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Revista de Modelamiento Matemático de Sistemas Biológicos

Grupo MatBio-UTEM Departamento de Matemática Facultad de Ciencias Naturales, Matemática y Medio Ambiente





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Editorial



El modelamiento matemático, como herramienta relevante en la comprensión de la realidad, juega un rol clave en el avance del conocimiento científico de los sistemas naturales y sociales. La creciente complejidad de los fenómenos abordados requiere niveles, cada vez mayores, de colaboración e interdisciplina. El gran universo que representa la biología, en sus múltiples facetas, es un claro ejemplo del fructífero diálogo entre matemática y ciencias naturales. Las últimas décadas han visto acrecentar el interés de los matemáticos en problemáticas biológicas y, asimismo, de los biólogos en entender y aplicar herramientas matemáticas sofisticadas en sus propios estudios. Nuestra región latinoamericana no es la excepción, y una importante comunidad de biomatemáticos se da cita regularmente en los múltiples eventos organizados en los países del continente.

En este contexto el Grupo de Investigación MatBio-UTEM, perteneciente al Departamento de Matemática de la Universidad Tecnológica Metropolitana, de Santiago de Chile, ha ido recorriendo un camino como polo de investigación, formación y difusión de la biomatemática. La revista, que se inaugura con este número, es parte de este proceso con un fuerte sentido colaborativo, interdisciplinar y regional. Esperamos que la Revista de Modelamiento Matemático de Sistemas Biológicos –MMSB– sea una vitrina y punto de encuentro que ayude a fortalecer más aún estos lazos. Aspiramos a que MMSB se transforme en un refrente para los científicos, de cualquier país, interesados en la relación entre matemática y biología. Esta propuesta editorial tiene un férreo compromiso con la circulación abierta y democrática del conocimiento. Creemos que la producción científica debe ser patrimonio de la humanidad, donde todos y todas tengan acceso libre a los avances de la ciencia.

Esta incitativa es el fruto del esfuerzo desinteresado de un gran número de personas que han colaborado en su concreción; el grupo de investigadores de MatBio-UTEM, los integrantes del Comité Editorial, con presencia de colegas de diversas universidades de Chile y América Latina, los autores que tan generosamente nos han regalado sus artículos para este primer número y el equipo de profesionales de Ediciones UTEM que han dado el soporte técnico y logístico para la puesta en marcha de MMSB; a todos, mis mayores agradecimientos.

> Dr. Ricardo Castro Santis Editor Jefe Modelamiento Matemático de Sistemas Biológicos

Editorial

Mathematical modeling, as a relevant tool in understanding reality, plays a key role in advancing scientific knowledge of natural and social systems. The increasing complexity of the phenomena addressed requires ever-increasing levels of collaboration and interdiscipline. The grand universe that biology represents, in its many facets, is a clear example of the meaninful dialogue between mathematics and natural sciences. In the last decades the interest of mathematicians in biological problems has increased and similarly, of biologists in understanding and applying sophisticated mathematical tools in their own studies. Our Latin American region is no exception, and an important community of biomathematicians regularly attends the many events organized in the countries of the continent.

In this context, the MatBio-UTEM Research Group, belonging to the Department of Mathematics of the Metropolitan Technological University of Santiago de Chile, has been opening an important path as a training, dissemination and research biomathematics center. The journal, which opens with this issue, is part of this process with a strong collaborative, interdisciplinary and regional sense. We hope that the Journal of Mathematical Modeling of Biological Systems –MMSB– will be a showcase and meeting point that will help to further strengthen these ties. We hope for MMSB to become a benchmark for scientists, from any country, interested in the relationship between mathematics and biology.

This editorial proposal has a strong commitment to the open and democratic circulation of knowledge. We believe that scientific production should be the heritage of humanity, where everyone has free access to the advances of science. This initiative is the result of the selfless effort of a large number of people who have collaborated in its realization; the group of researchers from MatBio-UTEM, the members of the Editorial Committee, with the presence of colleagues from various universities in Chile and Latin America, the authors who have so generously given us their articles for this first issue, and the team of professionals from Ediciones UTEM who have provided technical and logistical support for the start-up of MMSB; to all, my sincere gratitude.

> **Ph.D. Ricardo Castro Santis** Editor in chief Mathematical Modeling of Biological Systems

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An Inverse Problem in the Mathematical Modelling of our Sense of Smell

Un problema inverso en el modelamiento matemático de nuestro sentido del olfato

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Abstract—The first step in our sensing of smell is the conversion of chemical odorants into electrical signals. This happens when odorants stimulate ion channels along cilia, which are long thin cylindrical structures in our olfactory system. Determining how the ion channels are distributed along the length of a cilium is beyond current experimental methods. Here we describe how this can be approached as a mathematical inverse problem. Precisely, two integral equations based mathematical models are studied for the inverse problem of determining the distribution of ion channels in cilia of olfactory neurons from experimental data. The Mellin transform allows us to write an explicit formula for their solutions. Proving observability and continuity inequalities for the second integral equation is then a question of estimating the Mellin transform of the kernel on vertical lines. For the first integral model, an identifiability and a non observability (in some weighted L^2 spaces) results are proven.

Keywords-Inverse problem, integral equation, ill-posed problem, Mellin transform

Resumen— El primer paso en nuestra percepción del olfato es la conversión de olores químicos en señales eléctricas. Esto sucede cuando los olores estimulan los canales iónicos a lo largo de los cilios olfatorios, estructuras cilíndricas largas y delgadas en el sistema olfativo. Determinar cómo se distribuyen estos canales iónicos a lo largo de un cilio supera los métodos experimentales actuales. Aquí describimos cómo es posible abordar esta pregunta como un problema matemático inverso. Precisamente, se estudian dos modelos basados en ecuaciones integrales para el problema inverso de determinar la distribución de los canales iónicos en los cilios de las neuronas olfativas, a partir de datos experimentales. La transformada de Mellin nos permite escribir una fórmula explícita para sus soluciones. Demostrar las desigualdades de observabilidad y continuidad para la segunda ecuación integral resulta así equivalente a estimar el núcleo de la transformada de Mellin de la solución en líneas verticales. Para el primer modelo integral, se prueban resultados de identificabilidad y de no observabilidad (en ciertos espacios de tipo L^2 con peso).

Palabras clave--- Problema inverso, ecuación integral, problema mal puesto, transformada de Mellin

INTRODUCTION

The first step in sensing smell is the transduction (or conversion) of chemical information into an electrical signal that goes to the brain. Pheromones and odorants, which are small molecules with the chemical characteristics of an odor are found all throughout our environment. The olfactory system (part of the sensory system we use to smell) performs the task of receiving these odorant molecules in the nasal mucosa, and triggering the physical-chemical

processes that generates the electric current that travels to the brain. See Fig. 1.

What happens next is a mystery. Intuition tells us that the electrical wave generated gives rise to an emotion in the brain, which in turn affects our behavior. Of course, the workings of our other four senses is similarly a mystery. And so, we quickly come to perhaps one of the most fundamental questions in neurosciences for the future: How does our consciousness processes external stimuli once reduced





Figure 1: Odorants reaching the nasal mucus (left) & Structure of an olfactory receptor neuron (right)

to electro-chemical waves and, over time, how does this mechanism lead us to become who we are?

How can we approach this problem with mathematics? Faced with these reflections, applied mathematicians take time to stop and wonder if it is possible to provide such farreaching phenomena with a mathematical representation that allows us to understand and act. Biology is synonymous with "function", so the study of biological systems should start by understanding the corresponding underlying physiology. Consequently, to obtain a proper mathematical representation of the transduction of an odor into an electrical signal, and before any mathematical intervention, we must first detect which atomic populations are involved in the process and identify their respective functions.

Transduction of olfactory signals

The molecular machinery that carries out this work is in the olfactory cilia. Cilia are long, thin cylindrical structures that extend from an olfactory receptor neuron into the nasal mucus (Fig. 1).

The transduction of an odor begins with pheromones binding to specific receptors on the external membrane of cilia. When an odorant molecule binds to an olfactory receptor on a cilium membrane, it successively activates an enzyme, which increases the levels of a ligand or chemical messenger named cyclic adenosine monophosphate (cAMP) within the cilia. As a result of this, cAMP molecules diffuse through the interior of the cilia. Some of the cAMP molecules binds to cyclic nucleotide-gated (CNG) ion channels, causing them to open. This allows an influx of positively charged ions into the cilium (mostly Ca^{2+} and Na^{+}), which causes the neuron to depolarize, generating an excitatory response. This response is characterized by a voltage difference on one side and another of the membrane, which in turn initiates the electrical current. This is the overall process that human beings share with all mammals and reptiles to smell and differentiate odors.

Experimental techniques for isolating a single cilium (from a grass frog) were developed by biochemist and neuroscientist Steven J. Kleene and his research team at the University of Cincinnati in the early 1990s [Kleene (1993); Kleene and Gesteland (1991)]. One olfactory cilium of a receptor neuron is detached at its base and stretched tight into a recording pipette. The cilium is immersed in a bath of

a chemical known as cAMP (by its chemical initials). This substance diffuses through the interior of the cilium, opening the so-called GNC channels as it advances, and generating a transmembrane electrical current. The intensity of the total current is recorded.

Although the properties of a single channel have been able to be described using these experimental techniques, the distribution of these channels along the cilia still remains unknown, and may well turn out to be crucial in determining the kinetics of the neuronal response. Ionic channels, in particular, CNG channels are called "micro-domains" in biochemistry, because of their practically imperceptible size. This makes their experimental description using the current technology very difficult.

Olfactory transduction via inverse modelling

Given the experimental and numerical difficulties, there is a clear opportunity for fundamental mathematics to inform biology. Determining ion channels distribution along the length of a cilium using measurements from experimental data on transmembrane current is usually categorized in physics and mathematics as an inverse problem. Around 2006, a multidisciplinary team (which brought together mathematicians with biochemists and neuroscientists, as well as a chemical engineer) developed and published a first mathematical model [French et al. (2006)] to simulate Kleene's experiments. The distribution of CNG channels along the cilium appears in it as the main unknown of a nonlinear integral equation model.

This model gave rise to a simple numerical method for obtaining estimates of the spatial distribution of CNG ion channels. However, specific computations revealed that the mathematical problem is poorly conditioned. This is a general difficulty in inverse models, where the corresponding mathematical problem is usually ill-posed (in the sense of Hadamard, which requires the problem to have a solution that exists, is unique, and whose behavior changes continuously with the initial conditions), or else it is unstable with respect to the data. As a consequence, its numerical resolution often results in ill-conditioned approximations.

The essential nonlinearity in the previous model arises from the binding of the channel activating ligand (cAMP molecules) to the CNG ion channels as the ligand diffuses along the cilium. In 2007, D. A. French and C. W. Groetsch introduced a simplified model, in which the binding mechanism is neglected, leading to a linear Fredholm integral equation of the first kind with a diffusive kernel. The inverse mathematical problem consists of determining a density function, say $\rho = \rho(x) \ge 0$ (representing the distribution of CNG channels), from measurements in time of the transmembrane electrical current, denoted $I_0[\rho]$. This mathematical equation for ρ is the following integral equation: for all $t \ge 0$,

$$\mathbf{I}_0[\boldsymbol{\rho}](t) = \int_0^L \boldsymbol{\rho}(x) \, \mathbb{P}(c(t,x)) \, \mathrm{d}x, \tag{1}$$

where \mathbb{P} is known as the Hill function of exponent n > 0 (see



Fig. 2). It is defined by:

$$\forall w \ge 0, \qquad \mathbb{P}(w) = \frac{w^n}{w^n + K_{1/2}^n}$$

In this definition, the exponent *n* is an experimentally determined parameter and $K_{1/2} > 0$ is a constant which represents the half-bulk (i.e., the ligand concentration for which half the binding sites are occupied); typical values for *n* in humans are $n \simeq 2$. Besides, in the linear integral equation above, c(t,x) denotes the concentration of cAMP that diffuses along the cilium with a diffusivity constant that we denote as *D*; *L* denotes the length of the cilium, which for simplicity is assumed to be one-dimensional. Here, by concentration we mean the molar concentration, i.e., the amount of solute in the solvent in a unit volume; it is a nonnegative real number.

Hill-type functions are extensively used in biochemistry to model the fraction of ligand bound to a macromolecule as a function of the ligand concentration and, hence, the quantity $\mathbb{P}(c(t,x))$ models the probability of the opening of a CNG channel as a function of the cAMP concentration. The diffusion equation for the concentration of cAMP can be explicitly solved if the length of the cilium *L* is supposed to be infinite. It is given by:

$$c(t,x) = c_0 \operatorname{erfc}\left(\frac{x}{2\sqrt{\mathrm{Dt}}}\right),$$

where $c_0 > 0$ is the maintained concentration of cAMP with which the pipette comes into contact at the open end (x = 0) of the cilium (while x = L is the closed end). Here, erfc is the standard complementary Gauss error function,

$$\operatorname{erfc}(\mathbf{x}) := 1 - \frac{2}{\sqrt{\pi}} \int_0^{\mathbf{x}} e^{-\tau^2} \, \mathrm{d}\tau.$$

Accordingly, it is straightforward to check that *c* is decreasing in both its variables and that it remains bounded for all (t,x), $0 < c(t,x) \le c_0$.

Despite its elegance (by virtue of the simplicity of its formulation), this new model does not overcome the difficulties encountered in its non-linear version. In fact the mathematical inverse problem associated to model (1) can be shown to be ill-posed. More precisely, since $\mathbb{P}(c(t,x))$ is a smooth mapping, the operator $\rho \mapsto I_0[\rho]$ is compact from $L^p(0,L)$ to $L^p(0,T)$ for every $L, T > 0, 1 . Thus, even if the operator <math>I_0$ were injective, its inverse would not be continuous because, if so, then the identity map in $L^p(0,L)$ would be compact, which is known to be false.

Non-diffusive kernels

This last result certainly has a more general character. In fact, it is clear from its proof that any model based on a first-order integral equation with a diffusive smooth kernel necessarily results in the problem of recovering the density from measurements of the electrical current being ill-posed.

An initial, natural approach to tackling this anomaly in model (1) was developed in Conca et al. (2014). This exploited the fact that the Hill function converges point-wise to a single step function as the exponent *n* goes to $+\infty$, the strategy was to approximate \mathbb{P} using a multiple step function.

Based on different assumptions of the spaces where the unknown ρ is sought, theoretical results of identifiability, stability and reconstruction were obtained for the corresponding inverse problem. However, numerical methods for generating estimates of the spatial distribution of ion channels revealed that this class of models is not satisfactory for practical purposes. The only feasible estimates for ρ are obtained for multiple step functions that are very close to a single-step function or, equivalently, for Hill functions with very large exponents, which imply the use of unrealistic models.

Another way to overcome the ill-posedness of the inverse problem in (1) consists of replacing the kernel of the integral equation with a non-smooth variant of the Hill function.

Specifically, let $a \in (0, c_0]$ be a given real parameter. A discontinuous version of \mathbb{P} is obtained by forcing a saturation state for concentrations higher than *a*. By doing so, one is led to introduce the following disruptive variant of \mathbb{P} (shown in Fig. 3):

$$\mathbb{H}(c) = \mathbb{P}(c) \mathbb{1}_{c \leq a} + \mathbb{1}_{a < c \leq c_0},$$

where $\mathbb{1}_J$ denotes the characteristic function of the interval *J*. The mathematical problem that recovers ρ from the electrical current data is therefore modelled by

$$\mathbf{I}_{1}[\boldsymbol{\rho}](t) = \int_{0}^{L} \boldsymbol{\rho}(x) \, \mathbb{H}(c(t,x)) \, \mathrm{d}x, \tag{2}$$

where c(t,x) is still defined as before. The introduction of this disruptive Hill function can be understood mathematically as follows: as $t \to \infty$, the factor x/\sqrt{Dt} in the complementary error function defining the concentration tends to 0, and consequently c(t,x) tends pointwise to c_0 . An inverse mathematical problem and a direct problem are associated with both models (1) and (2). In the first, the electric current is measured and the unknown is the density ρ of ion channels, while in the direct problem the opposite is true. Since these are Fredholm equations of the first type, it is natural to tackle them using convolution. Once the variable ρ has been extended to $[0,\infty)$ by zero, the Mellin transform is revealed as being the most appropriate tool for carrying out this task (see the overview section "Mellin transform" in Appendix).





A GENERAL CONVOLUTION EQUATION

The Mellin transform is the appropriate tool to study model (2). It allows to reduce it in a convolution equation of the Mellin type. To do so, the key observation is the fact that $\mathbb{H}(c(t,x))$ can be written in terms of $\frac{\sqrt{t}}{x}$. Indeed, defining *G* as

$$G(z) \stackrel{\text{(def)}}{=} \mathbb{H}\left(c_0 \text{erfc}\left(\frac{1}{2\sqrt{D}z}\right)\right)$$

we have $I_1[\rho](t) = \int_0^L \rho(x)G(\frac{\sqrt{t}}{x}) dx$. Thus, by extending ρ by zero to $[0,\infty)$, and rescaling time *t* in t^2 , we obtain

$$I_1[\rho](t^2) = \int_0^\infty x \rho(x) G\left(\frac{t}{x}\right) \frac{dx}{x} = \left(x\rho(x)\right) * G$$

which is a convolution equation in $x\rho(x)$.

Taking Mellin transform on both sides and using its operational properties, we formally obtain

$$\frac{1}{2}\mathcal{M}\mathrm{I}_{1}[\rho](s/2) = \mathcal{M}G(s)\mathcal{M}\rho(s+1)$$

or equivalently,

$$\mathscr{M}\rho(s+1) = \frac{1}{2} \frac{\mathscr{M}I_1[\rho](s/2)}{\mathscr{M}G(s)}.$$
(3)

A priori estimates

Seeking continuity and observability inequalities for model (2) is then reduced to find lower and upper bounds for $\mathcal{M}G(\cdot)$ in suitable weighted Lebesgue's spaces¹. Doing so, one obtains

Theorem 1 (A priori estimates) Let $k \in \mathbb{N} \cup \{0\}$ and $r \in \mathbb{R}$ be arbitrary. Assume that the Mellin transforms of ρ and $I_1[\rho]$ satisfy (3), then

$$C_{\ell}^{k} \| \boldsymbol{\rho} \|_{L_{r}^{2}} \leq \| (I_{1}[\boldsymbol{\rho}])^{(k)} \|_{L_{2k+\frac{r-3}{2}}^{2}} \leq C_{u}^{k} \| \boldsymbol{\rho} \|_{L_{r}^{2}},$$

where

$$\begin{aligned} C_{\ell}^{k} \stackrel{(\text{def})}{=} & \sqrt{2} \inf_{s \in \frac{r-1}{2} + i \mathbb{R}} \left| \left(\frac{s}{2} \right)_{k} \mathscr{M}G(s) \right| \\ C_{u}^{k} \stackrel{(\text{def})}{=} & \sqrt{2} \sup_{s \in \frac{r-1}{2} + i \mathbb{R}} \left| \left(\frac{s}{2} \right)_{k} \mathscr{M}G(s) \right|, \end{aligned}$$

¹Details on the notation used for theses spaces are found in the Appendix on the Mellin transform.

and $L_q^p = L^p([0,\infty), x^q)$ stands for the Lebesgue space with the weight x^q , $p \ge 1, q \in \mathbb{R}$.

Remark 1 It is worth noting that C_{ℓ}^k, C_u^k could a priori range from 0 to $+\infty$.

Proof. Using the properties of the Mellin transform in equation (3), it follows that

$$(s-k)_k \mathscr{M}I[\rho](s-k) =$$

= 2(s-k)_k \mathscr{M}G(2(s-k)) \mathscr{M}\rho(2(s-k)+1) (4)

Thanks to Parseval-Plancherel's isomorphism, for every *s* in $q + i \mathbb{R}$, we have

=

$$\begin{split} \left\| (\mathbf{I}[\boldsymbol{\rho}])^{(k)} \right\|_{\mathbf{L}^{2}_{2q-1}} &= \\ \frac{1}{\sqrt{(2\pi)}} \left\| (-1)^{k} (s-k)_{k} \mathscr{M} \mathbf{I}[\boldsymbol{\rho}](s-k) \right\|_{\mathbf{L}^{2}(q+i\mathbb{R})} = \\ \frac{2}{\sqrt{(2\pi)}} \left\| (s-k)_{k} \mathscr{M} G(2(s-k)) \mathscr{M} \boldsymbol{\rho}(2(s-k)+1) \right\|_{\mathbf{L}^{2}(q+i\mathbb{R})} \\ &= \frac{2}{\sqrt{(2\pi)}} \left\| (s)_{k} \mathscr{M} G(2s) \mathscr{M} \boldsymbol{\rho}(2s+1) \right\|_{\mathbf{L}^{2}(q-k+i\mathbb{R})} \\ &= \frac{1}{\sqrt{\pi}} \left\| \left(\frac{s}{2} \right)_{k} \mathscr{M} G(s) \mathscr{M} \boldsymbol{\rho}(s+1) \right\|_{\mathbf{L}^{2}(2(q-k)+i\mathbb{R})} \end{split}$$
(5)

As \mathscr{M} is an isometry from $L^2(2(q-k)+1+i\mathbb{R})$ on $L^2_{4(q-k)+1}$ (see Theorem 8 in the Appendix),

$$\|\mathscr{M}\rho(s+1)\|_{L^{2}(2(q-k)+i\mathbb{R})} = \|\mathscr{M}\rho(s)\|_{L^{2}(2(q-k)+1+i\mathbb{R})}$$

= $\sqrt{2\pi} \|\rho\|_{L^{2}_{4(q-k)+1}}.$ (6)

Thanks to (5), (6) and the definitions of C_l^k, C_u^k , we get

$$C_{l}^{k} \|\rho\|_{\mathrm{L}^{2}_{4(q-k)+1}} \leq \left\| (\mathrm{I}[\rho])^{(k)} \right\|_{\mathrm{L}^{2}_{2q-1}} \leq C_{u}^{k} \|\rho\|_{\mathrm{L}^{2}_{4(q-k)+1}}$$

Taking r = 4(q - k) + 1, that is $q = k + \frac{r-1}{4}$, provides the result.

OBSERVABILITY OF CNG CHANNELS

The a priori estimates in the theorem above also allow to determine a unique distribution of ion channels along the length of a cilium from measurements in time of the transmembrane electric current.

Theorem 2 (Existence and uniqueness of ρ) Let a > 0 and r < 1 be given. If $I_1 \in L^2([0,\infty), t^{\frac{r-3}{2}})$, $I'_1 \in L^2([0,\infty), t^{2+\frac{r-3}{2}})$ and a is small enough, then there exists a unique $\rho \in L^2([0,\infty), x^r)$ which satisfies the following stability condition:

$$\|I_1\|_{L^2([0,\infty),t^{\frac{r-3}{2}})} + \|I_1'\|_{L^2([0,\infty),t^{2+\frac{r-3}{2}})} \ge C \|\rho\|_{L^2_r},$$

where C > 0 depends only on a and r.

Proof. The proof is based on the following technical lemmas and its corollaries :

Lemma 1 Let A and B be two elements of $[0,\infty]$, $k \in \bigcup\{0\}\mathbb{N}$ be a nonnegative integer and f a function such that $f^{(j)}$ is in $L^1_j(A,B)$ for every $j = 0, \ldots, k$. For every real number t, we have

$$\begin{split} \int_{A}^{B} f(x) x^{it} \, \mathrm{d}x &= \sum_{j=0}^{k-1} (-1)^{j} Q_{j} \left[x^{j+1} f^{(j)}(x) x^{it} \right]_{A}^{B} + \\ &+ (-1)^{k} Q_{k-1} \int_{A}^{B} x^{k} f^{(k)}(x) x^{it} \, \mathrm{d}x, \end{split}$$
where $Q_{j} &= Q_{j}(t) = \left(\prod_{l=0}^{j} (1+l+it) \right)^{-1}. \end{split}$

Proof. We use induction on $k \in \mathbb{N}$. For k = 0, since $Q_{-1} = 1$, there is nothing to prove. We assume that the formula is true for an integer $k \in \mathbb{N}$. As $(k + 1 + it)Q_k = Q_{k-1}$, it remains to prove that

$$(k+1+it) \int_{A}^{B} x^{k} f^{(k)}(x) x^{it} \, \mathrm{d}x = \left[x^{k+1} f^{(k)}(x) x^{it} \right]_{A}^{B} - \int_{A}^{B} x^{k+1} f^{(k+1)}(x) x^{it} \, \mathrm{d}x$$

As $\frac{d}{dx}x^{it} = \frac{it}{x}x^{it}$, the previous relation follows by integration by parts. Indeed, we have

$$it \int_{A}^{B} x^{k} f^{(k)}(x) x^{it} dx = \int_{A}^{B} x^{k+1} f^{(k)}(x) (x^{it})' dx =$$
$$= \left[x^{k+1} f^{(k)}(x) x^{it} \right]_{A}^{B} - (k+1) \int_{A}^{B} x^{k} f^{(k)}(x) x^{it} dx - \int_{A}^{B} x^{k+1} f^{(k+1)}(x) x^{it} dx$$

Corollary 1 Let $f: [A,B] \to \mathbb{R}$ with $A, B \in [0,\infty]$ be a piecewise C^1 function. If f is non-negative, f' is non-positive, $f \in L^1(A,B), f' \in L^1_1(A,B)$ and for all $t \in \mathbb{R}$: $[xf(x)x^{it}]^B_A = 0$, then

$$\sqrt{1+t^2} \left| \int_A^B f(x) x^{it} \, \mathrm{d}x \right| \leq \int_A^B f(x) \, \mathrm{d}x$$

Proof. From Lemma 1 with k = 1 one obtains

$$\forall t \in \mathbb{R}, \quad (1+it) \int_A^B f(x) x^{it} \, \mathrm{d}x = -\int_A^B x f'(x) x^{it} \, \mathrm{d}x.$$

As $A, B \ge 0$ and $f' \le 0$, using this previous identity twice, for $t \ne 0$ and for t = 0, we get

$$\sqrt{1+t^2} \left| \int_A^B f(x) x^{it} \, \mathrm{d}x \right| \leq \int_A^B \left| x f'(x) \right| \, \mathrm{d}x = \int_A^B f(x) \, \mathrm{d}x.$$

Lemma 2 Let $n, K > 0, q \in \mathbb{R}$ and $f = \frac{\operatorname{erfc}^n}{\operatorname{erfc}^n + K}$. There exists $x_q > 0$ such that the function $g_q : x \in [x_q, \infty) \mapsto f(x) x^{q-1}$ is decreasing. Let $\tilde{q} = \inf E_q$ where $E_q = \{c \ge 0 \mid g'_q(x) < 0 \forall x \ge c\}$. The function $q \mapsto \tilde{q}$ is increasing and $\tilde{q} = (q/(2n))^{1/2} + o(q^{1/2})$ as $q \to \infty$.

Proof. As f > 0, the inequality $g'_q(x) \leq 0$ is equivalent to

$$\frac{f'(x)}{f(x)} \leqslant -\frac{q-1}{x}.$$
(7)

Let us compute $\frac{f'}{f}$. To do so, let $u = \operatorname{erfc}^n$, so that $f = \frac{u}{u+K}$. We have

$$\frac{f'}{f} = \frac{u'}{u}\frac{K}{u+K} = n\frac{\operatorname{erfc}'}{\operatorname{erfc}}\frac{K}{u+K}$$
(8)

Since $\operatorname{erfc}'(x) = -2\pi^{-1/2}e^{-x^2}$, for *x* large enough, $\operatorname{erfc}(x) = \pi^{-1/2}x^{-1}e^{-x^2} + o(x^{-1}e^{-x^2})$, and so

$$\frac{f'(x)}{f(x)} = n \frac{\text{erfc}'(x)}{\text{erfc}(x)} (1 + o(1)) = -2nx + o(x)$$
(9)

This asymptotic expansion proves that the inequality (7) is satisfied for large enough values of *x*. As a consequence, for every *q* in \mathbb{R} , the set E_q is not empty, which justifies the definition of \tilde{q} . Note that the definition of \tilde{q} implies $g'_q(\tilde{q}) = 0$, and hence, thanks to (7), $\frac{f'(\tilde{q})}{f(q)} = -\frac{q-1}{\tilde{q}}$. Let $q_1 \ge q_2$ be two real numbers. In order to show that $\tilde{q}_2 \le \tilde{q}_1$, it is enough to prove that $g'_{q_1}(\tilde{q}_2) \ge 0$. This holds true because

$$g'_{q_1}(\widetilde{q_2}) = \widetilde{q_2}^{q_1-2}(f'(\widetilde{q_2})\widetilde{q_2} + f(\widetilde{q_2})(q_1-1)) \geqslant$$

$$\widetilde{q_2}^{q_1-2}(f'(\widetilde{q_2})\widetilde{q_2} + f(\widetilde{q_2})(q_2-1)) = \widetilde{q_2}^{q_1-q_2}g'_{q_2}(\widetilde{q_2}) = 0.$$

To find an expansion for \tilde{q} , let us recall the following classical lower bound on $\operatorname{erfc}(\mathbf{x})$ for $x \ge 0$,

$$\frac{1}{x + (x^2 + 2)^{1/2}} \leqslant \frac{1}{2} \pi^{1/2} \exp(x^2) \operatorname{erfc}(x).$$

As the function $u = \operatorname{erfc}^n$ takes its values in (0, 1], $\frac{nK}{1+K} \leq \frac{nK}{u+K} \leq n$. Consequently, the identities (8) yield

$$-n\left(x + (x^2 + 2)^{1/2}\right) \leqslant \frac{f'(x)}{f(x)}$$
(10)

Let q > 1 and set $x_q = \frac{q-1}{(2n)^{1/2}(n+q-1)^{1/2}}$. The inequality $-\frac{q-1}{x} \leq -n\left(x+(x^2+2)^{1/2}\right)$ is equivalent to $x\left(x+(x^2+2)^{1/2}\right) \leq \frac{q-1}{n}$. A simple computation shows that this inequality is satisfied for $x = x_q$ (and becomes and equality). Thanks to (10), we conclude that x_q satisfies $\frac{f'(x_q)}{f(x_q)} \geq -\frac{q-1}{x_q}$, which leads to $\tilde{q} \geq x_q$, by definition of \tilde{q} and by (7). This last inequality implies that \tilde{q} tends to $+\infty$ as q tends to $+\infty$. Finally, from (9), we get the asymptotic for \tilde{q} , namely

$$-2n\widetilde{q} + o(\widetilde{q}) = \frac{f'(\widetilde{q})}{f(\widetilde{q})} = -\frac{q-1}{\widetilde{q}}$$

This completes the proof of Lemma 2.

Proof of Theorem 2

We are now in a position to conclude the proof of Theorem 2. To do so, we begin by introducing

$$J(x) \stackrel{(\text{def})}{=} \mathbb{H}(c_0 \operatorname{erfc}(x)) = f(x) \mathbb{1}_{x \ge \alpha} + \mathbb{1}_{0 < x < \alpha},$$

where $f(x) = \frac{\operatorname{erfc}(x)^n}{\operatorname{erfc}(x)^n + \operatorname{c}_0^{-n} K_{1/2}^n}$, $\alpha = \operatorname{erfc}^{-1}\left(\frac{a}{c_0}\right)$. A brief calculation shows that *G* and *J*, and their corresponding Mellin transforms are related as follows

$$G(x) = J\left(\frac{1}{2\sqrt{D}x}\right), \ \mathcal{M}G(s) = \frac{\mathcal{M}J(-s)}{2^s\sqrt{D^s}}$$
(11)

Thus, in terms of J, the equation (3) becomes

$$\mathscr{M}\rho(s+1) = 2^{s-1}\sqrt{D^s}\frac{\mathscr{M}\mathrm{I}_1[\rho](s/2)}{\mathscr{M}J(-s)}$$
(12)



From the estimate for erfc at $+\infty$, given in the proof of Lemma 2, the function J_1 is in L_k^1 for every k > -1. Thus $\mathcal{M}J_1$ is holomorphic on the right half-plane, see Proposition 1 in Appendix. Using Lemma 3.2 in [Bourgeron et al. (2018)] on the vertical line $\frac{1-r}{2} + i\mathbb{R}$ with $\frac{1-r}{2} > 0$, one deduces that bounds for $\mathcal{M}J(-s)$ amount to estimate $|s\mathcal{M}J(s)|$ from above or from below, on the vertical lines $q + i\mathbb{R}$, for q > 0. The Mellin transform of J at s = q + it is given by

$$\mathcal{M}J(s) = \int_0^\alpha x^{s-1} dx + c_0^n \int_\alpha^{+\infty} f(x) x^{s-1} dx =$$

= $\frac{\alpha^s}{s} + c_0^n \int_\alpha^{+\infty} f(x) x^{q-1} x^{it} dx.$

For any $a \ge 0, q > 0$ and $s \in q + i \mathbb{R}$ we have

$$|\mathscr{M}J(s)| \leq \frac{\alpha^q}{q} + c_0^n \int_{\alpha}^{+\infty} f(x) x^{q-1} \,\mathrm{d}x,$$

which is finite. Let q > 0. According to Lemma 2 the function $x \mapsto f(x)x^{q-1}$ is decreasing for $x \ge x_0$. Let $a < c_0 \operatorname{erfc}(x_0)$ so that $\alpha = \operatorname{erfc}^{-1}(a/c_0) \ge x_0$. Let $g(x) = f(x)x^{q-1} \mathbbm{1}_{x \ge \alpha}$. For every $t \in \mathbb{R}$, $[f(x)x^{il}]_{x_0}^{\infty} = 0$ because f vanishes for $x \le \alpha$ and $x_0 \le \alpha$, and $g(x) = \pi^{-n/2}x^{-n+q-1}e^{-nx^2} + o\left(x^{-n+q-1}e^{-nx^2}\right)$. Then Corollary 1 can be applied to the function g, with $A = \alpha, B = +\infty$, for $s \in q + i \mathbb{R}$, to give

$$\begin{split} |s\mathcal{M}J(s)| &\leqslant |\alpha^{s}| + c_{0}^{n} \frac{|s|}{\sqrt{1+t^{2}}} \sqrt{1+t^{2}} \left| \int_{\alpha}^{\infty} f(x) \, x^{s-1} \, \mathrm{d}x \right| \\ &\leqslant \alpha^{q} + c_{0}^{n} \max(1,q) \int_{\alpha}^{\infty} f(x) x^{q-1} \, \mathrm{d}x < \infty, \end{split}$$

because $\frac{|s|}{\sqrt{1+t^2}} \in [q,1] \cup [1,q]$, either $q \leq 1$ or $q \geq 1$. For small values of *a*, the first term dominates the second one. The same calculation as above leads to

$$|s\mathcal{M}J(s)| \ge \alpha^q - c_0^n \max(1,q) \int_{\alpha}^{\infty} f(x) x^{q-1} dx.$$

This latter expression is equivalent to α^q as α tends to $+\infty$, so it is positive for large values of α . This finishes the proof of Theorem 2.

