Modeling symbiosis by interactions through species carrying capacities

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Abstract

We introduce a mathematical model of symbiosis between different species by taking into account the influence of each species on the carrying capacities of the others. The modeled entities can pertain to biological and ecological societies or to social, economic and financial societies. Our model includes three basic types: symbiosis with direct mutual interactions, symbiosis with asymmetric interactions, and symbiosis without direct interactions. In all cases, we provide a complete classification of all admissible dynamical regimes. The proposed model of symbiosis turned out to be very rich, as it exhibits four qualitatively different regimes: convergence to stationary states, unbounded exponential growth, finite-time singularity, and finite-time death or extinction of species.

Keywords: Mathematical models of symbiosis, Nonlinear differential equations, Dynamics of symbiotic systems, Functional carrying capacity

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1 Introduction

The term symbiosis describes close and usually long-term interactions between different biological species. Symbiotic relationships are well known in biological and ecological societies. Numerous examples can be found in the books [1–5]. Arguably, the symbiosis that is the most important to us as humans is the one between the typical human body and the multitudes of commensal organisms representing members of five of the six kingdoms of life. Specifically, the microbiome, with more than 2000 bacterial species and some $10^{14}$ microorganisms (about ten times the number of cells of the human body), is a key partner to the human immune system, and to the human metabolism as it participates in the synthesis of essential vitamins and amino acids, as well as in the degradation of otherwise indigestible plant material, and of certain drugs and pollutants in the guts [6]. Let us also mention the associations between plant roots and fungi, that are a feature of many terrestrial ecosystems, and without which the kingdom of plants would not exist as we know it.

In biology, one distinguishes three main types of symbiotic relations: mutualism, commensalism, and parasitism. Below, we briefly define these types of symbiosis, as they are described in the books [1–5], and give some examples illustrating these relations.

**Mutualism** is any relationship between individuals of different species where both individuals derive a benefit. Generally, only lifelong interactions involving close physical and biochemical contact can properly be considered symbiotic. A large percentage of herbivores have mutualistic gut fauna that help them digest plant matter, which is more difficult to digest than animal prey. Coral reefs are the result of mutualisms between coral organisms and various types of algae that live inside them. Most land plants and land ecosystems rely on mutualisms between the plants, which fix carbon from the air, and mycorrhizal fungi, which help in extracting minerals from the ground. An example of mutual symbiosis is the relationship between the ocellaris clownfish that dwell among the tentacles of Ritteri sea anemones. The territorial fish protects the anemone from anemone-eating fish, and in turn the stinging tentacles of the anemone protect the clownfish from its predators. A special mucus on the clownfish protects it from the stinging tentacles. See details and more examples in Refs. [1–5].

**Commensalism** is a class of relationship between two organisms where one organism benefits but the other is neutral (there is no harm or benefit). An example of commensalism: cattle egrets foraging in fields among cattle or other livestock. As cattle, horses and other livestock graze on the field, they cause movements that stir up various insects. As the insects are stirred up, the cattle egrets following the livestock catch and feed upon them. The egrets benefit from this relationship because the livestock have helped them find their meals, while the livestock are typically unaffected by it. Another example of commensalism is between tigers and golden jackals. In India, lone golden jackals expelled from their pack have been known to form commensal relationships with tigers. These solitary jackals will attach themselves to a particular tiger, trailing it at a safe distance in order to feed on the big cat’s kills. Tigers have been known to tolerate these jackals though having no profit from them. One more example of commensalism: birds following army ant raids on a forest floor. As the army ant colony travels on the forest floor, they stir up various flying insect species. As the insects flee from the army ants, the birds following the ants catch the fleeing insects. In this way, the army ants and the birds are in a commensal relationship because the birds benefit while the army ants are unaffected [1–5].

**Parasitism** is a type of symbiotic relationship between organisms of different species where
one organism, the parasite, benefits at the expense of the other, the host. Traditionally parasite referred to organisms with lifestages that needed more than one host. These are now called macroparasites (typically protozoa and helminths). The word parasite now also refers to micro-parasites, which are typically smaller, such as viruses and bacteria, and can be directly transmitted between hosts of the same species. Parasites that live on the surface of the host are called ectoparasites (e.g. some mites). Those that live inside the host are called endoparasites (including all parasitic worms). A typical example of endoparasites are bacteria and viruses [1–5].

Generally speaking, symbiosis is not restricted to biological systems. Many relations in social and economic societies can also be interpreted as examples of symbiosis. For instance, the economic and intellectual levels of human societies can be considered as symbiotic to each other. The interconnections between basic and applied research are symbiotic as well [7–9]. Economic and financial relations between different firms or between firms and banks can be treated as symbiotic. The notion of symbiosis has a very wide applicability to various relations, whether in biology, ecology, economy, or finance. Therefore, when we shall refer to societies, we keep in mind different kinds of societies, including biological, human, economic, and others, whose interactions can be considered from the point of view of symbiotic relations.

Extending the notion of symbiosis to social and economic systems, one meets the same types of symbiosis in many different forms and structures. As in biology, there can occur relations between different more or less independent parts or species, illustrated by the relations between plant roots and fungi [10], or in economics, the relations between firms and banks, or between economies and arts. Social systems are also often characterized by the existence of complicated relations, e.g., corresponding to the relations between a general system and a particular subsystem. Examples are the relations between the economy of a country and a particular branch of the economy, or between culture and language. Biological counterparts are widespread, as illustrated by the endosymbiotic origin of mitochondria and plastids of eukaryotic cells, by some marine annelid worms lacking mouth, guts and anus, and which rely on multiple extracellular bacterial endosymbionts for their excretory system [11], and more generally between the microbiome network and the mammal body [12].

Recently, the novel term industrial symbiosis has appeared to describe a certain type of eco-industrial development within the larger framework of industrial ecology. Industrial ecology is a relatively new field that is based on the ideology of nature. It claims that industrial ecosystem may behave similar to the natural ecosystem. In the same way as in nature, where symbiosis refers to an association between at least two different species, industrial symbiosis is an association between two or more industrial facilities or companies. For example, the wastes or byproducts of one company can become the raw materials for another [13–15]. Tyre shred, plastic pellets or waste steam from a factory are examples of outputs that can be sold on to other businesses. Mutual collaboration between different firms in many cases can be characterized as mutualistic symbiosis [16]. In this way, the notion of symbiosis is now applicable to biological as well as to economical societies.

Interactions between different co-existing species are usually modeled by equations of the Lotka-Volterra type [17,18]. Such equations are adequate for predator-prey relations between different species, whether one studies the simple co-existence of two species [17,18], or more complicated cases corresponding to high-dimensional dynamical systems, such as multiply connected food webs [19,20], or the inter-relations between different cells and pathogens inside biological organisms [21,22]. However, the symbiotic relations are known to be principally different from the predator-prey relations [1–5]. Hence, they require another
mathematical representation.

To be precise, we keep in mind the dynamical representation of symbiotic relations and the evolution of coexisting symbiotic species characterized by their concentrations. There are particular models describing the biological co-evolution of species by considering equations for some distributions, whether over size, or over age, or over phenotypes [23–26]. But our aim is to obtain the equations for the concentrations themselves, so that these equations could describe the variety of possible symbiotic relations.

Monod [27, 28] considered the microbial growth in a chemostat, which is a liquid phase of a chemical substrate nutrient. The Monod equations have been widely used for describing fermentation processes [29, 30]. These equations can also describe the situation when two or more bacterial species compete for the same growth substrate [31–34]. When the populations of microorganisms, inhabiting a common nonliving environment, compete for nutrients, this is, of course, an example of coexistence and coevolution. This, however, is not symbiosis in its direct sense, though it may share many features of the latter. The usual end of the evolution, when two species compete for the same food substrate, is that the one attaining the higher growth rate, under the given conditions, competes more successfully and ultimately displaces the slower-growing competitor [32–34]. It is well known [1–5, 32–34] that competition processes are quite different from symbiosis. Therefore several bacterial species competing for the same food substrate [31–34], strictly speaking, do not illustrate symbiosis or, in the best case, represent its very particular form.

The Holling [35] second type functional relation between predators and prey describes the situation when predators meet, not the amount of prey proportional to their total number, but an effective number of attacked prey that is proportional to the prey density \( D \) over \( 1 + cD \), with a parameter \( c > 0 \). This relation takes into account that predators, in order to consume prey, need to search for it, chase, kill, eat, and digest. This is why predators attack not all prey but a limited number of them, which saturates to a constant when the prey density increases [30]. Such predator-prey relations, clearly, do not characterize symbiosis.

The main aim of the present paper is to suggest a mathematical model of symbiosis characterizing the overall dynamics of this process for various systems. We concentrate in the present paper on the general mathematical properties of the considered model and on the classification of admissible types of symbiotic behavior in the frame of this model.

We stress that our aim is not the reinvention of a novel qualitative classification of symbiotic relations. Such a classification is well developed and widely employed in the biological literature [1–5]. And we accept this classification, as most other authors do. Our aim is to suggest a model of symbiosis that would fit well the known classification and would provide the possibility for studying dynamical as well as mathematical consequences of different symbiosis types.

The basic point that allows us to suggest a model of symbiosis is the idea that in symbiotic relations it is not the species that interact directly with each other, as in the Lotka-Volterra equation, but that symbiotic species act on the carrying capacities of each other.

The carrying capacity of a biological species in an environment is generally understood as the maximum population size of the species that the environment can sustain indefinitely, given the food, habitat, water and other necessities available in the environment. In population biology, carrying capacity is defined as the environment maximal load [37]. Historically, carrying capacity has been treated as a given fixed value [38, 39]. But later it has been understood that the carrying capacity of an environment may vary for different numbers of species and may change over time due to a variety of factors, including food availability,
water supply, environmental conditions, living space, and, the most important, population activity.

Mutual coexistence and symbiosis of several species strongly influence the carrying capacities of the species, with the changes being, to a first approximation, proportional to the species numbers. For example, humans have increased the carrying capacity of the environment for a few other species, including those with which we live in a mutually beneficial symbiosis. Those companion species include more than about 20 billion domestic animals such as cows, horses, pigs, sheep, goats, dogs, cats, and chickens, as well as certain plants such as wheat, rice, barley, maize, tomato, and cabbage. Clearly, humans and their selected companions have benefited greatly through active management of mutual carrying capacities [40].

Interactions between two or more biological species are known to essentially influence the carrying capacity of each other, by either increasing it, when species derive a mutual benefit, or decreasing it, when their interactions are antagonistic [41–43]. The same applies to economic and financial interactions between firms, which also form a kind of symbiosis, where the interacting firms develop the carrying capacity of each other also roughly proportionally to their sizes [16]. When species coexist, their carrying capacities are influenced by the species mutual interactions, either facilitating the capacity development or damaging it. Being functions of the species populations, such nonequilibrium carrying capacities can be naturally represented as polynomials over the population numbers [44].

Thus, it is now generally accepted that symbiotic organisms influence the carrying capacities of each other, hence the carrying capacities of symbiotic species are not fixed quantities, but should be considered as functions of population sizes [45, 46]. In the present paper, we suggest a mathematical formulation of this idea and investigate its consequences.

