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A Liebig's Principle of Limiting Factors based Single-Species Population Growth Model I: Qualitative Study of Trajectories and Fitting Results

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Abstract

Index terms—

1 I. INTRODUCTION

The optimal settings for biological processes often occur at the minimum and maximum values of relevant variables (Ghaleb et al., 2020;Peeters & Gardeniers, 1998). The concept of extreme value control ascended from results reported by K. Sprengel in 1839 (Sprengel, 1839; El-Sharkawy, 2011) and later popularised by Justus von Liebig, stating that the nutrient present in the minimum determines the rate of growth of a particular organism (Liebig, 1843). This observation led to the establishment of Liebig's Principle of Limiting Factors, also known as Liebig's Law of the Minimum (Rizhinashvili, 2022;Anees, 2022). Agents that slow down growth in an ecosystem constitute limiting factors. Control exerts by either the minimum or maximum values that the factor can assume over a gradient of variation. Based on lower and upper tolerance limits, Liebig's Law of the Minimum was generalised into the Law of the Tolerance of London Journal of Research in Science: Natural and Formal

2 II. THEORETICAL APPROACH

For present aims, we denote through a quantitative measure of the size of a single-species ?(?) population at a time . It could be understood by , for example, the biomass of all animals composing the population, or their number, if it is suitably large and changes continuously. We additionally assume that the maintenance of the population depends on the presence of an external resource or agent whose extent at time denotes using For instance, could ? ?(?). ?(?) a ?(?) ? London Journal of Research in Science: Natural and Formal stand for: the food solution for a culture of bacteria; the amount of solar energy with which the primary producers photosynthetically elaborate carbohydrates; the biomass of autotrophs upon which herbivores fed or the biomass of these later that provide nourishment for carnivores; the pool of antibiotics that limit the proliferation of a bacterial population; the number of nests available for a bird species.

We now explain how Liebig's Law of the Minimum statement can produce a population growth model under a limiting resource. For that aim, we use the symbol to denote the natural ? ?? ( ) growth rate of population size at a time . Formally, the proposed model states that ? ? ( ) ?

where at time stands for the amount of a resource that the population requires to stand by, ?(?) ? and is a function depending on both and and represents the intrinsic ð ??"(? ? ( ), ?(?)) ? ? ( ) ? ? ( ) population growth rate at a time .Along Equation (1), we take on the initial conditions ? ? 0 = ? 0 ( ) and ? 0 = ? 0 ( ).

Following Charlebois and Balázsi (2018) and Echavarria-Heras et al. (**??**021), we assume that the natural population growth rate and resource consumption relate such that (2) where is a positive constant. Integration yields ?

In order to provide a representation of Equation (1)

The minimum operation extends to all values of considered in a specific interval, say of the ? type , where can be any real number. [0, ?] ? ?( ) = ( ), ( ) ( ) ( ) = - ( ) ( ) = -(( ) -) ( ) = min { ( ), ( )}

Combining Equations (4) through (6) the intrinsic population growth rate ð ??" ? ? ( ), ? ? ( ) ( ) introduced in Equation (1), takes the form, Therefore, Equation (1) gets the piece wisely defined form (8) Moreover, replacing as given by Equation (3) into Equation (**??**) and simplifying leads to ?(?) (9) where (10) and (11) Note that the expressions of the second member of (**??**) are continuous functions by virtue that we can suppose that as much as are continuous functions of time.The first of the ?(?) ?(?) differential equations of (**??**) is a homogeneous linear equation whose solution is immediate, and the second of these equations is a non-homogeneous linear equation which using an integration factor or via the parameter variation method, can also be solved. Then, the solution to ?(?) Equation (**??**) will be (12) where (13) and (14) with and given by Equations (10) and (11) ? ? ( ) = ( ) ?( ) = ( ) -( ) ( ), ( ) = (( ), ( )) ( ) - ? ?( ) = (-) ( ) ( ) ? ( ) ( ) -( ) ( ) > ( ) ?( ) = (-) ( ) ( ) ? (+)(-( )) ( ) > = (+) (1 +) ? = (+ 1)(+) ( ) = ( ) ( ) ? ( ) ( ) > ( ) = ( ) ( ) = ( ) + (1 -( ))