UNSTABLE IDENTIFIABILITY, NON EXISTEN-CE OF OBSERVABILITY INEQUALITIES

Since the French-Groetsch model is also a Fredholm integral equation of the first kind, it is natural to apply a Mellin transform here too. This leads to interesting results: neither an observability inequality nor a proper numerical algorithm for recovering ρ can be established. However, a kind of identifiability result holds whenever the current is measured over an open time interval (see Theorem 4 below).

Defining G as

$$\widetilde{G}(z) = \mathbb{P}\left(c_0 \operatorname{erfc}\left(\frac{1}{2\sqrt{\mathrm{D}}z}\right)\right),$$

and rescaling time t in t^2 , we obtain a convolution equation very similar to (3):

$$\mathscr{M}\rho(s+1) = \frac{1}{2} \frac{\mathscr{M}I_0[\rho](s/2)}{\mathscr{M}\widetilde{G}(s)}$$
(13)

A close study of the transform of G(s) allows us to establish the following two theorems, which provide information about the behavior of the inverse problem associated with model (1). The proof of Theorems 3 and 4 below requires to extend Mellin transform to functions in the Schwartz space and to prove that the Mellin transforms of such smooth and rapidly decreasing functions decay faster than polynomials on vertical lines.

The starting point to do this is the following

Definition 1 Let $\mathscr{S}[0,\infty)$ be the Schwartz space of functions f in $C^{\infty}([0,\infty), \mathbb{C})$ which satisfy

$$\forall j \in \mathbb{N}, k \in \mathbb{N} \quad \lim_{x \to \infty} f^{(j)}(x) x^k = 0.$$

If f is a function in $\mathscr{S}(\mathbb{R})$, then $f \mathbb{1}_{x \ge 0}$ is in $\mathscr{S}[0,\infty)$ (the converse is also true thanks to Borel's lemma).

Lemma 3 If $f \in \mathscr{S}[0,\infty)$, then its Mellin transform $\mathscr{M} f$ is holomorphic on the right half-plane, and $\forall q > 0 \ \forall k \in \mathbb{N}$ there exists $C \ge 0$ such that

$$|\mathscr{M}f(q+it)| \leqslant \frac{C}{(1+t^2)^{k/2}} \quad \forall t \in \mathbb{R}$$

Proof. Let $f \in \mathscr{S}[0,\infty)$, q > 0. By the definition of $\mathscr{S}[0,\infty)$, for every l in \mathbb{N} and k > -1 the function $x \mapsto x^k f^{(l)}(x)$ is in L^1 . Proposition 1 in the Appendix implies that $\mathscr{M}f$ is holomorphic on the right half-plane, and hence Lemma 1 with $g(x) = f(x)x^{q-1}$ yields

$$\mathcal{M}f(q+it) = \int_0^\infty f(x)x^{q-1}x^{it} \, dx =$$

= $\sum_{j=0}^{k-1} (-1)^j Q_j(t) \left[x^{j+1}g^{(j)}x^{it} \right]_0^\infty +$
+ $(-1)^k Q_{k-1}(t) \int_0^\infty x^k g^{(k)}(x)x^{it} \, dx,$
where $Q_j(t) = \left(\prod_{l=0}^j (1+l+it) \right)^{-1}.$

The proof of this Lemma will be finished if we show that the terms between brackets vanish and that the last integral is finite.

Let $l, k \in \mathbb{N}$. By the Leibniz rule, we have

$$\begin{aligned} x^{l}g^{(k)}(x) &= \sum_{j=0}^{k} \binom{k}{j} f^{(k-j)}(x) (x^{q-1})^{(j)} x^{l} = \\ &= \sum_{j=0}^{k} \binom{k}{j} (q-1)_{j} f^{(k-j)}(x) x^{q+l-1-j} \end{aligned}$$

For l = k + 1 and for x = 0 this expression vanishes because $f^{(k-j)}(0)$ is finite and $q + k - j \ge q > 0$. As *x* tends to $+\infty$ the expression tends to 0 as $f^{(k-j)}(x) x^{q+k-j} \to 0$. For l = k this expression shows that the integral $\int_0^\infty x^k |g^{(k)}(x)| dx$ is finite because for every $j \in \{0, \dots, k\}$, since $x \mapsto x^{q-1+j} f^{(j)}(x)$ is in L^1 because $q - 1 + j \ge q - 1 > -1$. Thus,

$$|\mathscr{M}f(q+it)| \leq C |Q_{k-1}(t)| = \frac{C}{(1+t^2)^{k/2}} + o\left(\frac{1}{(1+t^2)^{k/2}}\right).$$

This completes the proof of Lemma 3.

Theorem 3 (Identifiability & Non observability) Let r < 1 be fixed. Then

• There exists C > 0 such that, for every ρ in L_r^2 , we have

$$\|I_0[\rho]\|_{\mathrm{L}^2_{\frac{r-3}{2}}} \leq C \|\rho\|_{\mathrm{L}^2_r}$$

 For every non-negative integer k there exists no constant C_k > 0 such that the observability inequality:

$$\|(I_0[\rho])^{(k)}\|_{L^2([0,\infty),t^{2k+\frac{r-3}{2}})} \ge C_k \|\rho\|_{L^2_r}$$

holds for every function $\rho \in L^2([0,\infty), x^r)$.

Remark 2 Note that the above result shows that $I_0 \in \mathscr{L}(L^2_r; L^2_{\frac{r-3}{2}})$, and that if the inverse problem were identificable (i.e, I_0 were injective), then I_0^{-1} could not be continuous.

Let us now observe that the model (1) can be seen as a particular choice of the parameter a in model (2), precisely, taking $a = c_0$, model (2) becomes (1). In this case, let us denote by J_0 the function J, that is,

$$J_0(x) \stackrel{\text{(def)}}{=} \mathbb{P}(c_0 \operatorname{erfc}(x)) = \frac{\operatorname{erfc}(x)^n}{\operatorname{erfc}(x)^n + c_0^{-n} K_{1/2}^n} \mathbb{1}_{x \ge 0}.$$

Proof of Theorem 3. It is based on showing that $\mathcal{M}J_0$ decays faster than polynomially on vertical lines, and this on the fact that J_0 belongs to some Schwartz space. For the proof that J_0 belongs to $\mathcal{S}[0,\infty)$, the reader is referred to Bourgeron et al. (2018) [Lemma 4.10].

As in the proof of Lemma 3.2 in the reference just quoted, thanks to (5), (6), the inequalities:

$$\left\| \left(\mathbf{I}_{0}[\boldsymbol{\rho}] \right)^{(k)} \right\|_{\mathbf{L}^{2}_{2k+\frac{r-3}{2}}} \ge C \| \boldsymbol{\rho} \|_{\mathbf{L}^{2}_{r}}, \tag{14}$$

and

$$\|(s)_{k} \mathcal{M} J_{0}(-2s) \mathcal{M} \rho(2s+1)\|_{L^{2}\left(\frac{r-1}{4}+i\mathbb{R}\right)} \geq \\ \geq C \|\mathcal{M} \rho(2s+1)\|_{L^{2}\left(\frac{r-1}{4}+i\mathbb{R}\right)}$$
(15)

are equivalent (up to some explicit constants depending on q,k). Furthermore, the same equivalence is true changing all \geq signs to \leq signs. Thus, Lemmas 3 implies that $|\mathcal{M}J_0|$ is bounded from above on $\frac{1-r}{2} + i \mathbb{R}$ so that (15), with \leq instead of \geq , holds, which concludes the proof of the first statement.

To prove the second statement, let us assume by absurd that there exists a constant C > 0 such that the inequality (15) holds for every $\rho \in L_r^2$. Let $s_0 \in \frac{r-1}{4} + i \mathbb{R}$ and $\delta > 0$. As the map $L_r^2 \ni \rho \mapsto \mathscr{M}\rho(2s+1) \in L^2\left(\frac{r-1}{4} + i\mathbb{R}\right)$ is onto (in fact it is an isometry up to a multiplicative constant), we can find $\rho \in L_r^2$ such that $\mathscr{M}\rho(2s+1) = \mathbb{I}_{s_0+i[-\delta,\delta]}(s)$. For this choice of ρ , (15) is localized in the following sense

$$\frac{1}{2\delta} \int_{s_0-i\delta}^{s_0+i\delta} |\mathscr{M}J_0(-2s)|^2 |(s)_k|^2 \, \mathrm{d}s \ge C$$

Thanks to Lemmas 3, and Lemma 4.10 in the reference quoted before, J_0 belongs to L_q^2 for every q > -1, and hence,

 $\mathcal{M}J_0 \in L^2(\tilde{q}+i\mathbb{R})$ for $\tilde{q} > 0$ (*cf.* Theorem 8). In particular, $|\mathcal{M}J_0(-2s)|^2 |(s)_k|^2$ is in L^1_{loc} , so, letting $\delta \to 0$, the Lebesgue differentiation theorem shows that at almost every point s_0 , we have

$$|\mathcal{M}J_0(-2s_0)| |(s_0)_k| \ge C.$$

In other words $|\mathcal{M}J_0|$ has at most a polynomial decay on vertical lines $\frac{1-r}{2} + i \mathbb{R}$, which is a contradiction with Lemma 3. This concludes the proof.

Theorem 4 (Identifiability) Let r < 0 and $\rho \in L^1([0,\infty), x^r)$ be arbitrary. If there exists a nonempty open subset \mathcal{U} of $(0,\infty)$ such that for all $t \in \mathcal{U}$, $I_0[\rho](t) = 0$, then $\rho = 0$ almost everywhere on $(0,\infty)$.

Proof. Lebesgue's dominated convergence theorem for analytic functions implies that $I_0[\rho]$ is an analytic function on $(0,\infty)$. For every $x \in [0,\infty)$, the function $\rho \mathbb{P}(c(\cdot,x))$ is analytic as erfc and all of its power functions are analytic. For the domination part let $\eta > 0$. As for $t \ge \eta$ we have that for all $x \ge 0$, $\rho(x) \mathbb{P}(c(t,x)) \le \rho(x) \mathbb{P}(c(\eta,x))$, it remains to show that $\rho \mathbb{P}(c(\eta,\cdot))$ is a L¹ function. At $+\infty$, we have

$$\mathbb{P}(c(\eta, x)) = \frac{1}{\pi^{n/2}} 2^n D^{n/2} \eta^{n/2} x^{-n} \exp\left(-\frac{nx^2}{4D\eta}\right) + o\left(x^{-n} \exp\left(-\frac{nx^2}{4D\eta}\right)\right),$$

so that $\int_1^{\infty} \rho(x) \mathbb{P}(c(\eta, x)) dx$ is finite because $\rho \in L_r^1$. At 0, $\mathbb{P}(c(\eta, 0)) = (1 + c_0^{-n} K_{1/2}^n)^{-1} > 0$, and since $r \leq 1$, $\int_0^1 \rho(x) dx \leq \int_0^1 \rho(x) x^{r-1} dx$ is finite so that $\int_0^1 \rho(x) \mathbb{P}(c(\eta, x)) dx$ is finite, too.

As $I_0[\rho]$ vanishes on U, the principle of permanence implies that it vanishes on the connected set $(0,\infty)$, i.e.,

$$\forall t \in (0, \infty) \quad \mathbf{I}_0[\boldsymbol{\rho}](t) = 0.$$

Taking the Mellin transform of this relation, using (12), we obtain

$$\forall s \in r+i \mathbb{R}, \quad \frac{1}{2^s \sqrt{D^s}} \mathscr{M} J_0(-s) \mathscr{M} \rho(s+1) = 0.$$

Thanks to Lemmas 3, and 4.10 in [Bourgeron et al. (2018)], $\mathcal{M}J_0$ is holomorphic on the right half-plane, which contains the line $-r + i\mathbb{R}$, because r < 0. The function $\mathcal{M}J_0$ is not identically zero, so $\mathcal{M}J_0$ can vanish only on a set -Z having no accumulation point. The previous relation implies that $\mathcal{M}\rho = 0$ on $r+1+i\mathbb{R} \setminus (1+Z)$. As $\rho \in L_r^1$ the function $\mathcal{M}\rho$ is continuous on the vertical line $r+1+i\mathbb{R}$, so that $\mathcal{M}\rho$ is identically zero on $r+1+i\mathbb{R}$. The Inversion Theorem 6 provides the result.

APPENDIX

Mellin transform

Austrian mathematician Robert Hjalmar Mellin (1854– 1933) gave his name to the so-called Mellin transform, whose definition and properties are recalled below. The interested reader is referred to E. Lindelöf (1933) for a summary of his work, and proof of the main results around this transform.



For $q \in \mathbb{R}$, $q + i\mathbb{R}$ will denote the vertical line $\{q + it, t \in \mathbb{R}\}$ of the complex plane having abscissa q, and for $p \in \mathbb{R}$ $(p \ge 1)$, $L^p([0,\infty), x^q)$, or simply L^p_q , will stand for the Lebesgue space with the weight x^q , *i.e.*,

$$\mathbf{L}_{q}^{p} = \left\{ f \colon [0, \infty) \to \mathbb{R} \mid \left\| f \right\|_{\mathbf{L}_{q}^{p}} < +\infty \right\},\$$

where $||f||_{L_q^p} = (\int_0^\infty |f(x)|^p x^q dx)^{1/p}$. L_q^p , endowed with this norm, is a Banach space.

Let f be in L¹($[0,\infty), x^q$). The Mellin transform of f is a complex-valued function defined on the vertical line $q + 1 + i \mathbb{R}$ by

$$\mathscr{M}f(s) = \int_0^\infty x^s f(x) \frac{\mathrm{d}x}{x}$$

From its very definition, it is observed that the Mellin transform maps functions defined on $[0,\infty)$ into functions defined on $q+1+i\mathbb{R}$. Like in the Fourier transform, $\mathcal{M}f$ is continuous whenever f is in $L^1([0,\infty), x^q)$. Specifically, we have

Theorem 5 (Riemann-Lebesgue) The Mellin transform is a linear continuous map from $L^1([0,\infty), x^q)$ into $\mathscr{C}^0(q+1+i\mathbb{R}; \mathbb{C}) \hookrightarrow L^{\infty}(q+1+i\mathbb{R}; \mathbb{C})$; its operator norm is 1.

Proposition 1 If f is in L^1_q for every real number q in (a,b), then its Mellin transform $\mathcal{M} f(\cdot)$ is holomorphic in the strip $S = \{s \in \mathbb{C} \mid a+1 < \operatorname{Re}(s) < b+1\}.$

The following table summarizes the main operational properties of the Mellin transform:

function	Mellin transform	
f(at), a > 0	$a^{-s}\mathcal{M}f(s)$	
$f(t^a), a \neq 0$	$ a ^{-1}\mathcal{M}f(a^{-1}s)$	
$f^{(k)}(t)$	$(-1)^k (s-k)_k \mathscr{M} f(s-k)$	

where, $\forall x \in \mathbb{R}$ and $\forall k \ge 1$, $(x)_k$ stands for the so-called Pochhammer symbol, which is defined by

$$(x)_k = x \cdots (x - k + 1) = \prod_{j=0}^{k-1} (x - j)$$
 if $k \ge 1$

and $(x)_0 = 1$, where *x* is in \mathbb{R} .

Theorem 6 (Inversion Theorem) If f is in L^1_q and if $\|\mathscr{M}f\|_{L^1(q+1+i\mathbb{R})}$ is finite, then one can define

$$\mathscr{M}_q^{-1}f(x) = \frac{1}{2\pi} \int_{\mathbb{R}} f(q+it) x^{-(q+it)} dt$$

The Inversion Theorem states that

$$f = \mathscr{M}_{q+1}^{-1}(\mathscr{M}f)$$
 a.e. in $(0,\infty)$.

Mellin convolution

For two given functions f, g, the *multiplicative convolu*tion f * g is defined as follows

$$(f * g)(x) = \int_0^\infty f(y) g\left(\frac{x}{y}\right) \frac{\mathrm{d}y}{y}$$

Theorem 7 (Mellin transform of a convolution)

Whenever this expression is well defined, we have

$$\mathcal{M}(f * g)(s) = \mathcal{M}f(s)\mathcal{M}g(s)$$

Finally, the classical L^2 -isometry has his Mellin counterpart, namely

Theorem 8 (Parseval-Plancherel's isomorphism) The

Mellin transform can be extended in a unique manner to a linear isometry (up to the multiplicative constant $(2\pi)^{-1/2}$) from L^2_{2q-1} onto the classical Lebesgue space $L^2(q+i\mathbb{R})$. Thus,

$$\mathcal{M} \in \mathscr{L}\left(\mathrm{L}^{2}_{2q-1}; \mathrm{L}^{2}(q+i\,\mathbb{R}, \mathrm{d}x)\right)$$

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Distribución de especies. Un punto de vista teórico

Species Distribution. A Theoretical Point of View

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Resumen— Entender los mecanismos y procesos que determinan la distribución de las especies, su abundancia y los patrones de biodiversidad que generan, es uno de los grandes retos para la ecología y de manera particular para la biogeografía. Si bien en la literatura existen varios cuerpos teóricos que tratan de explicar tales mecanismos, la formalización de cómo se relacionan los procesos fundamentales de la ecología (fisiología, conducta, demografía y dispersión) con los patrones espaciales de la biodiversidad, es un campo aún en desarrollo. En este trabajo exponemos algunos problemas relevantes en la modelación de nichos ecológicos y áreas de distribución; estos incluyen la conceptualización teórica de la relación entre nicho ecológico y los atributos de adecuación, el efecto de las interacciones bióticas, el movimiento y los mecanismos de defensa de la presa en los patrones espaciales de co-presencia de las especies. Se muestran resultados de diversos análisis que los autores han obtenido en el estudio de estos problemas con el uso de la modelación matemática.

Palabras clave— Teoría de Nicho Ecológico, Distribución de Especies, Centroide del Nicho, Modelos de Distribución y Abundancia, Modelos Metapoblacionales

Abstract—Understanding mechanisms and processes that determine the distribution and abundance of species as well as biodiversity patterns over time are one of the most interesting and challenging problems in Ecology, and particularly in Biogeography. Although in scientific literature diverse theoretical bodies have been proposed to explain these mechanisms, the formalization of how fundamental ecological processes (physiology, behavior, demography, and dispersal) and the spatial patterns of biodiversity are related is a field that remains in continuous development. In this work, we describe some of the relevant problems that arise from modeling the ecological niche and the spatial distribution of biodiversity. These problems include the theoretical conceptualization of the relationship between fitness attributes and the ecological niche, the effect of biotic interactions, dispersal and, defense mechanisms on the spatial distribution of a set of species that share a given environment. Results of various analyzes obtained by the authors in the study of these problems with the use of mathematical modeling are shown.

Keywords—Ecological Niche Theory, Species Distributions, Niche-Centroid, Models of Species Distributions and Abundance, Metapopulation models

INTRODUCCIÓN

E ntender los mecanismos y procesos que determinan la distribución de las especies, su abundancia y los patrones de biodiversidad que generan, es uno de los grandes retos para los ecólogos y biogeógrafos (Brown, 1995). Si bien en la literatura existen varios cuerpos teóricos que tratan de explicar tales mecanismos, la formalización de cómo se relacionan los procesos fundamentales de la ecología (fisiología, conducta, demografía y dispersión) con los patrones espaciales de la biodiversidad, es un campo aún en desarrollo.

La idea de representar el área de distribución de una especie como parte de un proceso ecológico, histórico, evolutivo y geográfico data desde los tiempos de Darwin, quien formalizó la hipótesis de un solo centro de origen (Darwin, 1902, chap. 12); hoy, gracias a las contribuciones de científicos como Grinnell (Grinnell, 1917), Elton (Elton, 1927), Hutchinson (Hutchinson, 1957) y MacArthur (Ma-





Figura 1: El diagrama BAM. En él se ilustra el área ocupada de una especie como la intersección de sus tres componentes, los bióticos, abióticos y movimientos ($G_0 = B \cap A \cap M$); el área invadible G_i ocurre en los sitios que son favorables tanto biótica como abióticamente, pero que la especie no ha podido acceder ($B \cap A \cap M^C$).

cArthur, 1972), se sabe que la presencia de una especie en una localidad determinada depende en gran medida de su "nicho ecológico" (Soberón, 2007), y que factores como las interacciones bióticas y el acceso a sitios con condiciones idóneas delimitan el área de distribución. Siguiendo este orden de ideas, Soberón y Peterson (2005) proponen el diagrama BAM (Fig. 1), un marco conceptual que, sintetizando ideas clásicas, ha servido como punto de referencia para entender la dinámica de las áreas de distribución. Así, el área ocupada por una especie G_0 ocurre en aquellos sitios en la geografía G que cumplen por lo menos tres condiciones: 1) el efecto neto de las interacciones bióticas (B) en la razón de cambio poblacional permite el crecimiento de una población; 2) que estos sitios posean condiciones abióticas (A) dentro de los rangos de tolerancia fisiológica, de modo tal que en presencia de fuentes de alimento, la tasa de natalidad es mayor que la de mortalidad; 3) finalmente, una condición aparentemente trivial pero necesaria es que estos lugares hayan sido accesibles (M) en periodos relevantes para la especie. Una zona del diagrama BAM que tiene importancia para el estudio de las invasiones biológicas es el área invadible Gi y representa aquellos sitios donde hay condiciones bióticas y ambientales favorables para la especie, sin embargo, no ha podido llegar.

Cada componente del **BAM** está estrechamente relacionado con un concepto de ecología clásica, así **B** hace referencia al nicho eltoniano (Chase y Leibold, 2003), el cual considera el efecto de las interacciones bióticas en la razón de cambio poblacional; **A** al nicho fundamental Grinnelliano (**N**_F), el cual está definido como una función matemática que mapea un vector de variables ambientales a valores de adecuación ("fitness") (Maguire, 1973); y (**M**) a los factores históricos y biogeográficos que permitieron la llegada de la especie a distintos sitios por medio de la dispersión (Sanín y Anderson, 2018).

Diferentes configuraciones en este esquema **BAM** revelan la importancia de cada uno de los procesos ecológicos mencionados. Así, habrá especies en las que los factores bióticos sean los que delimiten su distribución, algunas en las que las barreras al movimiento lo hagan y otras en las que los tres factores sean determinantes (Peterson, 2012; Soberón et al., 2017). Si bien, lo anterior representa algunos de los cimientos de una teoría sobre las áreas de distribución, varias preguntas de interés teórico y práctico sobre cada elemento BAM aún no están resueltas, por ejemplo para A: ¿cuál es la forma del nicho fundamental Grinnelliano? y ¿cómo es la relación entre los atributos de adecuación y la posición de una población en el espacio de nicho?; sobre M, ¿cuál es la relación entre la dispersión y la capacidad de acceder a sitios donde las condiciones ambientales A son favorables? y finalmente, sobre **B**, ¿cuál es el efecto de los mecanismos de interacción como los de la relación depredador-presa en la relación nicho-adecuación de las especies que interactúan?

LA FORMA DEL NICHO Y SU RELACIÓN CON LA ADECUACIÓN

Para entender cómo se relacionan el nicho y adecuación es necesario introducir algunas ideas conceptuales sobre los nichos. Aunque existen diversas concepciones de nicho (ver definiciones), en este trabajo distinguiremos tres tipos de nichos: el fundamental N_F , el fundamental existente N^* y el realizado N_R. El primero hace referencia a todo el conjunto de condiciones ambientales, que denotamos con \vec{e} (un vector constituido por variables como la temperatura, precipitación, pH, entre otras), donde la tasa de crecimiento es positiva $r(\vec{e}) > 0$; este nicho está definido por la fisiología de las especies, en general se conjetura que tiene una forma convexa donde solo hay un punto $\vec{\mu}$ donde la adecuación es máxima (Jiménez et al., 2019); es decir, donde $r(\vec{e}) < r(\vec{\mu}) = r_{max}$ para todo $\vec{e} \neq \vec{\mu}$ y además se espera que $r(\vec{e})$ decrezca como una función de la distancia al punto $\vec{\mu}$. Por otra parte, el nicho fundamental existente N*, es el conjunto de condiciones ambientales presentes en un tiempo t, donde la tasa de crecimiento es positiva; este concepto es de particular interés en la modelación de nichos y áreas de distribución, ya que permite considerar el efecto de los cambios ambientales (i.e. cambio climático) en las áreas de distribución geográfica. El nicho realizado N_R se refiere a las condiciones ambientales en las cuales la especie puede subsistir bajo el efecto de las interacciones bióticas. Las condiciones ambientales que comprende el nicho fundamental son en general más amplias que las del nicho realizado debido a que las interacciones actúan como factores restrictivos (Soberón y Nakamura, 2009). De hecho, tanto el nicho fundamental existente como el realizado son subconjuntos del nicho fundamental (Soberón y Arroyo-Peña, 2017); es decir,

$N_F \supseteq N^* = N_F \cap E(t,G) \supseteq N_R,$

donde $\mathbf{E}(\mathbf{t},\mathbf{G})$ es el conjunto de todas las condiciones ambientales al tiempo \mathbf{t} en el área \mathbf{G} .

En este orden de ideas, un problema que es de especial interés en la biogeografía, es la modelación de N_F y los atributos de adecuación, por medio de técnicas estadísticas que utilizan información ambiental en escalas geográficas (extensiones de por lo menos decenas de km²). Aquí el espacio geográfico **G** se divide mediante una retícula regular

constituida por i = 1, ... n parches. Cada parche i está caracterizado por condiciones ambientales que tienen un efecto en la adecuación r_i y por lo tanto, en la distribución. Debido a que es difícil obtener datos demográficos a lo largo de la distribución geográfica para la mayoría de las especies, estos métodos, conocidos como modelos de nicho ecológico (MNE), utilizan presencias y en ocasiones ausencias para estimar una función de idoneidad ambiental S, que relaciona los valores ambientales (\vec{e}_i) de estas observaciones con la adecuación, bajo el supuesto de que las combinaciones más frecuentes donde se ha observado a la especie, son las que tienen mayor adecuación. Generalmente la función $S(\vec{e}_i)$ toma valores en el intervalo [0,1], donde uno es el punto de mayor adecuación y cero significa no nicho o cero adecuación. Estas herramientas de modelación, han permitido la estimación de las distribuciones potenciales de muchas especies (Peterson, 2011), sin embargo, al carecer de los componentes dinámicos de la distribución (los movimientos e interacciones bióticas) no son capaces de tener estimaciones precisas de la distribución y de los atributos de adecuación.

Por medio de los así llamados MNE, diversos estudiosos han tratado de mostrar con evidencia empírica la conjetura de que existe una relación entre la salida de estos modelos y la abundancia (un atributo de adecuación); sin embargo, los resultados a favor de esta son variados. Por ejemplo, Dallas et al. (2017) y otros (Santini et al., 2018; Dallas y Hastings, 2018), encontraron poca evidencia que apoye a la conjetura en las especies que analizaron (118 de 1419 y 20 de 118, respectivamente). Por otro lado, Martínez-Meyer et al. (2013) y diversos autores (Yáñez-Arenas et al., 2012; Osorio-Olvera et al., 2020; Altamiranda-Saavedra et al., 2020; Ángeles-González et al., 2021), han hallado soporte a la misma, remarcando que la relación podría depender de otros factores como el grupo taxonómico, sus características biológicas y sus capacidades de dispersión. En Osorio-Olvera et al. (2019), los autores estudiaron diversas causas por las cuales la relación nicho-abundancia es difícil de observar; dichas causas van desde los mecanismos dinámicos de las distribuciones como los metapoblacionales, hasta los métodos empleados para estimar la función de idoneidad utilizada para relacionar la abundancia con el nicho. En la siguiente sección retomamos un par de trabajos donde investigamos el efecto de la dispersión, la estructura espacial de las idoneidades y la función de idoneidad S, en la relación nicho-abundancia.

Algunas Definiciones de nicho

Definición 1 (Nicho Fundamental Grinnelliano)

Conjunto de condiciones ambientales donde tasa de crecimiento es positiva, es decir, r > 0 (Soberón y Nakamura, 2009).

Definición 2 (Nicho Eltoniano) Rol funcional de una especie en la comunidad, resultado de la dinámica de las interacciones tipo consumidor-recurso. También llamado "nicho funcional" (Elton, 1927).

Definición 3 (Nicho Hutchinsoniano) Espacio abstracto y multidimensional donde tanto las variables bióticas y abióticas constituyen los ejes del espacio de nicho de la especie

(Hutchinson, 1957).

Definición 4 (Nicho Fundamental Existente) Subconjunto del nicho fundamental que incluye las condiciones ambientales bajo las cuales la tasa intrínseca de crecimiento es positiva, en un espacio geográfico y en un tiempo determinado (Soberón y Nakamura, 2009).

Definición 5 (Nicho Realizado) Condiciones ambientales bajo las cuales la especie puede subsistir en la presencia de competidores u otras especies con las que interactúa negativamente y factores restrictivos (Soberón y Nakamura, 2009).

LA DISPERSIÓN Y SU EFECTO EN LOS ATRIBU-TOS DE ADECUACIÓN

Es importante notar que los trabajos empíricos mencionados anteriormente, tratan de explicar los patrones de abundancia como función de la distancia al centro del nicho ecológico, sin modelar de manera explícita los otros factores **BAM**; es decir, el efecto del movimiento y de las interacciones bióticas. A continuación presentamos algunas predicciones teóricas sobre el efecto de la dispersión en la relación nicho-abundancia, obtenidas a partir de la simulación numérica utilizando modelos metapoblacionales. El primer modelo que presentamos es uno a tiempo y espacio discreto, mientras que el segundo es a tiempo continuo y espacio discreto. En general en ambos modelos suponemos:

- Existe una relación entre la estructura interna del nicho ecológico fundamental N_F y los atributos de adecuación de una población (Maguire, 1973).
- El nicho ecológico a través de los parámetros demográficos determina las posibilidades de que una especie pueda colonizar un área geográfica determinada (Osorio-Olvera et al., 2016).
- El espacio geográfico G, está dividido por una retícula discreta constituida por *i* = 1,2,...,*n* celdas.
- Hay una función matemática que permite relacionar un punto en la geografía con un punto en el espacio ambiental (ecológico) abstracto (Colwell y Rangel, 2009).
- Cada celda *i*, está caracterizada por diversas condiciones ambientales que tienen un efecto en la tasa intrínseca de crecimiento *r_i*.
- Las poblaciones en las celdas crecen de acuerdo a un modelo metapoblacional donde hay un proceso de dispersión

Modelo a tiempo y espacio discreto

El modelo que presentamos a continuación se utilizó en (Osorio-Olvera et al., 2016) para estudiar la relación entre abundancia poblacional y posición en el espacio de nicho bajo diferentes escenarios de dispersión en un espacio con n parches. El modelo está dado por

$$N^{i}(t+1) = \mathbf{S}^{i} \mathbf{M} N^{i}(t) + \Delta^{i} \left(N^{\overline{i}} \right), \tag{1}$$



donde S_i es una matriz diagonal con la idoneidades de cada estadio. M es la matriz de proyección poblacional con entradas $(a_{r,s})$; $N^i(t)$ es un vector con el número de individuos de cada estadio en el parche *i*.

$$\mathbf{S}^{i} = \begin{pmatrix} S_{1}^{i} & 0 & \dots & 0\\ 0 & S_{2}^{i} & \dots & 0\\ \vdots & \vdots & \ddots & \vdots\\ 0 & 0 & \dots & S_{m}^{i} \end{pmatrix}$$
(2)

Finalmente $\Delta^{i}\left(N^{\overline{i}}\right)$ es el flujo neto de inmigrantes a *i*.

$$\Delta^{i}\left(N^{\bar{i}}\right) = \left(\sum_{i,h} \Delta_{i,h} N_{1}^{i}(t), \sum_{i,h} \Delta_{i,h} N_{2}^{i}(t), \cdots, \sum_{i,h} \Delta_{i,h} N_{m}^{i}(t)\right).$$
(3)

con $\Delta_{i,h}N_s^i(t) = \delta_{i,h}N_s^i(t) - \delta_{h,i}N_s^i(t)$. Los parámetros $\delta_{i,h}$ y $\delta_{h,i}$ determinan la proporción de inmigrantes y emigrantes, respectivamente en un parche *i* y están determinados por un kernel de dispersión que depende de la distancia.