The paper proceeds as follows. Section 2 presents the general structure of the model. In Section 3, we specify the classification of different types of symbiotic interactions, in the frame of the suggested mathematical model. Sections 4, 5, and 6 focus on the structure of the model of symbiosis in the presence of mutual, respectively, asymmetric, and in the absence of direct interactions. Section 7 concludes, explaining the principal difference of our model from the Lotka-Volterra model, and proposes a way to avoid the finite-time singularities arising under parasitic interactions. Also, we described several concrete examples demonstrating that the suggested mathematical models can be directly applied to different types of symbiotic relations, whether in biological symbiosis or in economic and industrial symbiosis. A discussion is given on the relation of the suggested approach to the processes describing the coexistence of microbial populations.

2 General model of symbiosis

Our basic suggestion, making our approach principally new, is to describe symbiotic relations by the mutual influence of the co-existing species on their respective carrying capacities. Indeed, in the presence of symbiotic relations, the species act on the livelihood of each other by creating resources that others exploit, by using resources created by others without feedbacks, or by destroying the livelihood in the case of parasitism. In mathematical language, the livelihood is nothing but the carrying capacity. This is the principal point of the approach we suggest, as compared to the predator-prey models, where the species directly predate or compete. Such direct interactions are appropriate for describing the predator-
prey relations, when predators eat prey. But this is not what one usually calls symbiosis. Predation and competition are commonly treated as different processes as compared to symbiosis [17]. The standard description of symbiosis [1-5] corresponds exactly to the mutual influence of species on the carrying capacities of each other. For example, in the tree-fungi symbiosis, neither of the species eats another, but they do influence the carrying capacities of each other, producing the chemical elements helping the growth of both species.

Let us consider several species, or system parts, quantified by their population number $N_i$, with the index $i$ enumerating the species. For instance, in biology, $N_i$ can be the number of individuals of the $i$-th species or, in finance, this can be the amount of money or, in economics, this could be the quantity of some goods. To study the mutual influence of varying carrying capacities, we start with the logistic-type equations

$$\frac{dN_i}{dt} = \gamma_i N_i - \frac{C_i N_i^2}{K_i},$$

(1)

for the variables $N_i = N_i(t)$ as functions of time $t \geq 0$. Here $\gamma_i$ is the birth rate of the biological species $i$ or the growth rate in economic systems. The coefficient $C_i$ characterizes the intensity of mutual competition between the agents of the $i$-th species. We will thus consider only the case where

$$\gamma_i > 0, \quad C_i > 0.$$  

(2)

The principal difference from the standard logistic equation is that the carrying capacity is here considered to be a function

$$K_i = A_i + B_i S_i(\{N_1, N_2, \ldots\})$$

(3)

of the quantities $N_i$, in order to account for the co-existing symbiotic species. The first term $A_i$ is the carrying capacity of the given surrounding livelihood. The second term characterizes the carrying capacity produced by other species. We thus capture the typical feature of symbiotic relations via the mutual influence of each species on the carrying capacities of others. The symbiotic coefficient $B_i$ defines the intensity of producing, or destroying, the carrying capacity in the process of symbiotic relations. We refer to $B_i$ as the production coefficient, when $B_i$ is positive, or as the destruction coefficient, when $B_i$ is negative. Thence, we shall consider that

$$A_i > 0, \quad B_i \in (-\infty, \infty).$$

(4)

Since the nature of the mutual interactions is characterized by the sign of the symbiotic coefficient $B_i$, the symbiosis function

$$S_i(\{N_1, N_2, \ldots\}) \geq 0,$$

(5)

describing the type of symbiotic relations, can be taken non-negative.

Accepting that the symbiotic functions depend on the species populations, we exemplify this in what follows by the simplest form of such a dependence, assuming that the effective carrying capacity is a linear combination of the natural carrying capacity, provided by nature, and by the carrying capacity produced (or destroyed) by the mutual species activity. Generally, we assume that the symbiotic functions are analytical functions, hence, they can be expanded in power series over the species populations. We shall consider the following particular cases of such expansions, corresponding to different types of mutual influence of
two symbiotic species. When the carrying capacity of an $i$-species is influenced by the mutual interactions with a $j$-species, the effective carrying capacity is represented as

$$K_i = A_i + B_i N_i N_j.$$  

And if the carrying capacity of the $i$-species is influenced by the $j$-species without direct interactions, as it happens in the case of commensalism, then the effective carrying capacity is given by the form

$$K_i = A_i + B_i N_j.$$  

The natural carrying capacity $A_i$ is supposed to be nonzero, which implies that the species could exist without their symbionts, though the existence of the latter can drastically change the species behavior. In general, there can happen situations when one symbiont is obligatory for another, so that one of the species cannot survive without their counterpart. Such a situation would correspond to zero carrying capacity. But this rare case is not treated here.

The mathematical structure of Eq. (1) with (3), describing symbiosis, is principally different from equations of the Lotka-Volterra type and cannot be reduced to the latter, as we shall show in the Discussion section.

As we mentioned in the Introduction, in biology and ecology, three main categories of symbiotic relations can be distinguished (mutualism, parasitism, and commensalism), depending on whether the influence of one species on another is positive, negative, or neutral. This classification is straightforwardly linked to our model. Below, we explain this for the case of two species, when $i = 1, 2$, which will be treated in what follows.

**Mutualism** implies the relations in which both species extract some benefit from their relationship. In our model, this is equivalent to

$$B_1 > 0, \quad B_2 > 0 \quad (\text{mutualism}).$$

**Parasitism** means that one of the species can benefit, while the other is harmed in the process. Generally, one can say that parasitism is the relation in which at least one of the species is harmed. This means that one of the following inequalities is valid: either

$$B_1 > 0, \quad B_2 < 0,$$

or

$$B_1 < 0, \quad B_2 > 0,$$

or

$$B_1 < 0, \quad B_2 < 0 \quad (\text{parasitism}).$$

**Commensalism** is the relation in which one of the species benefits, while another is not affected. Hence, one of the following inequalities is satisfied: either

$$B_1 > 0, \quad B_2 = 0,$$

or

$$B_1 = 0, \quad B_2 > 0 \quad (\text{commensalism}).$$

In addition to this classification, it is possible to distinguish different kinds of mutual interactions embodied in the form of the symbiosis function $S_i (\{N_i\})$ obeying inequality (5), which will be specified later.
Before specifying this function \( S_i(\{N_i\}) \), it is convenient to introduce dimensionless units. For this purpose, we may choose two characteristic scales, \( N_{eff} \) and \( Z_{eff} \), to serve as the measuring units for the species variables \( N_1 \) and \( N_2 \), respectively. We thus define the dimensionless species characteristics

\[
x \equiv \frac{N_1}{N_{eff}}, \quad z \equiv \frac{N_2}{Z_{eff}}
\]

and the dimensionless carrying capacities

\[
y_1 \equiv \frac{\gamma_1 K_1}{C_1 N_{eff}}, \quad y_2 \equiv \frac{\gamma_1 K_2}{C_2 Z_{eff}}.
\]

Let us measure time in units of \( 1/\gamma_1 \) and introduce the ratio

\[
\alpha \equiv \frac{\gamma_2}{\gamma_1}.
\]

If the life times of the co-existing species were essentially different, then their mutual influence would be rather limited, inducing just local in time perturbations. The most interesting case is when the species co-exist in the long time scale comparable to their life times. This implies that the most important case is when the ratio \( \alpha \) is close to one, which we shall take into account in what follows.

Then, for two symbiotic species, Eqs. (1) take the form

\[
\frac{dx}{dt} = x - \frac{x^2}{y_1}, \quad \frac{dz}{dt} = z - \frac{z^2}{y_2}.
\]

These equations, controlling the time evolution of the functions \( x = x(t) \) and \( z = z(t) \), must be complemented by the initial conditions

\[
x(0) = x_0, \quad z(0) = z_0.
\]

By definition, the quantities \( N_i \), measuring the amount of the corresponding species, are positive. Hence, we are interested only in the non-negative solutions of Eqs. (9):

\[
x(t) \geq 0, \quad z(t) \geq 0.
\]

We then need to specify the forms of the symbiosis functions \( S_i(\{N_i\}) \) obeying inequality \( (5) \) and, respectively, the forms of the carrying capacities \( (3) \). The forms of functions \( (5) \) can vary, depending on the kind of symbiotic relations between the considered species.

At the end of this section, formulating the general idea of our approach, it is worth stressing again the meaning of the chosen type of the equations. We start with Eqs. (1) having the form of logistic equations, with all terms enjoying the known straightforward underpinning. The quantity \( K_i \) here is the carrying capacity of the \( i \)--th species. There can be numerous interpretations of what in particular cases could be this capacity, depending on whether biological, or social, or financial systems are considered. For concreteness, let us talk about food. So, the carrying capacity is the amount of food available for the species.

Our basic point is that the carrying capacity is not a fixed number, characterizing the amount of given food, but it consists of two parts, as in Eq. (3). The first part is the naturally provided amount of food, while the second part is the additional food produced during
the interaction of symbiotic species. It is possible to give an infinite number of examples illustrating this. The most classical example is the symbiosis of trees with mushrooms, or, more generally, plants with fungi. In such interactions, as is well known, the elements are produced that serve as additional food for both symbiotic species. That is, there appears additional food created by the collaboration of the species.

We consider the simple case where more agents in species lead to the increase of food production during their interactions. In a reduced formalism at the macro-level, the simplest and most robust way to account for this effect is to take the symbiotically produced amount of food to be proportional to the number of agents in each of the species. This is equivalent to writing the additionally produced food for the 1–th species as \( B_1 N_1 N_2 \), where \( N_i \) is the number of agents in the \( i \)-th species group. Similarly, for the second species the additional food is \( B_2 N_2 N_1 \). From this definition, it immediately follows that the symbiotic coefficient \( B_i \) is the amount of food produced in the process of symbiotic relations by the collaboration of an agent from the first type of species with an agent from the second species type.

The idea that the amount of food can be created in the process of symbiotic relations, or destroyed, when these relations are parasitic, is the pivotal new point we have advanced. This is exactly what happens in symbiotic relations. And this provides a novel mathematical approach to describing symbiotic relations. As we demonstrate in the following sections, our model allows for the description of all types of symbiosis.

3 Classification of forms of symbiotic relations

There can exist three main types of symbiotic relations.

3.1 Influencing livelihood through mutual interactions

A common case is when the symbiotic species influence the livelihood of each other by means of mutual interactions. Known biological examples are plant trees and mushrooms and many other plants and fungi [1-5]. In the social sciences, this could be the relationship between the economic level of a country and the intellectual level of society. Or this can be the relation between two firms, producing different kinds of goods in close collaboration with each other. Another example is the relation between basic and applied research [7-9].

