |\nabla_y \tilde{g}(y^{(k)})| < \epsilon/2, \quad k = 1, \dots, N(\epsilon). \tag{A13}$$

Then, due to conditions (21) on g , and the definition of \bar{g} , we have

$$|\tilde{g}|_{C^2(\mathbb{B}^n)} < C_1,$$

where a positive constant C_1 is independent of m . Therefore, for each $y \in \mathbb{B}^n$ one can find such a point $y^{(k)}$ that there hold the estimates

$$|\tilde{g}_i(y^{(k)}) - \tilde{g}_i(y)| < r\epsilon,$$

$$\left| \frac{\partial \tilde{g}_i(y^{(k)})}{\partial y_j} - \frac{\partial \tilde{g}_i(y)}{\partial y_j} \right| < r\epsilon.$$

Those last inequalities and (A13) imply

$$|\tilde{g}(y)| + |\nabla_y \tilde{g}(y)| < \epsilon/2 + C_2 r\epsilon, \quad y \in U_\epsilon, \tag{A14}$$

where C_2 is a positive constant. We set $r = 1/2C_2$. Due to conditions (29) and (30) the vector fields g and \bar{g} are directed towards the interior of \mathbb{B}^n that allows us to apply now the definition of structural stability [41]. Then for positive $\epsilon \leq \epsilon_0(\bar{g})$ the attractor of the original system is topologically equivalent to the attractor of the averaged system. Note that ϵ_0 does not depend on m and it is defined by the averaged system only.

Furthermore, we compute the probability that all the events defined by (A13) take place by Lemmas 1–3. This finishes the proof. ■

Theorem 2. Suppose condition (29) holds and that the averaged system defined by (26) has a Lyapunov function such that

$$\nabla L(y) \cdot \bar{g}(y) \leq -\epsilon, \quad y \in \mathbb{V}, \tag{A15}$$

where \mathbb{V} is an open subdomain of \mathbb{R}^n with a compact closure, and moreover,

$$|L|_{C^2(\mathbb{V})} < C_L$$

for a positive constant C_L . Then with the probability $\Pr_{L,\epsilon}$ the original system (20) has the same Lyapunov function such that

$$\nabla L(y) \cdot g(y) \leq -\epsilon/2, \quad y \in \mathbb{V}. \tag{A16}$$

The probability $\Pr_{L,\epsilon}$ satisfies the inequality

$$\Pr_{L,\epsilon} > 1 - \bar{C}_1 \exp(-\bar{C}_2 m \epsilon^2 - \ln \epsilon),$$

where \bar{C}_1, \bar{C}_2 are positive constants uniform in m .

Let us note that, similarly to the previous theorem, if $\epsilon > 0$ is small, the estimate from that theorem makes sense only for sufficiently large $m > m_0(\epsilon)$.

Proof. We apply the same idea used in the previous proof. The domain \mathbb{V} can be covered by $N(r\epsilon) \sim (r\epsilon)^{-n}$ balls $\Omega_{\epsilon,k}$

of the radius ϵ centered at some points $y^{(k)} \in \mathbb{B}^n$. Here, r is a positive constant uniform in ϵ . Let us introduce the functions

$$\bar{H}(y) = \nabla_y L(y) \cdot \bar{g}(y), \quad H(y) = \nabla_y L(y) \cdot g(y, \Phi(y)).$$

Consider the events

$$\mathcal{H}_{\text{out},\epsilon}(k) = \{|H(y^{(k)}) - \bar{H}(y^{(k)})| > \epsilon/4\}, \quad (\text{A17})$$

$$\mathcal{H}_\epsilon(k) = \text{Not } \mathcal{H}_{\text{out},\epsilon}(k) = \{|H(y^{(k)}) - \bar{H}(y^{(k)})| \leq \epsilon/4\}. \quad (\text{A18})$$

Suppose that all events defined by (A18) take place. Then

$$|H(y^{(k)}) - \bar{H}(y^{(k)})| < \epsilon/4, \quad \forall k = 1, \dots, N(\epsilon). \quad (\text{A19})$$

Now we use the estimate

$$|H(y^{(k)}) - H(y)| < \text{Lip}_H |y^{(k)} - y|, \quad (\text{A20})$$

where Lip_H is a Lipschitz constant of H . Let us estimate that constant. By definition of H one has

$$\frac{\partial H}{\partial y_k} = m^{-1} \sum_{i=1}^n \sum_{j=1}^m c_{ij} \frac{\partial(Lf_j)}{\partial y_k}.$$