Los resultados de la simulación numérica muestran que a pesar de que el modelo de la Ecuación (1) está diseñado para que haya una relación entre nicho y abundancia, la dispersión es un mecanismo que regula su fortaleza, de tal modo que entre más grande sea la proporción de individuos que se dispersan, la relación tiende a hacerse más débil (Fig. 2). Lo anterior sugiere una conjetura acerca de las condiciones en las que los procesos demográficos y de dispersión pueden hacer que la correlación entre abundancia y distancia al centroide del nicho se oscurezca; por ejemplo, se espera que las especies cuyas tasas de migración son altas, muestren una correlación baja entre abundancia y nicho. Esto concuerda con los hallazgos recientes de Osorio-Olvera et al. (2020), quienes estudiando diversos grupos de aves, encontraron que tanto el tamaño del nicho y la capacidad de dispersión influyen en la fuerza de la relación; de manera particular, se encontró que el patrón nicho-abundancia es menos marcado en especies migratorias y en las que presentan nichos amplios. Este resultado se relaciona con otros obtenidos anteriormente (Pulliam, 2000), donde también se hace énfasis del papel de la migración en la persistencia de poblaciones sumidero. Pese a que el modelo (1) es sencillo, notamos su relevancia para obtener conjeturas plausibles de los mecanismos que determinan la distribución de las especies y su abundancia. Un aspecto relevante del modelo (1) en términos ecológicos, es que considera de manera explícita que hay una idoneidad ambiental diferenciada a lo largo de las etapas de desarrollo (ecuación 2), lo cual ha sido poco explorado, en gran parte por la falta de datos empíricos.

Modelo a tiempo continuo y espacio discreto

En Osorio-Olvera et al. (2019) utilizamos un modelo metapoblacional a tiempo continuo en un espacio discreto para mostrar la forma en que diversos factores naturales pueden modificar la relación esperada entre abundancia y distancia al centro del nicho. Estudiamos por una parte, el efecto de tener barreras biológicas al proceso de dispersión y por otra, el papel de la estructura espacial de las idoneidades en la dinámica de crecimiento de las poblaciones que se



Figura 2: Valores del coeficiente de determinación \mathbb{R}^2 de la relación nicho-abundancia como función de la proporción de individuos δ que se dispersan de un parche a otros. Imagen modificada de (Osorio-Olvera et al., 2016).

desarrollan en un área donde ocurren las simulaciones. Para ello, creamos una especie hipotética, cuyo nicho fundamental presenta dos sitios de alta idoneidad ubicados cerca del centroide; además, se considera que en el espacio geográfico, estos sitios se encuentran claramente separados por parches donde la idoneidad es cero (Fig. 3, para saber los detalles de cómo se creó la especie *ver* (Osorio-Olvera et al., 2019)).

El mecanismo para modelar el papel de las barreras biológicas a la dispersión, fue el efecto Allee (Keitt et al., 2001). Estudiamos dos casos de interés general: el primero fue un escenario donde todos los parches son accesibles (no hay efecto Allee) y el segundo uno donde el efecto Allee es lo suficientemente fuerte como para evitar la llegada de los propágulos de A a B, y viceversa. A continuación mostramos el modelo

$$\dot{x}_i = \left(r_i x_i - a_i x_i^2\right) \left(x_i - M_i\right) + \sum_h \delta_{hi} x_h - \sum_h \delta_{ih} x_i, \qquad (4)$$

donde \dot{x}_i es la tasa de cambio de la población en la celda *i* en el tiempo *t*. La tasa intrínseca de crecimiento en el parche *i* es r_i . El factor de denso-dependencia es a_i . El efecto Allee es M_i . La tasa de inmigración a la celda *i* es δ_{hi} .

El análisis estadístico de las simulaciones numéricas, mostró que la relación entre distancia al centroide del nicho y la abundancia, depende en gran parte de la capacidad de los propágulos de colonizar sitios con baja idoneidad, ya que estos son utilizados como *stepping stones* para alcanzar las zonas de alta idoneidad. En este modelo, el mecanismo que regula dicha capacidad es el efecto Allee. Para el caso donde M = 0, los propágulos son capaces de invadir prácticamente todos los parches que conforman la arena; la relación nichoabundancia se hace más fuerte conforme las poblaciones en los parches alcanzan su estado de equilibrio (Fig. 4).

Por otro lado, cuando $M_i > 0$, se comienza a observar zonas no colonizables, de modo tal que, si M_i es suficientemente grande, la especie tendrá una distribución muy



Figura 3: El nicho fundamental y el mapa de idoneidad de la especie hipotética. Panel izquierdo: el elipsoide azul representa al el nicho fundamental de la especie (N_F), definido por la temperatura del mes más cálido (Bio 5), la temperatura en el mes más frío (Bio 6) y la precipitación anual acumulada (bio12); los puntos rojos son las combinaciones ambientales del espacio geográfico que caen fuera del nicho; y en naranja, verde y azul los puntos que caen dentro de éste. Panel izquierdo: valores de idoneidad de los parches en el espacio geográfico; la intensidad del verde corresponde a sitios con mayor idoneidad (más cercanos al centroide). A y B denotan el mismo conjunto de parches tanto en el espacio de nicho como en el geográfico. Observando los dos paneles se puede notar que A y B están muy cercanos en el espacio de nicho, pero que a su vez están separados por regiones no idóneas.

Figura 4: Simulación numérica de la relación entre abundancia y distancia al centroide del nicho para las poblaciones modeladas sin efecto Allee. A la izquierda, se muestra el mapa de la distribución geográfica de la abundancia como función del tiempo. A la derecha, la relación estadística entre distancia al centroide del nicho y la abundancia para distintos tiempos

restringida. Más aún, la relación entre distancia al centroide del nicho y abundancia tiende a cero, pese a que la especie hipotética fue diseñada para que presentara esta relación (Fig. 5). Lo anterior es interesante desde un punto de vista de la teoría ecológica, ya que se pueden utilizar estos mecanismos para simular atributos específicos de la distribución de las especies, por ejemplo; en Owens et al. (2013), los autores notaron que las especies pueden ser clasificadas de acuerdo con la relación que guardan los componentes **BAM**. Estos autores distinguen por lo menos tres tipos de especies: 1) las especies *Hutchinsonianas*, caracterizadas porque tienen la capacidad de acceder a todos lo sitios en el área **G** (la distribución de estas especies está determinada

principalmente por A); 2) las especies *Wallaceanas*, en las cuales su distribución está fuertemente determinada por su baja capacidad de dispersión (la distribución depende mucho de M), por lo que les es muy difícil de acceder sitios idóneos, alejados de su área de distribución nativa; 3) finalmente, las del **BAM** clásico (ver Fig. 1), donde los tres factores se sobrelapan parcialmente y ninguno de ellos domina la distribución.

El modelo del Sistema (4) puede ser utilizado como base para generar/modelar especies Hutchisonianas o Wallaceanas, utilizando como mecanismo al efecto Allee.



En la siguiente sección analizaremos cómo los mecanismos de interacción biótica (el componente **B** del **BAM**) pueden influir en los patrones de abundancia y distribución de las especies.

SOBRE LOS MECANISMOS DE INTERACCIÓN

Como se ha explicado en las líneas anteriores, la relación teórica entre el nicho y la tasa de crecimiento de una especie puede alterarse debido a múltiples factores como son las variaciones ambientales, condiciones geográficas y la biodiversidad del medio que necesariamente introduce mecanismos de interacción que afectan la distribución de las especies. La literatura donde se tratan estas cuestiones es muy abundante y en constante desarrollo, ya que el campo de investigación es muy amplio como resultado, por ejemplo, del gran número de interacciones entre especies y entre organismos de una misma población.

Un fenómeno de interés cuya importancia ha sido resaltada en muchos estudios es la reproducción estacional. En Quintero et al. (2014), los autores estudian como la disponibilidad de alimentos regula o interactúa con los distintos ciclos reproductivos que muestran algunas especies y el impacto que esto tiene en la diferenciación genética de las mismas. En Blé et al. (2011), los autores analizan la dinámica de una población con dos estaciones reproductivas A y B por cada unidad de tiempo (un año), con el fin de analizar el efecto de la superposición de dos dinámicas reproductivas diferentes en el crecimiento poblacional de una especie semélpara. La población se reproduce en la estación de acuerdo con un modelo logístico con parámetro a y en la estación B con parámetro b. El modelo resultante que determina el tamaño población anual es la composición de dos aplicaciones logísticas $F_a(x) = ax(1-x)$ y $F_b(x) = bx(1-x)$. Se encontró que largos periodos con una escasa reproducción en una de las estaciones puede llevar a la extinción de la población, aún cuando haya una rica reproducción en la otra. El modelo muestra la Coexistencia de dinámicas; es decir, dos poblaciones bajo las mismas condiciones ambientales puede mostrar fluctuaciones anuales diferentes que solo dependen de su densidad inicial. Este hecho contrasta fuertemente con los resultados que se obtienen cuando la superposición de las dos dinámicas es aleatoria; en Blé et al. (2007) se utilizó como modelo el proceso de Markov $X_n = F_a \circ F_b^{c_n} \circ F_a \circ \cdots \circ F_b^{c_i}$, en el que $\{c_i | i \in \mathbf{N}\}$ es un proceso de Poisson y se demostró que para cierto subconjunto de la región de parámetros $[a,b] \times [a,b]$, el sistema tiene una única medida invariante, por lo tanto, el comportamiento asintótico es el mismo para casi cualquier densidad inicial.

Las especies no viven aisladas; por el contrario, forman complejas redes de interacción que conducen a que las fuerzas evolutivas inducidas por el medio ambiente se alteren e induzcan nuevos mecanismos adaptativos que permitan la supervivencia de la especie, aunque tal vez alejados de aquellas que determinan su nicho fundamental. Uno de estos mecanismos, es el comportamiento diferenciado de los individuos en ciertas etapas etarias de su desarrollo como ya se mencionó en este trabajo (ver Sistema (1)). A. Hastings en Hastings (1983) y Hastings (1984) ha resaltado la importancia de la depredación selectiva por grupo de edad de la presa, como factor que promueve la persistencia de las poblaciones. A lo largo de su ciclo de vida, los cambios de tamaño y morfología que presentan los individuos de algunas especies tienen efectos importantes en la dinámica poblacional. Por ejemplo, B. Ebenman en Ebenman y Persson (1988) analiza cómo estos cambios afectan la competencia intraespecífica entre los diferentes grupos de edad y las consecuencias de esto sobre las variaciones temporales de la población. Más allá del interés teórico que guarda el entender la relación entre estructura de edad y crecimiento poblacional, la comprensión de este proceso puede ser útil para el manejo y conservación de las especies, ver Lingle et al. (2008), Quinn y Cresswell (2004). Los mecanismos y características de la depredación diferenciada por edad de la presa son muy variados y lo que uno observa actualmente, es el resultado de la coevolución de las especies involucradas. En Falconi et al. (2015), se consideró una presa con dos clases de edad: la densidad de la clase no reproductiva es denotada con x y la densidad de la clase reproductiva es y. Los juveniles presentan un mecanismo de defensa denso-dependiente y cada clase interfiere en la actividad de captura del depredador, de modo que la tasa de depredación sobre una clase, disminuye si la densidad de la otra aumenta. Con el propósito de estudiar el efecto en la supervivencia del depredador de la riqueza del medio en el que se desarrolla la presa se analizó el modelo

$$\dot{x} = r(1 - \frac{x}{K})y - vx - \frac{xz}{1 + x^2 + y},$$

$$\dot{y} = vx - \mu y - \frac{yz}{1 + x + y},$$

$$\dot{z} = (\frac{\gamma x}{1 + x^2 + y} - \frac{\lambda y}{1 + x + y} - D)z.$$

Una alta población de la clase adulta o reproductiva afecta de dos formas a la tasa de crecimiento del depredador: 1) hace que aumente la tasa de crecimiento de la clase juvenil y por lo tanto, se refuerza su mecanismo de defensa; y 2) se incrementa la interferencia sobre la depredación de la clase juvenil. Así, el depredador se extingue ya que el beneficio que obtiene de x disminuye y no lo puede compensar el incremento de su tasa de reproducción debido a y, si $\lambda < D$. Más aún, si la tasa de mortalidad de la clase reproductiva es suficientemente baja, la coexistencia de las dos especies es posible solo si la riqueza del medio, no es muy pequeña ni muy grande. En el primer caso, porque no habría suficiente biomasa para alimentar al depredador y en el segundo caso, como resultado de la riqueza del medio, la población de presas sería grande y entonces los efectos de defensa e interferencia se incrementarían a niveles no soportables para el depredador. La interferencia entre depredadores de distintas especies es también un tema relevante en la distribución de las especies y se ha tratado en Falconi et al. (2020).

La forma en la que la depredación influye en la distribución de las especies depende en buena medida de la conducta particular que haya desarrollado para perseguir a su presa. La eficiencia de la búsqueda también ha recibido atención por sus consecuencias en la adaptación de ambas especies; sin embargo, evaluar esta eficiencia es en general complicado, debido entre otros factores, a que las estrategias de búsqueda pueden cambiar por las condiciones ambientales, las cuáles **Figura 5:** Simulación numérica de la relación entre abundancia y distancia al centroide del nicho para las poblaciones modeladas con efecto Allee (M = 10). A la izquierda, se muestra el mapa de la distribución geográfica de la abundancia como función del tiempo. A la derecha, la relación estadística entre distancia al centroide del nicho y la abundancia para distintos tiempos

presentan a menudo bruscas fluctuaciones, ver Bartumeus et al. (2002), Zollner y Lima (1999). En Ross y Winterhalder (2015), han contrastado la estrategia de búsqueda activa con la de sentarse y esperar cuando las presas y depredadores se mueven aleatoriamente. De acuerdo con este trabajo, la búsqueda activa se correlaciona bien con presas que se mueven a bajas velocidades; en cambio, la emboscada es una mejor estrategia para presas veloces. Esta última estrategia también se ve favorecida si la interferencia aumenta debido a la velocidad del depredador. En Zoroa et al. (2011), se hace un estudio comparativo de estas dos estrategias utilizando la teoría de juegos. Establecer si ciertos rasgos, por ejemplo de conducta, conducen a diferencias funcionales es un tema que resulta de interés en la Ecología; un trabajo en esta dirección es War et al. (2012), en el que los autores analizan un numerosa cantidad de especies de arácnidos y encontraron que las diferencias funcionales crecen si las diferencias en las estrategias de caza, crecen y concluyen que estas estrategias influyen en las redes tróficas por medio de interacciones depredador-presa específicas.

El movimiento de los individuos inducidos por la emisión de substancias químicas es una característica presente en una gran variedad de especies; es frecuente que las plantas atraigan a sus polinizadores por la emisión de sustancias volátiles. En muchas especies, la búsqueda de alimento está regulada por los olores que emanan de los recursos. Con ensayos de laboratorio, en Dormont et al. (2006) mostraron que los escarabajos se dirigían hacia los volátiles del estiércol del mismo tipo que preferían en el campo. Los elementos volátiles también son utilizados por algunas especies como mecanismos indirectos de defensa, ya que estos sirven para atraer a los enemigos de sus depredadores; véase War et al. (2012) y la bibliografía ahí citada.

Ambos aspectos, estrategias de búsqueda de la presa y defensa indirecta inducidos por la emisión de volátiles, se abordan en Anaya et al. (2021) en una red tritrófica. El recurso es consumido por un mesodepredador, y este es depredado por un superdepredador. Las tres especies se dispersan en un medio S de acuerdo con la ley de difusión de Fick. Para simular un medio ambiente variable, la riqueza K del medio es una función positiva, definida en S. Las densidades del recurso, del mesodepredador y del superdepredador se denotan con u, v, w, respectivamente. Para estudiar el efecto de la defensa indirecta del recurso, en el modelo se considera que este produce un volátil que es percibido por el superdepredador y lo induce a moverse en la dirección del gradiente de u; así, la dispersión de w queda determinada por $d_2\Delta w - \nabla \cdot (\chi_1(u, w)\nabla u))$, en la que $\chi_1(u, w)$ es la sensibilidad del superdepredador al volátil; en el modelo, $\chi_1(u, w)$ es una función creciente de u y w y depende de un parámetro q que mide la rapidez conque el superdepredador se mueve hacia el recurso. Se analiza la dinámica del modelo en tres escenarios: E1) las tres especies viven en un mismo sitio por lo que no hay difusión ni atracción; E2) Las tres especies se difunden en una región acotada sin flujo hacia el exterior y no hay atracción, i.e q = 0; E3) Las tres especies se difunden y el recurso atrae al superdepredador (q > 0). El análisis del modelo en los casos E2) y E3) se realiza bajo condiciones sobre los parámetros que en el escenario E1) conducen a la extinción del superdepredador. Los resultados dan evidencia del rol que juega la migración en la supervivencia de las poblaciones y distribución de las especies. En el escenario E1, aunque inicialmente la población del recurso decrece fuertemente y ambos depredadores mantienen altos niveles, finalmente el superdepredador tiende a extinguirse; esto se explica porque la tasa de depredación del superdepredador es pequeña respecto a su tasa de mortalidad. En la situación correspondiente a E2) es el mesodepredador el que mantie-



ne una baja densidad y las tres especies tienden a sobrevivir. Aparentemente, la dispersión de las tres especies produce un flujo de mesodepredadores hacia zonas de baja densidad lo que permite que el número de encuentros con los superdepredadores sea suficientemente alto, y evita que la población de mesodepredadores aumente en estos sitios. Este mecanismo hace que la población de meso y superdepredadores se distribuyan homogénemente y el recurso se concentre en las zonas de mayor capacidad de carga del ambiente. Esta distribución espacial de las especies cambia si se considera el escenario E3; la atracción del superdepredador hacia el recurso favorece que el meso depredador tienda a ocupar espacios distintos al del superdepredador, el cual se concentra en los sitios de mayor densidad del recurso. En la naturaleza, un ejemplo que no es completamente análogo al caso E3, porque no hay un volátil (aparentemente) de por medio, pero en términos del patrón espacial es parecido, ha sido observado con los guepardos (Acynonyx jubatus) y los perros salvajes africanos (Lycaon pictus), los cuales evitan las áreas con alta densidad de presas porque estas son sitios donde competidores y superdepredadores, como las hienas manchadas (Crocuta crocuta) y los leones (Panthera leo), alcanzan densidades poblacionales altas (Laurenson, 1994; Creel y Creel, 1996; Mills y Gorman, 1997).

CONCLUSIONES Y REFLEXIONES

En este trabajo se hace una revisión de estudios donde los autores utilizan modelos matemáticos como herramientas para ayudar a entender el papel de diferentes mecanismos ecológicos en la distribución de las especies. Se puso especial énfasis, en aquellos que influyen la relación entre posición en el espacio de nicho con los atributos de adecuación desde el contexto del diagrama BAM; en particular, se estudió la relación entre distancia al centroide del nicho y la abundancia poblacional, y se hizo mención tanto a trabajos empíricos que han reportado resultados donde no se observa un patrón claro sobre la existencia de la relación, como otros en los que es posible observarla, aunque suele ser débil. Con base en los análisis (numéricos y matemáticos) de los modelos presentados aquí, conjeturamos que en la naturaleza es difícil observar la relación nicho-abundancia, debido a que hay una gran variedad de procesos que la pueden oscurecer, como por ejemplo, el efecto Allee, conductas diferenciadas por estadío, tipos de interacción biótica, la forma en que covarían los mecanismos de interacción y migración, entre otros. Por lo tanto, lejos de querer mostrar solo con datos empíricos la existencia de la relación, consideramos que es de vital importancia comprender el papel de cada uno de estos mecanismos en la dinámica espacio-temporal de las poblaciones que conforman el área de distribución de cada especie. Es de esperarse que haya especies en las que un mecanismo tenga mayor relevancia que otros; por ejemplo, se ha documentado que especies de aves no migratorias cuyos nichos son pequeños, suelen presentar relaciones nicho-abundancia más fuertes, que aquellas con nichos amplios y con estaciones migratorias marcadas (Osorio-Olvera et al., 2020). Es importante también notar, que la relevancia de los mecanismos de distribución y abundancia es dinámica, por lo que puede cambiar a lo largo del tiempo, presentándose así, casos donde en un periodo

determinado los tres factores **BAM** tengan importancia similar en la determinación de la distribución y abundancia, sin embargo perturbaciones sobre ellos (como lo pueden ser extinciones asociadas a factores de estocasticidad ambiental y/o demográfica (Dallas y Santini, 2020)), cambien de manera dramática estas relaciones. Lo anterior se ha observado en una serie de experimentos realizados por Paine (Paine, 1966, 1969, 1974), donde la extracción selectiva del depredador (*Pisaster ochraceous*), provocaba el rápido crecimiento de su presa principal (*Mytilus californianus*) y la extinción local de varias especies por exclusión competitiva (aquí es claro que el factor **B** toma un papel determinante).

Con todo lo anterior, en este trabajo se ha buscado resaltar la importancia de fortalecer la relación entre los estudios teóricos sobre la dinámica poblacional de las comunidades ecológicas y los trabajos experimentales y de campo, con el fin de entender mejor los patrones empíricos que se observan en la naturaleza.

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Growth and extinction in randomly varying environments: modelling and optimization using stochastic differential equations

Crecimiento y extinción en ambientes que varían aleatoriamente: modelamiento y optimización mediante ecuaciones diferenciales estocásticas

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Abstract—This paper presents a brief overview of a range of applications of stochastic differential equations (SDE) in describing the growth of wildlife populations living in randomly varying environments and the associated risks of extinction, including profit optimization issues in the particular case of fish or other populations subjected to harvesting. The same basic ideas apply also to the growth of individual animals and how to optimize the profit of the farmers that raise such animals.

Keywords—Stochastic differential equations, random environments, population growth models, extinction, fisheries, individual growth models, profit optimization

Resumen— Este artículo presenta una breve descripción de una gama de aplicaciones de las ecuaciones diferenciales estocásticas (SDE) para describir el crecimiento de poblaciones de vida silvestre que viven en condiciones ambientales que varían aleatoriamente y los riesgos asociados de extinción, incluidos los problemas de optimización de ganancias en el caso particular de peces u otras poblaciones sometido a recolección. Las mismas ideas básicas se aplican también al crecimiento de animales individuales y cómo optimizar las ganancias de los granjeros que crían tales animales.

Palabras clave— Ecuaciones diferenciales estocásticas, ambientes aleatorios, modelos de crecimiento poblacional, extinción, pesquerías, modelos de crecimiento individual, optimización de ganancias

INTRODUCTION

T he growth of a wildlife population over time or the growth of an individual animal from birth to maturity are often described by a deterministic growth curve, usually the solution of an ordinary differential equation (ODE) that describes the dynamics of the growth process. For example, if we have Gompertz growth dynamics, the size X(t) of the population at time $t \ge 0$ or of an individual animal at age

 $t \ge 0$ would be described by the ODE

$$\frac{dX(t)}{dt} = rX(t)\ln\frac{K}{X(t)},$$

where K > 0 is the asymptotic size and r > 0 is a speed of growth parameter, the solution of which is the Gompertz curve $X(t) = K\left(\frac{x_0}{K}\right)^{\exp(-rt)}$, where $x_0 = X(0) > 0$ is the initial size. Of course, $X(t) \to K$ when $t \to +\infty$ and K is called the *carrying capacity* of the environment in the population growth literature and it is the *size at maturity* for



Figure 1: Time evolution of the population size (measured in individuals per cm³) of a lab protozoan population (data from (Gause, 1934)). The solid broken line represents the observed data and the dashed smooth curve is the estimated Gompertz curve.



Figure 2: Age evolution of the size (in kg) of an individual cow of the Mertolengo breed (data from (Filipe et al., 2007)). The solid broken line represents the observed data and the dashed smooth curve is the estimated Gompertz curve.

an individual animal growth.

However, when we look at the data, what we observe is not this nice very smooth growth curve but rather a more irregular curve somewhat fluctuating around it, accompanying the effect of the random fluctuations that occur in nature on the internal and external environmental conditions. In Figures 1 and 2 we can see the observed irregular data for the size (in individuals per cm³) of a lab population of the protozoan *Paramecium caudatum* (data from (Gause, 1934)) and for the size (in kg) of a cow of the Mertolengo breed raised in the Alentejo region of Portugal (data taken from (Filipe et al., 2007)), respectively, together with the estimated smooth Gompertz curve that would occur under constant environmental conditions.

The usual literature on individual animal growth considers a growth curve (the Gompertz curve or some other function of age) and uses a regression model in which, typically, the observed deviations from the curve are assumed to be independent and identically distributed. That would be quite appropriate if they were due to measurement errors, which are negligible with our weighting apparatus. With such a model, looking at a cow that has now a weight quite below the growth curve, the prediction for its weight next week will be the weight given by the growth curve, a miraculous weight recovery in just a week. The deviations from the growth curve are, in fact, due to fluctuations in the growth rate induced by internal and external random environmental conditions and so, a good prediction for the weight next week should instead use today's weight as a starting point and project it to next week using the growth dynamics given by the differential equation. But we have to take into account that the growth rate is not exactly given by the deterministic differential equation because it keeps suffering the influence of the environmental conditions, which will introduce some amount of uncertainty on the prediction.

To take into account the influence of the random environmental fluctuations on the growth rate, that influence should be included in the differential equation that drives the growth process dynamics, making it a *stochastic differential equation* (SDE). The same applies to population growth dynamics.

There are many other dynamical phenomena in Biology and in several other different areas of Science and Technology where the descriptive variable(s) change in time according to some rules concerning its rate of change (i.e., its time derivative), rules that are conveniently described by an ODE. For simplicity of notation, we consider here the unidimensional case of a single variable X(t) following the ODE

$$\frac{dX(t)}{dt} = F(t, X(t)) \quad \text{or} \quad dX(t) = F(t, X(t)) \ dt,$$

with initial condition $X(0) = X_0$ (we consider for simplicity 0 as the starting time, but it can be replaced by some other time t_0). The extension to the multidimensional case is relatively simple, working with the column vector of the several descriptive variables involved.

Such dynamical phenomena are often influenced by many other variables not considered in the model, either for parsimonious reasons due to their less relevant effect or for the simple reason that they are unknown or impossible to measure and predict. But such factors have an effect on the rate of change of X(t). So, it is quite natural to group that effect in a single temporal variable having a necessarily random behavior, i.e., a stochastic process, and include it as an additional term in the equation. So, the original terms in the equation describe the deterministic dynamics that result from the variables explicitly considered in the model and the additional term describes the perturbation caused on such dynamics by other factors. That is similar to the probabilistic treatment we use to describe the result of throwing a coin instead of trying to model the gravity, air resistance and hand movement forces involved.

Assuming that there are many such perturbating factors that affect the rate of change of X(t), when grouping their effect on a single stochastic process the central limit theorem



would lead to an approximately Gaussian behavior, and so we assume here that such stochastic process is Gaussian.

Let us look at the integral of such stochastic process, i.e. the stochastic process of the accumulated perturbations between time 0 and time t > 0. It is likely that the effect of the perturbations acting on a given time interval is approximately independent of the effect of the perturbations on another non-overlapping time interval, so we will assume that this stochastic process, besides being Gaussian, has independent increments. If the many perturbations have approximately independent additive effects and occur with a relatively uniform frequency, the number of perturbations occurring in a time interval is approximately proportional to the interval's length and so their accumulated effect on that time interval has a variance also approximately proportional to the length of the interval. Even if such proportionality is not correct and the "constant" of proportionality is in fact variable with time and X(t), we can incorporate such variability in a multiplicative factor G(t, X(t)) that modifies an underlying perturbing process truly proportional and for which we can choose the constant of proportionality to be = 1. From all of the above, and assuming time continuity of the perturbations, we can assume that the underlying process behind the accumulated perturbations in the time interval [0,t] is a Wiener process, the only continuous Gaussian processes with independent increments and variance of the increment over a time interval exactly proportional to the interval's length. Since obviously the accumulated effect of perturbations on the time interval [0,0] should be = 0 and we can choose the constant of proportionality to be = 1 (so that the increment on a time interval has variance equal to the length of the interval), we can take as underlying process the standard Wiener process W(t), also known in the literature as Brownian motion (since it was used as a model of the Brownian motion of a particle suspended in a fluid). The square of the multiplicative factor $G^2(t, X(t))$ should take care of the variance of the perturbations per unit time and it may be constant or may depend on t and X(t).

In an infinitesimal time interval dt, the effect of the perturbations will then be given by the effect of the underlying perturbations, i.e. the increment dW(t) of the cumulative underlying process on that time interval, multiplied by the multiplicative factor G(t, X(t)). So, our general initial ODE becomes the general stochastic differential equation

$$dX(t) = F(t, X(t)) dt + G(t, X(t)) dW(t),$$
(1)

with the same initial condition $X(0) = X_0$; since the initial value X_0 may in some cases be unknown, nothing prevents X_0 from being a random variable, as long as it is independent of the Wiener process W(t).

All this can be generalized to the multidimensional case (with also multidimensional Wiener processes) and also to non-continuous underlying processes (processes with jumps).

The randomness of the perturbations is associated to a probability space $(\Omega, \mathscr{F}, \mathscr{P})$, where Ω can be considered the set of all possible environmental "states", from which an observed state $\omega \in \Omega$ is "chosen by chance" according to the probability law *P*, which is defined for the sets of states belonging to the σ -algebra \mathscr{F} . Notice that a state

 ω describes a concrete whole history of environmental conditions over the full time span for which we are using the SDE. The stochastic process W(t) depends also on "chance", i.e. on ω , so W(t) is an abbreviation of $W(t, \omega)$. For a fixed ω , $W(t, \omega)$ is a function of time (called a trajectory, realization or sample path) that describes the evolution over time of the underlying cumulative effect of the perturbations between time 0 and time *t* when the state of the environment is ω . Different states will in general have different trajectories. Of course, a solution (when it exists) of the SDE is also a stochastic process and so, when we write X(t), that should be taken as an abbreviation of $X(t, \omega)$. When we make predictions about a future fixed time *t*, we should remember that they must assume a probabilistic nature since $X(t) = X(t, \omega)$ is a random variable.

One may think that there are always perturbing factors not explicitly considered in a ODE deterministic model and so one should always use SDE models to take the uncertainty they cause in due consideration. Indeed, there are cases (sometimes even with relatively small *G* values) where the results obtained using the SDE model are quantitatively, and sometimes qualitatively, quite different from the results obtained using the ODE model with mean values of the variables or of the parameters, making the ODE models useless. That is certainly the case in many biological phenomena, in epidemiology, in seismology, in finance (stocks, futures, options, etc.) or in telecommunications. However, considering the added complexity of SDE models, it is not worth using them if the perturbing factors are relatively irrelevant.

In the next section we give a brief introduction to the treatment of stochastic differential equations following the steps of (Braumann, 2018). Of course, the reader interested in using SDE should follow up using a textbook like, for example, (Braumann, 2019), (Arnold, 1974) or (Øksendal, 2003).

Among the many areas of application, we are here just illustrating some biological applications related to population growth and individual animal growth. We start by looking at the modeling of population growth in a randomly varying environment and the associated extinction issues. The particular case of populations subject to harvesting, like it is the case in fisheries and forestry, is treated next, focusing on how to optimize the profit from the harvesting activity. After that, we deal with individual growth models for farm animals and some issues on profit optimization for farmers raising those animals. Finally, we present some conclusions and suggest further reading on related issues.

BRIEF INTRODUCTION TO STOCHASTIC DIF-FERENTIAL EQUATIONS

The solution of the SDE (1) with the initial condition $X(0) = X_0$ is the solution of the corresponding integral equation

$$X(t) = X_0 + \int_0^t F(s, X(s)) \, ds + \int_0^t G(s, X(s)) \, dW(s).$$
 (2)

Please keep in mind that W and X both depend also on ω , although we use the common convention of not writing

that dependence explicitly. But, if we fix the trajectory ω , we will only have functions of time and, under sufficient regularity conditions, the first integral in (2) can be interpreted as an ordinary Riemann integral. However, the second integral cannot be interpreted as a Riemann-Stieltjes integral since the integrator W(t) has unbounded variation for almost all trajectories. For that reason, when we approximate the second integral (the stochastic integral) by Riemann-Stieltjes sums for a sequence of tagged partitions $0 = t_{n,0} < t_{n,1} < \ldots < t_{n,n-1} < t_{n,n} = t$ $(n = 1, 2, \ldots)$ of the [0,t] interval with mesh $\delta_n = \max_{k=1,\ldots,n}(t_{n,k} - t_{n,k-1})$ converging to zero, the limit of such sums depends on the choice of the tags (i.e. the intermediate points $\tau_{n,k} \in [t_{n,k-1}, t_{n,k}]$) where the integrand function G(s, X(s)) is computed. Different choices lead to different stochastic integrals.