The simplest form of the carrying capacities, representing livelihoods that are influenced by mutual interactions, can be written as

\[
K_1 = A_1 + B_1 N_1 N_2 , \quad K_2 = A_2 + B_2 N_2 N_1 .
\]

The first terms \( A_1 \) and \( A_2 \) define the given carrying capacities, which in dimensionless units are

\[
a_1 \equiv \frac{\gamma_1 A_1}{C_1 Z_{eff}} , \quad a_2 \equiv \frac{\gamma_1 A_2}{C_2 Z_{eff}} .
\]

The second terms characterize the produced carrying capacities, corresponding to the mutual influence of symbiotic species on the livelihood of each other. The dimensionless symbiotic coefficients are

\[
b \equiv \frac{\gamma_1 B_1 Z_{eff}}{C_1} , \quad g \equiv \frac{\gamma_1 B_2 N_{eff}}{C_2} .
\]
The dimensionless carrying capacities (7) become

\[ y_1 = a_1 + bxz, \quad y_2 = a_2 + gxz. \tag{15} \]

The given carrying capacities are taken positive,

\[ a_1 > 0, \quad a_2 > 0, \tag{16} \]

which means that each of the two species can survive in the absence of the other one. The interaction coefficients \( b \) and \( g \) can be of any sign, depending on whether the relations are beneficial or parasitic.

The scaling units \( N_{\text{eff}} \) and \( Z_{\text{eff}} \) can be chosen arbitrarily. It is convenient to choose them as

\[ N_{\text{eff}} = \frac{\gamma_1 A_1}{C_1}, \quad Z_{\text{eff}} = \frac{\gamma_1 A_2}{C_2}. \tag{17} \]

Then one has

\[ a_1 = a_2 = 1, \tag{18} \]

and the symbiotic coefficients are

\[ b \equiv \gamma_1^2 B_1 A_2 \frac{Z_{\text{eff}}}{C_1 C_2}, \quad g \equiv \gamma_1^2 A_1 B_2 \frac{N_{\text{eff}}}{C_1 C_2}. \tag{19} \]

Therefore, the carrying capacities (15) become

\[ y_1 = 1 + bxz, \quad y_2 = 1 + gxz. \tag{20} \]

### 3.2 Influencing livelihood through asymmetric interactions

Another possibility is when the interactions of symbiotic species are not symmetric, such that the carrying capacity of one of them is influenced by mutual interactions, while the carrying capacity of another is influenced solely by the other species, not involving their mutual interactions. This type of symbiosis is common to many biological as well as social systems, when one of them is a subsystem of a larger one. For example, the relation between the economic level of a country and the development level of a particular branch of economics, say between the country gross domestic product and the level of science; or the relation between culture and language; or the relation between the size of social groups and the size of brain [48, 49]. In that asymmetric case, the carrying capacities are

\[ K_1 = A_1 + B_1 N_1 N_2, \quad K_2 = A_2 + B_2 N_1. \tag{21} \]

In dimensionless units, \( a_1 \) and \( a_2 \) have the same form as in Eq. (13), while the symbiotic coefficients are

\[ b \equiv \gamma_1 B_1 Z_{\text{eff}} \frac{N_{\text{eff}}}{C_1}, \quad g \equiv \gamma_1 B_2 N_{\text{eff}} \frac{Z_{\text{eff}}}{Z_{\text{eff}}}. \tag{22} \]

The carrying capacities (7) are given by the expressions

\[ y_1 = a_1 + bxz, \quad y_2 = a_2 + gx. \tag{23} \]
Opting for the scaling units (17) yields normalization (18), with the symbiotic coefficients
\[ b \equiv \frac{\gamma_1^2 B_1 A_2}{C_1 C_2} , \quad g \equiv \frac{\gamma_1^2 A_1 B_2}{C_1 A_2} . \] (24)
Thus, the dimensionless carrying capacities (23) become
\[ y_1 = 1 + bxz , \quad y_2 = 1 + gx . \] (25)

### 3.3 Influencing livelihood without direct interactions

This is, probably, the most common of biological and ecological symbiosis. Numerous examples can be found in the books [1–5]. In this case, the livelihood of each species is influenced by the presence of another species without involving their direct interactions. The carrying capacities are correspondingly given by
\[ K_1 = A_1 + B_1 N_2 , \quad K_2 = A_2 + B_2 N_1 . \] (26)
The terms \( A_1 \) and \( A_2 \) are the a priori given carrying capacities, in the absence of the other species. Their dimensionless forms are the same as in Eq. (13), but the symbiotic coefficients are
\[ b \equiv \frac{\gamma_1 B_1 Z_{\text{eff}}}{C_1 N_{\text{eff}}} , \quad g \equiv \frac{\gamma_1 B_2 N_{\text{eff}}}{C_2 Z_{\text{eff}}} . \] (27)
The dimensionless carrying capacities (7) take the forms
\[ y_1 = a_1 + bz , \quad y_2 = a_2 + gx . \] (28)
Choosing again the same scaling units (17) gives the same normalization (18), but with the symbiotic coefficients
\[ b \equiv \frac{\gamma_1 B_1 A_2}{A_1 C_2} , \quad g \equiv \frac{\gamma_1 A_1 B_2}{C_1 A_2} . \] (29)
This results in the dimensionless carrying capacities
\[ y_1 = 1 + bz , \quad y_2 = 1 + gx . \] (30)

Note that here, as well as in the previous cases, the symbiotic coefficients \( b \) and \( g \) can take different values, depending on the strength of the mutual influence between the symbiotic species. And these coefficients can be of different signs, describing either beneficial or parasitic relations. In the following sections, we give a detailed analysis of each type of symbiosis classified above.

### 4 Symbiosis with mutual interactions

We study the equations (9), with the carrying capacities (20), leading to the coupled system of two ordinary differential equations:
\[ \frac{dx}{dt} = x - \frac{x^2}{1 + bxz} , \quad \frac{dz}{dt} = z - \frac{z^2}{1 + gxz} . \] (31)
This system of equations is symmetric with respect to the change \( x \to z \) and \( b \to g \). Three kinds of qualitatively different solutions are found for these equations, which we describe in turn.
4.1 Convergence to Stationary States

Formally, there are five fixed points for Eqs. (31). However, as expressed by Eq. (11), we are looking for non-negative solutions. For each of the non-negative solutions, we accomplish the Lyapunov stability analysis and select the stable solutions. We assume that the reader is sufficiently qualified in the Lyapunov technique, so that we do not discuss the details of the stability analysis and present only the final results of the analysis for the stable stationary solutions that are non-negative.

Equations (31) can possess a single stable fixed point given by the expressions

\[ x^* = \frac{1 - b + g - \sqrt{(1 + b - g)^2 - 4b}}{2g}, \quad z^* = \frac{1 + b - g - \sqrt{(1 + b - g)^2 - 4b}}{2b}. \]  

(32)

This point is stable in the stability region shown in Fig. 1 characterized by one of the conditions, either

\[ b < 0, \quad -\infty < g < \infty, \]  

(33)

or

\[ 0 < b < 1, \quad g \leq g_c \equiv \left( \sqrt{b} - 1 \right)^2 \leq 1, \]  

(34)

or

\[ b \geq 1, \quad g \leq 0. \]  

(35)

On the boundaries of the stability region, we have

\[ x^* = 1, \quad z^* = \frac{1}{1 - g} \quad (b = 0, \ g < 1), \]

\[ x^* = \frac{1}{1 - b}, \quad z^* = 1 \quad (b < 1, \ g = 0), \]

\[ x^* = \frac{1}{1 - \sqrt{b}}, \quad z^* = \frac{1}{\sqrt{b}} \quad (0 < b < 1, \ g = g_c). \]  

(36)

The solution to Eqs. (31) tends to the stationary point (32), provided that the symbiosis parameters \( b \) and \( g \) are in the stability region defined above, and when the initial conditions are in the attraction basin of this fixed point. For positive \( b \) and \( g \), the attraction basin can be found only numerically while, if at least one of these parameters is negative, the attraction basin is characterized by one of the conditions, when either

\[ x_0 z_0 < \frac{1}{|b|} \quad (b < 0, \ g > 0), \]  

(37)

or when

\[ x_0 z_0 < \frac{1}{|g|} \quad (b > 0, \ g < 0), \]  

(38)

or when

\[ x_0 z_0 < \min \left\{ \frac{1}{|b|}, \frac{1}{|g|} \right\} \quad (b < 0, \ g < 0). \]  

(39)

The approach to the stationary solution (32) can be either monotonic or non-monotonic, from above or from below, depending on the parameters \( b \) and \( g \) and on the initial conditions \( x_0 \) and \( z_0 \). In Figs. 2, 3, and 4, the typical behavior of the solutions is shown for different
parameters and initial conditions: when $x_0 > x^*$ and $z_0 > z^*$ (Fig. 2), when $x_0 > x^*$ but $z_0 < z^*$ (Fig. 3), and when $x_0 < x^*$ with $z_0 < z^*$ (Fig. 4). The case when $x_0 < x^*$ but $z_0 > z^*$ is similar to the case when $x_0 > x^*$ but $z_0 < z^*$, with changing $x$ by $z$ and $b$ by $g$.

It is instructive to compare the behavior of the symbiotic solutions, described by the coupled Eqs. (31), with that of the solutions of the decoupled equations ($b = g = 0$)

$$\frac{dx}{dt} = x - x^2, \quad \frac{dz}{dt} = z - z^2 \quad (b = g = 0). \tag{40}$$

The solutions for these non-symbiotic species tend to the stable fixed point $x^* = z^* = 1$.

The comparison, explicitly showing the role of symbiosis, is demonstrated in Figs. 5 and 6. These two figures illustrate the general property that beneficial (respectively, parasitic) symbiosis leads to the increase (respectively, decrease) of the stationary solutions. Another important message is that stationary states can exist even in the presence of parasites.

### 4.2 Unbounded Exponential Growth

The solutions to the symbiotic equations (31) grow to infinity with increasing time $t \to \infty$, when there are no stable fixed points, that is, when either

$$0 < b < 1, \quad g > g_e, \tag{41}$$

or when

$$b > 1, \quad g > 0. \tag{42}$$

A similar exponential divergence at infinity occurs when the stable fixed points exist, but the initial conditions are taken outside of the attraction basin, so that either

$$x_0 z_0 > \frac{1}{|b|} \quad (b < 0, \ g > 0), \tag{43}$$

or when

$$x_0 z_0 > \frac{1}{|g|} \quad (b > 0, \ g < 0), \tag{44}$$

or when

$$x_0 z_0 > \max \left\{ \frac{1}{|b|}, \ \frac{1}{|g|} \right\} \quad (b < 0, \ g < 0). \tag{45}$$

The typical behavior of such increasing solutions is shown in Fig. 7. When the initial conditions are outside of the attraction basin, this means that at least one of them is sufficiently large, that is, the initial population is so large that even the existence of parasites cannot suppress the development of this species.

### 4.3 Finite-Time Death and Singularity

A specific behavior occurs under parasitic symbiotic relations, when stable fixed points can exist, but the initial conditions are taken outside of the attraction basin, so that

$$\frac{1}{|b|} < x_0 z_0 < \frac{1}{|g|} \quad (b < g < 0). \tag{46}$$
Then, at the critical time \( t_c \), defined as the solution of the equation
\[
x(t_c)z(t_c) = \frac{1}{|b|},
\]
the first variable \( x(t) \) sharply drops to zero, while the second one rises to infinity:
\[
x(t) \to 0, \quad \dot{x}(t) \to -\infty \quad (t \to t_c), \quad z(t) \to +\infty, \quad \dot{z}(t) \to +\infty \quad (t \to t_c).
\]
Here the overdot means time derivative.
The behavior is inverted for the case when
\[
\frac{1}{|g|} < x_0z_0 < \frac{1}{|b|} \quad (g < b < 0),
\]
for which the critical time is given as the solution of the equation
\[
x(t_c)z(t_c) = \frac{1}{|g|}.
\]
At this time, the first solution rises to infinity, while the second one quickly dies:
\[
x(t) \to +\infty, \quad \dot{x}(t) \to +\infty \quad (t \to t_c), \quad z(t) \to 0, \quad \dot{z}(t) \to -\infty \quad (t \to t_c).
\]
The situation corresponding to the case (46) is illustrated in Fig. 8. The meaning of this phenomenon, when one of the species dies, while the other rises, is easily understandable. Under the mutually parasitic relations, each species destroys the livelihood of the other one. That species, whose livelihood is destroyed faster, dies out, while the other species grows at the expense of the former one.