such that Note also that according to equations (**??**) and (**??**2

where, as we have specified around Equation (14), and are integration constants to be ? The stationary characterisation of Equation (**??**2) provides a resource availability model for ? ? ? ( ) autotrophic organisms, including photosynthetic bacteria, algae, and plants, that rely on a consistent energy source to withstand their growth and population sustainability. These organisms possess the ability to produce their food through photosynthesis, which entails the transformation of sunlight into chemical energy. As long as there is a stable availability of sunlight, the autotrophic population can thrive and grow. Another instance of a population dependent on a steady energy source is a group of chemosynthetic organisms inhabiting environments with a continuous supply of chemical compounds, such as sulfur or methane. They can generate sustenance using the energy derived from these compounds to support growth and reproduction. In addition, certain heterotrophic populations, such as specific kinds of fungi, can subsist and multiply on a steady energy supply sourced from decomposing organic matter given a constant supply.

The logistic model proposed initially by Verhulst (1838) as a way of modelling population growth under limited availability of resources formally represents employing the differential Equation (19) = (-) ( ) ( ) ? - ( ) ( ) > ( ) = ( ) ( ) ? ( ) ( ) > ( ) = ( ) ( ) = + (1 -) ?( ) = ( )(1 -( )) ? London Journal of

3 III. RESULTS

4 Qualitative study of the global trajectory ? ? ( )

As shown in the appendix, if we have that , then for , the global trajectory? -? < 0 ? 0 ? ? ?(?)

acquires the form given by Equation (**??**3 Consider now the order. Then, we will also have . Then, for , at the beginning of ? > ? ? > ? ? 0 ?? the growth process, population size will describe according to the exponentially increasing path . Furthermore, since by continuity, there will be a time such that ?1 (?) ? 0 ?? ? ? ? 1 ? ? ( ) = ?.

Afterwards, the dynamics will switch to being modelled by the stem. Therefore, as the ?(?) ? 2 ? ( ) asymptotically approaches the threshold (Figure **??**). ?appendix

5 Fitting Results

In what follows, we explain the performance of LLPM, Liebig's law population model of Equation (**??**), as an exploratory tool given different data sets. We address data on yeast grown under ideal conditions in a test tube and the growth of a harbour seal population, both reported by Avissar et al. **??**2013). We also consider data reported by R. Pearl on the growth of Drosophila melanogaster (Pearl, 1927) stands for CCC value linking to the LLPM of Equation (**??**), denotes CCC produced by a fit of ? ???? ? ??? the logistic model of Equation (19).

We first considered data on yeast growing under ideal conditions in a test tube portrayed in (2013) do not refer to whatever energy source the yeast population depended on, but in any event, the shape of the fitted form of suggests that independently of bulk consumption, the ?(?) yeast population and its feeding resource stabilised one to one. **??**), to the yeast growth data adapted from Panel (a) (blue lines). Panel (c) also shows the shape of the fitted form of the resource abatement function as given by ?(?) Equation (3) (red lines). that the steady form of the LLPM given by Equation (**??**5) also fits consistently. This fact explains by the small fitted value for the parameter Moreover, Panel (d) displays a close-up look at the ?.

variation of corroborating that this function remained close to its initial value ?(?), independently of consumption by the seal population. of the minimum-driven model of Equation (**??**) to the available seal population growth data-panel (d) variation of the fitted resource availability function .

6 ?(?)