If, for each subinterval *k* of the partition, we choose as tag $\tau_{n,k} = t_{n,k-1}$ the initial point of the subinterval, that has the advantage of being *non-anticipative* (the present dynamics is not affected by the future random fluctuations) and we obtain, assuming appropriate regularity conditions, the *Itô integral*

$$\int_{0}^{t} G(s, X(s)) \, dW(s)$$

= $\lim_{n \to \infty} \sum_{k=1}^{n} G(t_{n,k-1}, X(t_{n,k-1})) (W(t_{n,k}) - W(t_{n,k-1})), \quad (3)$

where we have used the mean square limit (L^2 convergence with respect to ω), represented by l.i.m., of the Riemann-Stieltjes sums. Under appropriate regularity conditions on *G*, the Itô integral has excellent probabilistic properties, like having a null mathematical expectation $\mathbb{E}\left[\int_0^t G(s,X(s))dW(s)\right] = 0$, having variance equal to $\int_0^t \mathbb{E}[G^2(s,X(s))]ds$ and being a martingale as a function of *t*. However, it does not follow the ordinary calculus rules and we need a new calculus, the *Itô stochastic calculus*, which is characterized by the following differentiation chain rule:

Itô formula (or Itô theorem). Let h(t,x) be $C^{1,2}$ (have a continuous partial derivative in t and first and second order continuous partial derivatives in x), assume F and G satisfy appropriate regularity conditions, let X(t) be unique solution of the SDE (1) and consider the stochastic process Y(t) = h(t, X(t)). Its differential, contrary to ordinary calculus rules (based on first order expansions), is based on the second order expansion in x, $dY(t) = \frac{\partial h}{\partial t}dt + \frac{\partial h}{\partial x}dX(t) +$ $\frac{1}{2}\frac{\partial^2 h}{\partial x^2}(dX(t))^2$. Note that the second order term $(dX(t))^2$ would be of lower order than dt in ordinary calculus and, therefore, would not appear, but, due to the irregularity of the trajectories of the Wiener process W(t), this is not true here (note that $\mathbb{E}\left[\left(W(t+\Delta t)-W(t)\right)^2\right] = \Delta t$). Therefore, now $(dX(t))^{2} = (Fdt + GdW(t))^{2} = F^{2}(dt)^{2} + 2FGdtdW(t) +$ $G^{2}(dW(t))^{2} = 0 + 0 + G^{2}dt$ (since the first two terms are of lower order that dt but the third term is of the same order as dt). Replacing dX(t) and $(dX(t))^2$ by their expressions and collecting terms, we obtain the Itô chain rule (with F, G and *h* and their derivatives computed at the point (t, X(t)):

$$dY(t) = \left(\frac{\partial h}{\partial t} + \frac{\partial h}{\partial x}F + \frac{1}{2}\frac{\partial^2 h}{\partial x^2}G^2\right)dt + \frac{\partial h}{\partial x}GdW(t).$$
 (4)

There are other stochastic integrals corresponding to other (anticipative) choices or combinations of choices of the tag points used in the Riemann-Stieltjes sums. The most popular of them is the *Stratonovich integral*

$$(S) \int_{0}^{t} G(s, X(s)) dW(s)$$

= l.i.m. $\sum_{k=1}^{n} G\left(t_{n,k-1}, \frac{X(t_{n,k-1}) + X(t_{n,k})}{2}\right) (W(t_{n,k}) - W(t_{n,k-1}))$
(5)

Since this expression contains a trajectory smoothing, the Stratonovich integral follows the ordinary rules of calculus, but in general lacks the nice probabilistic properties of the Itô integral. Also, for the same functions *F* and *G*, the solution of the Stratonovich SDE (i.e. the solution of the SDE one obtains by using Stratonovich integrals) is in general different from the Itô SDE solution. Using (3) and (5), it is easy to show that the Itô SDE dX = Fdt + GdW is equivalent to (has the same solution as) the Stratonovich SDE (*S*) $dX = F^*dt + GdW$ with $F^* = F - \frac{1}{2}G\frac{\partial G}{\partial x}$.

Whether one uses Itô calculus or Stratanovich (ordinary rule) calculus, existence and uniqueness of the corresponding SDE requires some regularity conditions on F and G and, with appropriate conditions, the solution is even a Markov process and a diffusion process, satisfying therefore the Kolmogorov equations. In the particular case of *autonomous* SDE, i.e., when $F(t,x) \equiv F(x)$ and $G(t,x) \equiv G(x)$, the solution is even a homogeneous diffusion process. For these issues, the reader can consult, for instance (Braumann, 2019).

The two calculi, Itô or Stratonovich, can give apparently different results, leading even to qualitative different conclusions. For example, in population growth models in a random environment, one calculus may predict, under certain conditions, the extinction of the population with probability one, while the other, under apparently the same conditions, may predict a zero probability of population extinction. Therefore, there has been some controversy in the literature on applications concerning which calculus is more appropriate to certain type of applications. Illustrating with population growth models (with and without harvesting), the controversy is solved in (Braumann, 2007a,b,c) by showing that the apparent discrepancy in results is due to the incorrect implicit assumption that F(t,x) ("average" population growth rate) has the same meaning under both calculi. That is not true since F always represents the arithmetic average when one uses Itô calculus but (except when the function G does not depend on x) it usually represents a different average under the Stratonovich calculus; in the illustrative models, it represented the geometric average when Stratonovich calculus was used. When one attends to the difference between the averages represented by F in the two calculi, the results of the two calculi completely coincide. The moral of the story is that one can use either calculus indifferently but should be careful when choosing the expression of F; it should be the correct expression for the arithmetic mean of the rate of change if one uses Itô calculus and it should be the correct expression for the appropriate mean (the geometric



mean in the illustrative models) of the rate of change if one uses Stratonovich calculus. More on that can be seen on (Braumann, 2019). Here we will use Itô calculus.

Let us now focus on Itô unidimensional autonomous SDE models

$$dX(t) = F(X(t)) dt + G(X(t)) dW(t),$$
 (6)

with known initial condition $X(0) = x_0$ and with functions F(x) and G(x) of class C^1 . It can be proved that the solution exists and is unique up to a possible explosion time and, if we can show that the probability of explosion is zero, then, with probability one, the solution exists and is unique for all $t \ge 0$ and is a homogeneous diffusion process with drift coefficient a(x) = F(x) and diffusion coefficient $b(x) = G^2(x)$ (so the process satisfies the Kolmogorov equations). If the state space, i.e. the space where X(t) takes values, has boundaries r_1 and r_2 with $-\infty \le r_1 < r_2 \le +\infty$ and G(x) > 0 for $x \in]r_1, r_2[$, we can define, for $x \in]r_1, r_2[$, the scale density s(x) and the speed density m(x) given by

$$s(x) = \exp\left(-\int_{z}^{x} \frac{2a(u)}{b(u)} du\right)$$
$$m(x) = \frac{1}{b(x)m(x)},$$
(7)

where z is a fixed but arbitrarily chosen point in the interior of the state space. A necessary and sufficient condition for the boundary r_1 to be *non-attractive* is that $\int_{r_1}^{c_1} s(x) dx = +\infty$ for some $c_1 \in]r_1, r_2[$ (it is enough to check for one such c_1 , because, if its true for some c_1 , it is true for all). Similarly, the boundary r_2 is non-attractive iff $\int_{c_2}^{r_2} s(x) dx = +\infty$ for some $c_2 \in]r_1, r_2[$. When both boundaries are non-attractive, whenever the process approaches a boundary, it is pushed away towards the interior of the state space and so it is possible that the transient probability distribution of X(t) may reach a stochastic equilibrium as $t \to +\infty$ in the sense of converging in distribution to a stationary distribution. If so, the pdf of such distribution is called the *stationary density* p(x) and is a time-invariant solution of the forward Kolmogorov equation. Indeed, it can be proved that, if both boundaries are nonattractive and the speed density is integrable, then the process is ergodic and such stochastic equilibrium occurs and has a stationary density given by

$$p(x) = \frac{m(x)}{\int_{r_1}^{r_2} m(z) dz} \quad (r_1 < x < r_2).$$
(8)

More details can be seen, for example, in (Braumann, 2019).

POPULATION GROWTH AND EXTINCTION IN RANDOMLY VARYING ENVIRONMENTS

Let X(t) be the size (number of individuals, biomass, density) of a wildlife population (of animals, plants or bacteria) at time *t* with known initial size $X(0) = x_0$. In the deterministic case, the contribution of an individual to the growth of the population is given by the *per capita* growth rate (abbreviately, growth rate, difference between the birth rate and the death rate) $R = \frac{dX(t)/dt}{X(t)}$, which expression may depend on the time *t* and the population size *x* at that time,

i.e. R = R(t,x). So, we have the deterministic ODE model $\frac{dX(t)/dt}{X(t)} = R(t,X(t))$ or $\frac{dX(t)}{X(t)} = R(t,X(t))dt$.

Assuming from now on a stable environment, we can assume an R = R(x) and obtain the autonomous ODE $\frac{dX(t)}{X(t)} = R(X(t))dt$. The function *R* may be constant if resources are unlimited but, since usually the available resources are limited, the amount of resources available per individual (*per capita*) tends to decrease when the population size *x* increases and, therefore, R(x) should be a strictly decreasing function. Several models satisfying this property have been proposed like the logistic R(x) = r(1 - x/K) or the Gompertz $R(x) = r\ln(K/x)$ (considered at the beginning of this paper), in which r > 0 is a speed of growth parameter and K > 0 is the *carrying capacity* of the environment, i.e. the stable equilibrium size towards which the population size X(t) converges when $t \to +\infty$.

If the environment has random fluctuations that affect the *per capita* growth rate, their cumulative effect in a time interval [0,t] can be described by an underlying standard Wiener process W(t) multiplied by an intensity factor $\sigma(x) \ge 0$. So we obtain the general SDE population growth model

$$\frac{dX(t)}{X(t)} = R(X(t)) dt + \sigma(X(t)) dW(t)$$

or, written in the traditional format,

$$dX(t) = R(X(t)) X(t) dt + \sigma(X(t)) X(t) dW(t).$$
(9)

We will assume the initial population size $X(0) = x_0$ known. Many specific models, i.e. models with specific forms of the functions R(x) (logistic, Gompertz, generalized logistic, etc.) and $\sigma(x)$ (constant or proportional to R(x)), have been proposed in the literature, starting with the pioneering works of (Levins, 1969; May, 1973; Capocelli and Ricciardi, 1974; Goel and Richter-Dyn, 1974; Kiester and Barakat, 1974; Tuckwell, 1974; Roughgarden, 1975).

Let us illustrate (see (Braumann, 2008)) with the Gompertz SDE model $R(x) = r \ln(K/x)$ with constant noise intensity $\sigma(x) \equiv \sigma > 0$:

$$dX(t) = r\left(\ln\frac{K}{X(t)}\right)X(t) dt + \sigma X(t) dW(t)$$
(10)

with known initial condition $X(0) = x_0 > 0$. Let us make the change of variable $Y(t) = \ln(X(t)/K)$ and use Itô formula to obtain, after simplifying,

$$dY(t) = \left(-rY(t) + \frac{\sigma^2}{2}\right)dt + \sigma dW(t).$$

Another change of variable $Z(t) = e^{rt}Y(t)$ and Itô formula lead to

$$dZ(t) = \frac{\sigma^2}{2}e^{rt}dt + \sigma e^{rt}dW(t)$$

and, by direct integration, to $Z(t) = \ln \frac{x_0}{K} + \frac{\sigma^2}{2} (e^{rt} - 1) + \sigma \int_0^t e^{rs} dW(s)$, from which we get

$$Y(t) = \left(\ln\frac{x_0}{K}\right)e^{-rt} + \frac{\sigma^2}{2}\left(1 - e^{-rt}\right) + \sigma e^{-rt}\int_0^t e^{rs}dW(s)$$
(11)

$$X(t) = K\left(\frac{x_0}{K}\right)^{\exp(-rt)} \exp\left(\frac{\sigma^2}{2}\left(1 - e^{-rt}\right) + \sigma e^{-rt} \int_0^t e^{rs} dW(s)\right).$$
(12)

When $\sigma = 0$, we retrieve the solution $X(t) = K \left(\frac{x_0}{K}\right)^{\exp(-rt)}$ of the deterministic Gompertz curve, but, while in the deterministic case, $X(t) \to K$ as $t \to +\infty$ (a stable deterministic equilibrium population size), this is not happening in the stochastic case. To see that, it is easier to work with Y(t) because it has a Gaussian distribution with mean $\left(\frac{x_0}{K}\right)e^{-rt} + \frac{\sigma^2}{2}(1-e^{-rt})$ and variance $\frac{\sigma^2}{2r}(1-e^{-2rt})$. This comes from (11) and the fact that the stochastic integral $\int_0^t e^{rs} dW(s)$ is Gaussian (because the integrand is deterministic) and has variance $\int_0^t e^{2rs} ds = \frac{1}{2}(e^{2rt} - 1)$. Of course, $X(t) = K \exp(Y(t))$ has a lognormal distribution. In this case, Y(t) has a stationary distribution towards which it converges as $t \to +\infty$, which is Gaussian with mean $\frac{\sigma^2}{2}$ and variance $\frac{\sigma^2}{2r}$. The stationary distribution in terms of the X process is lognormal and its pdf, called *stationary density*, is therefore

$$p(x) = \frac{1}{x \sqrt{2\pi \frac{\sigma^2}{2r}}} \exp\left(-\frac{\left(\ln \frac{x}{K} - \frac{\sigma^2}{2}\right)^2}{2\frac{\sigma^2}{2r}}\right) \quad (x > 0).$$
(13)

So, for the Gompertz model, while in the deterministic case the population size X(t) settles down for large t at the deterministic equilibrium K, in the stochastic case the environmental fluctuations will keep the population fluctuating randomly somewhat around K. It is rather a stochastic equilibrium, where what settles down is not X(t) but its probability distribution, which settles down to the stationary distribution.

Using the techniques at the end of the previous section and noting that $a(x) = r \left(\ln \frac{K}{x} \right) x$ and $b(x) = \sigma^2 x^2$, one can easily show that the boundaries $r_1 = 0$ and $r_2 = +\infty$ are both non-attractive and that the speed density is integrable. So, without solving the equation, we could have concluded that the solution exists and is unique always (because we have C^1 functions and the non-attractiveness of the $+\infty$ boundary prevents explosions), that "mathematical" extinction of the population (in the sense of population size converging to zero) has zero probability of occurring and that there is a stochastic equilibrium with a stationary density. For large *t*, the pdf of the X(t) distribution can be approximated by the stationary density.

This observation is particularly important since, like for ODE, we are often unable to determine the explicit solution of an SDE model. We can also, like in ODE, use numerical methods. In the SDE case, we recur to Monte Carlo techniques (taking advantage of the Markov property) to simulate trajectories. That technique, or the numerical solution of the forward Kolmogorov equation, can be used to approximate the transient probability distribution of X(t)when t is not large enough to use the stationary distribution as an approximation.

The specific models considered in the literature are certainly useful. However, one would like to have model robust properties that do not depend on the specific model considered but rather on the biological properties and so it is better to use general functions R(x) and $\sigma(x)$ (defined

for $x \in [0, +\infty[)$ satisfying only assumptions dictated by biological considerations and mild technical assumptions. From now on, we use the general model (9) and assume R(x)to be of class C^1 , strictly decreasing, with limit $R(+\infty) < 0$ (since, due to limited resources, a very large population must have a negative growth rate) and with $\lim_{x\to 0^+} R(x)x = 0$ (closed to immigration). We assume $\sigma(x) > 0$ and of class C^1 . In (Braumann, 1999), using the techniques described at the end of last Section, we studied the properties of this general SDE model (also in the case of harvested populations) for the particular case of constant $\sigma(x) \equiv \sigma > 0$ and in (Braumann, 2002, 2008) we have extended to general C^1 functions $\sigma(x) > 0$ satisfying an additional mild technical assumption (which all bounded functions automatically satisfy). Now the drift coefficient is a(x) = R(x)x and the diffusion coefficient is $b(x) = \sigma^2(x)x^2$.

We have shown first that the solution exists and is unique. Notice that the *per capita* growth rate is affected by the random environmental fluctuations and so we should look at some appropriate average. What matters for the fate of the population in terms of "mathematical" extinction is its average in the limit when population size $\rightarrow 0^+$, when the population grows at the fastest rate per capita since resource limitations have almost no effect. But, being growth a multiplicative process, we should not look at the arithmetic average $R(0^+)$ (implied in the Itô calculus we are using here), but rather to the geometric average given by $R(0^+) - \frac{\sigma^2(0^+)}{2}$. If this quantity is negative, it means that even the fastest growth is negative on the appropriate average and "mathematical" extinction will occur with probability one. If that quantity is positive, then "mathematical" extinction has zero probability of occurring, the process is ergodic and there is a stochastic equilibrium with stationary density, which we can compute using (7) and (8).

There is always some approximation involved when one uses continuous state models, like ODE or SDE, for the population size X(t). For large populations sizes, having a noninteger number of individuals is, in relative terms, a negligible error and so we can use these models as excellent approximations. But that is not the case when the population is very small, particularly so when we are talking about extinction. We have spoken about "mathematical" extinction (population size converging to zero) and, under certain conditions, we saw that it does not happen, but, since the process is ergodic under those conditions, the solution X(t) of the SDE will sooner or later take values like 0.4 individuals before coming back to higher numbers. When that happens, although not "mathematically" extinct, the population is extinct in realistic terms. If we set up a small extinction threshold a with $0 < a < x_0$ and consider realistic extinction happens when the population crosses the threshold, then all populations will become realistically extinct, even those that have a zero probability of becoming 'mathematically" extinct.

So, the real issue is not whether realistic extinction will occur (it will), but rather how long does it take, i.e., we are interested in the *extinction time* T_a , the first passage time of X(t) through the extinction threshold a. We can also study





Figure 3: Plot of $r\mathbb{E}[T_a]$ as a function of $z = x_0/a$ for the SDE Gompertz model (10) and two parameter combinations. Notice that the vertical axis in the bottom plot is not in the natural scale, so the mean number of ideal generations to extinction is of the order of 10^{90} . Figure taken from (Carlos and Braumann, 2006).

 T_b when b is a high threshold $b > x_0$, as well as $T_{a,b}$, the first passage time through either threshold. Expressions for the moments and the study of the behavior of the expected value and the variance of such passage times for these type of models and its applications can be seen in (Carlos and Braumann, 2005, 2006; Carlos et al., 2013; Braumann, 2008; Filipe et al., 2015; Braumann, 2019). As a function of x_0 , the mean extinction time is very low when x_0 is close to a but, as x_0 increases, it rapidly reaches a plateau and becomes almost insensitive to the initial population size. Depending on the specific models and parameters, that plateau can range from a few generations to times far larger than the age of the universe. For the SDE Gompertz model (10), Fig. 3 plots $r\mathbb{E}[T_a]$ (expected value of T_a measured in number of "ideal" generations, since 1/r is a proxy of generation time) as a function of $z = x_0/a$ (so values of z close to one correspond to x_0 close to a) for two parameter combinations.

Some populations, however, are subjected to Allee effects (see (Allee et al., 1949)), in which small population sizes, instead of having the highest *per capita* growth rates as would be expected since resource limitations barely affect them, have on the contrary depressed growth rates. That may be due to individuals having difficulty in finding mating partners (being few they might be very dispersed geographically) or requiring a minimum population size to mount an effective group defense from predators or, the other way around, requiring a minimum size to effectively

group hunt their prey. With Allee effects, R(x) will only be strictly decreasing due to resource limitations for population sizes above a certain threshold size *L* but, for sizes lower than *L*, Allee effects will prevail and R(x) will be an increasing function (since Allee effects will become weaker, and so the growth rate less depressed, as the population size increases). Specific models were studied, for instance, by (Dennis, 2002; Engen et al., 2003). The study of Allee effect models with a general R(x) function was held in (Carlos and Braumann, 2017).

HARVESTING AND HARVESTING OPTIMIZA-TION

If the population (say a population of fish, but it could be a population of trees or of wild birds) is being harvested, we can use the general model

$$dX(t) = \left(R(X(t)) - qE(t,X(t))X(t) dt + \sigma(X(t))X(t) dW(t)\right)$$
(14)

where qE(t,x) is, at time t when the population has size x, the additional *per capita* mortality rate of the population caused by the harvesting activity. It is assumed proportional to the *harvesting effort* $E(t,x) \ge 0$ (measured, in the case of fishing effort, by the number of fishing vessels adjusted by their efficiency and fraction of time they are in use). The constant of proportionality q > 0 is called the *catchability* in the fishing literature. Now, the arithmetic average of the *per capita* growth rate is the arithmetic average of the *net growth rate* R(x) - qE(t,x), the difference between the arithmetic average natural growth rate R(x) and the additional mortality rate qE(t,x) caused by fishing. The amount of fish caught per unit time is H(t,x) = qE(t,x)x and is called the *yield* in the harvesting literature.

The pioneer works (Beddington and May, 1977; Gleit, 1978; May, 1973; Braumann, 1985) were on specific models assuming specific functions R(x) and $\sigma(x)$. They also assumed the fishing efforts to depend only on the size of the population, i.e. $E(t,X(t)) \equiv E(X(t))$, so that the SDE (14) would become autonomous and we could determine conditions on the effort to avoid "mathematical" extinction of the fish population and to allow for a stochastic equilibrium with a stationarity density.

The study of general autonomous models with arbitrary R(x) and $\sigma(x)$ satisfying the assumptions mentioned in the previous Section and arbitrary C^1 autonomous effort E(x) can be seen in (Braumann, 1999) for the case of constant noise intensity σ) and in (Braumann, 2002) for the most general case. The conclusions are similar to the general SDE population growth models, except that now one should use, instead of the natural growth rate of the population, its net growth rate (natural growth rate minus the additional mortality rate caused by fishing).

If, for vanishing population sizes, the geometric average net growth rate $R(0^+) - \frac{\sigma^2(0^+)}{2} - qE(0^+)$ is negative, "mathematical extinction" of the population will occur with probability one. That happens if we are overfishing, i.e. if,

when the population size is small, the fishing effort $E(0^+)$ is so high that the additional mortality rate caused by fishing $qE(0^+)$ exceeds the geometric average natural growth rate $R(0^+) - \frac{\sigma^2(0^+)}{2}$.

If we are not overfishing, i.e. if the geometric average net growth rate at small population sizes is positive, "mathematical" extinction has zero probability of occurring and the process is ergodic with a stochastic equilibrium and a stationary density p(x) (pdf of the limiting probability distribution as $t \to +\infty$). Let $X(+\infty)$ denote the equilibrium random variable having pdf p(x). One can then study the effect at the stochastic equilibrium of the fishing effort E(x) on the expected yield $\mathbb{E}[H(+\infty, X(+\infty))] = \int_0^{+\infty} qE(x)x \ p(x)dx$ or on the expected profit. Usually, one takes a simple profit structure in which the profit per unit time is $\Pi(t,x) = p_1 H(t,x) - c_0 - c_1 E(x)$ (where $p_1 > 0$ is the unit price, for example the price per kg, at which the fish is sold, $c_0 \ge 0$ are the fixed costs and $c_1 > 0$ is the cost per unit effort) and looks at $\mathbb{E}[\Pi(+\infty, X(+\infty))] =$ $\int_{0}^{+\infty} (p_1 q E(x) x - c_0 - c_1 E(x)) p(x) dx.$

Another approach tries to keep adjusting the effort E(t,x) over time according to the evolution of the population size in order to maximize the overall expected profit (with a discount rate $\delta > 0$ that takes care of depreciation costs such as the cost of opportunity of the investment) over some time horizon [0,T] (where *T* can be finite or infinite). So, it tries to optimize $\mathbb{E}\left[\int_0^T e^{-\delta t} \Pi(t,X(t)) dt\right]$, called the *present value*, not caring if the optimal policy leads or not to the extinction of the population. We can cite pioneering works of (Lungu and Øksendal, 1997; Alvarez and Shepp, 1997; Alvarez, 2000).

One of the techniques, considering that we can control the effort E(t,x) and so can use it as a control, is based on stochastic optimal control theory and the use of the Hamilton-Jacobi-Bellman (HJB) equation. In (Brites and Braumann, 2017) and (Brites and Braumann, 2019b) that technique was used, together with Monte Carlo simulations of the SDE and a Crank-Nicholson discretization of the HJB equation, for the case of constant noise intensity $\sigma(x) \equiv \sigma$ and a more complex profit struture $\Pi(t,x) =$ $(p_1 - p_2 H(t,x))H(t,x) - c_0 - (c_1 + c_2 E(t,x))E(t,x)$ (with $p_2 \ge 0$ and $c_2 > 0$). Those papers consider the application to specific real fisheries using, respectively, the logistic model $R(x) = r\left(1 - \frac{x}{K}\right)$ and the Gompertz model $R(x) = r\ln\left(\frac{K}{x}\right)$. The growth parameters r and K and the cost and price parameters of those specific fisheries came from (Hanson and Ryan, 1998) and (Kar and Chakraborty, 2011), respectively.

In those papers, one can see in the optimal variable effort policy (the one obtained from stochastic optimal control theory that maximizes the present value, i.e. the expected discounted profit over a time horizon) a serious applicability problem not found when using optimal control theory in deterministic models. Namely, the optimal effort $E^*(t,x)$ keeps changing all the time accompanying the random fluctuations of population size induced by the effect of environmental fluctuation on the natural growth rate. Those changes include frequent periods with zero or low effort (where the fishery stops or has very little activity) and periods of fishing at the highest possible effort. Therefore, since in practice it is operationally not possible to keep changing the fishing effort all the time and so abruptly, this optimal fishing policy is not applicable. Also, in the periods of no or low fishing, fishermen unemployment occurs, with the corresponding social problems (or hidden unemployment compensation costs not taken into account in the used profit structure). Furthermore, at every time, we need to know the population size of fish since we need it to compute the optimal fishing effort to apply at that time. But estimating the population size cannot be done all the time because it is a difficult and costly process (another hidden cost not contemplated in the profit structure); also, the estimates are innaccurate, so we may compute an innaccurate value for the fishing effort to apply.

In those papers, it was also determined what would happen if one applies a constant effort fishing policy with $E(t,x) \equiv E$. This is operationally extremely easy to apply because the fishing effort is the same all the time and does not change with the changes in the population size. So, there are no periods of zero or low effort and so there are no social problems or hidden costs. There is also no need to estimate the population size all the time since it is not required in the computation of the effort. We chose the optimal sustainable effort, i.e. the value E^{**} of the constant effort E that maximizes the expected profit at the stochastic equilibrium $\mathbb{E}[\Pi(+\infty, X(+\infty))] = \int_0^{+\infty} ((p_1 - p_2 \ qEx) \ qEx - c_0)$ $-(c_1+c_2E) E$ p(x)dx, which can be easily obtained. Then we compare this sustainable policy with the previous optimal variable effort policy in terms of their present values in a T = 50 years horizon. Of course, the previous optimal variable effort policy, if it could be applied in practice, would maximize the present value and so it gives a better present value than the optimal sustainable policy. The question is: how worse is the present value of the sustainable constant effort policy (which is easily applicable and free of social problems) compared to the present value of the (inapplicable) optimal variable effort policy? It is only 4,1% worse for the logistic model and 1,5% worse for the Gompertz model! For lack of information, those papers did not take into account the hidden costs of the inapplicable policy, but it is possible that, if they did, it might turn out that the sustainable constant effort policy would be better even in terms of profit.

Fig. 4, taken from (Brites and Braumann, 2017), shows the comparison for the logistic model of the two policies in terms of population size, effort and profit per unit time dynamics. The thin lines correspond to one simulated trajectory chosen at random and correspond to what the fishermen will typically experience (maybe they will experience a different trajectory but with a similar typical behavior). The solid lines are the average over 1000 simulated trajectories, which is a good approximation of the expected values. Looking at the effort, one can see the problems with the optimal variable effort policy. Looking at the profit per unit time, although the optimal effort policy has usually a better expected value (as seen looking at the solid lines), if we look at the thin lines



to see what the fishermen will typically experience, it is obvious that the profit is very unsteady over time in the optimal variable effort policy. On the contrary, although not having a constant profit (even though the effort is constant, the population size fluctuates and so does the profit), one can see that the constant effort policy provides a much steadier profit.

Other fishing policies, somewhere in between the constant effort and the optimal variable effort, could be used to try to improve the profit in comparison with the constant effort policies while attenuating the problems of the optimal variable effort policy we have mentioned. Their study can be seen in (Brites and Braumann, 2019a,b,c). The treatment of fish populations having Allee effects can be seen in (Brites and Braumann, 2020).

INDIVIDUAL ANIMAL GROWTH MODELS IN RANDOM ENVIRONMENTS

In the Introduction we have mentioned that the traditional use of regression models based on growth curves to study the individual growth of animals (or, for that matter, of plants, particularly trees) is inappropriate because it ignores the dynamics of the growth process and the influence on the growth rate of random variations in internal and external environmental conditions. We have even given as example of a typical deterministic growth curve used in the literature, the Gompertz curve and showed on Fig. 2 that the observed evolution of the size of a cow indicates the existence of such fluctuations. The Gompertz growth curve in fact results from growth dynamics governed by a Gompertz ODE model $\frac{dX(t)}{dt} = rX(t)\ln\frac{K}{X(t)}$, where X(t) is the size of the animal, K > 0 is the size at maturity and r > 0 is a parameter that characterizes the speed of approach to maturity. So, if one takes into account the effect of random fluctuations, one should use an SDE model. This was proposed by (Garcia, 1983) and applied to the growth of trees.

But the Gompertz curve is just one of the several deterministic models proposed in the literature for individual growth. However, as also shown in (Garcia, 1983), the classical most used deterministic growth curves can be described as the result of growth dynamics driven by a common ODE model $\frac{dY(t)}{dt} = r(A - Y(t))$ with r > 0, where Y(t) is not the actual size of the individual at age t but rather a modified size by some strictly increasing C^1 function h, i.e. Y(t) = h(X(t)), where X(t) is the actual size. When h(x) = x we get the monomolecular growth curve, when $h(x) = x^c$ (c > 0) we get the Bertalanffy-Richards curve, when $h(x) = \ln x$ we get the Gompertz curve (which can be considered a limiting case of the Bertalanffy-Richards curve when $c \rightarrow 0^+$), and when h(x) = -1/x we get the logistic curve. Of course, the modified size at maturity is A = h(K), where K > 0 is the actual size at maturity. Then, one can consider also a common SDE model that takes into account the effect of environmental fluctuations on the growth process, namely

$$dY(t) = r(A - Y(t)) dt + \sigma dW(t) \quad (t \ge t_0, Y(t_0) = y_0),$$
(15)

where $\sigma > 0$ measures the intensity of the effect on *Y* of the environmental fluctuations, t_0 is the age of the initial (assu-

med known) size observation $X(t_0) = x_0$ and $y_0 = h(x_0)$. The solution of (15) is, for $t > t_0$,

$$Y(t) = A + e^{-r(t-t_0)}(y_0 - A) + \sigma e^{-r(t-t_0)} \int_{t_0}^t e^{rs} dW(s).$$
 (16)

Notice that Y(t) is Gaussian with mean $A + e^{-r(t-t_0)}(y_0 - A)$ and variance $\frac{\sigma^2}{2r} \left(1 - e^{-2r(t-t_0)}\right)$. Likewise, since Y(t) is a homogeneous diffusion process, the transition distribution between two ages *s* and t > s (both $\ge t_0$), given the value of $Y(s) = y_s$, is also Gaussian with mean $A + e^{-r(t-s)}(y_s - A)$ and variance $\frac{\sigma^2}{2r} \left(1 - e^{-2r(t-s)}\right)$. The stationary distribution of *Y*, obtained by letting $t \to +\infty$, is also Gaussian with mean *A* and variance $\frac{\sigma^2}{2r}$. Of, course, using the transformation *h*, one can easily obtain from the transient, transition and stationary distributions of the *Y* process the corresponding distributions of the actual size process *X*.

Modifications of this model have been proposed. We might have two (or more) growth phases (as may happen in cows before and after weaning due to different food diets) with two different growth parameters, r_1 for ages $t \leq u$ and r_2 for t > u; these *biphasic models* were studied in (Filipe et al., 2012). It is also possible that, due to genetic differences for instance, different animals have different parameter values, say different maturity sizes K; so, when we study a certain animal breed, we may need to take that into account and assume, for example that the modified maturity size A varies randomly among the individual animals of the breed, with a Gaussian distribution. These are mixed models that have been studied and applied to the Mertolengo breed of cows (data provided by the producer's association ACBM, Associação de Criadores de Bovinos Mertolengos) in (Braumann et al., 2009).

For the applications, one needs to deal with statistical issues of estimation, model choice and prediction, which pose more complex issues for modified models (like the biphasic or the mixed models), but can be easily handled for the basic model (15) if we have (as we do) a reasonable number and age range of observed sizes for many different animals (Filipe et al., 2010; Braumann et al., 2009). We may assume different animals correspond to independent realizations of the stochastic process so that the likelihood function of the observations is just the product of the likelihoods of the individual animals. By the Markov property of the Y process, the likelihood function for one animal is just the product of the transition densities between the consecutive observations made on that animal, and such transition densities are, as we have seen, Gaussian. So, one easily obtains the likelihood function and can maximize it to obtain the maximum likelihood estimates of the parameters r, A and σ ; their approximate confidence intervals can be obtained by the traditional method, using the inverse of the empirical Fisher information matrix. For example, from the data on 16201 bovine Mertolengo males provided by ACBM and using the Gompertz model, the 95% confidence intervals were 630.1 \pm 6.4 kg for $K = e^A$, 1.422 \pm 0.012 per year for r and 0.340 ± 0.002 per year^{1/2} for σ , as can be seen in (Filipe, 2018).



Figure 4: On the left is the optimal variable effort policy and on the right the optimal sustainable constant effort policy. Thin lines correspond to one randomly chosen simulated trajectory (representing what fishermen typically experience) and solid lines to the average of a 1000 simulated trajectories (an approximation of the expected values). The Figure is taken from Brites and Braumann (2017) and shows, using the application of an SDE logistic model with fishing, the evolution with time (in years) of the population size (on top, in kg), of the fishing effort (in the middle, in standardized fishing units) and of the profit per unit time (at the bottom, in US dollars per year).

If we have enough data and no assumptions on the growth dynamics, we may wish to use a general model $dY(t) = f(Y(t))dt + \sigma(Y(t))dW(t)$ and estimate the drift coefficient f(y) and the diffusion coefficient $\sigma^2(y)$ by nonparametric methods; this was done in (Filipe et al., 2010), where it turned out that the estimated coefficients were relatively close to the coefficients of the Gompertz model and also of the Bertalanffy-Richards model with c = 1/3, so that this specific models were somewhat "validated" as reasonable models. Actually, comparisons of several specific models using AIC show that these two models have the best performances.

Prediction issues were discussed in (Filipe et al., 2013).