5 Symbiosis with asymmetric interactions

If the symbiotic relations between species are characterized by asymmetric interactions with the carrying capacities (25), then Eqs. (9) take the form
\[
\frac{dx}{dt} = x - \frac{x^2}{1 + bxz}, \quad \frac{dz}{dt} = z - \frac{z^2}{1 + gx}.
\]
The following qualitatively different dynamic regimes can occur.

5.1 Convergence to stationary states

There can exist just one stable fixed point, given by
\[
x^* = \frac{1 - b - \sqrt{(1 - b)^2 - 4bg}}{2bg}, \quad z^* = \frac{1 + b - \sqrt{(1 - b)^2 - 4bg}}{2b}.
\]
Let us introduce the critical parameter value

\[ g_c \equiv \frac{(1 - b)^2}{4b} \].

The fixed point (53) is stable and non-negative if either

\[ b \leq -1, \quad g \geq g_c, \] (55)

or if

\[ -1 < b \leq 0, \quad g > -1, \] (56)

or if

\[ 0 < b < 1, \quad -1 \leq g \leq g_c, \] (57)

or when

\[ b \geq 1, \quad -1 < g < 0. \] (58)

The overall region of stability is depicted in Fig. 9.

The marginal values of the fixed point, occurring at the boundary of the stability region, are

\[ x^* = 1, \quad z^* = 1 + g \quad (b = 0, \ g > -1), \]
\[ x^* = \frac{1}{1 - b}, \quad z^* = 1 \quad (b < 1, \ g = 0), \] (59)

if \( g \neq g_c \), and

\[ x^* = \frac{2}{1 - b}, \quad z^* = \frac{1 + b}{2b} \quad (g = g_c), \] (60)

if \( g = g_c \) and either \( b < -1 \) or \( 0 < b < 1 \).

The solutions tend to the fixed point, provided that the related initial conditions are in the basin of attraction. When one of the symbiotic coefficients is negative, the basin of attraction is defined so that either

\[ x_0z_0 < \frac{1}{|b|} \quad (b < 0, \ g > 0), \] (61)

or if

\[ x_0 < \frac{1}{|g|} \quad (b > 0, \ g < 0), \] (62)

or when

\[ x_0 < \frac{1}{|g|}, \quad x_0z_0 < \frac{1}{|b|} \quad (b < 0, \ g < 0). \] (63)

The convergence to the stationary state can be monotonic or non-monotonic, as illustrated in Figs. 10 and 11 for various initial conditions and different symbiotic coefficients. The convergence of solutions to the stable fixed point is qualitatively similar to that documented in the case of symmetric interactions.
5.2 Exponential growth at infinity

Another regime, which is similar to that found for symmetric interactions, is the exponential growth at increasing time $t \to \infty$. This happens when there are no stable fixed points and either

\[ 0 < b < 1, \quad g > g_c, \quad (64) \]

or when

\[ b > 1, \quad g > 0, \quad (65) \]

with the critical parameter $g_c$ given in Eq. (54). The same kind of exponential growth arises when there exist stable fixed points, but the initial conditions are outside of their basin of attraction, which occurs for

\[ 0 < b < 1, \quad 0 < g < g_c, \quad (66) \]

or when

\[ x_0 z_0 > \frac{1}{|b|} \quad (b < 0, \; g > 0) \quad (67) \]

The temporal behavior is qualitatively similar to that of Fig. 7.

5.3 Finite-time singularity

A different regime occurs when the parameter $g$ is negative, and no stable fixed point exists, which occurs when

\[ 0 < b < \infty, \quad g < -1, \quad (68) \]

or if

\[ -1 < b < 0, \quad g < -1, \quad (69) \]

or if

\[ b \leq -1, \quad g < g_c < -1. \quad (70) \]

When the initial conditions obey the inequalities

\[ x_0 > \frac{1}{|g|}, \quad x_0 z_0 > -\frac{1}{b} \quad (b > 0, \; g < 0) \quad (71) \]

or the inequalities

\[ x_0 > \frac{1}{|g|}, \quad x_0 z_0 > \frac{1}{|b|} \quad (b < 0, \; g < 0) \quad (72) \]

then the solutions live only a finite life until the critical time $t_c$. The value of this critical point can only be determined numerically. As time approaches $t_c$, the first variable remains finite, while the second one diverges:

\[ x(t) \to x(t_c) > 0, \quad \dot{x}(t) \to \dot{x}(t_c) \quad (t \to t_c), \quad (73) \]

\[ z(t) \to \infty, \quad \dot{z}(t) \to \infty \quad (t \to t_c). \quad (73) \]

Here $x(t_c)$ and $\dot{x}(t_c)$ imply finite values of the corresponding functions at the critical time $t_c$.

The main difference with the case of Eq. (68) is the finiteness of the solution $x(t_c)$ at the critical time. The typical behavior of the two variables in this regime is shown in Fig.
12. The explosive divergence of one of the species announces a change of regime: beyond $t_c$, the system of two species will change their characteristics and, possibly, the nature of their interactions.

The same kind of behavior also happens when the stable fixed points exist for $b$ and negative $g$ in the region

$$b > -1 , \quad -1 < g < 0 ,$$

or if

$$b < -1 , \quad g_c < g < 0 ,$$

but initial conditions are taken outside of the basin of attraction, so that $x_0, z_0$ are defined by Eqs. (71) or (72), correspondingly.

### 5.4 Finite-time death

An interesting behavior appears for some parameters, in particular, when the parameter $g$ is negative, meaning parasitism, so that no stable fixed points exist or when fixed points exist but the initial conditions are outside their domain of attraction. For $g < 0$, when the symbiosis coefficients are taken outside of the stability region presented in Fig. 9, and initial conditions obey the following inequalities, either

$$x_0 < \frac{1}{|g|} , \quad x_0z_0 > -\frac{1}{b} \quad (b > 0, \ g < 0) , \tag{74}$$

or if

$$x_0 < \frac{1}{|g|} , \quad x_0z_0 < \frac{1}{|b|} \quad (b < 0, \ g < 0) , \tag{75}$$

or if

$$x_0 < \frac{1}{|g|} , \quad x_0z_0 > \frac{1}{|b|} \quad (b < 0, \ g < 0) , \tag{76}$$

or when

$$x_0 > \frac{1}{|g|} , \quad x_0z_0 < \frac{1}{|b|} \quad (b < 0, \ g < 0) , \tag{77}$$

then the solutions have a finite life and one of the species dies or exhibits a gradient catastrophe at the death time $t_d$ (see below) found as the solution to the equation

$$|g|x(t_d) = 1 , \tag{78}$$

at which either $\dot{z}(t) = -\infty$ or $\dot{x}(t) = -\infty$ for $t \to t_d$.

When the parameters are taken outside of the stability region and the initial conditions obey inequalities (74) or (75), then

$$x(t) \to \frac{1}{|g|} , \quad \dot{x}(t) \to \dot{x}(t_d) \quad (t \to t_d) ,$$

$$z(t) \to z(t_d) , \quad \dot{z}(t) \to -\infty \quad (t \to t_d) . \tag{79}$$

When the initial conditions obey inequality (76), then

$$x(t) \to \frac{1}{|g|} , \quad \dot{x}(t) \to +\infty \quad (t \to t_d) ,$$

$$z(t) \to z(t_d) , \quad \dot{z}(t) \to -\infty \quad (t \to t_d) . \tag{79}$$
\[ z(t) \to \frac{|g|}{|b|}, \quad \dot{z}(t) \to -\infty \quad (t \to t_d) , \]  
\[ x(t) \to \frac{1}{|g|}, \quad \dot{x}(t) \to -\infty \quad (t \to t_d) , \]
\[ z(t) \to \frac{|g|}{|b|}, \quad \dot{z}(t) \to +\infty \quad (t \to t_d) . \]  

(80)  

(81)

In the cases (74) and (75), the solutions (79) remain non-zero at \( t \to t_d \), but the time derivative of \( z(t) \) tends to \(-\infty\). Such a behavior corresponds to the so-called gradient catastrophe. The value \( z(t_d) \) is close to zero, as shown in Fig. 13. This kind of behavior can be interpreted as the extinction of the species described by the variable \( z(t) \). Therefore, after \( t_d \), we can set
\[ z(t) \equiv 0 \quad (t \geq t_d) . \]  

(82)

Then the continuation of the evolution of the population \( x(t) \) after \( t_d \) is characterized by the single equation \( \dot{x} = x - x^2 \). The death of the species \( z(t) \) is due to the large negative (parasitic) symbiosis coefficient \( g \), which leads the species \( x \) to suppress the population \( z \) of the other species, until its complete demise occurring at the time \( t_d \).

A behavior similar to that, described by Eqs. (80) and (81), occurs for \( g < 0 \), when the symbiosis coefficients are in the stability region, but the initial conditions obey inequalities (76) or (77).

When \( \{x_0, z_0\} \) obey Eq. (76), then again there is a death time \( t_d \), given by the same Eq. (78). Here \( z(t_d) \) is not necessarily close to zero, but it experiences the same gradient catastrophe as in Eq. (79). Contrary to the case of Eq. (79), the derivative \( \dot{x}(t) \) tends to \(+\infty\). Strictly speaking, the coupled system of Eqs. (52) has no solution after the time \( t_d \). However, we can again interpret the gradient catastrophe, with \( \dot{z}(t) \to -\infty \) as the death of the species \( z(t) \), extending the solution \( x \) after \( t_d \) using condition (82), as is shown in Fig. 14.

In the case when the initial conditions obey Eq. (77), the evolution also ends at the death time \( t_d \), defined by the same Eq. (78). At this point, conditions (81) hold true. The difference with the case of Eqs. (80) is that here the gradient catastrophe happens with \( \dot{x}(t) \to -\infty \) while \( \dot{z}(t) \to +\infty \) for \( t \to t_d \). Hence, interpreting \( t_d \) as the time of extinction of the species \( x \) that are killed by the species \( z \), the subsequent evolution of the dynamics after \( t_d \) is obtained by setting
\[ x(t) \equiv 0 \quad (t > t_d) . \]  

(83)

The overall behavior is presented in Fig. 15. Comparing Figs. 14 and 15, we see that the dynamics essentially depends on the initial conditions.

6 Symbiosis without direct interactions

When symbiosis is characterized by the influence of species on the livelihood of each other without direct mutual interactions, the corresponding carrying capacities are given by Eqs. (30). Then, the symbiotic Eqs. (9) take the form
\[ \frac{dx}{dt} = x - \frac{x^2}{1 + bz} , \quad \frac{dz}{dt} = z - \frac{z^2}{1 + gx} . \]  

(84)
These equations are symmetric with respect to the replacement $b \rightarrow g$ and $x \rightarrow z$. The different possible regimes exhibited by Eqs. (84) are described as follows.