Correspondingly, Figure 6a presents the spread of data reported by R. Pearl on the growth of Drosophila melanogaster (Pearl, 1927) about the logistic curve fitted by the model of Equation (19). Fitted parameter values were , , and with Concordance ? = 6. 19 ? = 329. 7 ? 0 = 0. 2194 Correlation Coefficient at a value of . Figure 6b shows the spread of captured ? = 99. 43 Drosophila melanogaster data about the trajectory produced by a fit of LLPM, Liebig's law of the minimum-based model of Equation (9). Fitted parameters values were , ? = 0. 4956 ? = 0. 3616 , , , , which through Equations (**??**0) and (**??**1

7 IV. DISCUSSION

In cellular structures such as mitochondria, the maxima or minima of a periodical chemical reaction proved to be determinants of observable patterns (Woodcock, 1978). In other processes, for instance, catalysis, limiting values of variables such as pH and temperature can cause enzymes to lose their functionality, thereby impairing the easing of essential chemical reactions within living organisms (Dyson & Noltmann, 1968). Besides, the maximum and minimum blood glucose levels, body temperature, or pH range are critical for maintaining homeostasis (Yildiz et al., 2020). Furthermore, maximum and minimum values can activate regulatory mechanisms in biological systems that help organisms deal with and adapt to challenging environmental conditions. Within these response mechanisms, we can include activation of heat shock proteins that shield cells from harm given extreme values of temperature or water conservation mechanisms in plants in response to extreme osmotic conditions (Bich et al., 2016;Sharp et al., 1999;Chaves & Oliveira, 2004). Another example of extreme value control of a biological process is the existence of a minimum light intensity needed for efficient photosynthesis in plants (Boardman, 1977;Madsen & Sand-Jensen, 1994). What is more, in this vein, it is worth mentioning that extreme levels of light intensity or CO2 concentrations can restrict the effectiveness of photosynthesis and, as a result, hamper the capability of plants to create energy (Jolliffe & Tregunna, 1968). Therefore, from a general perspective, comprehending the upper and lower limits of biologically relevant variables delivers an understanding of organisms' underlying limits, adaptive responses, and constraints.

In ecological settings, extreme values are often more descriptive of relevant dynamics than standard measures of central tendency (Gaines & Denny, 1993;Montiel et al., 2004). Issues relating to physical stress, such as high or low temperatures, salinity, soil water content, wind velocities, and varying durations of air exposure, serve as examples (Denny & Deines, 1990). Moreover, characterising extreme values not only aids in defining the optimal operational boundaries for ecological processes and contributes to our interpretation of the correlation between organisms and their environment (Ruthsatz, Dausmann, and Peck, 2022). For instance, species interaction dynamics and community formation depend on the maximum and minimum values of different variables (Checa et al., 2014). Furthermore, the availability of particular resources can limit the distribution of species or the sizes of their populations (Wright, 1983), while the sizes of predator populations below or above given edges can impact the distribution and behaviour of prey species (Schneider, 2001). Also, from an ecological perspective, acknowledging the relevance of maximum and minimum values of pertinent variables contributed to conceiving the concept of tolerance bounds (Niinemets & Valladares, 2008;Pörtner, 2001;Goss & Bunting, 1976). For example, the minimum oxygen concentration required for aquatic organisms' survival sets their tolerance lower limit (Seibel, 2011;Gaufin et al., 1974). Likewise, the maximum temperature at which an organism can survive or reproduce entails its thermal tolerance upper limit (Madeira et al., 2012;Buckley & Huey, 2016). Ecological niches, characterised by certain variables' upper and lower limits, determine a species' optimal environmental conditions (Galparsoro et al., 2009). Therefore, including maximum and minimum thresholds for factors such as temperature, moisture, or nutrient availability helps to understand how organisms distribute and their ecological requirements (Kearney, 2006) (Hutchinson, 1957;Hutchinson, 1978;Polechová & Storch, 2008).