In (Filipe et al., 2015), a farmer optimization issue was studied. Suppose a farmer buys an animal having weight x_0 at age t_0 (usually right after weaning) in order to raise (finishing phase) and sell it to the meat market at a later age $t > t_0$ with weight X(t) yet unknown. In the process, the farmer makes a profit $\Pi(t) = p_1X(t) - c_0 - c_1(t - t_0)$, where p_1 is the selling price per kg of live weight, c_0 are the fixed costs (like, for example, the price the farmer paid for the animal at age t_0 , transportation costs, veterinary costs, certain licenses and taxes) and c_1 are the variable costs per unit time of raising the animal (such as feeding and handling costs). The paper shows how to determine the optimal selling age t in order to maximize the expected profit $\mathbb{E}[\Pi(t)]$ and ap-



plies the results to the Mertolengo breed using information on typical costs and market meat prices. Instead of choosing a fixed age *t* (preferably the optimal one) to sell the animal, one could alternatively choose a fixed weight *M* and sell the animal when it reaches that weight (irrespective of its age). To choose the optimal *M*, one needs to maximize the expected profit $\mathbb{E}[P(M)]$ where $P(M) = p_1M - c_0 - c_1(T_M - t_0)$ and T_M is the first age at which the animal reaches the weight *M*. That problem was also solved in (Filipe et al., 2015) using the study made on first passage times T_M in (Carlos et al., 2013). Curiously, this second approach turns out to give a slightly better average profit that the first approach, but it has the inconvenience of having to keep weighting the animal until it reaches the target optimal weight.

CONCLUSIONS

We have given a general birds eye view on how to model the growth of a wildlife population living in a randomly varying environment by using stochastic differential equations, and use the models to study important issues such as the risk of extinction. Since we are dealing with similar models, the paper also presents the modeling of the growth of individual animals (or plants like trees). These models have many important applications, for which we gave two examples concerning profit optimization in fisheries and in animal production farming.

Many other biological applications could be given, in ecosystems management, in epidemiology, in physiology, in medical applications, in demography and in many other areas traditionally handled by ordinary differential equation models but for which random fluctuations in non-directly modelled internal and external environmental factors do require a stochastic differential equation approach.

On the technical side, here we have just treated unidimensional models where the "underlying environmental noise" can be handled (in its cumulative form over time) by a Wiener process, which is characterized by the continuity of its trajectories and by its independent increments. There are, however, extensions to multidimensional models (for instance, if we have to consider different interacting populations). There are also extensions to "noises" with jumps or with correlated increments, although for most practical applications, the approach taken here of using a Wiener process approximation, besides being much simpler, is sufficiently accurate.

Also the statistical issues were just briefly mentioned and only for an ideal situation in which we can explicitly obtain the likelihood function, which involves the exact knowledge of the transition densities. But, in most cases, one cannot solve explicitly the SDE and needs to use approximate expressions for the transition densities or recur to Monte Carlo simulation techniques, issues that are out of the scope of this paper.

Of course, in order to give the reader a flavor on SDE, we have also given here a quick and dirty introduction to its theory, but, for those interested in pursuing work on modeling with SDE, we recommend further consolidating reading, like, for example, (Braumann, 2019), (Arnold, 1974) or (Øksendal, 2003). The reading of a few papers from the ones recommended in the References or others in application subjects that might interest the reader will be also recommended.

I am sure the reader understands that my main purpose is not to give a comprehensive treatment, nor that would be feasible in a short dissemination paper. Rather, the aim is to introduce the subject, using mostly material that I have worked with, to give a rough idea of its usefulness and potential range of applications to the reader not yet acquainted with it. If this managed to attract a few readers to the subject and maybe drive some to develop further ideas and new areas of application, all the better.

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Sobre el conjunto de umbrales sostenibles

On the Set of Sustainable Thresholds

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Resumen— Hacer operativo el concepto de sostenibilidad es un desafío importante en la gestión de recursos naturales, problemas de conservación de la biodiversidad, el cambio climático y la epidemiología, entre otros. Diferentes enfoques se han propuesto, basados en restricciones y umbrales que consideran no sobrepasar indicadores biológicos, ecológicos, económicos o sociales como metas para los objetivos de una gestión sostenible. Cuando las restricciones inducidas por umbrales deben satisfacerse a lo largo del tiempo, estos problemas pueden formularse en el marco matemático de la *teoría de la viabilidad*, como han propuesto numerosos autores durante las últimas décadas. El eje central de estos enfoques ha sido principalmente el cálculo del *núcleo de viabilidad*, concepto clave en la mencionada teoría, que consiste en el conjunto de estados iniciales del sistema a partir del cual es posible satisfacer las restricciones prescritas a lo largo del tiempo. Nuestro enfoque en los últimos años ha sido en el sentido inverso, consistente en determinar los umbrales para los que existe una trayectoria que satisface las restricciones parametrizadas por dichos umbrales, a partir del estado actual de un sistema. El conjunto de todos estos umbrales se denomina *conjunto de umbrales sostenibles*, que corresponde al operador inverso del núcleo de viabilidad. Este nuevo concepto, y su cálculo, proporciona una herramienta para la gestión y visualización de múltiples objetivos relacionados con la sostenibilidad que se puede alcanzar, permitiendo observar la (in)compatibilidad y compensaciones entre ellos. En este trabajo revisamos la definición del conjunto de umbrales sostenibles, presentando algunas interpretaciones y un método para calcularlo, resumiendo trabajos recientes desarrollados con varios coautores.

Palabras clave-sostenibilidad, teoría de la viabilidad, umbrales sostenibles, maximin, programación dinámica

Abstract—Operationalizing sustainability is a major challenge in natural resource management, biodiversity conservation problems, the climate change, and epidemiology, among others. Approaches based in constraints and thresholds have been proposed considering not to exceed biological, ecological, economic, or social indicators as goals for sustainable management objectives. Whenever the constraints induced by thresholds have to be satisfied over time, such problems can be formulated into the mathematical framework of *viability theory*, as has been proposed by numerous authors during the last decades. The focus of these approaches, has been mainly the computation of the *viability kernel*, the key concept in the mentioned theory, and consisting in the set of initial states of the system from which is possible to satisfy prescribed constraints along the time. Our approach in the last years has been in the inverse sense, consisting in determining the thresholds for which there exists a trajectory satisfying constraints parametrized by such thresholds. The set of all these thresholds is called the *set of sustainable thresholds*, that corresponds to the inverse operator of the viability kernel. This new concept and its computation, provide a tool for the management and visualization of multiple objectives related to sustainability that can be accomplished, allowing to observe their (in)compatibility and trade-offs. In this paper, we review the definition of the set of sustainable thresholds presenting some interpretations and a method to compute it, summarizing recent works developed with several co-authors.

Keywords-sustainability, viability theory, sustainable thresholds, dynamic programming.

INTRODUCCIÓN

A partir del Informe Brundtland et al. (1987), que proporciona una definición unificadora del desarrollo sostenible, se pueden identificar varios estudios que proponen cómo hacer operativa esa definición en diversos contextos: Asheim (2007); Cairns y Long (2006); Doyen y Martinet (2012); Fleurbaey (2015), en particular en el de la economía ecológica, ambiental y de los recursos. En esa perspectiva, el enfoque de maximizar una función de utilidad con una tasa de descuento, es calificado como *la dictadura del presente* por Chichilnisky (1996), debido

a que este criterio descuida la utilidad a largo plazo, lo que conlleva a trayectorias insostenibles para las futuras generaciones. Entre los enfoques y criterios alternativos relacionados con la sostenibilidad cuantitativa, se encuentra el maximin Solow (1974), definido como el nivel de utilidad más alto que puede sostenerse en el tiempo, promoviendo así la equidad intergeneracional. Sin embargo, el uso de métodos de optimización para cuantificar la sostenibilidad, incluido el criterio maximin, es criticado globalmente en Howarth (1995); Martinet (2011), donde se argumenta que es necesario imponer condiciones de sostenibilidad antes de la maximización de cualquier función de bienestar social.

En este sentido, la consideración de restricciones biológicas, ecológicas, sociales o físicas para cumplir los objetivos a lo largo del tiempo surge como una cuestión crucial. El enfoque en términos de restricciones y objetivos está bien adaptado para abordar problemas de conservación de la biodiversidad, en los que se suelen preferir las limitaciones ecológicas a las evaluaciones de utilidad o monetarias (véase, por ejemplo, los objetivos de biodiversidad de Aichi, formulados por el Convenio sobre la Diversidad Biológica), o para abordar la cuestión del cambio climático, como ilustra el protocolo de Kioto, en el que los objetivos físicos se definen en términos cuantitativos. En este marco, los puntos de referencia que no deben traspasar los indicadores biológicos, ecológicos, económicos o sociales representan objetivos de gestión sostenible. Como ejemplos de este enfoque, se pueden mencionar el concepto de Estándares Mínimos de Seguridad (SMS) Margolis y Naevdal (2008), donde se introducen umbrales de inflexión y zonas de riesgo, o el Enfoque de Ventanas Tolerables (TWA) Bruckner et al. (1999), basado en límites seguros y regiones de viabilidad. Del mismo modo, en Rockström et al. (2009) desarrollan un marco basado en restricciones que definen el espacio operativo seguro (SOS) para la humanidad, asociado a los subsistemas o procesos biofísicos del planeta.

Con una perspectiva de equidad intergeneracional, si las restricciones inducidas por los puntos de referencia, umbrales, límites, normas o puntos de inflexión deben satisfacerse a lo largo del tiempo, estos problemas relacionados con la sostenibilidad pueden formularse en el marco matemático de la teoría de la viabilidad Aubin (1990); De Lara y Doyen (2008); Doyen et al. (2019). Interpretando las restricciones como derechos mínimos que deben garantizarse a todas las generaciones, la teoría de la viabilidad puede utilizarse para abordar estos problemas de sostenibilidad Baumgartner y Quaas (2009); Doyen y Martinet (2012). De hecho, este enfoque ha sido aplicado por numerosos autores a la gestión sostenible de recursos renovables a los que se refieren Béné y Doyen (2000); Béné et al. (2001); Doyen et al. (2017); Krawczyk et al. (2013); Péreau et al. (2012); Pereau et al. (2018). En Oubraham y Zaccour (2018), los autores ofrecen una visión completa de estos estudios, destacando la aplicación de conceptos y herramientas de la teoría de la viabilidad a la gestión sostenible de recursos renovables, incluidos los ecosistemas y las poblaciones, como la pesca y especies no marinas, el medio ambiente y otros recursos.

Los enfoques de maximin y viabilidad están fuertemente

conectados, ya que el maximin surge como una *viabilidad máxima* - Doyen y Gajardo (2020); Doyen y Martinet (2012); Martinet y Doyen (2007) -. Más concretamente, en Doyen y Martinet (2012) se demuestra que la función valor de un problema maximin es la solución de un problema de optimización estático que involucra al núcleo de viabilidad como restricción.

Las aplicaciones tradicionales de la teoría de la viabilidad a la gestión sostenible de recursos naturales (incluyendo aspectos ecológicos, económicos o sociales) se basan en la determinación del llamado *núcleo de viabilidad*, un conjunto formado por las condiciones iniciales de las variables de estado, que aseguran la existencia de al menos una trayectoria (viable) de estados que puede satisfacer las restricciones impuestas que representan la sostenibilidad (ver Baumgartner y Quaas (2009); Béné et al. (2001); Cissé et al. (2013); De Lara y Doyen (2008); Doyen et al. (2017); Doyen y Martinet (2012); Krawczyk et al. (2013); Péreau et al. (2012) y sus referencias). Si el estado actual de los recursos no es viable, es decir, si no hay una trayectoria futura viable capaz de satisfacer las restricciones de sostenibilidad, se sugiere entonces la recuperación de los recursos.

A pesar de las diversas aplicaciones de la teoría de la viabilidad, uno de los inconvenientes del núcleo de viabilidad es que puede contener estados que no son alcanzables desde el estado actual de los recursos a estudiar, lo que hace inútil su cálculo, tarea que, en general, es muy difícil. En lugar del núcleo de viabilidad, en los últimos años hemos propuesto centrarnos en el conjunto de umbrales sostenibles, un conjunto de umbrales que parametrizan las restricciones de sostenibilidad que pueden satisfacerse en el futuro, dado el estado actual de los recursos. Este conjunto representará la capacidad (o incapacidad) de los recursos para sostener las restricciones de sostenibilidad especificadas, además de mostrar todas las restricciones que pueden satisfacerse a partir del estado actual, que puede ser muy malo, en caso de que solo puedan sostenerse en el tiempo restricciones muy poco exigentes.

Desde el punto de vista matemático, el uso del núcleo de viabilidad y el del conjunto de umbrales sostenibles son enfoques equivalentes, ya que uno es el mapeo inverso del otro. Sin embargo, para asistir al proceso de toma de decisiones, creemos que el conjunto de umbrales sostenibles es visualmente más atractivo porque contiene más información útil que el núcleo de viabilidad y tiene propiedades matemáticas (no compartidas por el núcleo de viabilidad) que deberían hacer de su cálculo una tarea más abordable.

En el presente artículo, consideraremos un sistema dinámico controlado a tiempo discreto (Sección Definiciones preliminares), donde las variables de estado pueden representar por ejemplo uno o varios recursos naturales, diferentes especies, emisiones, o diversas cantidades de interés que evolucionan en el transcurso del tiempo. El o los controles serán las decisiones exógenas que modifican la evolución del sistema. El objetivo es que tanto las trayectorias de estado y controles satisfagan restricciones, parametrizadas por umbrales, a lo largo del tiempo. En ese contexto,



definiremos el conjunto de umbrales sostenibles y veremos su relación con el núcleo de viabilidad (Sección Núcleo de viabilidad y el conjunto de umbrales sostenibles). Luego presentaremos caracterizaciones que involucran estos objetos, mediante problemas de optimización de tipo maximin (Sección Umbrales sostenibles y maximin), estableciendo un estrecho vínculo entre tal tipo de problemas, estudiados hace mucho tiempo en sostenibilidad cuantitativa, y la teoría de la viabilidad. Finalmente en la Sección Principio de Programación Dinámica presentaremos un resultado que permite diseñar un método numérico, basado en el principio de la programación dinámica, para calcular los umbrales sostenibles eficientes (frontera débil de Pareto), y de esa forma obtener el conjunto completo.

DEFINICIONES PRELIMINARES

El contexto matemático general en el cual se plantea esta revisión, es un sistema dinámico determinista en tiempo discreto, que se escribe de la siguiente forma:

$$\begin{cases} x(t+1) = D(x(t), u(t)) & t_0 \le t < T \\ x(t_0) = x_0 \text{ dado,} \end{cases}$$
(1)

donde $x(t) \in X \subset \mathbb{R}^n$ es la variable de estado (e.g., niveles de uno o varios recursos naturales, de diversas especies, o la cantidad de individuos en compartimentos en modelos epidemiológicos), $u(t) \in U \subset \mathbb{R}^m$ es el control o decisión que afecta la evolución de las variables de estado (e.g., esfuerzo de captura, cosecha, o medidas de mitigación de una enfermedad), $D: X \times U \longrightarrow X$ representa la dinámica, $t_0 \in \mathbb{N}$ es el periodo de tiempo inicial en el que se realiza el análisis y $T \in \mathbb{N} \cup \{+\infty\}$ ($T \ge t_0$) es el horizonte de tiempo.

Para simplificar la presentación, consideraremos solo sistemas autónomos, pero todo lo que expondremos es fácilmente extendible a sistemas no-autónomos.

Establecido el sistema dinámico (1), lo que en esencia es un trabajo multidisciplinario que involucra el modelamiento, identificación y estimación de parámetros, nos situaremos en un contexto donde es deseable que las trayectorias de estados y controles satisfagan restricciones a lo largo del periodo de tiempo en estudio. Un ejemplo ilustrativo es el caso en que (1) representa la evolución de un sistema medioambiental sujeto a restricciones de preservación y producción (De Lara y Doyen (2008); Doyen et al. (2017); ICES (2004)). En un contexto general, escribiremos

$$I_j(x(t), u(t)) \ge \theta_j, \quad j = 1, \dots, p; \quad t_0 \le t \le T, \quad (2)$$

donde para j = 1, ..., p, las funciones $I_j : X \times U \longrightarrow \mathbb{R}$ representan indicadores de calidad, métricas u observaciones y $\theta = (\theta_1, ..., \theta_p) \in \mathbb{R}^p$ es el vector donde la componente *j* es el umbral correspondiente a la restricción I_j . De esta forma, el sistema dinámico controlado con restricciones que estudiaremos es

$$\begin{cases} x(t+1) = D(x(t), u(t)) & t_0 \le t < T \\ x(t_0) = x_0 \text{ dado} & (3) \\ I_j(x(t), u(t)) \ge \theta_j, \quad j = 1, \dots, p, \quad t_0 \le t \le T \end{cases}$$

En la literatura de los últimos años, podemos encontrar diversas investigaciones cuyo objeto de estudio se puede escribir de la forma anterior (en tiempo discreto o continuo), y que han sido motivados por la gestión de recursos pesqueros - Cissé et al. (2013); De Lara et al. (2007a); Doyen et al. (2017, 2012); Eisenack et al. (2006); Mullon et al. (2004); Péreau et al. (2012) -, la gestión de recursos forestales - Bernard (2010); Bernard y Martin (2013); Mathias et al. (2015); Rapaport et al. (2006) -, el cambio climático Aubin et al. (2005, 2012), los sistemas agro-ecológicos - Baumgartner y Quaas (2009); Durand et al. (2017); Sabatier et al. (2015), y el control de epidemias Barrios et al. (2018); De Lara y Sepulveda-Salcedo (2016); Sepulveda-Salcedo y De Lara (2019) -.

Al observar el sistema (3), representando este una situación ideal o deseable, la pregunta natural que nos podemos hacer es si existe una trayectoria de controles (decisiones) $u(\cdot) = (u(t_0), u(t_0 + 1), \dots, u(T))$ tal que las restricciones estipuladas en (3) se puedan satisfacer. Evidentemente, la respuesta dependerá del estado inicial del sistema x_0 y de las restricciones que están parametrizadas por el vector de umbrales $\theta = (\theta_1, \dots, \theta_p) \in \mathbb{R}^p$. La compatibilidad entre ambos objetos, es lo que abordamos en la próxima sección.

NÚCLEO DE VIABILIDAD Y EL CONJUNTO DE UMBRALES SOSTENIBLES

En el contexto del sistema dinámico controlado (3) con restricciones mixtas (de estado y control), la *teoría de la viabilidad* se ha concentrado en analizar y calcular el *núcleo de viabilidad* (ver Aubin (1991)), concepto clave en dicha teoría, y que consiste en el conjunto de condiciones iniciales x_0 para las cuales el sistema (3) es factible, es decir, existe una secuencia de decisiones $u(\cdot)$ que permite satisfacer las restricciones. El núcleo de viabilidad se define entonces por

$$\mathbb{V}_{T}(t_{0},\theta) \stackrel{\text{def}}{=} \left\{ x_{0} \in X \middle| \begin{array}{c} \exists u(\cdot) \neq x(\cdot) \text{ satisfaciendo} \\ x(t_{0}) = x_{0} \\ x(t+1) = D(x(t),u(t)) \\ u(t) \in U \neq y \\ I_{j}(x(t),u(t)) \geq \theta_{j} \quad \forall i = 1,\ldots,p \\ \forall t_{0} \leq t \leq T \end{array} \right\}$$

$$(4)$$

El núcleo de viabilidad $\mathbb{V}_T(t_0, \theta) \subset X \subset \mathbb{R}^n$, asociado al vector de umbrales $\theta \in \mathbb{R}^p$, juega un rol fundamental (en tiempo discreto y continuo) en el análisis de la consistencia entre un sistema dinámico controlado y las restricciones a las cuales está sujeto, siendo clave también en el diseño de controles viables. Desafortunadamente, su cálculo presenta diversas complejidades.

De la definición del núcleo de viabilidad, se obtiene que si la condición inicial x_0 no está en $\mathbb{V}_T(t_0, \theta)$, entonces independiente de lo que hagamos (i.e., de la secuencia de controles $u(\cdot)$ que se elija), tarde o temprano alguna de las restricciones no será respetada, información relevante cuando se analizan problemas de sostenibilidad.

En la literatura podemos encontrar una gran cantidad de trabajos cuyo foco es la caracterización y el cálculo del núcleo de viabilidad - Aubin et al. (2011); Béné et al. (2001); Bonneuil y Boucekkine (2014); De Lara y Doyen (2008); De Lara et al. (2007b); Krawczyk et al. (2013); Saint-Pierre (1994) -. Recientemente en Oubraham y Zaccour (2018), los autores proveen una exhaustiva revisión sobre la utilización de la teoría de la viabilidad y en particular del núcleo de viabilidad, en el estudio de problemas asociados a la gestión sostenible de recursos renovables, incluyendo ecosistemas y medio ambiente, concluyendo que la teoría de la viabilidad es un marco metodológico muy útil para analizar problemas de sostenibilidad. En Schuhbauer y Sumaila (2016) también se hace una revisión de aplicaciones de la teoría de la viabilidad, pero en dicho trabajo estas se concentran en la gestión de recursos pesqueros.

Menos atención, con la excepción de Doyen y Gajardo (2020); Doyen y Martinet (2012); Gajardo y Hermosilla (2021); Gajardo et al. (2018); Martinet (2011); Martinet et al. (2010), ha recibido el problema de viabilidad inverso, consistente en determinar, dada una condición inicial x_0 , las restricciones parametrizadas por el vector de umbrales $\theta = (\theta_1, \dots, \theta_p)$, para las cuales el sistema (3) es factible. En términos matemáticos, lo que se busca es determinar el siguiente conjunto

$$\mathscr{S}_{T}(t_{0}, x_{0}) \stackrel{\text{def}}{=} \left\{ \boldsymbol{\theta} \in \mathbb{R}^{p} \middle| \begin{array}{c} \exists u(\cdot) \neq x(\cdot) \text{ satisfaciendo} \\ x(t_{0}) = x_{0} \\ x(t+1) = D(x(t), u(t)) \\ u(t) \in U \neq \mathbf{y} \\ I_{j}(x(t), u(t)) \geq \boldsymbol{\theta}_{j} \\ \forall i = 1, \dots, p \\ \forall t_{0} \leq t \leq T \end{array} \right\}$$
(5)

El conjunto $\mathscr{S}_T(t_0, x_0) \subset \mathbb{R}^p$ es denominado *conjunto de umbrales sostenibles* a partir del estado inicial x_0 . La definición de este conjunto se puede encontrar en Doyen y Gajardo (2020); Gajardo y Hermosilla (2021); Gajardo et al. (2018); Martinet et al. (2010, 2011) (en tiempo discreto) y en Barrios et al. (2018); Martinet (2011) (en tiempo continuo).

Directamente de las definiciones (4) y (5), el conjunto de umbrales sostenibles puede considerarse como el mapeo inverso del núcleo de viabilidad, en el siguiente sentido

$$\boldsymbol{\theta} \in \mathscr{S}_T(t_0, x_0) \iff x_0 \in \mathbb{V}_T(t_0, \boldsymbol{\theta})$$
 (6)



Figura 1: Ilustración tomada de Gajardo et al. (2018) del conjunto de umbrales sostenibles $\mathscr{S}_T(t_0, x_0) \cap \mathbb{R}^2_+$ (i.e., considerando solo restricciones no negativas en (5)).

Similar a lo que sucede con el núcleo de viabilidad, identificar y calcular $\mathscr{S}_T(t_0, x_0)$ plantea diversos desafíos. Sin embargo, en muchas situaciones prácticas, el conjunto de umbrales sostenibles visualmente es más interpretable que el núcleo de viabilidad y podría proporcionar una valiosa información cualitativa a los tomadores de decisiones. Por ejemplo, en problemas de gestión de recursos naturales, en los que el estado de los recursos estudiados está representado por varias variables de estado (como en los modelos en clases de edades en la gestión pesquera), el núcleo de viabilidad no puede proporcionar información visual a los tomadores de decisiones que están considerando diversas restricciones. Este caso no se da cuando se tienen pocas restricciones que satisfacer, por ejemplo, dos: una restricción de tipo preservación (e.g., mantener al menos un nivel mínimo del recurso) y una restricción de tipo producción (e.g., mantener al menos un nivel mínimo de cosecha o beneficio). En esta situación, el conjunto de umbrales sostenibles puede ilustrarse en el plano (dos dimensiones asociadas a las dos restricciones) como se muestra en Barrios et al. (2018) y Gajardo et al. (2018). De esta forma, este conjunto representa la buena o mala salud del sistema en estudio en términos de la sostenibilidad, permitiendo visualizar las compensaciones o trade-offs existentes entre las diferentes restricciones, que usualmente están en conflicto, subyacentes en la definición de sostenibilidad. En la Figura 1 ilustramos el conjunto $\mathscr{S}_T(t_0, x_0)$ con dos restricciones en conflicto, en el sentido de que cuanto más exigentes seamos con una restricción (i.e., imponiendo un umbral más alto), menos exigentes deberíamos ser con la otra restricción (i.e., imponiendo un umbral más bajo). Esto último ocurre muy a menudo en problemas relacionados con la sostenibilidad o más generalmente en problemas sociales.

Durante los últimos años, hemos creído que el conjunto $\mathscr{S}_T(t_0, x_0)$ entrega información muy relevante sobre la sos-





Figura 2: Esquema tomado de Gajardo et al. (2021) del conjunto de umbrales sostenibles para dos estados iniciales diferentes x_0 y x'_0 .

tenibilidad del estado actual del recurso x_0 , en el sentido de que informa sobre los niveles de las diferentes métricas u observaciones I_j que pueden garantizarse tanto hoy como en el futuro. En particular, un conjunto $\mathscr{S}_T(t_0, x_0)$ pequeño, indica que el estado actual x_0 es vulnerable en el sentido de que hay pocas opciones para operar en el sistema en términos de su sostenibilidad. De esta forma, el conjunto $\mathscr{S}_T(t_0, x_0)$ pretende proporcionar una imagen del estado actual del sistema, dado por x_0 , en términos de los umbrales que pueden mantenerse de forma sostenible en el tiempo. La Figura 2 muestra el conjunto de umbrales sostenibles para dos diferentes estados iniciales x_0 y x'_0 en el caso en que el espacio de umbrales es de dimensión dos. En esta imagen, teniendo $\mathscr{S}_T(t_0, x'_0) \subset \mathscr{S}_T(t_0, x_0)$, se puede inferir que el estado x'_0 está en una peor situación que x_0 .

Por otro lado, en varias aplicaciones el estado inicial x_0 suele ser conocido o al menos estimado, por lo que puede ser más fácil y práctico determinar $\mathscr{S}_T(t_0, x_0)$ en lugar del núcleo de viabilidad completo $\mathbb{V}_T(t_0, \theta)$. Además, el conjunto de umbrales sostenibles tiene propiedades matemáticas que no comparte el núcleo de viabilidad, como ser un conjunto inferior en el sentido de que

$$\mathscr{S}_T(t_0, x_0) - \mathbb{R}^p_+ = \mathscr{S}_T(t_0, x_0), \tag{7}$$

propiedad que se obtiene directamente de la definición (5), la que hace el cálculo numérico del conjunto $\mathscr{S}_T(t_0, x_0)$ más abordable, dado que gracias a la propiedad (7), este conjunto queda completamente caracterizado por su frontera, propiedad que mencionaremos más adelante. Por lo tanto, para problemas con varias variables de estado, el cálculo de $\mathbb{V}_T(t_0, \theta)$ puede ser demasiado costoso o poco práctico en términos del tiempo computacional, incluso si solo hay pocas restricciones. Sin embargo, en la misma situación (varias variables de estado con pocas restricciones), el tiempo computacional de estimar $\mathscr{S}_T(t_0, x_0)$ puede reducirse considerablemente porque, esencialmente, la complejidad de calcular $\mathbb{V}_T(t_0, \theta)$ y $\mathscr{S}_T(t_0, x_0)$ es la misma, pero este último es un objeto en un espacio de menor dimensión. Antes de terminar esta sección, veamos una propiedad de monotonía del conjunto $\mathscr{S}_T(t_0, x_0)$, que es útil para la identificación y aproximación del conjunto cuando se tiene horizonte infinito:

$$\mathscr{S}_T(t, x_0) \subset \mathscr{S}_T(t+1, x_0)$$

 $\mathscr{S}_{T+1}(t, x_0) \subset \mathscr{S}_T(t, x_0)$

La demostración de estas inclusiones es directa de la definición (5) y simplemente subrayan que los umbrales que son sostenibles durante un período de tiempo, también son sostenibles durante un período más corto. De acuerdo con dicha propiedad de monotonía, se puede deducir que el conjunto de umbrales sostenibles en el caso de horizonte infinito se puede caracterizar a través de umbrales sostenibles en tiempo finito como sigue:

$$\mathscr{S}_{\infty}(t_0, x_0) = \bigcap_{T \ge t_0} \mathscr{S}_T(t_0, x_0)$$

En virtud de la anterior propiedad, a partir de ahora supondremos que el horizonte de tiempo T es finito.

UMBRALES SOSTENIBLES Y MAXIMIN

En esta sección, procederemos a caracterizar el conjunto de umbrales sostenibles $\mathscr{S}_T(t_0, x_0)$ a través de problemas de optimización de tipo maximin. Si bien hay una amplia literatura matemática sobre problemas de optimización maximin, desde el punto de vista de la sostenibilidad cuantitativa, el concepto maximin fue propuesto en los años setenta Solow (1974), definiéndolo como el nivel de utilidad más alto que puede sostenerse en el tiempo, promoviendo así la equidad intergeneracional. Por lo tanto, establecer una relación entre el maximin de un problema de sostenibilidad (por definir aun) y el respectivo conjunto de umbrales sostenibles, establece un puente entre dos enfoques *a priori* diferentes, utilizados para abordar este tipo de problemas.

En primera instancia, relacionaremos al conjunto $\mathscr{S}_T(t_0, x_0)$ con un problema maximin multicriterio. Para ello tendremos que definir qué se entiende por soluciones de este tipo de problemas, las cuales entenderemos en el sentido de Pareto. En segunda instancia caracterizaremos el conjunto $\mathscr{S}_T(t_0, x_0)$, como el conjunto de nivel de una función valor de un problema maximin usual (i.e., monocriterio). Dicha caracterización nos permitirá establecer un método para identificar puntos que están en la frontera de $\mathscr{S}_T(t_0, x_0)$, recuperando de aquella forma el conjunto completo. Los resultados matemáticos que enunciaremos para ambas partes, fueron establecidos en Doyen y Gajardo (2020) y Gajardo y Hermosilla (2021), referencias donde se pueden encontrar las demostraciones.

Antes de comenzar con las dos caracterizaciones mencionadas, definiremos los puntos de Pareto o frontera de Pareto de un conjunto. Para ello utilizaremos el concepto de dominancia en el sentido de Pareto.

Definición 1 Dados dos vectores $\theta = (\theta_1, ..., \theta_p)$ y $\tilde{\theta} = (\tilde{\theta}_1, ..., \tilde{\theta}_p)$ en \mathbb{R}^p , se dice que θ está fuertemente dominado



Figura 3: Ilustración de las fronteras de Pareto de un conjunto $\mathscr{S} \subset \mathbb{R}^2$. En verde se indica la frontera débil y los puntos en rojo corresponden a la frontera (fuerte).

por $\tilde{\theta}$ en el sentido de Pareto, si $\theta < \tilde{\theta}$ (componente a componente) y se dirá que está debilmente dominado en el sentido de Pareto, si $\theta \le \tilde{\theta}$ y existe una coordenada $j \in \{1, ..., p\}$ tal que $\theta_j < \tilde{\theta}_j$.

Definición 2 Dado un conjunto $\mathscr{S} \subset \mathbb{R}^p$, su frontera de Pareto débil se define por

 $\mathscr{P}_{w}(\mathscr{S}) \stackrel{\text{def}}{=} \{ \theta \in \mathscr{S} \mid \nexists \, \tilde{\theta} \in \mathscr{S} \, ; \, \tilde{\theta} \, \text{ domina fuertemente a } \, \theta \};$

Es decir, $\theta \in \mathcal{P}_w(\mathcal{S})$ *si y solamente si* $\theta \in \mathcal{S}$ *y para todo* $\tilde{\theta} \in \mathcal{S}$ *, existe una coordenada j* $\in \{1, ..., p\}$ *tal que* $\theta_j \ge \tilde{\theta}_j$ *. La frontera (fuerte) de Pareto de* \mathcal{S} *estará dada por*

 $\mathscr{P}(\mathscr{S}) \stackrel{\text{def}}{=} \{ \theta \in \mathscr{S} \mid \nexists \ \tilde{\theta} \in \mathscr{S} \ \text{tal que} \ \tilde{\theta} \ \text{domina debil a} \ \theta \}.$

En otras palabras, $\theta \in \mathscr{P}(\mathscr{S})$ si y solamente si $\theta \in \mathscr{S}$ y para todo $\tilde{\theta} \in \mathscr{S}$ (diferente de θ) se tiene $\tilde{\theta} \leq \theta$ y además, existe una coordenada $j \in \{1, ..., p\}$ tal que $\theta_j > \tilde{\theta}_j$.

Observe que de las definiciones anteriores, se obtiene que $\mathscr{P}(\mathscr{S}) \subset \mathscr{P}_w(\mathscr{S})$ para todo conjunto $\mathscr{S} \subset \mathbb{R}^p$. En las próximas secciones trabajaremos con las fronteras de Pareto del conjunto de umbrales sostenibles $\mathscr{P}_T(t_0, x_0)$.