### 6.1 Convergence to stationary states

There can exist the single stable fixed point

$$x^* = \frac{1 + b}{1 - bg}, \quad z^* = \frac{1 + g}{1 - bg},$$

which is positive and stable if either

$$-1 \leq b < 0, \quad g \geq -1$$

or if

$$b \geq 0, \quad 0 \leq g < g_c \equiv \frac{1}{b}.$$  

The corresponding stability region is shown in Fig. 16. On the boundary of the stability region, the fixed point degenerates to one of the values

$$x^* = 0, \quad z^* = 1 \quad (b = -1, \ g > -1),$$

$$x^* = 1, \quad z^* = 0 \quad (b > -1, \ g = -1),$$

$$x^* = 1 - z^*, \quad 0 \leq z^* \leq 1 \quad (b = g = -1).$$

For $b > 0$ and $g > 0$, the basin of attraction is the whole region in the $b - g$ plane, where inequalities (87) are valid. When one of the parameters $b$ or $g$ is negative, or both are negative, then the attraction basin is defined by one of the following conditions, either

$$x_0 < \frac{1}{|g|} \quad (b > 0, \ g < 0),$$

or by

$$z_0 < \frac{1}{|b|} \quad (b < 0, \ g > 0),$$

or by

$$x_0 < \frac{1}{|g|}, \quad z_0 < \frac{1}{|b|} \quad (b < 0, \ g < 0).$$

The convergence to the stationary solution can be monotonic or non-monotonic, depending on the symbiosis parameters and initial conditions, similarly to Figs. 2, 3, 4, and 10, 11.

### 6.2 Exponential growth at infinity

This behavior, which is analogous to that displayed in Fig. 7, occurs when

$$b > 0, \quad g > g_c \equiv \frac{1}{b}.$$  

Then, both solutions $x(t)$ and $z(t)$ exponentially increase as $t \rightarrow \infty.$
6.3 Finite-time singularity

When one or both of the symbiosis parameters are negative, implying parasitic symbiotic relations, a finite-time singularity can occur. For the initial conditions

\[ x_0 > \frac{1}{|g|}, \quad z_0 > -\frac{1}{b} \quad (b > 0, \ g < 0), \]  

(93)

there exists a critical time \( t_c \), such that

\[ x(t) \to x(t_c) , \quad \dot{x}(t) \to \dot{x}(t_c) \quad (t \to t_c) , \]
\[ z(t) \to +\infty , \quad \dot{z}(t) \to +\infty \quad (t \to t_c) . \]  

(94)

This behavior is similar to that shown in Fig. 12. Because of the equation symmetry, there is the opposite case, occurring for

\[ x_0 > -\frac{1}{g} , \quad z_0 > \frac{1}{|b|} \quad (b < 0, \ g > 0), \]  

(95)

when

\[ x(t) \to +\infty , \quad \dot{x}(t) \to +\infty \quad (t \to t_c) , \]
\[ z(t) \to z(t_c) , \quad \dot{z}(t) \to z(t_c) \quad (t \to t_c) . \]  

(96)

If both symbiosis parameters are negative, and

\[ x_0 > \frac{1}{|g|} , \quad z_0 > \frac{1}{|b|} \quad (b < 0, \ g < 0), \]  

(97)

there exists a finite-time singularity of the same type as above, with the particular behavior depending on the parameter values and initial conditions.

6.4 Finite-time death

The occurrence of a gradient catastrophe, of the type described previously in Sec. 5, depends on the values of the symbiotic parameters and initial conditions. If the symbiotic parameters are outside of the stability region and the initial conditions are such that

\[ x_0 < \frac{1}{|g|} , \quad z_0 > -\frac{1}{b} \quad (b > 0, \ g \leq -1) , \]  

(98)

then there exists a finite time \( t_d \), determined as the solution of the equation

\[ |g|x(t_d) = 1 , \]  

(99)

where

\[ x(t) \to \frac{1}{|g|} , \quad \dot{x}(t) \to \dot{x}(t_d) \quad (t \to t_d) , \]
\[ z(t) \to z(t_d) , \quad \dot{z}(t) \to -\infty \quad (t \to t_d) . \]  

(100)

The gradient catastrophe occurs for the species \( z \), whose gradient tends to \(-\infty\). This can be interpreted as an abrupt collapse of \( z \) to 0 and thus as the extinction of this species. The
continuation of the solution $x$ is then obtained by setting $z \equiv 0$ for $t > t_d$. The extinction of the species $z$ is caused by the strong parasitic action of the species $x$ onto species $z$, represented by the negative value of the symbiotic parameter $g$.

Under the condition
\begin{equation}
    x_0 > -\frac{1}{g}, \quad z_0 < \frac{1}{|b|} \quad (b \leq -1, \; g > 0),
\end{equation}
the role of $x$ and $z$ is interchanged and the finite-time extinction is observed for the species $x$. At the finite time $t_d$, given as the solution to the equation
\begin{equation}
    |b|z(t_d) = 1,
\end{equation}
we have
\begin{align*}
    x(t) &\to x(t_d), \quad \dot{x}(t) \to -\infty \quad (t \to t_d) \\
    z(t) &\to \frac{1}{|b|}, \quad \dot{z}(t) \to \dot{z}(t_d) \quad (t \to t_d).
\end{align*}
(103)
Again, interpreting the gradient catastrophe for $x$ as the extinction of $x$, the continuation of the solution for $z$ is obtained by setting $x \equiv 0$ for $t > t_d$. The extinction of the species $x$ is caused by the strong parasitic action of $z$ on $x$, due to the negative symbiotic parameter $b$.

The gradient catastrophe can occur even when the symbiotic parameters are inside the stability region, but with initial conditions that are outside of the basin of attraction. Thus, if
\begin{equation}
    x_0 < \frac{1}{|g|}, \quad z_0 > \frac{1}{|b|} \quad (b < 0, \; g < 0),
\end{equation}
then there exists a finite time $t_d$, given as the solution of the equations
\begin{equation}
    |g|x(t_d) = |b|z(t_d) = 1,
\end{equation}
at which
\begin{align*}
    x(t) &\to \frac{1}{|g|}, \quad \dot{x} \to +\infty \quad (t \to t_d) \\
    z(t) &\to \frac{1}{|b|}, \quad \dot{z} \to -\infty \quad (t \to t_d).
\end{align*}
(106)
Again, here the gradient catastrophe for $z$ can be understood as the extinction of $z$. Conversely, when the initial conditions are such that
\begin{equation}
    x_0 > \frac{1}{|g|}, \quad z_0 < \frac{1}{|b|} \quad (b < 0, \; g < 0),
\end{equation}
then there is the finite time $t_d$, given by the same Eqs. (105), when
\begin{align*}
    x(t) &\to \frac{1}{|g|}, \quad \dot{x}(t) \to -\infty \quad (t \to t_d) \\
    z(t) &\to \frac{1}{|b|}, \quad \dot{z}(t) \to +\infty \quad (t \to t_d).
\end{align*}
(108)
This can be interpreted as the extinction of the species $x$, after which it can be set zero for $t > t_d$. The overall behavior is presented in Fig. 17.
7 Discussion

7.1 Summary of the main results and outlook

We have proposed an approach to describe the dynamics of symbiotic relations between several species. We have argued that the notion of symbiosis can be applied not merely to biological systems but can also be generalized to social systems of different nature.

The principal point of our approach is the description of symbiosis through the influence of each species on the carrying capacities of the others. This is in agreement with the common understanding that symbiotic species act on the livelihood of each other, either improving it, under beneficial relations, or destroying it, under parasitic relations.

The general symbiotic model can be represented by several variants characterizing different types of symbiotic relations. We have considered three basic types of such relations, symbiosis with mutual interactions, symbiosis with asymmetric interactions, and symbiosis without direct interactions. In all cases, we have provided a complete classification of all admissible dynamical regimes.

The functional dependence of the carrying capacities on the species variables $x$ and $z$ constitutes the principal difference between our model and the logistic equation, where the carrying capacity is fixed. We have chosen here the simplest functional form of the carrying capacity characterizing symbiotic interactions. The carrying capacity has been taken as a combination of terms not exceeding the bilinear order in terms of the species variables. In general, it would be possible to describe the carrying capacity as an expansion in increasing powers of $x$ and $z$. Then, we could use an effective summation of the expansion, obtaining a more complicated expression, e.g., in the form of the self-similar exponentials, as has been done for the model describing the dynamics of a nonequilibrium financial system [50]. Another modification could be by including the effects of delays into the carrying capacity, as has been done for the model of punctuated evolution [51].

Even in its simplest form, the proposed model of symbiosis turned out to be sufficiently rich, exhibiting four qualitatively different regimes: convergence to stationary states, unbounded exponential growth, finite-time singularity, and finite-time death or extinction of species.

The suggested model of symbiosis can be applied to a variety of systems, biological, social, economic, financial, and so on. We have just mentioned some of the possible applications. The main goal of the present paper has been to advance a general parsimonious model of symbiosis and to analyze its main dynamical regimes. Here, we limit ourselves by the mathematical side of the problem. Particular applications require separate investigations and will be studied in future publications.

7.2 Recipe to avoid finite-time singularities

We have shown that singularities appear under parasitic relations, when at least one of the symbiosis coefficients is negative. The characteristics of real systems, of course, cannot diverge. Therefore, the occurrence of finite-time singularities should be understood as the manifestation of an instability developing in the system, which signals a change of regime into a new structural phase described by different mechanisms and thus different equations [52]. In some cases, the singularity can be avoided by slightly modifying the model, e.g., by taking
into account higher-order powers of the variables $x$ and $z$. Such higher orders can remove the finite-time singularity \[50\]. In any case, when a finite-time singularity does happen, this can be understood as the signal that the system behavior is drastically changing at this point, somewhat similar to the changes occurring under phase transitions \[53, 54\].

In order to be more specific, let us delineate how the model can be modified in order to avoid the appearance of finite-time singularities, leading to a more realistic behavior. Recall that finite-time singularities appear under parasitic relations, when at least one of the symbiosis coefficients is negative. The divergence occurs when the effective carrying capacity either becomes zero or is negative owing to the choice of initial conditions. Hence, mathematically, to avoid the occurrence of such divergences, it would be sufficient to have always positive-definite carrying capacities. This also would be reasonable for the majority of biological systems, though for economic and financial systems, a transient effective negative carrying capacity can have sense, representing the leverage of an economy over-stretching its borrowing level beyond its capacity for reimbursement, leading to crises and bankruptcies as illustrated by the sovereign default issues in Greece, Ireland, and in Europe that were revealed in 2010.