Due to Assumption 1, one has

$$\left| \sum_{i=1}^n \sum_{j=1}^m c_{ij} \frac{\partial(Lf_j)}{\partial y_k} \right| < mnc_1 R_0, \quad (\text{A21})$$

where

$$c_1 = \max_{i,j,y \in \mathbb{V}} (|f_{ij}(y)| |\nabla L(y)| + |\nabla f_j(y)| |L(y)|). \quad (\text{A22})$$

The same estimate holds for the Lipschitz constant of \bar{H} . Therefore, (A19) and (A20) give

$$\sup_{y \in \mathbb{V}} |H(y) - \bar{H}(y)| < \epsilon/4 + rC_3\epsilon, \quad (\text{A23})$$

where $C_3 > 0$ is a constant uniform in m . Let us set $r = 1/4C_3$. Then condition (A15) of Theorem 2 in this Appendix and (A23) show that (A16) is satisfied. Furthermore, to complete the proof, we compute the probability that all the events defined by (A13) take place by estimates analogous to those obtained in Lemmas 1–3. ■

[1] W. Chen, T. O. Suzuki, and M. Lackner, *Handbook of Climate Change Mitigation and Adaptation* (Springer, New York, 2014).

[2] IPCC, *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge University Press, Cambridge, UK, 2013) p. 1535.

[3] IPCC, *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (IPCC, Geneva, 2014).

[4] C. H. Mortimer, Modelling of lakes as physico-biochemical systems—present limitations and needs, in *Modelling of Marine Systems*, edited by J. C. J. Nihoul, Elsevier Oceanography Series Vol. 10 (Elsevier, Amsterdam, 1975), pp. 217–232.

[5] J. E. Lovelock and L. Margulis, Atmospheric homeostasis by and for the biosphere: The Gaia hypothesis, *Tellus* **26**, 2 (1974).

[6] J. Lovelock, *Gaia: A New Look at Life on Earth* (Oxford University Press, Oxford, U.K., 2000).

[7] O. D. N. Alcabes, S. Olson, and D. S. Abbot, Robustness of Gaian feedbacks to climate perturbations, *Mon. Not. R. Astron. Soc.* **492**, 2572 (2020).

[8] R. A. Boyle and T. M. Lenton, Fluctuations in the physical environment as a mechanism for reinforcing evolutionary transitions, *J. Theor. Biol.* **242**, 832 (2006).

[9] T. Lenton, S. Daines, J. Dyke, A. Nicholson, D. Wilkinson, and H. Williams, Selection for Gaia across multiple scales, *Trends Ecol. Evol.* **33**, 0169 (2018).

[10] T. M. Lenton, H. Held, E. Kriegler, J. W. Hall, W. Lucht, S. Rahmstorf, and H. J. Schellnhuber, Tipping elements in the Earth’s climate system, *Proc. Natl. Acad. Sci. USA* **105**, 1786 (2008).

[11] P. Ashwin, S. Wieczorek, R. Vitolo, and P. Cox, Tipping points in open systems: Bifurcation, noise-induced and rate-dependent examples in the climate system, *Philos. Trans. R. Soc. A* **370**, 1166 (2012).

[12] A. Kleidon, Beyond Gaia: Thermodynamics of life and earth system functioning, *Clim. Change* **66**, 271 (2004).

[13] A. Kleidon, Understanding the Earth as a whole system: From the Gaia hypothesis to thermodynamic optimality and human societies, [arXiv:2005.09216](https://arxiv.org/abs/2005.09216).

[14] R. J. Charlson, J. E. Lovelock, M. O. Andreae, and S. G. Warren, Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate, *Nature (London)* **326**, 655 (1987).

[15] J. W. Hurrell, M. M. Holland, P. R. Gent, S. Ghan, J. E. Kay, P. J. Kushner, J.-F. Lamarque, W. G. Large, D. Lawrence, K. Lindsay, W. H. Lipscomb, M. C. Long, N. Mahowald, D. R. Marsh, R. B. Neale, P. Rasch, S. Vavrus, M. Vertenstein, D. Bader, W. D. Collins *et al.*, The Community Earth System Model: A framework for collaborative research, *Bull. Am. Meteorol. Soc.* **94**, 1339 (2013).

[16] A. Katok and B. Hasselblatt, *Introduction to the Modern Theory of Dynamical Systems*, Encyclopedia of Mathematics and its Applications (Cambridge University Press, Cambridge, U.K., 1995).