Maximin multicriterio

El enfoque maximin usual en sostenibilidad cuantitativa - Cairns y Long (2006); Doyen y Martinet (2012); Solow (1974) -, busca maximizar el mínimo nivel en el tiempo de un beneficio *I*. En otras palabras, el criterio maximin define el nivel máximo de beneficio que se puede sostener en el tiempo a partir de un estado inicial x_0 . De esta forma, si el sistema dinámico controlado viene dado por

$$\begin{cases} x(t+1) = D(x(t), u(t)) & t_0 \le t < T \\ x(t_0) = x_0, \end{cases}$$
(8)

y un beneficio en el transcurso del tiempo está representado por la función $I: X \times U \longrightarrow \mathbb{R}$, es decir, en cada periodo de tiempo t se obtiene un beneficio I(x(t), u(t)), lo que se busca es maximizar el mínimo nivel de I a lo largo del tiempo. Esto lo escribimos como

$$V(t_0, x_0) \stackrel{\text{def}}{=} \sup_{\substack{(x(\cdot), u(\cdot))\\\text{satisfacen (8)}}} \min_{t_0 \le t \le T} I(x(t), u(t)),$$

daf

donde $V(t_0, \cdot) : X \longrightarrow \mathbb{R}$ será la función valor maximin asociada a la métrica *I*. Cuando el supremo en la definición de $V(t_0, x_0)$ es alcanzado, entonces corresponde a un máximo y esta función valor tiene asociada al menos una trayectoria óptima $x^*(\cdot)$ junto a la trayectoria de controles o decisiones óptima $u^*(\cdot)$. Si el conjunto de controles $U \subset \mathbb{R}^m$ es compacto, la dinámica $D : X \times U \longrightarrow X$ es continua y la función $I : X \times U \longrightarrow \mathbb{R}$ es semicontinua superior, entonces se puede demostrar que el supremo en la anterior definición se alcanza, por lo que podemos remplazarlo por un máximo escribiendo

$$V(t_0, x_0) \stackrel{\text{def}}{=} \max_{\substack{(x(\cdot), u(\cdot))\\\text{satisfacen (8)}}} \min_{t_0 \le t \le T} I(x(t), u(t))$$
(9)

El valor $V(t_0, x_0)$ tiene una interpretación simple: es el máximo valor que se puede asegurar de la métrica *I* en todos los periodos de tiempo (i.e., para todas las generaciones) a partir del estado inicial x_0 del sistema. Esta métrica puede representar el nivel de un recurso natural, lo que se cosecha de este, un beneficio económico, o cualquier otra medida de interés que se busque preservar a futuro.

Desde un punto de vista de la sostenibilidad, el objetivo es equilibrar no una, sino que diversas métricas relacionadas con objetivos ecológicos, económicos y sociales dentro de una perspectiva intergeneracional. Para abordar esto, estudiaremos un problema maximin multiobjetivo, en donde el problema de optimización maximin involucrará múltiples métricas I_1, \ldots, I_p . En términos matemáticos, este problema lo formulamos como

$$\begin{array}{l}
\max_{\substack{(x(\cdot),u(\cdot))\\\text{satisfacen (8)}}} \left(\min_{t_0 \le t \le T} I_1(x(t),u(t)), \dots, \min_{t_0 \le t \le T} I_p(x(t),u(t)) \right) \\
\end{array}$$
(10)

La anterior formulación corresponde a un problema de optimización multicriterio (o multiobjetivo), dado que la función que se está maximizando tiene más de una componente. En consecuencia, es necesario establecer qué se entiende por una solución del problema de optimización (10) pues generalmente, no existe una trayectoria $(x(\cdot), u(\cdot))$ que maximice todos los criterios objetivos $\min_{t_0 \le t \le T} I_j(x(t), u(t))$; j = 1, ..., p de manera simultánea. Nuestro enfoque se centrará en las soluciones óptimas en el sentido de Pareto, que son soluciones que no pueden ser mejoradas en todos los criterios sin deteriorar alguno de ellos Miettinen (1999). En términos matemáticos, una trayectoria factible $(x^*(\cdot), u^*(\cdot))$ que satisface (8) se dice que domina débilmente a otra trayectoria factible $(x(\cdot), u(\cdot))$ si $\forall j \in \{1, 2, ..., p\}$

$$\min_{t_0 \le t \le T} I_j(x^*(t), u^*(t)) \ge \min_{t_0 \le t \le T} I_j(x(t), u(t)),$$

 $\exists j^* \in \{1, 2, \dots, p\}$ tal que

$$\min_{t_0 \le t \le T} I_{j^*}(x^*(t), u^*(t)) > \min_{t_0 \le t \le T} I_{j^*}(x(t), u(t))$$



Una trayectoria factible $(x^*(\cdot), u^*(\cdot))$ se denominará una solución fuerte del problema (10), en el sentido de Pareto, si no existe otra trayectoria factible que la domine débilmente. El conjunto de todas las soluciones fuertes lo denotaremos por $\mathscr{A}_m(t_0, x_0)$.

El conjunto de valores de los criterios que se están optimizando en (10) asociados a las soluciones fuertes, lo denotaremos por $\mathscr{V}_m(t_0, x_0)$ y corresponde a

$$\begin{aligned} \mathcal{V}_m(t_0, x_0) \stackrel{\text{def}}{=} \\ \left\{ \left(\min_{t_0 \le t \le T} I_1(x^*(t), u^*(t)), \dots, \min_{t_0 \le t \le T} I_p(x^*(t), u^*(t)) \right) \ \middle| \\ (x^*(\cdot), u^*(\cdot)) \in \mathscr{A}_m(t_0, x_0) \right\} \subset \mathbb{R}^p \quad (11) \end{aligned}$$

Es decir, el conjunto $\mathscr{V}_m(t_0, x_0) \subset \mathbb{R}^p$ contiene los valores del problema (10) que se alcanzan con soluciones fuertes.

Similar a los conceptos introducidos previamente, diremos que una trayectoria factible $(x^*(\cdot), u^*(\cdot))$ que satisface (8), domina fuertemente a otra trayectoria factible $(x(\cdot), u(\cdot))$ si

$$\min_{t_0 \le t \le T} I_j(x^*(t), u^*(t)) > \\
\min_{t_0 \le t \le T} I_j(x(t), u(t)) \quad \forall \ j \in \{1, 2, \dots, p\}.$$
(12)

Una trayectoria $(x^*(\cdot), u^*(\cdot))$ se dirá es una solución débil del problema (10) en el sentido de Pareto, si no existe otra trayectoria factible que la domine fuertemente de acuerdo a como se define en (12). De esta forma, el conjunto de soluciones débiles lo denotaremos por $\mathscr{A}_m^w(t_0, x_0)$ y el conjunto de los valores (multicriterio) asociados a las soluciones débiles corresponderá a

$$\mathcal{V}_m^w(t_0, x_0) \stackrel{\text{def}}{=} \left\{ \left(\min_{t_0 \le t \le T} I_1(x^*(t), u^*(t)), \dots, \min_{t_0 \le t \le T} I_p(x^*(t), u^*(t)) \right) \mid (x^*(\cdot), u^*(\cdot)) \in \mathscr{A}_m^w(t_0, x_0) \} \subset \mathbb{R}^p \quad (13) \right\}$$

De estas definiciones, directamente se deducen las siguientes inclusiones

$$\mathscr{A}_m(t_0, x_0) \subset \mathscr{A}_m^w(t_0, x_0); \qquad \mathscr{V}_m(t_0, x_0) \subset \mathscr{V}_m^w(t_0, x_0),$$

enfatizando que la optimalidad fuerte de Pareto es más demandante que la optimalidad débil.

Observe que si se tiene un solo criterio $(p = 1; I_1 = I)$, entonces $\mathscr{V}_m(t_0, x_0) = \mathscr{V}_m^{w}(t_0, x_0)$ y estos conjuntos contienen un solo valor, que coincidirá con $V(t_0, x_0)$ definido en (9).

Siendo (10) un problema de optimización dinámico, determinar los valores óptimos fuerte y débil en el sentido de Pareto, entregados por los conjuntos $\mathscr{V}_m(t_0,x_0)$ y $\mathscr{V}_m^w(t_0,x_0)$, presenta varios desafíos y complejidades, pues se está optimizando sobre trayectorias $(x(\cdot), u(\cdot))$ que satisfacen (8). A continuación presentaremos una caracterización de estos conjuntos, establecida como un problema de optimización multicriterio estático, es decir, que no involucra trayectorias, caracterizaciones en las cuales intervendrán el conjunto de umbrales sostenibles $\mathscr{S}_T(t_0, x_0)$ y el núcleo de viabilidad $\mathbb{V}_T(t_0, \theta)$ definidos por (5) y (4) respectivamente. Tales representaciones permiten interpretar las soluciones del problema maximin multicriterio (10), como un caso extremo de viabilidad.

Las caracterizaciones establecen que los valores máximos (débiles y fuertes) de Pareto del problema maximin (10), asociados a un estado x_0 , corresponden a los valores máximos (en el sentido débil y fuerte de Pareto) del conjunto de umbrales sostenibles (ver Definición 2), que también se pueden interpretar como los niveles máximos de las restricciones del sistema (3) tal que el estado actual x_0 se encuentre en el núcleo de viabilidad subyacente.

Proposición 1 *Para todo estado inicial* $x_0 \in X$ *, se tendrá*

al (W)

$$\mathcal{V}_m^{rr}(t_0, x_0) = \mathscr{P}_w\Big(\mathscr{S}_T(t_0, x_0)\Big) = \mathscr{P}_w\Big(\{\theta \in \mathbb{R}^p \mid x_0 \in \mathbb{V}_T(t_0, \theta)\}\Big)$$
$$\mathcal{V}_m(t_0, x_0) = \mathscr{P}\Big(\mathscr{S}_T(t_0, x_0)\Big) = \mathscr{P}\Big(\{\theta \in \mathbb{R}^p \mid x_0 \in \mathbb{V}_T(t_0, \theta)\}\Big)$$

La demostración de la anterior proposición, puede encontrarse en Doyen y Gajardo (2020). Observe que las segundas igualdades en cada línea, son una consecuencia directa de la equivalencia (6), pues se tendrá la igualdad

$$\{\boldsymbol{\theta} \in \mathbb{R}^p \mid x_0 \in \mathbb{V}_T(t_0, \boldsymbol{\theta})\} = \mathscr{S}_T(t_0, x_0).$$

El resultado de la Proposición 1 puede interpretarse de la siguiente forma. Sabemos que los umbrales $\theta = (\theta_1, \dots, \theta_p)$ son sostenibles desde el estado inicial x_0 si pertenecen al conjunto $\mathscr{S}_T(t_0, x_0)$. Por lo tanto, los máximos umbrales sostenibles (i.e., la frontera de Pareto, débil o fuerte, del conjunto $\mathscr{S}_T(t_0, x_0)$) corresponden a los máximos niveles de las métricas, indicadores u observaciones I_j que se pueden sostener en el tiempo, al ser estos los valores óptimos del problema maximin multicriterio (10). La Proposición 1 significa también, que a partir de un estado x_0 dado, no se puede garantizar ningún umbral mayor a los valores óptimos de Pareto dados por los conjuntos $\mathscr{V}_m^w(t_0, x_0, T)$ y $\mathscr{V}_m(t_0, x_0, T)$.

Aunque la interpretación de esta proposición es bastante sencilla, tiene importantes consecuencias, pues establece que los valores óptimos del problema maximin multicriterio (10) pueden definirse en el marco de la la teoría de la viabilidad, utilizando un problema de optimización multicriterio sobre el conjunto de umbrales sostenibles o sobre el núcleo de viabilidad. Aunque este método no es necesariamente más sencillo que el enfoque estándar para resolver problemas maximin, permite mostrar algunas propiedades ocultas de sus soluciones. Siempre que la solución de un problema de optimización dado pueda formularse en términos de un núcleo de viabilidad, la solución hereda las propiedades del núcleo. Dichas propiedades incluyen una estructura de programación dinámica que se utiliza para obtener aproximaciones numéricas de los valores óptimos maximin multicriterio y también de los umbrales sostenibles, como describimos más adelante.

Conjunto de nivel

En esta parte, estableceremos la relación entre el conjunto de umbrales sostenibles $\mathscr{S}_T(t_0, x_0)$ y un problema de optimización maximin. La diferencia con la anterior sección, es que en esta ocasión el problema de optimización a considerar será monocriterio.

En primer lugar, para un estado inicial x_0 , una trayectoria de estados y controles $(x(\cdot), u(\cdot))$ que satisface el sistema (8) y un vector $\theta = (\theta_1, \dots, \theta_p) \in \mathbb{R}^p$, definimos la función

$$R_{\theta}(t_0, x_0, x(\cdot), u(\cdot))) \stackrel{\text{def}}{=} \min_{t_0 \le t \le T} \min_{j \in \{1, \dots, p\}} (I_j(x(t), u(t)) - \theta_j)$$

Asociado a la anterior función, definimos el problema de optimización

$$W(\theta, t_0, x_0) \stackrel{\text{def}}{=} \max_{\substack{(x(\cdot), u(\cdot))\\\text{satisfacen (8)}}} R_{\theta}(t_0, x_0, x(\cdot), u(\cdot)), \quad (14)$$

que consiste en maximizar, sobre todas las trayectorias factibles del sistema sin restricciones (8), la función R_{θ} .

El siguiente resultado establece una caracterización del conjunto de umbrales sostenibles $\mathscr{S}_T(t_0, x_0)$ en términos de un conjunto de nivel de la función $W(\theta, t_0, x_0)$.

Proposición 2 *Para todo estado inicial* $x_0 \in X$ *se tendrá*

$$\mathscr{S}_T(t_0, x_0) = \{ \boldsymbol{\theta} \in \mathbb{R}^p \mid W(\boldsymbol{\theta}, t_0, x_0) \ge 0 \}$$

Además, un vector $\theta \in \mathbb{R}^p$ pertenecerá a la frontera débil de Pareto del conjunto $\mathscr{S}_T(t_0, x_0)$, si y solamente si, $W(\theta, t_0, x_0) = 0$, es decir,

$$\boldsymbol{\theta} \in \mathscr{P}_{w}\Big(\mathscr{S}_{T}(t_{0},x_{0})\Big) \Leftrightarrow W(\boldsymbol{\theta},t_{0},x_{0}) = 0$$

Este resultado, establecido en Gajardo y Hermosilla (2021), entrega una herramienta para chequear si un vector de umbrales $\theta \in \mathbb{R}^p$ es o no sostenible a partir del estado inicial x_0 , que consistirá en resolver el problema (14). Más aún, la Proposición 2 nos entrega también una caracterización de la frontera de Pareto débil de $\mathscr{I}_T(t_0, x_0)$, como el conjunto de nivel cero de la función $W(\cdot, t_0, x_0)$. Esto tiene una considerable relevancia, dado que los vectores θ en la frontera de Pareto son los mejores (i.e., máximos) umbrales que se pueden sostener, de acuerdo con lo analizado en la sección anterior.

Por otro lado, gracias a la propiedad (7), bajo ciertas hipótesis no muy demandantes, como que el conjunto $U \subset \mathbb{R}^m$ donde se encuentran los controles sea compacto, que la dinámica $D: X \times U \longrightarrow X$ sea continua, y las funciones $I_j:$ $X \times U \longrightarrow \mathbb{R}$ sean semicontinuas superiores y acotadas inferiormente, se tendrá que (ver Gajardo y Hermosilla (2021)) el conjunto $\mathscr{S}_T(t_0, x_0)$ queda completamente determinado a partir de sus fronteras de Pareto, mediante las igualdades

$$\mathscr{S}_{T}(t_{0},x_{0}) = \mathscr{P}_{w}\left(\mathscr{S}_{T}(t_{0},x_{0})\right) - \mathbb{R}^{p}_{+} = \mathscr{P}\left(\mathscr{S}_{T}(t_{0},x_{0})\right) - \mathbb{R}^{p}_{+}$$
(15)

Las hipótesis mencionadas son bastante habituales en el modelamiento de problemas de recursos naturales o, más en

general, en el modelamiento de problemas de sostenibilidad De Lara y Doyen (2008). La compacidad del conjunto de controles U simplemente representa las limitaciones que generalmente los tomadores de decisiones suelen tener. El que las funciones I_j sean acotadas inferiormente, es bastante natural si dichas métricas representan indicadores biológicos, ecológicos, económicos o sociales que no son negativos. Una consecuencia de esta hipótesis, es que el conjunto de umbrales sostenibles nunca será vacío. De hecho, si $\underline{\theta} = (\underline{\theta}_1, \dots, \underline{\theta}_p)$ es un vector de cotas inferiores de las funciones I_j , entonces se obtiene inmediatamente que $\underline{\theta} \in \mathscr{S}_T(t_0, x_0)$ para cualquier condición inicial x_0 . Por supuesto, si $\mathscr{S}_T(t_0, x_0)$ se reduce a $\{\underline{\theta}\} - \mathbb{R}^m_+$, entonces estamos en presencia del peor escenario para operar de forma sostenible.

En consecuencia, poder calcular alguna de las fronteras de Pareto del conjunto $\mathscr{S}_T(t_0, x_0)$, es suficiente para determinar el conjunto completo. El siguiente resultado, establecido en Gajardo y Hermosilla (2021), permitirá identificar de una manera directa elementos en la frontera débil $\mathscr{P}_w(\mathscr{S}_T(t_0, x_0))$.

Proposición 3 *Para un estado inicial* $x_0 \in X$ *y un vector* $\theta \in \mathbb{R}^p$, *si* $W(\theta, t_0, x_0) < 0$, *es decir (ver la Proposición 2)* $\theta \notin \mathscr{S}_T(t_0, x_0)$, *entonces*

$$p(\boldsymbol{\theta}) \stackrel{\text{def}}{=} \boldsymbol{\theta} + W(\boldsymbol{\theta}, t_0, x_0)(1, \dots, 1) \in \mathscr{P}_w\left(\mathscr{S}_T(t_0, x_0)\right)$$
(16)

Lo que este resultado nos está indicando, es que si consideramos un vector $\theta \in \mathbb{R}^p$ con coordenadas suficientemente grandes de tal forma de que $\theta \notin \mathscr{S}_T(t_0, x_0)$, entonces, resolviendo el problema de optimización (14) para ese vector θ , obtendremos un vector en la frontera débil de Pareto del conjunto $\mathscr{S}_T(t_0, x_0)$, simplemente sumando en cada componente de θ el valor $W(\theta, t_0, x_0)$. En otras palabras, desde fuera del conjunto de umbrales sostenibles, estamos obteniendo puntos de su frontera, como se ilustra en la Figura 4.

PRINCIPIO DE PROGRAMACIÓN DINÁMICA

A partir de la caracterización obtenida en la sección anterior, dada por las proposiciones 2 y 3 donde interviene un problema de optimización de tipo maximin, a continuación expondremos un resultado, obtenido en Gajardo y Hermosilla (2021), que establece el principio de programación dinámica para poder encontrar el valor $W(\theta, t_0, x_0)$ definido en (14). Dicha estructura de programación dinámica proviene de la propiedad subyacente al núcleo de viabilidad en tiempo discreto, como se detalla en De Lara y Doyen (2008). A partir de dicho principio se podrá diseñar un esquema numérico para calcular el conjunto de umbrales sostenibles $\mathscr{S}_T(t_0, x_0)$.

Proposición 4 Para todo vector $\theta = (\theta_1, ..., \theta_p) \in \mathbb{R}^p$ la función valor $W(\theta, \cdot, \cdot)$, definida en (14), satisface la ecuación inversa de programación dinámica

$$\begin{split} W(\theta,T,x) &= \max_{u \in U} \min_{j \in \{1,\dots,p\}} (I_j(x,u) - \theta_j) \\ W(\theta,t,x) &= \max_{u \in U} \min \left\{ W(\theta,t+1,D(x,u,w)), \\ \min_{j \in \{1,\dots,p\}} (I_j(x,u) - \theta_j) \right\} \quad t = t_0,\dots,T-1 \end{split}$$





Figura 4: Ilustración tomada de Gajardo y Hermosilla (2021), de la Proposición 3 mostrando cómo utilizarla para la construcción de la frontera débil de Pareto a partir de vectores de umbrales θ_a , θ_b y θ_c que no son sostenibles cuando p = 2 (i.e., dos restricciones). La frontera débil de Pareto en este ejemplo se indica con la línea punteada negra.

Lo que señala el anterior principio, es que si para un vector $\theta \in \mathbb{R}^p$ y un tiempo t + 1 se conoce la función $W(\theta, t + 1, x)$, para todo estado $x \in X$, entonces resolviendo un problema de optimización estático (no involucra trayectorias), se puede obtener el valor de la función $W(\theta, t, x)$. Por ello se comienza resolviendo el problema desde el final (t = T)hacia atrás. Cada uno de estos problemas es simple de resolver, pues solo se está optimizando sobre el conjunto (compacto) de controles U en lugar de optimizar sobre un conjunto de trayectorias. Sin embargo, para poder hacer lo anterior, es necesario, en cada tiempo t, conocer el valor de la función $W(\theta, t+1, x)$ en todo estado x. Si bien el principio de programación dinámica es muy útil para resolver problemas de optimización dinámicos, dividiéndolos en varios sub-problemas estáticos, el inconveniente es que se necesitan resolver muchos de estos subproblemas, número que crece de manera exponencial respecto al periodo de tiempo analizado $T - t_0$ y a la cantidad de variables de estado. Es por ello que en la literatura se señala que la programación dinámica sufre la maldición de la dimensionalidad, que la transforma en un método eficaz solo cuando el sistema considerado tiene pocas variables de estado.

De esta forma, dado un estado inicial x_0 en un tiempo inicial t_0 , para un vector de umbrales $\theta \in \mathbb{R}^p$, utilizando el esquema señalado en la Proposición 4 es posible determinar el valor $W(\theta, t_0, x_0)$. Con este valor calculado, utilizando la Proposición 3, se obtiene de inmediato un elemento en la frontera débil de Pareto del conjunto $\mathscr{S}_T(t_0, x_0)$, utilizando la propiedad (16). Repitiendo este procedimiento para varios vectores θ , es posible estimar la frontera débil del conjunto $\mathscr{S}_T(t_0, x_0)$ y, por lo tanto, el conjunto completo (ver igualdad (15)).

OBSERVACIONES FINALES

En la gestión de recursos naturales, problemas de conservación de la biodiversidad o cambio climático, hacer operativas las definiciones de sostenibilidad es un desafío mayor. Al respecto, el criterio maximin desempeña un papel importante como el valor máximo de alguna cantidad de interés que se puede sostener desde un punto de vista intergeneracional - Asheim (2007); Cairns y Long (2006) -. Por otro lado, son diversos los enfoques propuestos basados en restricciones y umbrales para indicadores biológicos, ecológicos, económicos o sociales, que son vistos como metas para alcanzar los objetivos de gestión sostenible. Cuando las restricciones inducidas por umbrales deben satisfacerse a lo largo del tiempo, estos problemas pueden formularse en el marco matemático de la teoría de la viabilidad, como han propuesto numerosos autores en las últimas décadas - Oubraham y Zaccour (2018) -. El enfoque de esta teoría, ha sido principalmente el cálculo o la estimación del núcleo de viabilidad, consistente en el conjunto de estados iniciales del sistema a partir de los cuales es posible satisfacer las restricciones prescritas a lo largo del tiempo. En este artículo, hemos hecho una revisión del enfoque inverso, consistente en determinar los umbrales para los que existe una trayectoria que satisface las restricciones parametrizadas por dichos umbrales. Este nuevo concepto y su cómputo proporcionan una herramienta para la gestión y visualización de múltiples objetivos relacionados con la sostenibilidad, permitiendo observar la (in)compatibilidad de múltiples objetivos y sus compensaciones.

Adicionalmente, en esta revisión se ha expuesto una extensión del enfoque maximin a un contexto multicriterio, combinando el enfoque de control viable y de optimalidad en el sentido de Pareto, mostrando los fuertes vínculos existentes entre los problemas maximin y el enfoque de la teoría de la viabilidad. En particular, se muestra cómo los valores del problema maximin son soluciones de un problema estático de optimización multicriterio, que implica al núcleo de viabilidad. En otras palabras, el maximin emerge como un óptimo de viabilidad de Pareto. Este resultado indica que las restricciones económicas, ecológicas o sociales sostenibles y las compensaciones o sinergias entre estas restricciones pueden identificarse a partir del núcleo de viabilidad y, en particular, del conjunto de umbrales sostenibles. Basándose en la estructura de programación dinámica en la que se basa el núcleo de viabilidad, en este documento se proporciona un resultado que permite diseñar algoritmos para la identificación y aproximación de los máximos de Pareto y, por tanto, de los umbrales sostenibles.

Los resultados expuestos confirman la pertinencia del enfoque de la teoría de la viabilidad para abordar problemas asociados a la sostenibilidad, considerando tanto la equidad intergeneracional como los objetivos multicriterio - Fleurbaey (2015); Doyen y Martinet (2012); Oubraham y Zaccour (2018) -. En particular, la teoría de la viabilidad identifica las decisiones que satisfacen las restricciones de sostenibilidad en el presente y mantienen la capacidad para satisfacer estas restricciones en el futuro. Desde este punto de vista, el enfoque de la viabilidad es coherente con la definición de sostenibilidad de Brundtland - Brundtland et al. (1987) -, que caracteriza el desarrollo sostenible como un desarrollo "que satisface las necesidades del presente sin comprometer la capacidad de las generaciones futuras para satisfacer sus propias necesidades". Así, nuestros resultados aportan importantes aspectos metodológicos para la operacionalización de la sostenibilidad - Baumgartner y Quaas (2009); Neumayer (2010) -.

Concluimos este artículo mencionando que el enfoque planteado bien puede ser extendido a sistemas controlados bajo restricciones como (3), pero en tiempo continuo (ver Barrios et al. (2018)). Las herramientas para poder determinar el conjunto de umbrales sostenibles en dicho contexto, son diferentes y las que se han establecido hasta ahora se sustentan en los teoremas de comparación de trayectorias de un sistemas de ecuaciones diferenciales ordinarias. Por otra parte, también se puede extender la noción a sistemas estocásticos en tiempo discreto. La noción de núcleo de viabilidad en tal contexto existe en la literatura (ver Aubin (1990); De Lara y Doyen (2008); Aubin et al. (2011)), por lo que no es difícil extender la definición de umbrales sostenibles, al menos en dos sentidos: umbrales que se pueden sostener en el tiempo con al menos un cierto nivel de probabilidad, o que se puedan sostener ante cualquier evento aleatorio futuro. Esta última opción, da pie a la definición de umbrales sostenibles robustos, concepto definido y estudiado recientemente en Gajardo et al. (2021).

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Elucidating the Role Played by Cancer Stem Cells in Cancer Growth

Esclareciendo el papel que juegan las células madre cancerosas en el crecimiento del cáncer

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Abstract— The cancer stem cell hypothesis states that cancer growth is propelled by a relatively small number of cancer stem cells (CSCs). These CSCs have been shown to play a crucial role in the growth and recurrence of many tumor types. The possibility that their elimination becomes an efficient cancer control procedure has even led to new therapeutic paradigms. On the other hand, from their early stages, most solid tumors grow in stressed environments. The stress field impacts on tumor evolution, and it is likely to affect different cancer cell populations in different ways. It is therefore of great interest to determine the nature and strength of the interactions between CSCs and differentiated tumor cells and how these interactions are affected by the mechanical properties of the environment. We have developed a two-population mathematical model suitable to describe the initial stages of cancer growth and applied it to extract information from three different experiments. Two of these experiments involve tumorspheres (spheroids resulting from the proliferation of a single CSC). In these cases, the model validates the concept of CSC niche (the microenvironment responsible for signals that stimulate or inhibit CSC growth), shows that interspecific interactions stimulate growth, while intraspecific interactions are generally inhibitory, and indicates how substrate hardness modifies growth. In the third experiment analyzed, where stress-induced growth suppression was measured in multicellular tumor spheroids, we were able to reconstruct the (unobserved) CSC fraction and found that medium rigidity eventually forces all cell interactions to be competitive. We find that, under adverse environmental conditions the CSC fraction always remains nonzero. This lends support to the hypothesis of the existence of the niche as a regulatory maintenance mechanism whose understanding will be crucial to the development of a successful therapy based on CSC elimination.

Keywords-cancer stem cell, tumor, populations, interaction modeling, substrate

Resumen— La hipótesis de las células madre cancerosas afirma que el crecimiento del cáncer es promovido por un número relativamente pequeño de células madre cancerosas (CSCs). Se ha demostrado que estas CSC juegan un papel crucial en el crecimiento y recurrencia de muchos tipos de tumores. La posibilidad de que su eliminación se transforme en un procedimiento eficiente para el control del cáncer ha conducido a nuevos paradigmas terapéuticos. Por otra parte, a partir de sus etapas iniciales la mayoría de los tumores sólidos crecen en ambientes sujetos a tensiones mecánicas. El campo de tensiones afecta a la evolución del tumor y es probable que afecte en forma diferente a las distintas poblaciones celulares. Es entonces de gran interés determinar la naturaleza e intensidad de las interacciones entre las CSC y las células cancerosas diferenciadas del tumor y cómo estas interacciones son influidas por las propiedades mecánicas del ambiente. Hemos desarrollado un modelo matemático de dos poblaciones, adecuado para describir las etapas iniciales del crecimiento del cáncer y lo hemos aplicado para obtener información a partir de tres experimentos diferentes. Dos de estos experimentos fueron realizados con tumoresferas (esferoides que resultan de la proliferación de una sola CSC). En estos casos, el modelo valida el concepto de nicho: el microambiente responsable por las señales que estimulan o inhiben la reproducción de las CSC, muestra que las interacciones interespecíficas estimulan el crecimiento, mientras que las interacciones intraespecíficas son generalmente inhibitorias, e indica cómo la rigidez del substrato modifica el crecimiento. En el tercer experimento que analizamos, en el que fue medido cómo la presión aplicada suprime el crecimiento de esferoides multicelulares, pudimos reconstruir la fracción de CSC (que no había sido medida) y encontramos que la rigidez del medio eventualmente hace que todas las interacciones intercelulares sean competitivas. Encontramos también que bajo condiciones ambientales adversas la fracción de CSC siempre es no nula. Estos resultados apoyan la hipótesis de la existencia del nicho como mecanismo de mantenimiento regulatorio cuya dilucidación es esencial para el desarrollo de una terapia exitosa basada en la eliminación de las CSC.

Palabras clave-célula madre cancerosa, tumor, poblaciones, modelado de interacciones, substrato



INTRODUCTION

he obvious interest and complexity of cancer has led to the formulation of numerous mathematical models of tumor growth. Surveys of the state of the art in cancer modeling have appeared at different times (Adam and Bellomo, 1997; Wodarz and Komarova, 2005; Tan and Hanin, 2008; Lowengrub et al., 2009). The models range from the deterministic differential equation descriptions (Murray, 2001) to the cellular automata (Scalerandi et al., 1999), to stochastic approaches (Tan and Hanin, 2008). The emergence of new experimental techniques continuously imposes further constraints on the growth models being developed. Multicellular tumor spheroids were developed to study the influence of the microenvironment on the regulation of cell development and viability (Freyer and Sutherland, 1986; Sutherland, 1988). Later, the identification of cancer stem cells in many tumor types (Al-Hajj et al., 2003; O'Brien et al., 2007) led to the formulation of the cancer stem cell hypothesis (Batlle and Clevers, 2017), which states that a subpopulation of stem cells drives cancer growth and may explain metastasis and tumor recurrence after therapy. As a consequence, new therapeutic paradigms have emerged, built on the idea of controlling cancer through the destruction or incapacitation of the CSCs (Jagust et al., 2019). Tumorspheres were developed as biological models to test the potential and weaknesses of CSC - driven tumor growth (Weiswald et al., 2015). They are spheroids grown from single-cell suspensions out of permanent cell lines or tumor tissue. When cultivated in a serum-free medium, they grow in a natural way, but their environment can be tuned-up to study particular phenomenologies. By adding growth factors such as EGF and FGF-2, the stem cells are forced to self-replicate without differentiating. Another possibility is to grow the spheroids in agarose gel to induce stress and examine how this stress modifies cell behavior and proliferation.

Associated with a stem cell is the *niche*, the set of cells and intercellular elements that provide the signals that define stem cell behavior and maintain stemness (Scadden, 2014). In the case of CSCs, the niche functionality is well known, but its design and structure are still not precisely defined, although its deregulation is certainly connected to the emergence of tumorigenesis. The cross-talk between the CSCs and their niches has now become a possible therapeutic target (Taniguchi et al., 2020). Mechanical stresses are important to the initiation and interpretation of the promoting and inhibitory signals that the niche sends to the CSC (Cheng et al., 2009). To shed light on the niche properties and on the effect of mechanical interactions, it is therefore important to have a mathematical model to describe stem-cell-fueled tumorsphere growth. We stress the importance of having a simple mathematical model: Tumorsphere experiments are notoriously difficult, and they yield key but relatively scarce data. Such sophisticated models as the one developed in (Scalerandi et al., 2002) to explain the growth of tumor cords under varying stresses are not useful to extract information of the available tumorsphere data.

We have recently developed a two-population mathematical model of tumor growth (Benítez et al., 2019, 2021), which we used to interpret the results of tumorsphere growth experiments performed under different mechanical and growth factor conditions and to extract information about the interaction between cancer stem cells and differentiated cancer cells. We also obtain the evolution of the CSC fraction, an important quantity which is in general not directly accessible to the experiments. Here we review the model, present its properties and applications, and indicate how to apply it to interpret the results of tumorsphere and spheroid growth experiments.

THE MATHEMATICAL MODEL

When a CSC undergoes mitosis, it may generate either two CSCs with a probability p_s , two differentiated cancer cells (DCCs) with a probability p_d , or one CSC and one differentiated CSC, with a probability $p_a = 1 - p_s - p_d$. To describe the interaction between the CSC and DCC populations we must generalize the standard equations for competing species to account for these three possible results of a CSC division. Since it is in general not possible to discriminate between the growth rates of the two populations, we will assume that all cells divide at the same basal reproductive rate r. The interactions between members of both populations will be quantified by four coefficients α_{ij} , which describe intraspecific (i = j) and interspecific $(i \neq j)$ interactions.