With the goal of removing finite-time singularities, let us consider the case of Sec. 4, where the finite-time singularity happens at a critical time, as is described in subsection 4.3, when either the carrying capacity $y_1$ or $y_2$ becomes zero. We may treat the carrying capacities $y_1 = 1 + bxz$ and $y_2 = 1 + gxz$ as the first terms of the general expansions

$$y_1 = \sum_{n=0}^{\infty} a_n (xz)^n, \quad y_2 = \sum_{n=0}^{\infty} b_n (xz)^n,$$

(109)

with $a_0 = 1$, $a_1 = b$, $b_0 = 1$, and $b_1 = g$. To find effective limits of such expansions, we can resort to some resummation, or renormalization, procedure. Probably, the most general procedure of this kind is based on the self-similar approximation theory \[55–52\]. Invoking the variant of this theory, employing self-similar exponential approximants \[63, 64\] yields renormalized effective sums that are always sign defined. For instance, the first-order exponential approximants for sums (109) read as

$$y_1^* = \exp(bxz), \quad y_2^* = \exp(gxz).$$

These forms are evidently positive for any signs of $b$ and $g$, which makes it straightforward to avoid the finite-time singularities caused by the occurrence of zero values of $y_i$ at some finite time. The same method of avoiding the finite-time singularities can be used for other cases, where such divergences arise. This method, e.g., was employed in Ref. \[50\] for removing the finite-time singularities in the dynamical models of financial markets. The use of the renormalized expressions for the effective carrying capacities makes the mathematical treatment more involved and requires separate consideration.

### 7.3 Comparison of symbiosis model with predator-prey Lotka-Volterra model

It is worth emphasizing that the suggested symbiosis model is basically different from the predator-prey Lotka-Volterra model. For two species, the general form of the latter can be
written as
\[
\begin{align*}
\frac{dx_1}{dt} &= \gamma_1 x_1 - a_1 x_1^2 + b_{12} x_1 x_2 , \\
\frac{dx_2}{dt} &= \gamma_2 x_2 - a_2 x_2^2 + b_{21} x_2 x_1 ,
\end{align*}
\]
where the coefficients \(a_1\) and \(a_2\) are positive. One gets the standard Lotka-Volterra model \[17, 18\] for prey, with the concentration \(x_1\), and predators, with the concentration \(x_2\), when \(\gamma_1 > 0, a_1 = 0, \) and \(b_{12} < 0\), while \(\gamma_2 < 0, a_2 = 0\) and \(b_{21} > 0\). In the general case, Eqs. \(110\) correspond to the competitive Lotka-Volterra model, if the coefficients \(b_{12}\) and \(b_{21}\) are negative, while if they are positive, one has the mutualistic Lotka-Volterra model \[65, 66\].

Let us compare the mathematical structure of these equations \(110\) with the symbiosis equations studied above, say, with Eqs. \(31\). It is easy to see that their nonlinearity is of rather different forms, which makes the behavior of their solutions principally different. One could ask the question whether there are, maybe, some particular cases when these equations are close to each other. For example, could it be that Eqs. \(31\) would reduce to Eqs. \(110\) at small values of \(xz\)? Expanding the expressions \(1/y_1\) and \(1/y_2\) in powers of \(xz\), and retaining the minimal terms containing the symbiosis coefficients, we get
\[
\begin{align*}
\frac{dx}{dt} &\approx x - x^2 + bx^3 z , \\
\frac{dz}{dt} &\approx z - z^2 + gx z^3 .
\end{align*}
\]
These equations, clearly, are very different from Eqs. \(110\).

But, maybe, the symbiosis and Lotka-Volterra equations could be equivalent for the dynamics close to stationary points, when the symbiosis equations could be reduced to polynomial forms? To check this, let us consider small deviations from fixed points \(x^*\) and \(z^*\), defined as
\[
x_1 \equiv x - x^* , \quad x_2 \equiv z - z^* .
\]
To compare with Eqs. \(110\), we need to represent Eqs. \(31\) in the polynomial form of second order with respect to the small deviations \(x_1\) and \(x_2\). This results in the following equations
\[
\begin{align*}
\frac{dx_1}{dt} &= A_{11} x_1 + A_{12} x_2 + B_{11} x_1^2 + B_{12} x_2^2 + C_{12} x_1 x_2 , \\
\frac{dx_2}{dt} &= A_{21} x_1 + A_{22} x_2 + B_{21} x_1^2 + B_{22} x_2^2 + C_{21} x_2 x_1 .
\end{align*}
\]
Again these equations are principally different from Eqs. \(110\).

Of course, if we would limit ourselves to only small deviations of first order in Eqs. \(31\) and \(110\), we would come to linear equations. All linear equations are formally similar to each other. However, the linearized forms obtained from Eqs. \(31\) and \(110\) will have absolutely different coefficients and will correspond to different fixed points, with different stability properties.

We should also mention the existence of a fundamental difference at the conceptual level. The Lotka-Volterra equations of the type \(110\) represent the dynamics of species as resulting from pairwise interactions, associated with the quadratic and bilinear terms. In contrast, the symbiosis equation \(31\) expresses the interactions through the impact of species concentrations on their carrying capacities. In principle, modeling explicitly the dynamics of the carrying capacities as genuine coupled dynamical variables provides a richer conceptual and technical approach to complex ecologies. The carrying capacities act as important relevant dynamical variables.
Therefore we have to conclude that the symbiosis and prey-predator equations are principally different and cannot be reduced to each other. They have different mathematical structure and different solutions. The mathematical difference of the suggested symbiosis model from the predator-prey models reflects the actual difference between the processes of symbiosis and predation [1-5, 47].

7.4 Examples of symbiotic types

In conclusion, we feel it is useful to return back to concrete examples of particular symbiotic relations treated in the paper. This would give the reader the feeling that the considered mathematical models are closely connected to real cases of symbiosis.

Probably, one of the best known examples of symbiosis is the mutualistic interaction between trees and fungi. Trees ability to generate large amounts of biomass or store carbon is underpinned by their interactions with soil microbes known as mycorrhizal fungi that are a crucial part of all forest ecosystems. Mycorrhizas are symbiotic relationships between certain fungi and the roots of plants. The fine fungal threads (called hyphae) either ensheathe or penetrate the host plant’s roots. The fungus helps the plant to extract nutrients and water from the soil. Fungi excel at procuring necessary, but scarce, nutrients such as phosphate and nitrogen. They also protect their hosts against harmful organisms. In return, the fungus receives sugars via the plant’s photosynthesis. The fungus within the root is protected from competition with other soil microbes and gains preferential access to carbohydrates within the plant. As with most mutualistic relationships, each partner grows better in association with the other than it would individually. For instance, birch (Betula spp.) has a number of these partnerships, the most familiar being with the red and white fly agaric (Amanita muscaria), as well as with the chanterelle (Cantharellus cibarius). Scots pine has mycorrhizal associations with over 200 species of fungi in Scotland, including another kind of chanterelle (Cantharellus lutescens). In fact, the majority of plants forests benefit from mycorrhizal relationships, and it is thought that mycorrhizas helped plants to colonize the land, millions of years ago [67].

In the frame of our approach, such a symbiotic relation is described by the carrying capacities (12). There, the carrying capacity $A_1$ is the amount of natural resources available for trees, and the carrying capacity $A_2$, the amount of natural resources of fungi. In their mutual interactions, trees and fungi produce additional resources that enlarge their carrying capacities by providing more food for each of them. Thus, $B_1 N_1 N_2$ and $B_2 N_2 N_1$ are the additional amounts of food for trees and fungi, respectively, produced in the process of their interaction.

As is explained in the Introduction, the ideas of biological symbiosis nowadays are widely used in economic relations, leading to the appearance of such terms as industrial symbiosis and economic symbiosis. For example, the relations between employers and employees can be described in the same way as symbiotic relations between some biological species [68]. The approach, known as Partner Fidelity Feedback, holds that, similarly to biological species, social symbionts have evolved to help their hosts because a healthy host automatically feeds back benefits to the symbionts. A cheating symbiont would seem to be treated like any other environmental setback, such as infertile soil, and a mutualistic symbiont elicits the same sort of investments that are triggered by the availability of new resources, like a patch of sunlight [68].

In the frame of our model, the symbiotic relations between employers and employees
should be characterized by the carrying capacities (21). Then, $A_1$ and $A_2$ are the natural carrying capacities available irrespectively of interactions. Employers provide tools to employees for producing additional capacity $B_1N_1N_2$. As a result of the growing firm or company, the employees also profit getting the increased capacity $B_2N_1$, say, in the form of increased salaries.

Another example of industrial symbiosis between different enterprises is the process of sharing of services, utility, and by-product resources among diverse industrial actors in order to add value, reduce costs, and improve the environment. Industrial symbiosis is a subset of industrial ecology, with a particular focus on material and energy exchange. Industrial ecology is a relatively new field that is based on a natural paradigm, claiming that an industrial ecosystem may behave in a similar way to the natural biological ecosystems [15]. A straightforward case is when companies collaborate to utilize each other’s by-products and otherwise share resources, enlarging by this their carrying capacities.

In our approach, this situation corresponds to the carrying capacities (26). Then the capacities $A_1$ and $A_2$ are the resources available to each of the industrial symbionts. Their additional resources come from the exchange of the companies by-products, increasing their capacities by the amounts $B_1N_2$ and $B_2N_1$, respectively. These by-products are produced by each of the companies, without direct interactions between them. And without this exchange, the by-products would be lost, while due to the exchange, they increase the carrying capacities of the symbiotic companies.

These examples illustrate that our main idea of modeling symbiotic relations by taking into account the mutual influence of symbiotic species on their carrying capacities allows us to describe various types of symbiosis for biological or social symbiotic systems.

### 7.5 Symbiosis in microbial systems

The symbiosis of microbial species is of special interest for several reasons:

- it is so much widespread in nature,
- it can be observed and studied in the laboratory, which is often impossible for other wild species,
- it can be modeled in artificial synthetic-biology games [69][70], and
- the specific features of microbial coexistence, such as resource enrichment [71][72], fluctuation enhancement [73], quorum sensing [74][75], group selection [76][77], development of cooperation [77][79], and evolutionary race [80][81], can be illuminating for understanding, characterizing, and organizing both technological as well as social systems [82].

Microbial symbiosis has been a survival feature of bacteria since their origin. The best example of this is the presence of the energy factories known as mitochondria in eukaryotic cells. Mitochondria arose because of the symbiosis between an ancient bacterium and a eukaryote. Over evolutionary time, the symbiosis became permanent, and the bacterium became part of the host. However, even to the present day, the differences in constitution and arrangement of the genetic material of mitochondria and the host cell’s nucleus attest to the symbiotic origin of mitochondria.
There are many well-known examples of bacterial mutualism. The first example is the presence of huge numbers of bacteria in the intestinal tract of warm-blooded animals such as humans [83]. About 10 percent of the dry weight of a human consists of bacteria. The bacteria act to break down foodstuffs, and so directly participate in the digestive process. As well, some of the intestinal bacteria produce products that are crucial to the health of the host. For example, in humans, some of the gut bacteria manufacture vitamin K, vitamin B12, biotin, and riboflavin. These vitamins are important to the host but are not produced by the host. The bacteria benefit by inhabiting an extremely hospitable environment. The natural activities and numbers of the bacteria also serve to protect the host from colonization by disease-causing microorganisms and to educate the host immune system. The importance of this type of symbiosis is exemplified by the adverse health effects to the host that can occur when the symbiotic balance is disturbed by antibiotic therapy.

The skin is colonized by a number of different types of bacteria, such as those from the genera Staphylococcus and Streptococcus [84]. The bacteria are exposed to a ready supply of nutrients, and their colonization of the skin helps protect that surface from colonization by less desirable microorganisms.