[17] S. Smale, Differentiable dynamical systems, *Bull. Am. Math. Soc.* **73**, 747 (1967).

[18] V. Lucarini, Response theory for equilibrium and non-equilibrium statistical mechanics: Causality and generalized Kramers-Kronig relations, *J. Stat. Phys.* **131**, 543 (2008).

[19] V. Lucarini, F. Ragone, and F. Lunkeit, Predicting climate change using response theory: Global averages and spatial patterns, *J. Stat. Phys.* **166**, 1036 (2017).

[20] T. N. Palmer, A nonlinear dynamical perspective on model error: A proposal for non-local stochastic-dynamic parametrization in weather and climate prediction models, *Q. J. R. Meteorol. Soc.* **127**, 279 (2001).

[21] M. Ghil and V. Lucarini, The physics of climate variability and climate change, *Rev. Mod. Phys.* **92**, 035002 (2020).

[22] V. Lucarini, Introduction to the special issue on the statistical mechanics of climate, *J. Stat. Phys.* **179**, 997 (2020).

- [23] K. Hasselmann, Stochastic climate models Part I. Theory, *Tellus* **28**, 473 (1976); C. Frankignoul and K. Hasselmann, Stochastic climate models, Part II Application to sea-surface temperature anomalies and thermocline variability, *ibid.* **29**, 289 (1977).
- [24] G. R. North and K.-Y. Kim, *Energy Balance Climate Models* (Wiley, Hoboken, NJ, 2017).
- [25] K. Fraedrich, Catastrophes and resilience of a zero-dimensional climate system with ice-albedo and greenhouse feedback, *Q. J. R. Meteorol. Soc.* **105**, 147 (1979).
- [26] A. J. J. van Woerkom, The astronomical theory of climate changes, in *Climatic Change: Evidence, Causes, and Effects*, edited by H. Shapley (Harvard University Press, Cambridge, MA, 1953).
- [27] J. Huisman and F. J. Weissing, Biodiversity of plankton by oscillations and chaos, *Nature (London)* **402**, 407 (1999).
- [28] V. Kozlov, S. Vakulenko, and U. Wennergren, Biodiversity, extinctions, and evolution of ecosystems with shared resources, *Phys. Rev. E* **95**, 032413 (2017).
- [29] S. Roy and J. Chattopadhyay, Towards a resolution of “the paradox of the plankton”: A brief overview of the proposed mechanisms, *Ecol. Complexity* **4**, 26 (2007).
- [30] A. L. Shields, V. S. Meadows, C. M. Bitz, R. T. Pierrehumbert, M. M. Joshi, and T. D. Robinson, The effect of host star spectral energy distribution and ice-albedo feedback on the climate of extrasolar planets, *Astrobiology* **13**, 715 (2013).
- [31] R. D. Cess, Biosphere-albedo feedback and climate modeling, *J. Atmos. Sci.* **35**, 1765 (1978).
- [32] I. Sudakov, S. Vakulenko, and K. Golden, Arctic melt ponds and bifurcations in the climate system, *Commun. Nonlinear Sci. Numer. Simul.* **22**, 70 (2015).
- [33] V. Kozlov, V. G. Tkachev, S. Vakulenko, and U. Wennergren, Global stability and persistence of complex foodwebs, *Ann. Mat. Pura Appl.* **198**, 1693 (2019).
- [34] D. Henry, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Mathematics (Springer, Berlin, 1981).
- [35] P. Constantin, C. Foias, B. Nicolaenko, and R. Temam, *Integral Manifolds and Inertial Manifolds for Dissipative Partial Differential Equations*, Applied Mathematical Sciences Vol. 70 (Springer, New York, 1989).
- [36] S. Smale, *The Mathematics of Time: Essays on Dynamical Systems, Economic Processes, and Related Topics* (Springer, Berlin, 1980).
- [37] D. Anosov, *Dynamical Systems with Hyperbolic Behavior* (Springer, Berlin, 1995).
- [38] S. Newhouse, D. Ruelle, and F. Takens, Occurrence of strange axiom-A attractors near quasiperiodic flows on t^m , $m \geq 3$, *Commun. Math. Phys.* **64**, 35 (1978).
- [39] D. Ruelle, A measure associated with axiom-A attractors, *Am. J. Math.* **98**, 619 (1976).
- [40] D. Ruelle, Ergodic theory of differentiable dynamical systems, *Publ. Math. de l’IHÉS* **50**, 27 (1979).