Let S(t) and D(t) be, respectively, the CSC and DCC populations at time *t*. Their evolution is then given by the following pair of equations:

$$\frac{dS}{dt} = r[p_s S] \left\{ \frac{p_s - p_d}{p_s} - \alpha_{SS} S - \alpha_{SD} D \right\}, \qquad (1a)$$

$$\frac{dD}{dt} = r[D + (1 + p_d - p_s)S] \{1 - \alpha_{DD}D - \alpha_{DS}S\}.$$
 (1b)

Positive (negative) values of the coefficient α_{ij} describe the inhibition (promotion) of population *i* growth by the presence of population *j*, i.e. positive values of α_{ij} correspond to competitive interactions, while negative values represent cooperation. The initial conditions for these equations depend on the system of interest. In the case of a tumorsphere, we start with a seed of a single cancer stem cell given by S(0) = 1 and D(0) = 0, but other choices are possible.

Since our system of equations is designed to describe cell populations, we should determine a positivity conditions for its solutions. A sufficient condition may be obtained following the method of Kirwa *et al.* (see Chen et al. (2016)), and noting that in all systems of interest S(0) > 0 and $D(0) \ge 0$. We thus have,

Theorem 1 Let S(t) and D(t) be continuous functions that solve Eqs. (1), and satisfy S(0) > 0 and D(0) = 0. Then $\alpha_{DS} \le 0$ is a sufficient condition for the positivity of S(t) and D(t).

Proof: Given that S(0) > 0, for S(t) to become nonpositive for the first time at a $t_0 > 0$, we must require that $S(t_0) = 0$ and $S'(t_0) < 0$. But replacing these in Eq. (1a), we arrive at a contradiction: while the left-hand side is negative definite, the right-hand side is zero. Therefore, S(t) must be positive for any finite times, without any conditions on the model parameters.

To obtain the positivity condition for D(t), we note that a sufficient condition for the initial growth of D(t) is $\alpha_{DS} \leq 0$.

(7c)

In this case, there must be at least an interval $(0,t_1)$ where D(t) > 0. If we now assume that t_1 is the first positive time for which *D* vanishes, $D(t_1) = 0$, then $D'(t_1) < 0$. Since r > 0 and $S(t_1) > 0$, Eq. (1b) requires that $[1 - \alpha_{DS}S(t_1)] < 0$, a condition that is never fulfilled because $\alpha_{DS} \le 0$. Thus, we have again arrived at a contradiction and D(t) must remain positive for all finite times.

The generalization of this theorem to the case D(0) > 0 is straightforward and we will not go into the details here.

The condition $\alpha_{DS} \le 0$ is likely to be generally fulfilled because we expect the cancer stem cells to promote the growth of the differentiated cells that make up their niche.

Initial size

A natural question for a biologist would be: If I want to create a tumorsphere, what is the minimum size that should be used to ensure growth? The answer to this question depends on the influence of differentiation inhibitors, as we can see by requiring that the time derivative S'(t) of the CMC number be positive at the start of the experiment. From Eq. (1a), we see that this is equivalent to demanding that the initial seed size satisfy the inequality,

$$1 - \Pi - \alpha_{SS}S(0) > 0,$$
 (2)

where $\Pi = p_d / p_s$. If $\alpha_{SS} < 0$ (the CMCs cooperate), this is equivalent to,

$$S(0) > \frac{\Pi - 1}{|\alpha_{SS}|}.$$
(3)

If $\Pi < 1$, i.e. $p_d < p_s$, any value of S(0) (for instance, a single cancer stem cell) will suffice to start a tumorsphere. If on the other hand, $\Pi > 1$, Eq. (3) provides us with a convenient estimate for the seed size.

If $\alpha_{SS} > 0$, the CMCs inhibit each other, and Eq. (3) is replaced by

$$S(0) < \frac{1 - \Pi}{\alpha_{SS}}.$$
(4)

Because of the intraspecific competition, even if $p_s > p_d$, the number of cancer stem cells will initially decrease unless Eq. (4) is satisfied.

To further investigate the mathematical properties of the System (1), it is convenient to write it in a dimensionless form. To do this, we will assume that $\alpha_{DD} \neq 0$. If we then define the dimensionless time $\tau = rt$ and the dimensionless populations,

$$X = \alpha_{DD}(1 - p_s + p_d)S, \tag{5a}$$

$$Y = \alpha_{DD}D, \tag{5b}$$

we obtain a set of dimensionless equations:

$$\dot{X} = (P - AX - BY)X,\tag{6a}$$

$$\dot{Y} = (1 - CX - Y)(X + Y),$$
 (6b)

where the dot signals a derivative with respect to τ and we have defined the new parameters

$$P = p_s - p_d, \tag{7a}$$

$$A = \frac{\alpha_{SS}}{\alpha_{DD}} \frac{p_s}{1 - p_s + p_d},\tag{7b}$$

and

$$C = \frac{\alpha_{DS}}{\alpha_{DD}} \frac{1}{1 - p_s + p_d}.$$
 (7d)

We have already shown that the sufficient condition for the positivity of the solutions to Eqs. (1) is that $\alpha_{DS} \leq 0$. From Eqs.(6) we see that X and Y will have the same (opposite) signs than their dimensional counterparts if $\alpha_{DD} > 0$ (< 0). Using Theorem 1 and Eq. (7d), we arrive at the following corollary:

 $B=\frac{\alpha_{SD}}{\alpha_{DD}}p_s,$

Corollary 1 The simultaneous satisfaction of the conditions $\alpha_{DS} \leq 0$ and $\alpha_{DD} > 0$ implies the positivity of $X(\tau)$ and $Y(\tau)$. The single condition $C \leq 0$ may be used instead.

Remark 1 In most cases, we expect cancer stem cells to compete for space and resources, which would lead to $\alpha_{DD} > 0$. If they cooperate instead, $\alpha_{DD} < 0$ and the positivity of S(t) and D(t) would imply the negativity of $X(\tau)$ and $Y(\tau)$.

Short-time behavior

Next, we investigate the short time behavior of system (6). This is given by,

Theorem 2 If the system evolution starts at $\tau = 0$ from a small mixed seed, such that $X(0) = X_0 > 0$ and $Y(0) = Y_0$ but AX_0 , CX_0 , BY_0 , and Y_0 are all much smaller than one, the representative point in the phase portrait of Eqs. (6) initially moves upwards and to the right. If $X_0 = 0$ but $Y_0 > 0$, the representative point moves straight towards the point (0, 1).

Proof: Let us consider first the case $X_0 > 0$. Under the theorem assumptions, Eqs. (6) may be linearized. The explicit solutions to the linearized form are easy to obtain. They are

$$X(\tau) = X_0 \exp(P\tau), \tag{8a}$$

and

$$Y(\tau) = \left(Y_0 + \frac{X_0}{1 - P}\right)e^{\tau} - \frac{X_0}{1 - P}e^{P\tau}.$$
 (8b)

From these equations, we immediately find that the shorttime location of the representative point in the X - Y plane is given by the equation

$$Y(t) = \left[Y_0 + \frac{X_0}{1 - P}\right] \left[\frac{X(t)}{X_0}\right]^{\frac{1}{P}} - \frac{X(t)}{1 - P}.$$
 (9)

Given that $0 \le P \le 1$ and that $X(\tau) > X(0)$ for all $\tau > 0$, the trajectory will be initially controlled by the first term of Eq. (9), starting as a curve that moves upwards and to the right, as we wanted to prove. If $X_0 = 0$, Eq. (6a) leads to $X(\tau) = 0, \forall \tau > 0$. Equation (6b) is therefore elementary to integrate, yielding

$$Y(\tau) = \left[1 + \left(Y_0^{-1} - 1\right) \exp(-\tau)\right]^{-1},$$
 (10)

an expression that is valid $\forall \tau > 0$. Equation (10) tells us that $Y(\tau \to \infty) = 1$ for any value of Y_0 .





Figure 1: System evolution in the X - Y plane for growth starting from a pure CSC seed when a mixed asymptotic population is reachable. Trajectories are obtained by varying the parameter *B*. Fixed parameter values: P = 0.5, A = 2, and C = 0.1. The red line corresponds to the bifurcation condition B = P. Lines to its left correspond to B > P and end at the stable coexistence fixed point $Q_1 = (0, 1)$. Lines to the right are obtained for B < P and end at the stable coexistence point. The blue line corresponds to $B = \tilde{B}$ (see text).

Fixed points and stability

The behavior of a cell colony can be studied by locating the equilibria (fixed points) of system (6) and analyzing their stability. The fixed points are determined by setting the righthand sides of Eqs. (6) equal to zero. Their stability is then found by looking at the real parts of the eigenvalues λ_1 and λ_2 of the Jacobian matrix,

$$J = \begin{pmatrix} P - 2AX - By & -BX \\ 1 - 2CX - (1+C)Y & 1 - (1+C)X - 2Y \end{pmatrix}$$
(11)

The fixed points Q_i are:

- The trivial point $Q_0 = (0,0)$, for which the eigenvalues are $\lambda_1 = 1$ and $\lambda_2 = P$. This point is unstable if P > 0, which is the most interesting case (cancer stem cells are stimulated to divide symmetrically), and the colony will grow. If P < 0, the origin is a saddle point.
- The differentiated cancer cell point, $Q_1 = (0, 1)$, whose eigenvalues are $\lambda_1 = -1$ and $\lambda_2 = P B$. This corresponds to a stable equilibrium if P < B and is otherwise a saddle point.
- The coexistence point,

$$Q_2 = (X^*, Y^*) = \frac{1}{\Delta}(P - B, A - PC),$$
 (12)

with $\Delta = A - BC$. The corresponding eigenvalues are too cumbersome for a direct interpretation, but extensive simulations confirm that Q_2 is unstable when P < B, which is the domain where Q_1 is stable. There is therefore a transcritical bifurcation at P = B, where an exchange of stability occurs: a stable equilibrium such that the system contains no cancer stem cells is found if P < B, while a stable equilibrium where both populations coexist occurs for P > B.



Figure 2: System evolution in the X - Y plane for growth starting from a pure CSC seed, when a mixed asymptotic population is not reachable. Trajectories are obtained by varying the parameter *B*. Fixed parameter values: P = 0.5, A = 0.1, and C = 1. The red line corresponds to the bifurcation condition B = P. Lines to its left (B > P) end at the stable fixed point at (0, 1), while lines to its right (B < P) end at the *X* axis. Q_2 is never a stable fixed point. The

fixed points, located along the dashed line, are not stable.

• The non-biological point $Q_3 = \frac{P}{A-B}(1,-1)$, for which one of the two populations would be negative.

The fixed points in the X - Y plane are located on the straight line $Y^* = 1 - CX^*$. Since we generally expect $\alpha_{DD} > 0$ (differentiated cancer cells compete for resources), the sign of the slope of the fixed-point line is determined by the sign of α_{DS} (see Eq. (7d). If CSCs promote the generation of new differentiated cells ($\alpha_{DS} < 0$), an increase in the number of CSCs in equilibrium would imply an increase of the number of differentiated cells. Conversely, if the CSCs inhibit the creation of new differentiated cells ($\alpha_{DS} > 0$), an increase in the number of CSCs in the equilibrium would imply fewer DCCs there.

Figure 1 depicts the system trajectories in the X - Y plane starting from a small CSC seed, for the parameter values indicated in the figure caption. After an initial stage where both populations increase in agreement with Theorem 2, we can identify three types of behavior: For B > P, all trajectories converge to the differentiated cancer cell fixed point Q_1 , which represents a stable tumorsphere that contains no cancer stem cells. The transcritical bifurcation occurs at B = P, where there is an exchange of stability between Q_1 and Q_2 , the last becoming the stable fixed point for B < P. If $P > B > \tilde{B}$, where \tilde{B} is determined numerically, the populations go through a maximum, and then converge to a *B*-dependent coexistence point. If $B < \tilde{B}$, the tumorsphere grows monotonically towards the coexistence fixed point. Since C < 0, the slope of the fixed-point line is positive.

If $\Delta < 0$, but B > P and A < PC, the coexistence fixed point is a saddle point located along the dashed line in the first quadrant. This case is shown in Fig. 2, where a typical value of Q_2 is represented by a square symbol. The trajectories cross into the fourth quadrant, but biological evolution ends on the X axis, which corresponds to a spheroid with no differentiated cancer cells.



Figure 3: Fit to the experimental data (dots) of (Chen et al., 2016) to reconstruct the CSC population, which is given by the orange line. The green line corresponds to the DCC population, and the blue line is the fit to the total cell population.

THE MATHEMATICAL MODEL IN THE REAL WORLD

As stated in the Introduction, the model can describe the possible outcomes of a spheroid growth assay. To illustrate the application of our results to experimental data, we selected three experiments designed to investigate very different properties of a growing spheroid. The fitting parameters we obtain are reported in Table 1 along with the predicted final cell population and the expected CSC fraction. Note that the spheroids final sizes, in the column labeled "Total", span five orders of magnitude. We briefly discuss our interpretation of these results bearing in mind that our main goal is to predict the dynamics of the cancer stem cell fraction.

The first experiment we analyze corresponds to tumorsphere assays performed by Chen et al. (2016) starting from three cancer cell lines. They found that, under suitable growing conditions, the final CSC fraction is rather large. Here we report only results for the T47D breast cancer line, but a more detailed account may be found in Benítez et al. (2019). As seen in Fig. 3, the fitting agrees well with the data, and allows us to reconstruct the evolution of the CSC population. Growth stops after about fifteen days, as is usually observed, leaving the final CSC fraction stable. By inspection of the corresponding parameters in Table 1, we conclude that growth is favored by the interspecific interactions. Stem cells promote the increase in the number of differentiated cells that consolidate their niche, which leads to an initial decrease in the CSC fraction (see Fig. 6). Although the location of the cell population in the tumorsphere was not studied in the experiment, it has been recently suggested (Barberis, 2021) that the relatively high differentiation probability in combination with the colony's geometry helps the CSCs to build a DCC shield around them. As expected, the coefficients α_{DD} and α_{SS} are positive, confirming that cells in the same population compete for resources.

The second experiment Wang et al. (2016) studied the influence of the substrate on tumorsphere growth in CSC-promoting media. Recently, we applied our model to this experiment (Benítez et al., 2021). Here we report only the case of a "soft" substrate, in which cells were cultured using



Figure 4: Fit to the experimental data (dots) of (Wang et al., 2016) to study tumorsphere growth on a soft substrate. The CSC population (red line) is much larger than the DCC population (green line).

0.05% agar as the contact matrix surface. Growth is slow at first, being apparently driven only by the tendency to build a suitable niche, hence the small basal growth rate (c.f. Table 1). As a result, a slow exponential growth of CSCs prevails in the early stages. As in the preceding example, the CSCs attempt to generate niche-building DCCs, but, due to the strong differentiation inhibition forced by the addition of differentiation-inhibiting agents (note the high value of p_s), the CSCs are only occasionally able to generate a differentiated cell. Thus, as shown in Fig. 4, the CSC fraction is close to one with only a very slow decay. The signs of the coefficients α_{ij} again indicate interspecific cooperation and intraspecific competition.

The third experiment is a classic (Helmlinger et al., 1997). These researchers prepared culture media that induced increasing stresses on the growing tumor spheroids, showing that stress may be a strong growth inhibitor for tumors. Although these experiments were satisfactorily described using an allometry-based mathematical model (Delsanto et al., 2004), no information was extracted about subpopulations or the nature of the intercellular interactions. Now we fitted their reported tumor sizes with our model and found an interesting fact: the fit is not possible without the assumption of the existence of at least one CSC to drive the tumor growth. Here we report only our fit to the 0.3% agarose concentration case, which corresponds to a relatively low stress environment. As shown in Fig. 5, the DCCs form an overwhelming majority of the cell population. We note that this experiment was performed at a time when the cancer stem cells were little more than a conjecture. The finding that those experiments must have been CSC-driven becomes evident today, because the currently accepted biological definition of a CSC states that it is a cell that can form a sphere in a tumorsphere assay (the original paper indicates that many cells were seeded but not all of them formed spheres). The CSC fraction represented in Fig. 6 for this experiment (green curve) shows that the pressure quickly kills the seed. As a result, the final size of the spheroid is reduced respect to the control one (not shown here), for which the CSC num-



TABLE 1: PARAMETERS OBTAINED BY FITTING THE DATA FROM THREE VERY DIFFERENT TUMORPHERE ASSAYS.

	α_{SS}	α_{SD}	α_{DS}	α_{DD}	r	p_s	p_d	Total	$\frac{S}{S+D}$
Chen	0.0519	-0.032816	-0.0175	0.020616	1.32	0.36	0.160	210	0.42
Wang	0.0844	-0.4082	-0.2005	0.483	0.07	0.969	0.004	7	0.92
Helmlinger	0.0202	0.000060	0.4007	0.000066	0.89	0.24	0.22	15178	0.00



Figure 5: Fit (green line) the experimental data (dots) of (Helmlinger et al., 1917) for the total number of cells yields the evolution of the CSC population (orange line). Cancer stem cells cannot thrive due to the external pressure. Spheroids were grown in 0.3% agarose gels.

ber becomes constant after a brief transient. The last result is consistent with the "control" experiment of Wang et al. (2016), analyzed by us in Benítez et al. (2021), and with the simulations reported in Barberis (2021).



Figure 6: Time evolution of the CSCs fractions generated by our model for the experiments described in Figs. 3 to 5. Environmental factors alter the CSC fraction drastically.

CONCLUSION

The mathematical properties of a model for tumor spheroid growth driven by cancer stem cells were discussed in detail and illustrated through representative phase portraits. The model was then shown to be able not only to reproduce the extant data for tumorsphere growth (which usually correspond to whole populations), but to yield in each case the cancer stem cell fraction, which had not been accessible to the experimentalists.

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Comparison of two mathematical models for the *Echinococcus multilocularis*-red foxes-rodents interactions

Comparación de dos modelos matemáticos para las interacciones de *Echinococcus multilocularis*zorros rojos-roedores

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Abstract— The paper sets up two mathematical models for the *Echinococcus multilocularis*'s life cycle in the environment. Herbivores are the intermediate hosts, harboring its larval stage, while carnivores host the adults. From the wild this helminth can spill to domestic animals and thus it could be potentially harmful for humans. The models differ in the way disese transmission is modeled. Feasibility and stability of the systems' equilibria are assessed. No persistent oscillations can arise. The study of the transcritical bifurcations between the steady states provides maps that are useful for the applied ecologist for possible parasite eradication.

Keywords—Mathematical Models, Mathematical Ecology, Mathematical Epidemiology, Zoonosis, Echinococcosis

Resumen— El trabajo considera dos modelos matématicos para el ciclo de vita natural del *Echinococcus multilocularis*. Los herbivores representan los huespes intermediarios, contienen las larvas; los carnivores en vez hospitan la forma adulta. Los animales domésticos pueden assumir el parasita y en consequencia lo trasmitir a los hombres, lo que representa una menaça potential. Los modelos son differentes en quanto las transmissión del *E. multilocularis* tiene duas formulationes matématicas diferentes. La admissibilidad y la estabilidad de los equilibrios son calculadas. Las poblaciones no pueden oscillar persistentemente. Las bifurcationes transcriticas entre los equilibrios permeten a los ecologistas de determinar las maneras possibles de eliminar el helminto.

Palabras clave— Modelos Matemáticos, Ecología Matemática, Epidemiología Matemática, Zoonosis, Echinococcosis

INTRODUCTION

Echinococcus, a genus of Cestoda, is a parasitic tapeworm with a life cycle where carnivores are the definitive hosts and herbivores represent the intermediate ones. The latter harbor the larval form, while the definitive hosts harbor the adult form. Its eggs are present in contaminated food and water. Upon ingestion, the eggs proliferate in the guts and cause Echinococcosis, a zoonosis as the parasite can be transmitted from the wild to domestic animals and then to humans, for whom it is therefore potentially harmful Houston et al. (2021); Luong et al. (2018).

Echinococcus multilocularis thrives only in the northern hemisphere. It is endemic in central Europe, where its definitive host is the red fox, *Vulpes vulpes*.

The adult parasite is composed of a head and a few segments (proglottids), the last of which contains the eggs. When it is expelled into the environment, the microscopic eggs can survive for a long time even at low temperatures and especially in humid environments. The intermediate hosts get infested by ingestion of the eggs, that hatch in their stomach, with the embryos crossing the intestinal wall and reaching the liver and the lungs. The definitive host feeding on raw parasitized prey viscera gets in turn infected and develops the adult form. Thus *Echinococcus Multilocularis* has a cycle closely linked with the environment, difficult to eradicate. In natural forests the human interference is scant of absent indeed, and the main control tool is administering antibiotics to foxes. It is therefore important to understand the life cycle of this helminth in the wild, to find possibly other ways of controlling it.

In part extending the works Baudrot (2016); Baudrot et al. (2016a,b, 2018), we construct two mathematical models to study the Echinococcus multilocularis life cycle, in which the parasite is not explicitly built in the system. They differ only in the transmission mechanism, considering also the ideas expounded previously in Bulai and Venturino (2016).

THE MODELS

We now present two ecoepidemic models for the foxesrodents interactions, affected by Echinococcus multilocularis. We must account for both animal species, but do not explicitly model the parasite. Thus the variables in consideration are the healthy foxes F, the infected, or rather carrier, foxes C, the susceptible rodents S and I, the infected rodents.

We will assume that there is no latency period in the parasites and epidemic spreading and that the transition rate from susceptibles to infected depends on the sizes of these populations. The disease transmission mechanism can be modeled in two alternative ways. First of all we can use the mass action law, good for low population densities, which produces the following equations:

$$\begin{aligned} \frac{dF}{dt} &= r(F+C) - mF + e(k_2S + k_3I)C + ek_1FS & (1) \\ &-F(b_1F + b_2C) - \lambda FI - \alpha FC + \gamma_1C, \\ \frac{dC}{dt} &= \lambda FI + \alpha FC - (m+\mu)C - C(c_1F + c_2C) - \gamma_1C, \\ \frac{dS}{dt} &= s(S+I) - nS - S(g_1S + g_2I) - S(k_1F + k_2C) \\ &-\theta SI - \beta SC + \gamma_2I, \\ \frac{dI}{dt} &= \beta SC + \theta SI - I(n+\nu) \\ &-I[(g_3S + g_4I) + (\lambda F + k_3C) + \gamma_2]. \end{aligned}$$

However, a more realistic approach is given by the standard incidence, in which the transmission rate is related to the proportion of infected in the whole population. This gives the alternative formulation

$$\frac{dF}{dt} = r(F+C) - mF + e(k_2S + k_3I)C + ek_1FS \quad (2)$$
$$-F(b_1F + b_2C) - \lambda F \frac{I}{L} - \alpha F \frac{C}{L} + \gamma_1C,$$

. ...

$$\frac{dC}{dt} = \lambda F \frac{I}{S+I} + \alpha F \frac{C}{F+C} - (m+\mu)G$$
$$-C(c_1F+c_2C) - \gamma C$$

$$\frac{dS}{dt} = s(S+I) - nS - S(g_1S + g_2I) - S(k_1F + k_2C)$$
$$-\theta S \frac{I}{S+I} - \beta S \frac{C}{F+C} + \gamma_2 I,$$
$$\frac{dI}{dt} = \theta S \frac{I}{S+I} + \beta S \frac{C}{F+C} - (n+v)I$$

$$S+I \qquad F+C \\ -I[(g_3S+g_4I)+(\lambda F+k_3C)+\gamma_2].$$

The first equation describes the dynamics of healthy red foxes. Both healthy and infected individuals grow with reproduction rate r due to food resources other than the rodents modeled in the system generating healthy offsprings. Thus, the parasite is not vertically transmitted. The second

term contains the natural mortality rate *m*, then we find the infected foxes reproduction due to capture of healthy and infected rodents, at respective rates k_2 and k_3 and with conversion coefficient e. Next, the births from healthy foxes hunting of susceptible rodents at rate k_1 , followed by the intraspecific competition among susceptible and infected foxes with respective rates b_1 and b_2 . The new infections are accounted for in the following two terms, with rates λ and α depending on the fact that they come from the infected foxes capturing and being contaminated by an infected rodent, or by other infected foxes. Note that it is the way these two terms are formulated that distinguishes model (1) from (2). The last term denotes possible disease recovery by elimination of the parasites, at rate γ_1 .

The second equation describes the dynamics of infected red foxes. They are recruited at rates λ and α from the susceptible ones, as described above, and experience natural as well as disease-induced mortality, the latter at rate μ . They further feel the intraspecific pressure due to healthy and infected individuals, at respective rates c_1 and c_2 and finally we allow them to possibly exit this class by recovery, migrating back into the susceptibles.

The third equation describes the healthy rodents dynamics. Newborns from both healthy and infected parents appear at rate s; here too vertical parasite transmission is not allowed. Natural mortality is experienced at rate *n*, and then the third and fourth terms contain the intra- (with rates g_1 and g_2) and interspecific (at rates k_1 and k_2) competition with both susceptible and infected individuals of both populations. The next two terms model disease transmission, at rates θ and β if respectively caused by rodents or foxes carriers. Finally the input due to recovered individuals at rate γ_2 is taken into consideration.

In the fourth equation infected rodents are recruited via parasite transmission from other infected rodents or diseased foxes. Then losses due to natural and infection-related mortality are accounted for, the latter at rate v. Intraspecific competition models additional deaths, at respective rates g_3 and g_4 if caused by healthy or infected individuals. The damage due to foxes is then accounted for, at rate λ by susceptible ones and k_3 by carriers. Finally, individuals leave the infected class if they recover, at rate γ_2 . Note that the possible administration of antibiotics can be modeled via the parameters γ_1 and γ_2 .

Table 1 contains a biological interpretation of the parameters, which are all assumed to be nonnegative.

A preliminary result

We address now the boundedness of the systems solution trajectories. For both (1) and (2) define the total environmental population A := F + C + S + I, and add the model equations. For any $\eta > 0$, then

$$\dot{A} + \eta A = F(r - m + \eta) + C(r - m - \mu + \eta)$$
(3)
+S(s - n + \eta) + I(s - n - v + \eta) - b_1 F^2 - c_2 C^2 - g_1 S^2
-g_4 I^2 - \lambda FI - FC(c_1 + b_2) - SI(g_2 + g_3)
+k_1 FS(e - 1) + k_2 CS(e - 1) + k_3 CI(e - 1).



(4)

 TABLE 1: SUMMARY AND INTERPRETATION OF THE PARAMETERS.

Rate	Biological interpretation		
r	foxes birth on other resources		
s	Rodents births		
m	healthy foxes natural mortality		
n	healthy rodents natural mortality		
μ	foxes disease-related mortality		
v	rodents disease-related mortality		
k_1	healthy foxes hunting on healthy rodents		
<i>k</i> ₂	infected foxes hunting on healthy rodents		
<i>k</i> ₃	infected foxes hunting on infected rodents		
e	conversion factor of rodents into foxes		
b_1	healthy foxes intraspecies competition		
b_2	healthy foxes competition on infected ones		
c_1	infected foxes competition on healthy ones		
c_2	infected foxes intraspecies competition		
<i>g</i> ₁	healthy rodents intraspecies competition		
<i>g</i> ₂	healthy rodents competition on infected ones		
<i>g</i> ₃	infected rodents competition on healthy ones		
<i>g</i> 4	infected rodents intraspecies competition		
γ1	infected foxes recovery		
γ2	infected rodents recovery		
α	disease transmission among foxes		
θ	disease transmission among rodents		
λ	foxes infection by capture of infected rodents		
β	healthy rodents infection by infected foxes		

Then taking $e \leq 1$, observing that concave parabolae have a maximum, so that we obtain

$$F(r-m+\eta-b_1F) \le \frac{(r-m+\eta)^2}{4b_1} = F_m,$$

$$C(r-m-\mu+\eta-c_2C) \le \frac{(r-m-\mu+\eta)^2}{4c_2} = C_m,$$

$$S(s-n+\eta-g_1S) \le \frac{(s-n+\eta)^2}{4g_1} = S_m,$$

$$I(s-n-\nu+\eta-g_4I) \le \frac{(s-n-\nu+\eta)^2}{4g_4} = I_m$$

and dropping the negative terms we obtain the final estimate

$$\dot{A} + \eta A \le F_m + C_m + S_m + I_m = D$$

from which

$$A(t) \leq \max\left\{\frac{D}{\eta}, A(0)\right\}.$$

From this, all the populations are bounded, giving a good biological ground of the models.

MASS LAW ACTION MODEL

Equilibrium points

System (1) allows the origin E_0 and the following points as equilibria:

$$E_1 = \left(\frac{r-m}{b_1}, 0, 0, 0\right), \quad E_2 = \left(0, 0, \frac{s-n}{g_1}, 0\right),$$

respectively feasible for

and

$$\geq n.$$
 (5)

Then we find the disease-free equilibrium

$$E_{3} = \left(\frac{ek_{1}s + g_{1}r - ek_{1}n - g_{1}m}{b_{1}g_{1} + ek_{1}^{2}}, 0, \frac{b_{1}s + k_{1}m - b_{1}n - k_{1}r}{b_{1}g_{1} + ek_{1}^{2}}, 0\right)$$

 $r \ge m$

S

with feasibility conditions

$$ek_1s + g_1r > ek_1n + g_1m, \quad b_1s + k_1m > b_1n + k_1r.$$
 (6)

The next two points need a more detailed investigation, reported below: the rodents-free point $E_5 = (F_5, C_5, 0, 0)$ and the corresponding foxes-free point $E_6 = (0, 0, S_6, I_6)$. Coexistence $E_4 = (F_4, C_4, S_4, I_4)$ will instead be investigated numerically.

The rodents-free point E_5

The last two equilibrium equations of (1) are identically satisfied. From the first two we obtain the system

$$-b_1 F^2 - FC(b_2 + \alpha) + F(r - m) + C(r + \gamma_1) = 0,$$
(7)
$$c_2 C + F(c_1 - \alpha) + (m + \gamma_1 + \mu) = 0,$$

which in the (C, F) plane represents the intersection of a conic section Ω with a straight line ℓ with slope

$$\frac{c_2}{c_1 - \alpha}.$$
 (8)

Determining the line intersections with the axes, we find

$$L_1 = \left(0, \frac{m+\gamma_1+\mu}{\alpha-c_1}\right), \quad L_2 = \left(-\frac{m+\gamma_1+\mu}{c_2}, 0\right),$$

h - $(m+\gamma_1+\mu)c_2^{-1} < 0$, while $(m+\gamma_1+\mu)(\alpha-c_1)^{-1} > 0$

with $-(m + \gamma_1 + \mu)c_2^{-1} < 0$, while $(m + \gamma_1 + \mu)(\alpha - c_1)^{-1} > 0$ if and only if

$$\alpha > c_1. \tag{9}$$

In the opposite case no part of the line crosses the first quadrant, so that no feasible intersections can exist.

Assuming nondegeneracy for the conic, i.e.

$$\widetilde{\Delta} = \begin{vmatrix} -b_1 & -\frac{b_2 + \alpha}{2} & \frac{r - m}{2} \\ -\frac{b_2 + \alpha}{2} & 0 & \frac{r + \gamma_1}{2} \\ \frac{r - m}{2} & \frac{r + \gamma_1}{2} & 0 \end{vmatrix}$$
$$-\frac{1}{4}(r + \gamma_1)[(b_2 + \alpha)(r - m) - (r + \gamma_1)b_1] \neq 0$$

and calculating the invariant, Woods (1939)

=

$$\widetilde{\Gamma} = \begin{vmatrix} -b_1 & -\frac{b_2 + \alpha}{2} \\ -\frac{b_2 + \alpha}{2} & 0 \end{vmatrix} = -\frac{(b_2 + \alpha)^2}{4} < 0$$

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we find that the conic is a hyperbola. Its intersections with the axes are

$$O = (0,0), \quad P_1 = \left(0, \frac{r-m}{b_1}\right).$$

To assess the slope of the hyperbola, we differentiate implicitly the conic, assuming F = F(C) to get

$$r + \gamma_1 - 2b_1FF' - (F'C + F)(b_2 + \alpha) + F'(r - m) = 0.$$
(10)

Evaluation at the intersections with the axes gives

$$F'(O) = \frac{r + \gamma_1}{m - r}, \quad F'(P_1) = \frac{r + \gamma_1}{r - m} - \frac{b_2 + \alpha}{b_1}$$

We now assess the asymptotes of Ω , recalling the asymptotes equation,

$$-b_1F^2 - FC(b_2 + \alpha) + F(r - m) + C(r + \gamma_1) - \frac{\widetilde{\Delta}}{\widetilde{\Gamma}} = 0.$$
(11)

Assume the form

$$F = \pi C + \sigma, \quad \pi, \sigma \in \mathbf{R}$$
 (12)

with the coefficients to be determined. Substituting into (11), we find

$$-b_1(\pi C + \sigma)^2 - (\pi C + \sigma)C(b_2 + \alpha) + (\pi C + \sigma)(r - m) +C(r + \gamma_1) - \frac{\widetilde{\Delta}}{\widetilde{\Gamma}} = 0.$$

Dividing by C^2 and letting $C \to +\infty$, we obtain $\pi = 0$, thus giving a horizontal asymptote or

$$\pi = -\frac{b_2 + \alpha}{b_1}$$

To assess the height of the horizontal asymptote, we substitute again (12), now with $\pi = 0$, into (11), to get

$$-b_1\sigma^2 - \sigma C(b_2 + \alpha) + \sigma(r - m) + C(r + \gamma_1) - \frac{\widetilde{\Delta}}{\widetilde{\Gamma}} = 0,$$

from which dividing by C and again letting $C \to +\infty$, we obtain

$$\sigma = \frac{r+\gamma_1}{b_2+\alpha} > 0.$$

Thus the horizontal asymptote lies above the C axis.