In summarising the passage above, it is worth emphasising that to understand better the underlying limits, changes, and necessities of living organisms; it is essential to determine the upper and lower limits that set the intervals of influence of their determining physical and biological variables. This understanding of suitable extreme values assists in setting the boundaries that biological processes must function within, leading to a better comprehension of how organisms work in conjunction with their surroundings to function efficiently. Notwithstanding, when referring to conceiving constructs aimed to model population dynamics, besides a reduced number of papers (e.g. Polyetayev, 1971 Law by the minimum between the size of the population and that of its feeding resource, ?(?) at a time t, (2) the accompanying natural mortality rate is supposed to be proportional ?(?), solely to population size, and (3) the rate of consumption of the external feeding resource ostensibly varies directly proportional to the natural growth rate of the population. Despite being partially founded on the assumption that mortality depends linearly on population size, the qualitative exploration of the behaviour of the global trajectory associated with the offered LLPM demonstrated a proven capability to mimic the typical s-shaped pattern associated with restricted growth models. The presented fitting results confer the LLPM of excellent reproducibility features and reveal that such a paradigm offers a remarkable interpretative strength. Firstly, the LLPM could identify the suggested form for the resource abatement function on the fly, entailing a feature that the typical logistic growth model of Equation ?(?) (19) lacks. Secondly, also compared to the presently addressed logistic model, the LLPM offers a consistent way to identify a declining pace in population size leading to extinction which the latter model could not suitably achieve. Besides, simplifying complexity has been proven advantageous in finding parameter estimates for consistent reproducibility of real data sets.

London Journal of Research in Science: Natural and Formal Nevertheless, performing research on further simplifying the nonlinear parameter estimation tasks deems necessary.

8 V. APPENDIX. ANALYTICAL APPROACH

9 Continuity property of the global trajectory ?(?)

Equation (**??**2) states that the global trajectory , associating to the piecewise-defined ODE ? ? ( )

given by Equation (**??**), expresses such that (A1) where agreeing to Equations (**??**0) and (**??**1 towards zero (see Figure **??**1b).

We can summarise what we have explored so far by stating that maintenance of the condition implies the disappearance of the population, regardless of its initial value (also ? < ? ? 0 regardless of whether this value is greater or equal or less than). ? [1] [2] [3] [4] [5] [6] [7] [8]

45

Figure 1: Figure 45 .

4

Figure 2: Figure 4 :

[1] A Liebigs Principle of Limiting Factors based Single-Species Population Growth Model I: Qualitative Study of Trajectories and Fitting Results

[2] Volume 23 | Issue 9 | Compilation 1.0 © 2023 Great Britain Journal Press A Liebigs Principle of Limiting Factors based Single-Species Population Growth Model I: Qualitative Study of Trajectories and Fitting Results