Bacteria themselves coexist with bacteriophages that are viruses attacking bacteria. Therefore, bacteria and virulent phages are often treated as prey and predators, respectively. Classical predator-prey systems are modeled by the Lotka-Volterra equations, whose solutions display oscillations in the populations of the competing species [85]. However, the experimental studies of bacteria-phage biology [86, 87] reveal the existence of stationary non-oscillating equilibrium states of populations and also the occurrence of extinction phenomena, when one of the species becomes completely extinct. It has therefore been necessary to modify the classical predator-prey equations for accounting for the non-oscillatory stable coexistence of bacteria and phages [88–92].

In this regard, we would like to emphasize that, in our approach, the coexisting equilibrium states, corresponding to stable fixed points, appear naturally for all three models (31), (52), and (84). Under strong parasitic relations, dynamics with death occurring in finite time are also present, characterizing the phenomenon of species extinction, as is shown in Figs. 13, 14, 15, and 17. Similar extinction of bacteria E.coli, attacked by a large population of bacteriophages T4, has been observed in experiments [87].

A detailed description of coexisting bacterial hosts and virulent phages requires to take into account the renewable environmental resources, satiation effects, the host lysis, when each infected host releases many phages, and also spatial heterogeneity. Including these processes into the consideration would need to add several more equations, essentially complicating the dynamical system, which is not the aim of our paper. Our main goal has been to suggest a new mechanism, not treated earlier, that of the mutual influence of symbionts on the carrying capacities of each other and to demonstrate that it is not less, but, probably, even more important than other known factors. Taking into account only this mutual influence makes it possible to get a rich variety of admissible types of the symbiotic behavior, including the stable coexistence of species as well as extinction of one of them, caused by parasitic relations.

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Figure Captions

Fig. 1. Region of stability (shaded) in the parameter plane \( b - g \) for the fixed points in the case of symbiosis with mutual interactions.

Fig. 2. Convergence to stationary states of the solutions \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line), as functions of time, in the case of symmetric mutual interactions, when \( x_0 > x^* \) and \( z_0 > z^* \), for different parameters \( b \) and \( g \) and initial conditions \( \{x_0, z_0\} \):
(a) \( b = -0.1, g = 1, \{0.75, 3.8\}_1, \{1, 3.8\}_2, \{2.5, 3.8\}_3 \); the fixed points being \( x^* = 0.730, z^* = 3.702 \). (b) \( b = 0.5, g = 0.01 < g_c = 0.086, \{2.5, 1.5\}_1, \{4, 1.5\}_2, \{7, 1.5\}_3 \); \( x^* = 2.043, z^* = 1.021 \). (c) \( b = -0.5, g = -0.1, \{0.8, 1\}_1, \{0.8, 1.5\}_2, \{0.8, 2.499\}_3 \); \( x^* = 0.681, z^* = 0.936 \). (d) \( b = 0.5, g = -0.1 < g_c = 0.086, \{3, 1\}_1, \{3, 3\}_2 \); \( x^* = 1.742, z^* = 0.852 \).

Fig. 3. Convergence to stationary states of the solutions \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line), as functions of time, in the case of symmetric mutual interactions, when \( x_0 > x^* \) but \( z_0 < z^* \), for different parameters \( b \) and \( g \) and initial conditions \( \{x_0, z_0\} \):
(a) \( b = 0.05, g = 0.5 < g_c = 0.603, \{4, 0.05\}_1, \{4, 0.5\}_2, \{4, 2\}_3 \); the fixed points being \( x^* = 1.130, z^* = 2.298 \). (b) \( b = 0.7, g = 0.02, \{6, 0.05\}_1, \{6, 0.5\}_2, \{6, 0.9\}_3 \); \( x^* = 4.258, z^* = 1.093 \). (c) \( b = -1, g = 0.1, \{0.45, 0.01\}_1, \{1, 0.01\}_2, \{1.5, 0.01\}_3 \); \( x^* = 0.438, z^* = 1.281 \). (d) \( b = -0.01, g = 1, \{3, 0.05\}_1, \{3, 2\}_2, \{3, 3.33\}_3 \); \( x^* = 0.730, z^* = 3.702 \).

Fig. 4. Convergence to stationary states of the solutions \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line), as functions of time, in the case of symmetric mutual interactions, when \( x_0 < x^* \) and \( z_0 < z^* \), for different parameters \( b \) and \( g \) and initial conditions \( \{x_0, z_0\} \):
(a) \( b = 0.1, g = 0.45 < g_c = 0.468, \{0.05, 2\}_1, \{0.5, 2\}_2, \{1, 2\}_3 \); the fixed points being \( x^* = 1.333, z^* = 2.5 \). (b) \( b = 0.7, g = 0.025 < g_c = 0.027, \{0.1, 0.01\}_1, \{1.4, 0.01\}_2, \{4.9, 0.01\}_3 \); \( x^* = 5, z^* = 1.143 \). (c) \( b = -1, g = 0.1, \{0.01, 0.1\}_1, \{0.2, 0.1\}_2, \{0.487, 0.1\}_3 \); \( x^* = 0.4874, z^* = 1.051 \). (d) \( b = -0.1, g = -1, \{0.01, 0.001\}_1, \{0.01, 0.3\}_2, \{0.01, 0.51\}_3 \); \( x^* = 0.951, z^* = 0.513 \).

Fig. 5. Comparison of the symbiotic solutions \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line) with the solutions \( x(t) = z(t) \) (dashed line) of the decoupled equations (40) for the same initial conditions \( x_0 = z_0 = 0.1 < 1 \), but for different symbiotic parameters \( b \) and \( g \):
(a) \( b = 0.25, g = 0.1 < g_c = 0.25 \); the stationary points of the symbiotic equations being \( x^* = 1.411, z^* = 1.164 \). (b) \( b = 2, g = -0.5 \), the fixed points of the symbiotic equations being \( x^* = 3.562, z^* = 0.360 \). (c) \( b = -1, g = 2 \), the symbiotic fixed points being \( x^* = 0.293, z^* = 2.414 \). (d) \( b = -1, g = -2 \), the symbiotic fixed points being \( x^* = 0.707, z^* = 0.414 \).

Fig. 6. Comparison of the symbiotic solutions \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line) with the solutions \( x(t) = z(t) \) (dashed line) of the decoupled equations (40) for the same initial conditions \( x_0 = z_0 = 1.8 > 1 \), but for different symbiotic parameters \( b \) and \( g \):
(a) \( b = 0.5, g = 0.080 < g_c = 0.086 \); the fixed points of the symbiotic equations being
\( x^* = 2.823, \ z^* = 1.292 \). (b) \( b = 0.5, \ g = -0.1 \), the fixed points of the symbiotic equations being \( x^* = 1.742, \ z^* = 0.852 \). (c) \( b = -0.3, \ g = 1 \), the symbiotic fixed points being \( x^* = 0.582, \ z^* = 2.393 \). (d) \( b = -0.1, \ g = -0.3 \), the symbiotic fixed points being \( x^* = 0.927, \ z^* = 0.782 \).

**Fig. 7.** Logarithmic behavior of the exponentially growing solutions \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line) for different symbiotic parameters and initial conditions: (a) \( b = 1, \ g = 0.1, \ x_0 = 148, \ z_0 = 0.135 \). (b) \( b = 0.5, \ g = 1 > \ g_c = 0.086, \ x_0 = 0.368, \ z_0 = 0.05 \). (c) \( b = 1, \ g = 0.1 > \ g_c = 0, \ x_0 = 0.135, \ z_0 = 2.72 \). (d) \( b = -1, \ g = 0.1, \ x_0 = 148, \ z_0 = 0.05 \).

**Fig. 8.** Logarithmic behavior of the solutions in the case of finite-time death and singularity, \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line), for the parasitic relations with the symbiotic coefficients \( b = -1, \ g = -2 \), under the initial conditions \( x_0 = 1.8, \ z_0 = 0.5 \). For these parameters, the critical time is \( t_c = 0.87 \).

**Fig. 9.** Region of stability (shaded) in the parameter plane \( b - g \) for the fixed points in the case of symbiosis with asymmetric interactions.

**Fig. 10.** Convergence to stationary states of the solutions \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line), as functions of time, in the case of asymmetric interactions, for the same initial conditions, such that \( x_0 > z_0 \), with \( x_0 = 1.8 \) and \( z_0 = 0.1 \), for different parameters \( b \) and \( g \): (a) \( b = 0.5, \ g = 0.1 < \ g_c = 0.125 \); the fixed points being \( x^* = 2.764, \ z^* = 1.276 \). (b) \( b = 2, \ g = -0.5 \); the fixed points being \( x^* = 1.618, \ z^* = 0.191 \). (c) \( b = -0.25, \ g = 2 \); with the fixed points \( x^* = 0.638, \ z^* = 2.275 \). (d) \( b = -0.3, \ g = -0.4 \); the fixed points being \( x^* = 0.833, \ z^* = 0.667 \).

**Fig. 11.** Convergence to stationary states of the solutions \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line), as functions of time, in the case of asymmetric interactions, for the same initial conditions, such that \( x_0 < z_0 \), with \( x_0 = 0.1 \) and \( z_0 = 1.8 \), for different parameters \( b \) and \( g \): (a) \( b = 0.5, \ g = 0.1 < \ g_c = 0.125 \); the fixed points being \( x^* = 2.764, \ z^* = 1.276 \). (b) \( b = 2, \ g = -0.5 \); the fixed points being \( x^* = 1.618, \ z^* = 0.191 \). (c) \( b = -0.25, \ g = 2 \); with the fixed points \( x^* = 0.638, \ z^* = 2.275 \). (d) \( b = -0.3, \ g = -0.4 \); the fixed points being \( x^* = 0.833, \ z^* = 0.667 \).

**Fig. 12.** Logarithmic behavior of the solutions in the case of asymmetric interactions, in the presence of the finite-time singularity, \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line), for the symbiotic coefficients \( b = 2, \ g = -1.5 \) and the initial conditions \( x_0 = 1.8, \ z_0 = 0.1 \). The critical time here is \( t_c = 4.43 \).
Fig. 13. Finite-time death in the case of asymmetric interactions. The species $x(t)$ (solid line) kill the species $z(t)$ (dashed-dotted line) at the death time $t_d$: (a) $b = -2, g = -1.5$; the initial conditions are $x_0 = z_0 = 0.1$; the death time is $t_d = 3.8$. (b) $b = 1, g = -1.5$; the initial conditions are $x_0 = 0.1, z_0 = 1.8$; the death time is $t_d = 2.6$.

Fig. 14. Finite-time death in the case of asymmetric interactions. The species $x(t)$ (solid line) kill the species $z(t)$ (dashed-dotted line) at the death time $t_d$. The symbiotic coefficients are $b = -2, g = -1.5$; the initial conditions are $x_0 = 0.1, z_0 = 6$; the death time is $t_d = 0.559$.

Fig. 15. Finite-time death in the case of asymmetric interactions. The species $z(t)$ (dashed-dotted line) kill the species $x(t)$ (solid line) at the death time $t_d$. The symbiotic coefficients are $b = -2, g = -1.5$; the initial conditions are $x_0 = 1.8, z_0 = 0.1$; the death time is $t_d = 1.016$.