- [41] D. Ruelle, *Elements of Differentiable Dynamics and Bifurcation Theory* (Elsevier, Amsterdam, 2014).
- [42] W. Hoeffding, Probability inequalities for sums of bounded random variables, *J. Am. Stat. Assoc.* **58**, 13 (1963).
- [43] I. Sudakov, S. A. Vakulenko, D. Kirievskaya, and K. M. Golden, Large ecosystems in transition: Bifurcations and mass extinction, *Ecol. Complexity* **32**, 209 (2017).
- [44] S. A. Vakulenko, I. Sudakov, and L. Mander, The influence of environmental forcing on biodiversity and extinction in a resource competition model, *Chaos* **28**, 031101 (2018).
- [45] V. Lucarini and T. Bódai, Transitions Across Melancholia States in a Climate Model: Reconciling the Deterministic and Stochastic Points of View, *Phys. Rev. Lett.* **122**, 158701 (2019).
- [46] R. van der Val and A. Steen, High-arctic plants like it hot: A long-term investigation of between-year variability in plant biomass, *Ecology* **95**, 3414 (2014).
- [47] V. Kozlov and S. Vakulenko, On chaos in Lotka-Volterra systems: An analytical approach, *Nonlinearity* **26**, 2299 (2013).
- [48] J. Norberg, M. C. Urban, M. Vellend, C. A. Klausmeier, and N. Loeuille, Eco-evolutionary responses of biodiversity to climate change, *Nat. Climate Change* **2**, 747 (2012).
- [49] H. Engler, H. G. Kaper, T. J. Kaper, and T. Vo, Dynamical systems analysis of the Maasch-Saltzman model for glacial cycles, *Physica D* **359**, 1 (2017).
- [50] A. Kazi, Paleoclimate changes and significance of present global warming, in *Handbook of Climate Change Mitigation and Adaptation* (Springer, New York, 2014), Chap. 1, pp. 1–14.
- [51] J. Sieber, C. Quinn, A. S. von der Heydt, and T. M. Lenton, The Mid-Pleistocene Transition induced by delayed feedback and bistability, *Dyn. Stat. Climate Syst.* **3**, dzy005 (2018).
- [52] K. Emanuel, A simple model of multiple climate regimes, *J. Geophys. Res.: Atmos.* **107**, ACL 4 (2002).
- [53] I. Sudakov and S. Vakulenko, Bifurcations of the climate system and greenhouse gas emissions, *Philos. Trans. R. Soc. A* **371**, 20110473 (2013).
- [54] I. M. Held and B. J. Soden, Water vapor feedback and global warming, *Annu. Rev. Energy Environ.* **25**, 441 (2000).
- [55] S. Petrovskii, Y. Sekerci, and E. Venturino, Regime shifts and ecological catastrophes in a model of plankton-oxygen dynamics under the climate change, *J. Theor. Biol.* **424**, 91 (2017).
- [56] D. Schulze-Makuch, L. N. Irwin, and A. G. Fairén, Drastic environmental change and its effects on a planetary biosphere, *Icarus* **225**, 775 (2013).
- [57] M. J. Russell, A. E. Murray, and K. P. Hand, The possible emergence of life and differentiation of a shallow biosphere on irradiated icy worlds: The example of Europa, *Astrobiology* **17**, 1265 (2017).
- [58] J. Yang, F. Ding, R. M. Ramirez, W. R. Peltier, Y. Hu, and Y. Liu, Abrupt climate transition of icy worlds from snowball to moist or runaway greenhouse, *Nat. Geosci.* **10**, 775 (2017).
- [59] A. L. Shields, The climates of other worlds: A review of the emerging field of exoplanet climatology, *Astrophys. J. Suppl. Ser.* **243**, 30 (2019).
- [60] S. K. B. William T. Hyde, Thomas J. Crowley, and W. R. Peltier, Neoproterozoic “snowball Earth” simulations with a coupled climate/ice-sheet model, *Nature (London)* **405**, 425 (2000).
- [61] L. M. van Maldegem, P. Sansjofre, J. W. H. Weijers, K. Wolkenstein, P. K. Strother, L. Wörmer, J. Hefter, B. J. Nettersheim, Y. Hoshino, S. Schouten, J. S. S. Damsté, N. Nath, C. Griesinger, N. B. Kuznetsov, M. Elie, M. Elvert, E. Tegelaar, G. Gleixner, and C. Hallmann, Bismorgammacerane traces predatory pressure and the persistent rise of algal ecosystems after Snowball Earth, *Nat. Commun.* **10**, 476 (2019).