[3] ©

[4] ©

[5] ©

[6] ©

[7] Volume 23 | Issue 9 | Compilation 1.0 © 2023 Great Britain Journal Press

[8] ©

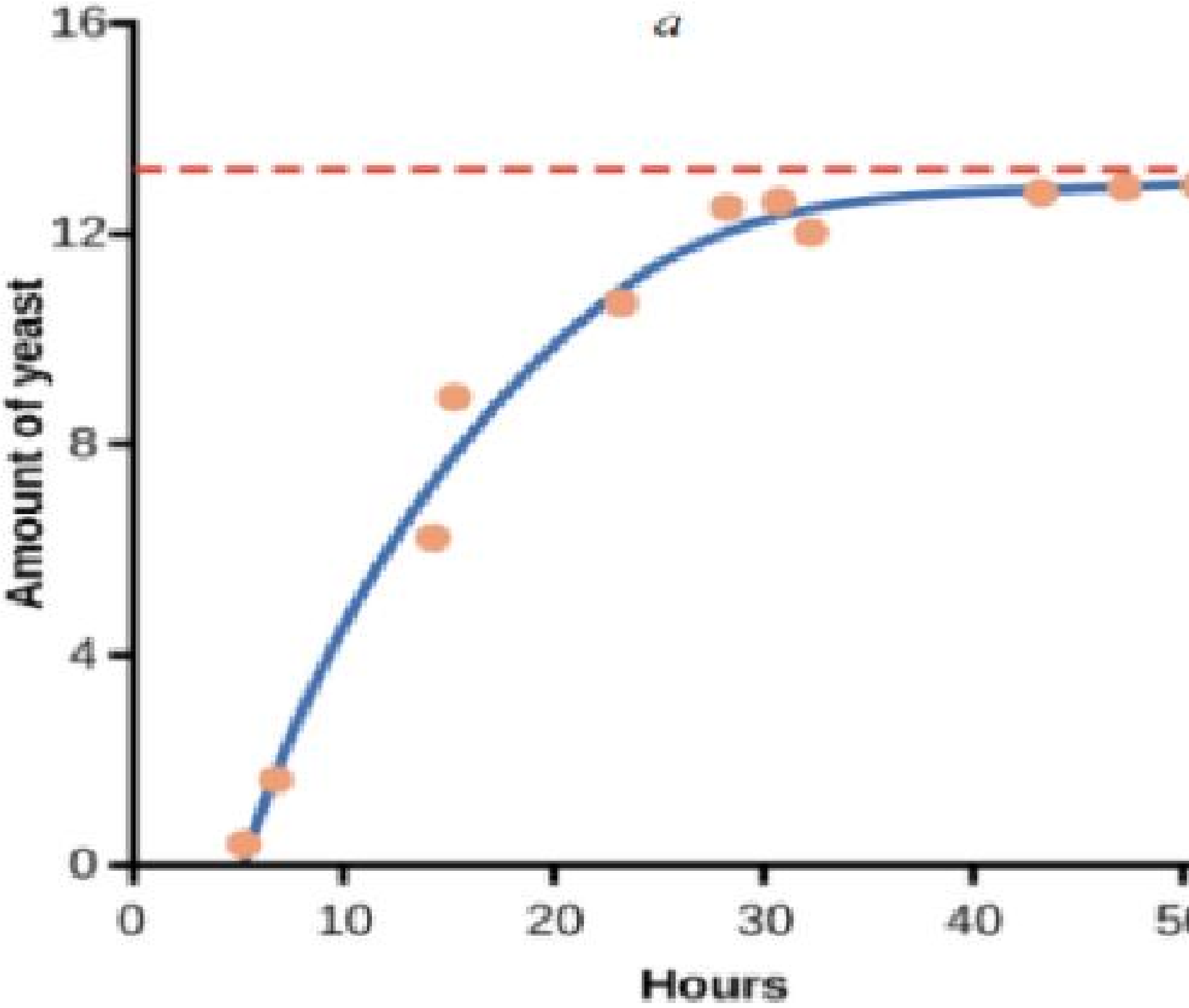
Figure 3: Figure

Figure 4:

5

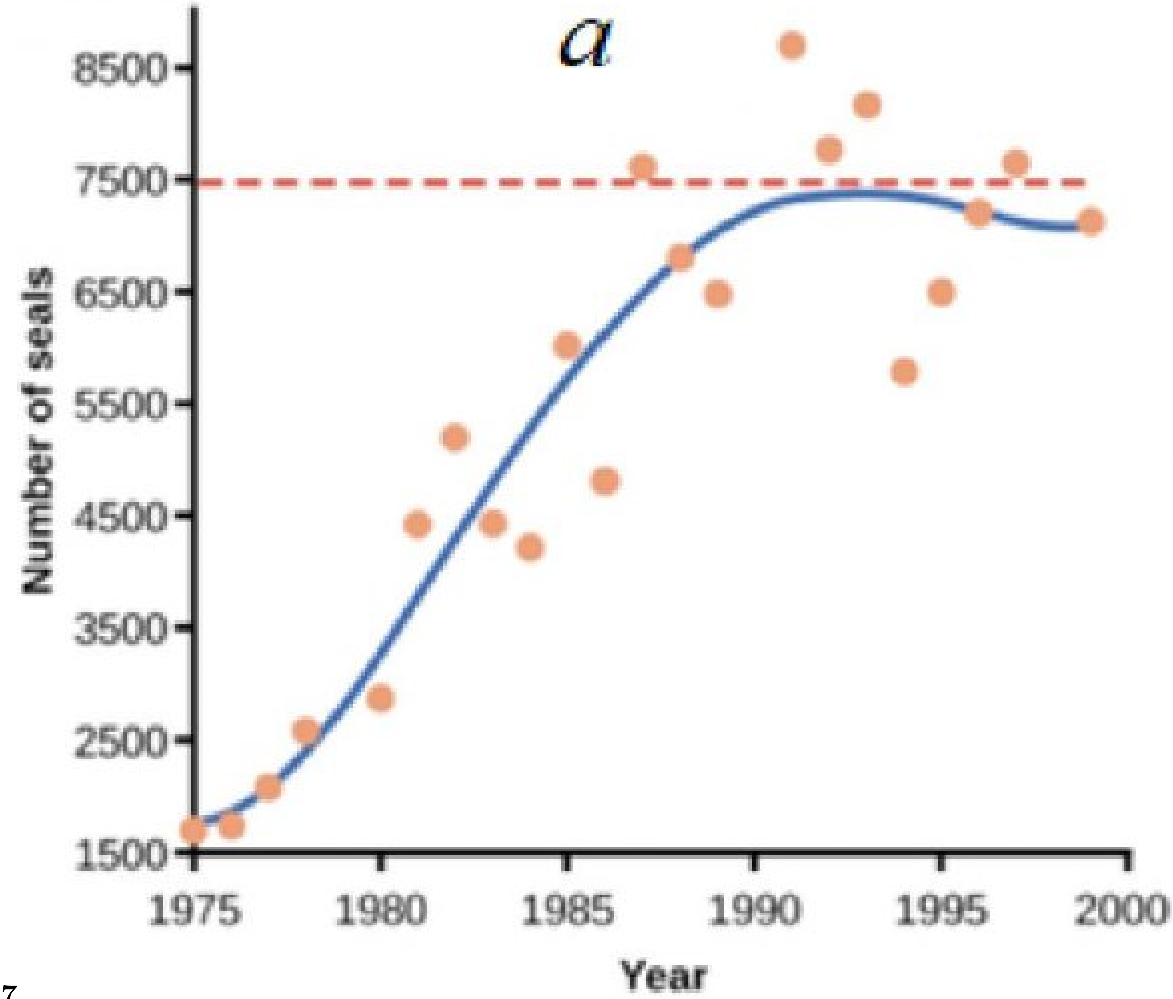
Figure 5: Figure 5 :

Figure 6:



6

Figure 7: Figure 6 :



7

Figure 8: Figure 7 :