Fig. 16. Region of stability (shaded) in the parameter plane $b - g$ for the fixed points in the case of symbiosis without direct interactions.

Fig. 17. Finite-time death in the case of symbiosis without direct interactions. Temporal behavior of solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line) for different symbiosis parameters and initial conditions: (a) $b = -0.75, g = -0.5, x_0 = 0.8, z_0 = 3$; the death time being $t_d = 0.204$. (b) $b = -1.5, g = 1, x_0 = 1, z_0 = 0.1$; with the death time $t_d = 2.412$. (c) $b = -1, g = -2, x_0 = 0.8, z_0 = 0.1$; with the death time $t_d = 4.279$. (d) $b = -2, g = -1, x_0 = 0.1, z_0 = 1$; the death time being $t_d = 1.459$. 
Figure 1: Region of stability (shaded) in the parameter plane $b - g$ for the fixed points in the case of symbiosis with mutual interactions.

$$g_c = |\sqrt{b} - 1|^2$$
Figure 2: Convergence to stationary states of the solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line), as functions of time, in the case of symmetric mutual interactions, when $x_0 > x^*$ and $z_0 > z^*$, for different parameters $b$ and $g$ and initial conditions $\{x_0, z_0\}$: (a) $b = -0.1$, $g = 1$, $\{0.75, 3.8\}_1$, $\{1, 3.8\}_2$, $\{2.5, 3.8\}_3$; the fixed points being $x^* = 0.730$, $z^* = 3.702$. (b) $b = 0.5$, $g = 0.01 < g_c = 0.086$, $\{2.5, 1.5\}_1$, $\{4, 1.5\}_2$, $\{7, 1.5\}_3$; $x^* = 2.043$, $z^* = 1.021$. (c) $b = -0.5$, $g = -0.1$, $\{0.8, 1\}_1$, $\{0.8, 1.5\}_2$, $\{0.8, 2.499\}_3$, $x^* = 0.681$, $z^* = 0.936$. (d) $b = 0.5$, $g = -0.1 < g_c = 0.086$, $\{3, 1\}_1$, $\{3, 3\}_2$, $x^* = 1.742$, $z^* = 0.852$. 
Figure 3: Convergence to stationary states of the solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line), as functions of time, in the case of symmetric mutual interactions, when $x_0 > x^*$ but $z_0 < z^*$, for different parameters $b$ and $g$ and initial conditions $\{x_0, z_0\}$: (a) $b = 0.05$, $g = 0.5 < g_c = 0.603$, $\{4, 0.05\}_1$, $\{4, 0.5\}_2$, $\{4, 2\}_3$; the fixed points being $x^* = 1.130$, $z^* = 2.298$. (b) $b = 0.7$, $g = 0.02$, $\{6, 0.05\}_1$, $\{6, 0.5\}_2$, $\{6, 0.9\}_3$; $x^* = 4.258$, $z^* = 1.093$. (c) $b = -1$, $g = 0.1$, $\{0.45, 0.01\}_1$, $\{1, 0.01\}_2$, $\{1.5, 0.01\}_3$, $x^* = 0.438$, $z^* = 1.281$. (d) $b = -0.01$, $g = 1$, $\{3, 0.05\}_1$, $\{3, 2\}_2$, $\{3, 3.33\}_3$, $x^* = 0.730$, $z^* = 3.702$. 
Figure 4: Convergence to stationary states of the solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line), as functions of time, in the case of symmetric mutual interactions, when $x_0 < x^*$ and $z_0 < z^*$, for different parameters $b$ and $g$ and initial conditions $\{x_0, z_0\}$: (a) $b = 0.1$, $g = 0.45 < g_c = 0.468$, $\{0.05, 2\}_1$, $\{0.5, 2\}_2$, $\{1.1, 2\}_3$; the fixed points being $x^* = 1.333$, $z^* = 2.5$. (b) $b = 0.7$, $g = 0.025 < g_c = 0.027$, $\{0.1, 0.01\}_1$, $\{1.4, 0.01\}_2$, $\{4.9, 0.01\}_3$; $x^* = 5$, $z^* = 1.143$. (c) $b = -1$, $g = 0.1$, $\{0.01, 0.1\}_1$, $\{0.2, 0.1\}_2$, $\{0.487, 0.1\}_3$, $x^* = 0.4874$, $z^* = 1.051$. (d) $b = -0.1$, $g = -1$, $\{0.01, 0.001\}_1$, $\{0.01, 0.3\}_2$, $\{0.01, 0.51\}_3$, $x^* = 0.951$, $z^* = 0.513$. 
Figure 5: Comparison of the symbiotic solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line) with the solutions $x(t) = z(t)$ (dashed line) of the decoupled equations (40) for the same initial conditions $x_0 = z_0 = 0.1 < 1$, but for different symbiotic parameters $b$ and $g$: (a) $b = 0.25$, $g = 0.1 < g_c = 0.25$; the stationary points of the symbiotic equations being $x^* = 1.411$, $z^* = 1.164$. (b) $b = 2$, $g = -0.5$, the fixed points of the symbiotic equations being $x^* = 3.562$, $z^* = 0.360$. (c) $b = -1$, $g = 2$, the symbiotic fixed points being $x^* = 0.293$, $z^* = 2.414$. (d) $b = -1$, $g = -2$, the symbiotic fixed points being $x^* = 0.707$, $z^* = 0.414$. 
Figure 6: Comparison of the symbiotic solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line) with the solutions $x(t) = z(t)$ (dashed line) of the decoupled equations (40) for the same initial conditions $x_0 = z_0 = 1.8 > 1$, but for different symbiotic parameters $b$ and $g$: (a) $b = 0.5, g = 0.080 < g_c = 0.086$; the fixed points of the symbiotic equations being $x^* = 2.823, z^* = 1.292$. (b) $b = 0.5, g = -0.1$, the fixed points of the symbiotic equations being $x^* = 1.742, z^* = 0.852$. (c) $b = -0.3, g = 1$, the symbiotic fixed points being $x^* = 0.582, z^* = 2.393$. (d) $b = -0.1, g = -0.3$, the symbiotic fixed points being $x^* = 0.927, z^* = 0.782$. 
Figure 7: Logarithmic behavior of the exponentially growing solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line) for different symbiotic parameters and initial conditions: (a) $b = 1$, $g = 0.1$, $x_0 = 148$, $z_0 = 0.135$. (b) $b = 0.5$, $g = 1 > g_c = 0.086$, $x_0 = 0.368$, $z_0 = 0.05$. (c) $b = 1$, $g = 0.1 > g_c = 0$, $x_0 = 0.135$, $z_0 = 2.72$. (d) $b = -1$, $g = 0.1$, $x_0 = 148$, $z_0 = 0.05$. 
Figure 8: Logarithmic behavior of the solutions in the case of finite-time death and singularity, \( x(t) \) (solid line) and \( z(t) \) (dashed-dotted line), for the parasitic relations with the symbiotic coefficients \( b = -1 \), \( g = -2 \), under the initial conditions \( x_0 = 1.8 \), \( z_0 = 0.5 \). For these parameters, the critical time is \( t_c = 0.87 \).
Figure 9: Region of stability (shaded) in the parameter plane $b - g$ for the fixed points in the case of symbiosis with asymmetric interactions.
Figure 10: Convergence to stationary states of the solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line), as functions of time, in the case of asymmetric interactions, for the same initial conditions, such that $x_0 > z_0$, with $x_0 = 1.8$ and $z_0 = 0.1$, for different parameters $b$ and $g$: (a) $b = 0.5$, $g = 0.1 < g_c = 0.125$; the fixed points being $x^* = 2.764$, $z^* = 1.276$. (b) $b = 2$, $g = -0.5$; the fixed points being $x^* = 1.618$, $z^* = 0.191$. (c) $b = -0.25$, $g = 2$; with the fixed points $x^* = 0.638$, $z^* = 2.275$. (d) $b = -0.3$, $g = -0.4$; the fixed points being $x^* = 0.833$, $z^* = 0.667$.  

Figure 11: Convergence to stationary states of the solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line), as functions of time, in the case of asymmetric interactions, for the same initial conditions, such that $x_0 < z_0$, with $x_0 = 0.1$ and $z_0 = 1.8$, for different parameters $b$ and $g$: (a) $b = 0.5$, $g = 0.1 < g_c = 0.125$; the fixed points being $x^* = 2.764$, $z^* = 1.276$. (b) $b = 2$, $g = -0.5$; the fixed points being $x^* = 1.618$, $z^* = 0.191$. (c) $b = -0.25$, $g = 2$; with the fixed points $x^* = 0.638$, $z^* = 2.275$. (d) $b = -0.3$, $g = -0.4$; the fixed points being $x^* = 0.833$, $z^* = 0.667$. 
Figure 12: Logarithmic behavior of the solutions in the case of asymmetric interactions, in the presence of the finite-time singularity, $x(t)$ (solid line) and $z(t)$ (dashed-dotted line), for the symbiotic coefficients $b = 2$, $g = -1.5$ and the initial conditions $x_0 = 1.8$, $z_0 = 0.1$. The critical time here is $t_c = 4.43$. 
Figure 13: Finite-time death in the case of asymmetric interactions. The species $x(t)$ (solid line) kill the species $z(t)$ (dashed-dotted line) at the death time $t_d$: (a) $b = -2, g = -1.5$; the initial conditions are $x_0 = z_0 = 0.1$; the death time is $t_d = 3.8$. (b) $b = 1, g = -1.5$; the initial conditions are $x_0 = 0.1, z_0 = 1.8$; the death time is $t_d = 2.6$. 
Figure 14: Finite-time death in the case of asymmetric interactions. The species $x(t)$ (solid line) kill the species $z(t)$ (dashed-dotted line) at the death time $t_d$. The symbiotic coefficients are $b = -2$, $g = -1.5$; the initial conditions are $x_0 = 0.1$, $z_0 = 6$; the death time is $t_d = 0.559$. 
Figure 15: Finite-time death in the case of asymmetric interactions. The species $z(t)$ (dashed-dotted line) kill the species $x(t)$ (solid line) at the death time $t_d$. The symbiotic coefficients are $b = -2$, $g = -1.5$; the initial conditions are $x_0 = 1.8$, $z_0 = 0.1$; the death time is $t_d = 1.016$. 
Figure 16: Region of stability (shaded) in the parameter plane $b - g$ for the fixed points in the case of symbiosis without direct interactions.
Figure 17: Finite-time death in the case of symbiosis without direct interactions. Temporal behavior of solutions $x(t)$ (solid line) and $z(t)$ (dashed-dotted line) for different symbiosis parameters and initial conditions: (a) $b = -0.75$, $g = -0.5$, $x_0 = 0.8$, $z_0 = 3$; the death time being $t_d = 0.204$. (b) $b = -1.5$, $g = 1$, $x_0 = 1$, $z_0 = 0.1$; with the death time $t_d = 2.412$. (c) $b = -1$, $g = -2$, $x_0 = 0.8$, $z_0 = 0.1$; with the death time $t_d = 4.279$. (d) $b = -2$, $g = -1$, $x_0 = 0.1$, $z_0 = 1$; the death time being $t_d = 1.459$. 