1513 $R(t)$

Figure 9: 15 13 ©

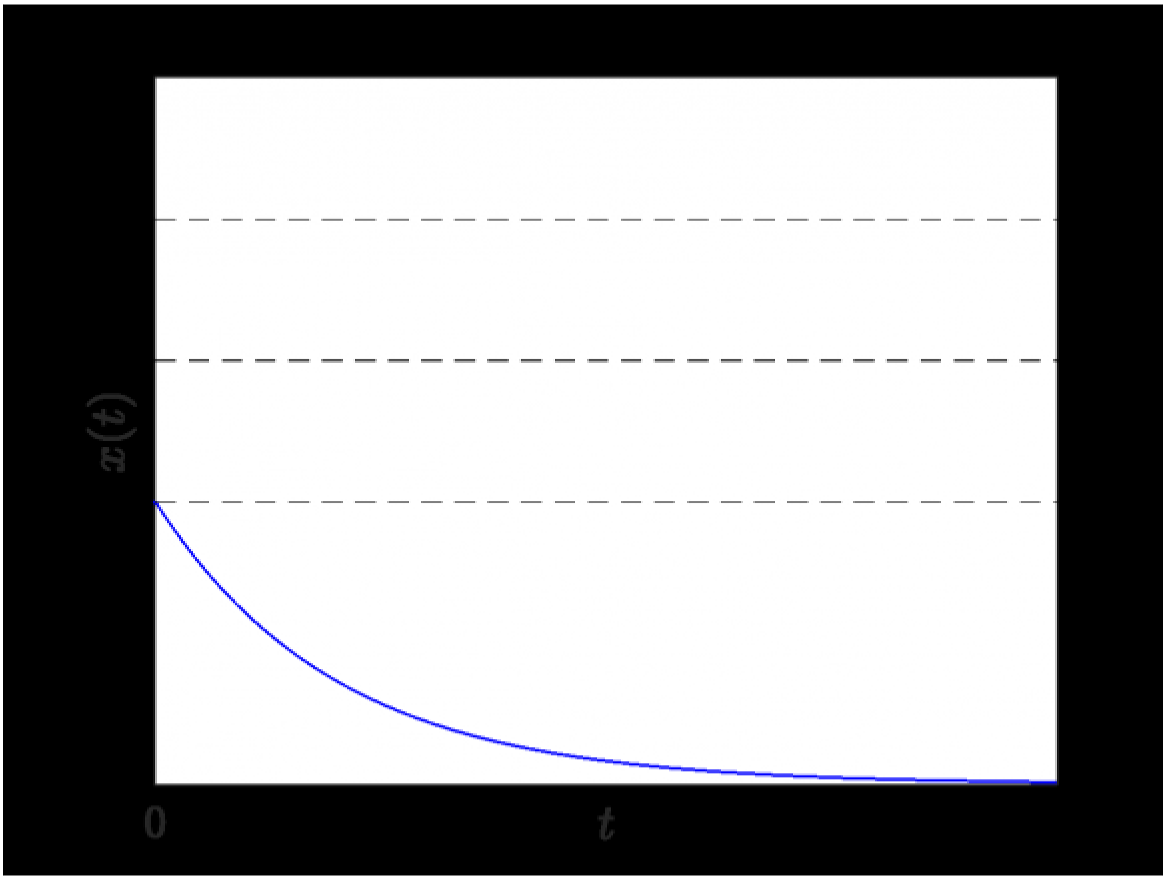


Figure 10:

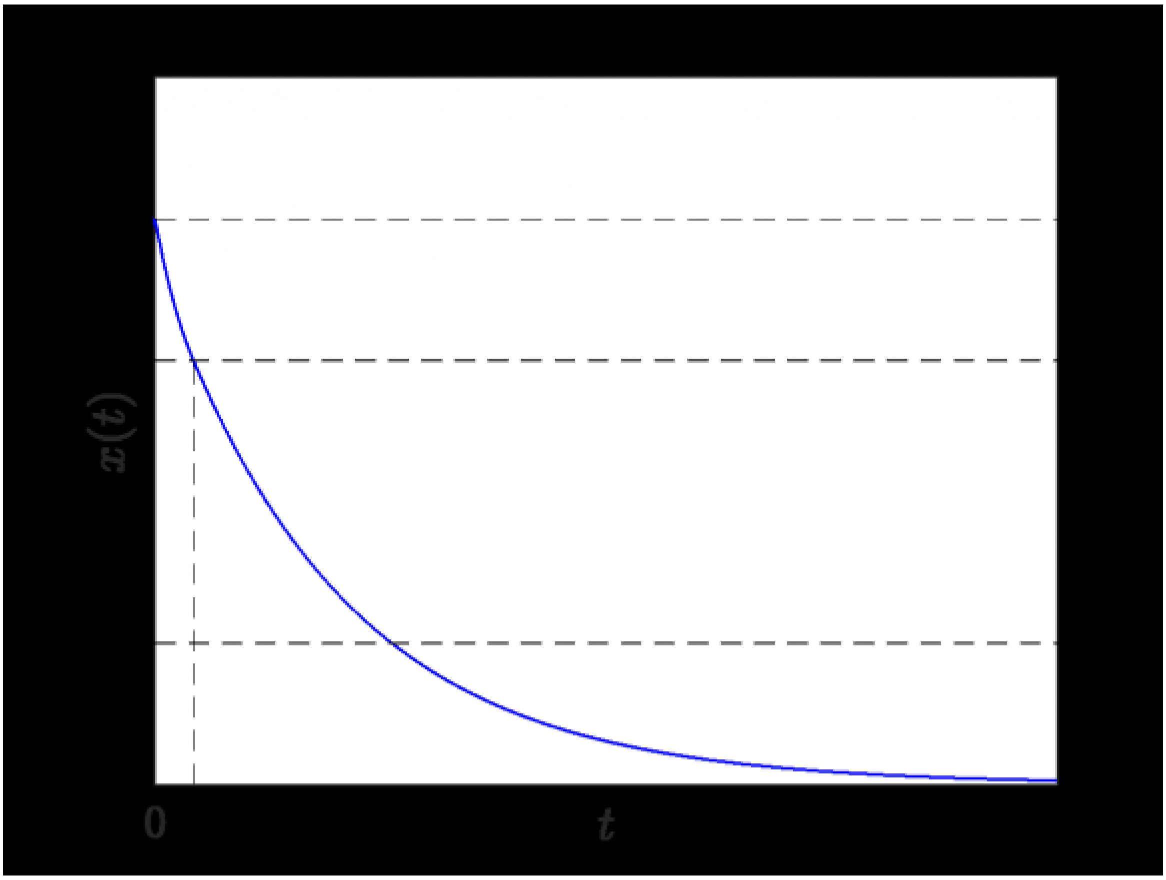


Figure 11: Figure

Figure 12:

Data set	x o	a	b	E	? 0	?	?	?????	????
Yeast	1.1	0.2549	0.0452	5.7925	8.1388	12.827	0.5	99.23%	98.19%
Seal	1634.24	0.3142	0.1748	4345.66	4350	7801	0.0016	92.97%	86.91%
Fruit fly	13.0039	0.4956	0.3616	235	279.39	303.31	0.2	99.43%	99.43%
Coral	142.62	0.1070	0.2565	376.49	376.871	157.20	0.0016	91.43%	88.99%

Figure 13:

1

? 0 and , as well as ? 0

Figure 14: Table 1 :

Figure 15:

Figure 16:

Therefore, the ? 2 ? ( ) path bears a horizontal asymptote ?. Note also that because

inequality (A11), we also have ? < ?. Therefore, the limiting value of ? 2 ? ( ) whenever

below . Then, necessarily the ? ? 2 ? ( ) trajectory keeps on decreasing until it reaches the value , ?

that is, there exists a time value ? = ? ? as given by Equation (A7) such that ? 2 ? ? ( ) = ?

that, the dynamics of ? ? ( ) will set by ? 1 ? ( ), that according to Equation (A1) bears a form

Then, choosing

adds the continuity condition , as much as setting ( ) = ? ? 1 ? ? ?(?) to decrease asymptotically

Figure 17:

.1 ACKNOWLEDGEMENTS

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hand, from Equation (A6), we also have that shall be decreasing and asymptotically approaching as progresses to infinity (Figure **??**3b).

.2 ? ?

In short, the case entitles a heterogeneous behaviour because if the magnitude of the ? = ? asymptotically approaches the threshold. ?

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