We can also determine the center of the hyperbola

$$C_{\text{center}} = \frac{r-m}{b_2+\alpha} - 2b_1 \frac{r+\gamma_1}{(b_2+\alpha)^2}, \qquad F_{\text{center}} = \frac{r+\gamma_1}{b_2+\alpha}.$$

Thus if

$$r < m, \tag{13}$$

the point P_1 lies on the negative F semiaxis, the slopes are F'(O) > 0 and $F'(P_1) < 0$, the center lies in the second quadrant and the hyperbola has a concave feasible branch emanating from the origin raising up to the horizontal asymptote of Ω . This is case (I).

If (4) holds instead, P_1 lies on the positive F semiaxis and F'(O) < 0. Thus

$$F'(P_1) = \frac{r + \gamma_1}{r - m} - \frac{b_2 + \alpha}{b_1} > 0$$

if and only if the center lies in the second quadrant and

$$(r+\gamma_1)b_1 > (b_2+\alpha)(r-m) > 0,$$
 (14)

giving Case (W), with a concave feasible branch emanating from P_1 . In the opposite case, $F'(P_1) < 0$,

$$(r+\gamma_1)b_1 < (b_2+\alpha)(r-m),$$
 (15)

Case (Z), the center lies in the second quadrant and the hyperbola has a convex branch in the first one decreasing to the horizontal asymptote.

We now assess the possible intersections of the straight line ℓ with the hyperbola Ω .

In case (Z) the intersection is guaranteed if L_1 lies below P_1 , namely for

$$b_1(m+\gamma_1+\mu) < (\alpha - c_1)(r-m).$$
 (16)

Similarly, in case (W), the intersection feasibility requires in the latter case the same above condition (16), and no further additional conditions are necessary.

In case (I) the conditions (13) and (9) must be satisfied, but given that Ω has a concave branch emanating from the origin to approach the horizontal asymptote, the intersection with ℓ is either non-existent or a pair of points. This situation gives rise to a saddle-node bifurcation that is not investigated further here.

The foxes-free point E_6

As for the previous equilibrium, for $E_6 = (0, 0, S_6, I_6)$ we reduce the problem to studying the feasible intersections of a conic section Θ and a straight line $\hat{\ell}$:

$$-g_1S^2 - SI(g_2 + \theta) + (s - n)S + (s + \gamma_2)I = 0,$$

(\theta - g_3)S - g_4I - (n + \nu + \nu_2) = 0.

The situation parallels the one of the rodents-free point. Without stating the details, we have the following results. Θ is again a hyperbola, calculating the invariants

$$\widehat{\Delta} = \begin{vmatrix} -g_1 & -\frac{g_2 + \theta}{2} & \frac{s - n}{2} \\ -\frac{g_2 + \theta}{2} & 0 & \frac{s + \gamma_2}{2} \\ \frac{s - n}{2} & \frac{s + \gamma_2}{2} & 0 \end{vmatrix}$$
$$-\frac{1}{4}(s + \gamma_2)[(g_2 + \theta)(s - n) - (s + \gamma_2)g_2] \neq 0,$$

assuming nondegeneracy, and

$$\widehat{\Gamma} = \begin{vmatrix} -g_1 & -\frac{g_2 + \theta}{2} \\ -\frac{g_2 + \theta}{2} & 0 \end{vmatrix} = -\frac{(g_2 + \theta)^2}{4} < 0$$

The straight line meets the first quadrant of the I - S plane only if

$$\theta > g_3, \tag{17}$$

has slope

$$\frac{g_4}{g_3 - \theta} > 0 \tag{18}$$

and intercepts the axes at the points

$$\widehat{L}_1 = \left(0, \frac{n+\gamma_2+\nu}{\theta-g_3}\right), \quad \widehat{L}_2 = \left(-\frac{n+\gamma_2+\nu}{g_4}, 0\right).$$

The intersections of Θ with the axes are

$$O = (0,0), \quad Q_1 = \left(0, \frac{s-n}{g_1}\right)$$

and the slopes at these points

$$S'(O) = \frac{s + \gamma_2}{n - s}, \quad S'(Q_1) = \frac{s + \gamma_2}{s - n} - \frac{g_2 + \theta}{g_1}$$

This hyperbola has a horizontal asympotote

$$S = \frac{s + \gamma_2}{g_2 + \theta} > 0$$

while the other one has a negative slope

$$-\frac{g_2+\theta}{g_1}<0.$$

For

$$s < n, \tag{19}$$

 Θ has a concave feasible branch emanating from the origin raising up to the horizontal asymptote. This is case (II).

Instead, for (5),

$$(s+\gamma_2)g_1 < (g_2+\theta)(s-n),$$
 (20)

giving Case (X), in which the convex feasible branch approaches the horizontal asymptote decreasing from the point Q_1 . In the opposite situation the feasible branch is concave and raises up from Q_1 toward the horizontal asymptote, giving Case (Y), $S'(Q_1) > 0$,

$$(s + \gamma_2)g_1 > (g_2 + \theta)(s - n) > 0.$$
 (21)

In case (X) the feasible intersection is guaranteed if the following condition holds

$$g_1(n+\gamma_2+\nu) < (\theta-g_3)(s-n).$$
 (22)

In case (Y) instead the intersection is guaranteed again by requiring (22). Instead we note also that if (22) is not satisfied, a pair of feasible points could arise through a saddlenode bifurcation, a situation that is not further explored here.

For Case (II) a possible saddle-node bifurcation could give rise to a pair of equilibria, but this case is not examined in detail.

Table 2 summarizes these results.

TABLE 2: EQUILIBRIA OF MODEL (1)

Equilibrium point	Feasibility condition
$E_0 = (0, 0, 0, 0)$	-
$E_1 = \left(\frac{r-m}{b_1}, 0, 0, 0\right)$	(4)
$E_2 = \left(0, 0, \frac{s-n}{g_1}, 0\right)$	(5)
$E_3 = (F_3, 0, S_3, 0)$	(6)
	(I): (9), (13), saddle-node;
$E_5 = (F_5, C_5, 0, 0)$	(Z): (9), (4), (15), (16);
	(W): (9), (4), (14), (16);
	(II): (17), (19), saddle-node;
$E_6 = (0, 0, S_6, I_6)$	(Y): (17), (5), (21), (22);
	(X): (17), (5), (20), (22);
$E_4 = (F_4, C_4, S_4, I_4)$	numerical

Equilibria stability

The Jacobian matrix $J_{i,j}$ of the system (1) has the entries

$$\begin{aligned} J_{1,1} &= ek_1S - \alpha C - b_2C - 2b_1F - \lambda I - m + r, & J_{2,3} = 0, \\ J_{1,2} &= r + e(k_2S + k_3I) - b_2F - \alpha F + \gamma_1, & J_{3,1} = -k_1S, \\ J_{1,3} &= ek_2C + ek_1F, & J_{2,4} = \lambda F, & J_{2,1} = \alpha C - c_1C + \lambda I, \\ J_{4,1} &= -\lambda I, & J_{2,2} = -2c_2C + \alpha F - c_1F - m - \mu - \gamma_1, \\ J_{3,2} &= -\beta S - k_2S, & J_{3,4} = -g_2S - \theta S + s + \gamma_2, \\ J_{3,3} &= -\beta C - k_2C - k_1F - 2g_1S - g_2I - \theta I - n + s, \\ J_{1,4} &= ek_3C - \lambda F, & J_{4,2} = \beta S - k_3I, & J_{4,3} = \beta C - g_3I + \theta I, \\ J_{4,4} &= -k_3C - \lambda F - g_3S + \theta S - 2g_4I - n - v - \gamma_2. \end{aligned}$$

For $E_0 = (0,0,0,0)$ the eigenvalues of the Jacobian are $r-m, -m-\mu-\gamma_1 < 0, s-n, -n-\nu-\gamma_2 < 0$ but from (4)-(5) this point is unconditionally unstable.

At $E_1 = (F_1, 0, 0, 0)$ the eigenvalues are $-b_1F_1 = m - r < 0$, $-m - \mu + (\alpha - c_1)F_1 - \gamma_1$, $s - n - k_1F_1$, $-n - \nu - \lambda F_1 - \gamma_2 < 0$, so that stability is ensured by

$$\frac{(\alpha - c_1)(r - m)}{b_1} < m + \mu + \gamma_1, \quad s + \frac{k_1(m - r)}{b_1} < n.$$
(23)

The eigenvalues at $E_2 = (0, 0, S_2, 0)$ are once again explicitly evaluated, $-n - \nu + S_2(\theta - g_3) - \gamma_2$, n - s, $r - m + ek_1S_2$, $-m - \mu - \gamma_1$, providing, after semplification from (4)-(5) the stability conditions

$$\frac{(\theta - g_3)(s - n)}{g_1} < n + \nu + \gamma_2, \quad r + \frac{ek_1(s - n)}{g_1} < m.$$
(24)

At $E_5 = (F_5, C_5, 0, 0)$ the Jacobian factorizes into two minors of order two, to both of which the Routh-Hurwitz conditions apply. But the trace of one of these minors is negative,

$$-b_1F_5 - c_2C_5 - \frac{C_5}{F_5}(r + \gamma_1) < 0, \qquad (25)$$

and from the remaining ones the stability conditions are found

$$\frac{\frac{c_2(r-m)+(\alpha-c_1)(r+\gamma_1)}{2b_1c_2F_5+(m+\gamma_1+\mu)(b_2+\alpha)} < 1, \quad (26)$$

$$\frac{s}{2n+F_5(k_1+\lambda)+C_5(k_2+k_3+\beta)+\nu+\gamma_2} < 1,$$

$$k_1F_5+C_5(k_2+\beta)-s > \frac{\beta C_5(s+\gamma_2)}{n+\nu+\lambda F_5+k_3C_5+\gamma_2}.$$

n+



The Jacobian of $E_3 = (F_3, 0, S_3, 0)$ again factorizes into the product of two minors of order two, for the first one of which the Routh-Hurwitz conditions are always satisfied, namely $b_1F_3 + g_1S_3 > 0$, $b_1g_1F_3S_3 + ek_1^2F_3S_3 > 0$. From the remaining ones, stability is ensured by

$$\frac{F_{3}(\alpha - c_{1} - \lambda) + S_{3}(\theta - g_{3})}{m + \mu + \gamma_{1} + \gamma_{2} + n + \nu} < 1, \qquad (27)$$
$$[m + \mu - F_{3}(\alpha - c_{1}) + \gamma_{1}][n + \nu + \lambda F_{3} - S_{3}(\theta - g_{3}) + \gamma_{2}] > \beta \lambda F_{3}S_{3}.$$

Also at $E_6 = (0, 0, S_6, I_6)$ the Jacobian factorizes into the product of two minors of order two. The trace condition of one of them holds unconditionally,

$$-g_1S_6 - \frac{I_6}{S_6}(s + \gamma_2) - g_4I_6 < 0, \tag{28}$$

while the remaining Routh-Hurwitz conditions provide the stability inequalities

$$g_{4}(s-n) + (\theta - g_{3})(s+\gamma_{2}) + (n+\gamma_{2}+\nu)(g_{2}+\theta)$$
(29)
> $2g_{1}g_{4}S_{6},$
 $r + ek_{1}S_{6} < \lambda I_{6} + \mu + \gamma_{1} + 2m,$
 $(r-m+ek_{1}S_{6} - \lambda I_{6})(-m-\mu - \gamma_{1})$
> $\lambda I_{6}(r+ek_{2}S_{6} + ek_{3}I_{6} + \gamma_{1}).$

Table 3 summarizes the stability conditions of the equilibria of the system (1).

TABLE 3: EQUILIBRIA STABILITY CONDITIONS OF (1)

Equilibrium	Stability conditions
$E_0 = (0, 0, 0, 0)$	unstable
$E_1 = \left(\frac{r-m}{b_1}, 0, 0, 0\right)$	(23)
$E_2 = \left(0, 0, \frac{s-n}{g_1}, 0\right)$	(24)
$E_3 = (F_3, 0, S_3, 0)$	(27)
$E_5 = (F_5, C_5, 0, 0)$	(26)
$E_6 = (0, 0, S_6, I_6)$	(29)
$E_4 = (F_4, C_4, S_4, I_4)$	numerical

Equilibria verification

The previous equilibria analysis is here supported by numerical results showing that the various sets of feasibility and stability conditions are indeed not empty. In the simulations we have used values for the biological parameters borrowed from the literature Caudera et al. (2021, 2020); Viale et al. (2021), for an analogous foxes-rodents ecosystem:

$$b_{1} = \log(3) - \frac{2}{7}, \quad e = 0,91, \quad g_{1} = \frac{1}{100}\log(4,5) - \frac{4}{500},$$

$$g_{2} = \frac{1}{100}\log(4,5) - \frac{4}{500} + 1, \quad g_{4} = \frac{1}{100}\log(4,5) - \frac{4}{500},$$

$$k_{1} = 0,5, \quad k_{3} = 0,5, \quad m = \frac{2}{7}, \quad n = \frac{4}{5},$$

$$r = \log(3), \quad s = \log(4,5). \quad (30)$$

The remaining parameter values are hypothetical. The initial conditions are always taken as follows:

$$F(0) = 1, \quad C(0) = 0, \quad S(0) = 8, \quad I(0) = 1$$
 (31)

Now E_0 is attained with (30) and m = 5, n = 3, $b_2 = 0,1$, $c_1 = 0,22$, $c_2 = 0,21$, $g_3 = 0,11$, $k_2 = 0,15$, $\alpha = 0,47$, $\beta = 0,83$, $\gamma_1 = 0,23$, $\gamma_2 = 0,12$, $\theta = 0,55$, $\lambda = 0,67$, $\mu = 2$, $\nu = 5$. For E_1 we need, in addition to (30), m = 10, n = 3, r = 12,

 $b_2 = 0,1, c_1 = 0,22, c_2 = 0,21, g_3 = 0,11, k_2 = 0,15, \alpha = 0,47, \beta = 0,83, \gamma_1 = 0,23, \gamma_2 = 0,12, \theta = 0,55, \lambda = 0,67, \mu = 2, \nu = 5.$

*E*₂ is obtained with the choice m = 16, s = 1, $b_2 = 0,2$, $c_1 = 0,22$, $c_2 = 0,21$, $g_3 = 0,11$, $k_2 = 0,1$, $\alpha = 6,91$, $\beta = 0,2$, $\gamma_1 = 0$, $\gamma_2 = 3$, $\theta = 0,2$, $\lambda = 15$, $\mu = 5$, v = 5.

For E_3 we choose n = 0,01, s = 8, $b_2 = 3$, $c_1 = 0,88$, $c_2 = 0,214$, $g_3 = 0,11$, $k_2 = 0,1$, $\alpha = 0,05$, $\beta = 0,2$, $\gamma_1 = 0,1$, $\gamma_2 = 3$, $\theta = 0,2$, $\lambda = 0,2$, $\mu = 0,22$, $\nu = 5$.

*E*₅ is found for *b*₂ = 0,2, *c*₁ = 0,22, *c*₂ = 0,21, *g*₃ = 0,11, *k*₂ = 0,1, $\alpha = 4$, $\beta = 0,2$, $\gamma_1 = 0,1$, $\gamma_2 = 3$, $\theta = 0,2$, $\lambda = 15$, $\mu = 0,22$, $\nu = 5$.

The parameters to attain E_6 are instead $g_2 = 0.2$, $g_3 = 0.22$, $\theta = 2$, $\gamma_2 = 0.1$, v = 0.22, $n = \frac{2}{7}$, $s = \log(3)$, $g_4 = 0.21$, $c_1 = 0.11$, $\gamma_1 = 3$, $\alpha = 0.2$, $\mu = 5$, $r = \log(4.5)$, $k_2 = 0.1$, $\beta = 0.2$, $\lambda = 15$, e = 0.91, $k_1 = 0.5$, $k_3 = 0.5$ and

$$g_1 = \log(3) - \frac{2}{7}, \quad b_1 = \frac{1}{100}\log(4,5) - \frac{4}{500}, \quad m = \frac{4}{5}$$
$$b_2 = \frac{1}{100}\log(4,5) - \frac{4}{500} + 1, \quad c_2 = \frac{1}{100}\log(4,5) - \frac{4}{500}.$$

The coexistence equilibrium is shown in Figure 1 together with the parameter values needed to achieve it.



Figure 1: Coexistence equilibrium E_4 is attained for the values $s = 5, b_2 = 3, c_1 = 0.88, c_2 = 0.21, g_3 = 0.01, k_2 = 0.1, \alpha = 0.05, \beta = 0.2, \gamma_1 = 0.1, \gamma_2 = 0.2, \theta = 2, \lambda = 15, \mu = 0.22, \nu = 0.2.$

BIFURCATIONS

We study the bifurcations using Sotomayor's theorem, Perko (2013), applied to (1) written in shorthand as $\dot{\mathbf{x}} = \mathbf{F}(\mathbf{x})$. To this end, we need to know $D^2\mathbf{F}$ and $D^3\mathbf{F}$. To evaluate $D^2\mathbf{F}$ are necessary:

$$F_{F,F}^{1} = -2b_{1} \quad F_{F,C}^{1} = -\alpha - b_{2} \quad F_{F,S}^{1} = ek_{1} \quad F_{F,I}^{1} = -\lambda$$

$$F_{C,S}^{1} = ek_{2} \quad F_{C,I}^{1} = ek_{3} \quad F_{F,C}^{2} = \alpha - c_{1} \quad F_{F,I}^{2} = \lambda$$

$$F_{C,C}^{2} = -2c_{2} \quad F_{F,S}^{3} = -k_{1} \quad F_{C,S}^{3} = -\beta - k_{2} \quad F_{S,S}^{3} = -2g_{1}$$

$$F_{S,I}^{3} = -g_{2} - \theta \quad F_{F,I}^{4} = -\lambda \quad F_{C,S}^{4} = \beta \quad F_{C,I}^{4} = -k_{3}$$

$$F_{S,I}^{4} = -g_{3} + \theta \quad F_{I,I}^{4} = -2g_{4},$$

while all other possible combinations $F_{A,B}^n$, $A, B \in \{F, C, S, I\}$, $n \in \{1, 2, 3, 4 \text{ vanish. Hence}\}$

$$D^{2}\mathbf{F}^{1} = \begin{pmatrix} -2b_{1} & -\alpha - b_{2} & ek_{1} & -\lambda \\ -\alpha - b_{2} & 0 & ek_{2} & ek_{3} \\ ek_{1} & ek_{2} & 0 & 0 \\ -\lambda & ek_{3} & 0 & 0 \end{pmatrix}$$



$$D^{2}\mathbf{F}^{2} = \begin{pmatrix} 0 & \alpha - c_{1} & 0 & \lambda \\ \alpha - c_{1} & -2c_{2} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \lambda & 0 & 0 & 0 \end{pmatrix}$$
$$D^{2}\mathbf{F}^{3} = \begin{pmatrix} 0 & 0 & -k_{1} & 0 \\ 0 & 0 & -\beta - k_{2} & 0 \\ -k_{1} & -\beta - k_{2} & -2g_{1} & -g_{2} - \theta \\ 0 & 0 & -g_{2} - \theta & 0 \end{pmatrix}$$
$$D^{2}\mathbf{F}^{4} = \begin{pmatrix} 0 & 0 & 0 & -\lambda \\ 0 & 0 & \beta & -k_{3} \\ 0 & \beta & 0 & -g_{3} + \theta \\ -\lambda & -k_{3} & -g_{3} + \theta & -2g_{4} \end{pmatrix}$$

It is also easily found that $D^3 \mathbf{F}$ is identically zero. Thus condition $\mathbf{w}^T [D^3 \mathbf{F}(\mathbf{x}_0, \mu_0)(\mathbf{v}, \mathbf{v}, \mathbf{v})] \neq 0$ cannot be satisfied and system (1) never experiences a pitchfork bifurcation.

Bifurcations at E₀

For E_0 the Jacobian has four explicit eigenvalues, $\Lambda_1 = r - m$, $\Lambda_2 = -m - \mu - \gamma_1$, $\Lambda_3 = s - n$, $\Lambda_4 = -n - v - \gamma_2$.

Eigenvalue Λ_1

Take as bifurcation parameter *m* and let $\tilde{m} := r$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (1,0,0,0)^T$, $\mathbf{w} = (\tilde{m} + \mu + \gamma_1, \tilde{m} + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_0,\tilde{m}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_m(E_0,\tilde{m}) = 0$, implying $D\mathbf{F}_m(E_0,\tilde{m})\mathbf{v} = (-1,0,0,0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_m(E_0,\tilde{m})\mathbf{v}] = -(\tilde{m} + \mu + \gamma_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_0,\tilde{m})(\mathbf{v},\mathbf{v})] = -2b_1(\tilde{m} + \mu + \gamma_1) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_0 and E_1 .

Eigenvalue Λ_3

Take as bifurcation parameter *n* and let $\tilde{n} := s$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (0,0,1,0)^T$, $\mathbf{w} = (0,0,\tilde{n}+\nu+\gamma_2,\tilde{n}+\gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_0,\tilde{n}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_n(E_0,\tilde{n}) = \mathbf{0}$, implying $D\mathbf{F}_n(E_0,\tilde{n})\mathbf{v} = (0,0,-1,0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_n(E_0,\tilde{n})\mathbf{v}] = -(\tilde{n}+\nu+\gamma_2) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_0,\tilde{n})(\mathbf{v},\mathbf{v})] = -2g_1(\tilde{n}+\nu+\gamma_2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_0 and E_2 .

Bifurcations at E_1

For E_1 the Jacobian has four explicit eigenvalues, $\Lambda_1 = m - r$, $\Lambda_2 = -m - \mu + (\alpha - c_1)F_1 - \gamma_1$, $\Lambda_3 = s - n - k_1F_1$, $\Lambda_4 = -n - v - \lambda F_1 - \gamma_2$.

Eigenvalue Λ_2

Take as bifurcation parameter m and let

$$\tilde{m} := \frac{(\alpha - c_1)r - b_1(\mu + \gamma_1)}{b_1 - c_1 + \alpha}$$

feasible for $(\alpha - c_1)r > b_1(\mu + \gamma_1)$ with $\alpha > c_1$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (r - F_1(b_2 + \alpha) + \gamma_1, b_1F_1, 0, 0)^T$, $\mathbf{w} = (0, n + v + \lambda F_1 + \gamma_2, 0, \lambda F_1)^T.$ Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_1, \tilde{m}) = (-F_1, 0, 0, 0)$, for which $\mathbf{w}^T \mathbf{F}_m(E_1, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_1, \tilde{m})\mathbf{v} = (-r + F_1(b_2 + \alpha) - \gamma_1, -b_1F_1, 0, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_m(E_1, \tilde{m})\mathbf{v}] = -b_1F_1(n + v + \lambda F_1 + \gamma_2) \neq 0.$ Further, $\mathbf{w}^T[D^2\mathbf{F}(E_1, \tilde{m})(\mathbf{v}, \mathbf{v})] = (n + v + \lambda F_1 + \gamma_2)2b_1F_1((\alpha - c_1)(r - F_1(b_2 + \alpha) + \gamma_1) - c_2b_1F_1).$ Now if $(\alpha - c_1)(r - F_1(b_2 + \alpha) + \gamma_1) \neq c_2b_1F_1$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_1 and E_5 .

Eigenvalue Λ_2

Taking instead as bifurcation parameter μ and let $\tilde{\mu} := -m - \gamma_1 + F_1(\alpha - c_1)$, feasible for $F_1(\alpha - c_1) > m + \gamma_1$ with $\alpha > c_1$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (r - F_1(b_2 + \alpha) + \gamma_1, b_1F_1, 0, 0)^T$, $\mathbf{w} = (0, n + \mathbf{v} + \lambda F_1 + \gamma_2, 0, \lambda F_1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_{\mu}(E_1, \tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_{\mu}(E_1, \tilde{\mu}) = 0$, implying $D \mathbf{F}_{\mu}(E_1, \tilde{\mu}) \mathbf{v} = (0, -b_1F_1, 0, 0)^T$ and therefore $\mathbf{w}^T[D \mathbf{F}_{\mu}(E_1, \tilde{\mu})\mathbf{v}] = -b_1F_1(n + \mathbf{v} + \lambda F_1 + \gamma_2) \neq 0$. Further, $\mathbf{w}^T[D^2 \mathbf{F}(E_1, \tilde{\mu})(\mathbf{v}, \mathbf{v})] = (n + \mathbf{v} + \lambda F_1 + \gamma_2)2b_1F_1((\alpha - c_1)(r - F_1(b_2 + \alpha) + \gamma_1) - c_2b_1F_1)$. Now if $(\alpha - c_1)(r - F_1(b_2 + \alpha) + \gamma_1) \neq c_2b_1F_1$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_1 and E_5 .

Eigenvalue Λ_3

Take as bifurcation parameter *n* and let $\tilde{n} := s - k_1 F_1$, feasible for $s > k_1 F_1$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (ek_1 F_1, 0, b_1 F_1, 0)^T$, $\mathbf{w} = (0, 0, s - F_1(k_1 - \lambda) + \mathbf{v} + \gamma_2, s + \gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_1, \tilde{n}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_n(E_1, \tilde{n}) =$ 0, implying $D\mathbf{F}_n(E_1, \tilde{n})\mathbf{v} = (0, 0, -b_1 F_1, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_n(E_1, \tilde{n})\mathbf{v}] = -b_1 F_1(s - F_1(k_1 - \lambda) + \mathbf{v} + \gamma_2) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_1, \tilde{n})(\mathbf{v}, \mathbf{v})] = -2b_1 F_1^2(ek_1^2 + b_1g_1)(s - F_1(k_1 - \lambda) + \mathbf{v} + \gamma_2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_1 and E_3 .

Bifurcations at E₂

For E_2 the Jacobian has four explicit eigenvalues, $\Lambda_1 = n - s$, $\Lambda_2 = -n - v + S_2(\theta - g_3) - \gamma_2$, $\Lambda_3 = r - m + ek_1S_2$, $\Lambda_4 = -m - \mu - \gamma_1$.

Eigenvalue Λ_2

Take as bifurcation parameter n and let

$$\tilde{n} := \frac{(\theta - g_3)s - g_1(\gamma_2 + \nu)}{g_1 - g_3 + \theta})$$

feasible for $(\theta - g_3)s > g_1(\gamma_2 + v)$ with $\theta > g_3$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (0, 0, s - S_2(g_2 + \theta) + \gamma_2, g_1S_2)^T$, $\mathbf{w} = (0, \beta S_2, 0, m + \mu + \gamma_1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_2, \tilde{n}) = (0, 0, -S_2, 0)$, for which $\mathbf{w}^T \mathbf{F}_n(E_2, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_2, \tilde{n})\mathbf{v} = (0, 0, S_2(g_2 + \theta) - s - \gamma_2, -g_1S_2)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_n(E_2, \tilde{n})\mathbf{v}] = -g_1S_2(m + \mu + \gamma_1) \neq 0$. Further, $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{n})(\mathbf{v}, \mathbf{v})] = 2g_1S_2(m + \mu + \gamma_1)((\theta - g_3)(s - S_2(g_2 + \theta) + \gamma_2) - g_1g_4S_2)$. Now if $(\theta - g_3)(s - S_2(g_2 + \theta) + \gamma_2) \neq g_1g_4S_2$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_2 and E_6 .

Eigenvalue Λ_2

Take as bifurcation parameter v and let $\tilde{v} := -n + S_2(\theta - g_3) - \gamma_2$, feasible for $S_2(\theta - g_3) > n + \gamma_2$ with $\theta > g_3$. The right v and left w eigenvectors of the Jacobian are $v = (0, 0, s - S_2(g_2 + \theta) + \gamma_2, g_1S_2)^T$, $w = (0, \beta S_2, 0, m + \mu + \gamma_1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_v(E_2, \tilde{v}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_v(E_2, \tilde{v}) = 0$, implying $D\mathbf{F}_v(E_2, \tilde{v})\mathbf{v} = (0, 0, 0, -g_1S_2)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_v(E_2, \tilde{v})\mathbf{v}] = -g_1S_2(m + \mu + \gamma_1) \neq 0$. Further, $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{v})(\mathbf{v}, \mathbf{v})] = 2g_1S_2(m + \mu + \gamma_1)((\theta - g_3)(s - S_2(g_2 + \theta) + \gamma_2) - g_1g_4S_2)$. Now if $(\theta - g_3)(s - S_2(g_2 + \theta) + \gamma_2) = g_1g_4S_2$ a transcritical bifurcation arises for the critical parameter value $v = \tilde{v}$, between E_2 and E_6 .

Eigenvalue Λ_3

Take as bifurcation parameter *m* and let $\tilde{m} := r + ek_1S_2$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (g_1S_2, 0, -k_1S_2, 0)^T$, $\mathbf{w} = (r + ek_1S_2 + \mu + \gamma_1, r + ek_2S_2 + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_2, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_m(E_2, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_2, \tilde{m})\mathbf{v} = (-g_1S_2, 0, 0, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_m(E_2, \tilde{m})\mathbf{v}] = -g_1S_2(r + ek_1S_2 + \mu + \gamma_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2g_1S_2^2(r + ek_1S_2 + \mu + \gamma_1)(b_1g_1 + ek_1^2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_2 and E_3 .

Bifurcations at E₃

At E_3 the Jacobian has four explicit eigenvalues,

$$\begin{split} \Lambda_{A_{1,2}} &= \frac{1}{2} \left[\pm \sqrt{b_1^2 F_3^2 + g_1^2 S_3^2 - 2b_1 g_1 F_3 S_3 - 4ek_1^2 F_3 S_3} \\ &\quad -b_1 F_3 - g_1 S_3 \right], \\ \Lambda_{B_{1,2}} &= \frac{1}{2} \left[-F_3 (c_1 - \alpha + \lambda) - S_3 (g_3 - \theta) \pm \sqrt{\Delta} \\ &\quad -m - n - \gamma_1 - \gamma_2 - \mu - \nu \right], \end{split}$$

where

$$\Delta = [\gamma_1 + \gamma_2 + \mu + \nu + F_3(c_1 - \alpha + \lambda) + S_3(g_3 - \theta)]^2 + m + n - 4\{[-m - \mu + F_3(\alpha - c_1) - \gamma_1][-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2] - \beta \lambda F_3 S_3\}$$

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter *m* and getting \tilde{m} from $(-m - \mu + F_3(\alpha - c_1) - \gamma_1)(-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2) - \beta \lambda F_3 S_3 = 0$, feasible for $(-m - \mu + F_3(\alpha - c_1) - \gamma_1)(-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2) < \beta \lambda F_3 S_3$. The right **v** and left **w** eigenvectors of the Jacobian are **v** = $(ek_1F_3, \lambda F_3, b_1F_3, \tilde{m} + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$. We $(g_1S_3, \beta F_3, ek_1F_3, \tilde{m} + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_3, \tilde{m}) = (-F_3, 0, 0, 0)$, for which $\mathbf{w}^T \mathbf{F}_m(E_3, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_3, \tilde{m})\mathbf{v} = (-ek_1F_3, -\lambda F_3, 0, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_m(E_3, \tilde{m})\mathbf{v}] = -ek_1g_1F_3S_3 - \beta \lambda F_3S_3 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{m})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_3 and E_4 .

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter *n* and getting \tilde{n} from $(-m - \mu + F_3(\alpha - c_1) - \gamma_1)(-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2) - \beta \lambda F_3 S_3 = 0$, feasible for $(-m - \mu + F_3(\alpha - c_1) - \gamma_1)(-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2) < \beta \lambda F_3 S_3$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda F_3, b_1F_3, m + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$. W = $(g_1S_3, \beta F_3, ek_1F_3, m + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_3, \tilde{n}) = (0, 0, -S_3, 0)$, for which $\mathbf{w}^T \mathbf{F}_n(E_3, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_3, \tilde{n})\mathbf{v} = (0, 0, -b_1F_3, -(m + \mu + \gamma_1 + F_3(c_1 - \alpha)))^T$ and therefore $\mathbf{w}^T [D\mathbf{F}_n(E_3, \tilde{n})\mathbf{v}] = -eb_1k_1F_3^2 - (m + \mu + \gamma_1 + F_3(c_1 - \alpha))^2 \neq 0$. Now if $\mathbf{w}^T [D^2\mathbf{F}(E_3, \tilde{n})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_3 and E_4 .

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter μ and let

$$\tilde{\mu} = -m + F_3(\alpha - c_1) - \gamma_1 + \frac{\beta \lambda F_3 S_3}{n + \nu + \lambda F_3 + S_3(g_3 + \theta) + \gamma_2}$$

feasible for

$$F_3(\alpha-c_1)+\frac{\beta\lambda F_3S_3}{n+\nu+\lambda F_3+S_3(g_3+\theta)+\gamma_2}>m+\gamma_1$$

The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda F_3, b_1F_3, m + \tilde{\mu} + \gamma_1 + F_3(c_1 - \alpha))^T$, $\mathbf{w} = (g_1S_3, \beta F_3, ek_1F_3, m + \tilde{\mu} + \gamma_1 + F_3(c_1 - \alpha))^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_{\mu}(E_3, \tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_{\mu}(E_3, \tilde{\mu}) = 0$, implying $D\mathbf{F}_{\mu}(E_3, \tilde{\mu})\mathbf{v} = (0, -\lambda F_3, 0, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_{\mu}(E_3, \tilde{\mu})\mathbf{v}] = -\beta\lambda F_3S_3 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{\mu})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_3 and E_4 .

Eigenvalue Λ_{B_1} ,

Take as bifurcation parameter v and let

$$\tilde{\nu} = -n - \lambda F_3 + S_3(\theta - g_3) - \gamma_2 + \frac{\beta \lambda F_3 S_3}{m + \mu + F_3(c_1 - \alpha) + \gamma_1}$$

feasible for

$$S_3(\theta-g_3)+\frac{\beta\lambda F_3S_3}{m+\mu+F_3(c_1-\alpha)+\gamma_1}>n+\gamma_2+\lambda F_3.$$

The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda F_3, b_1F_3, m + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$, $\mathbf{w} = (g_1S_3, \beta F_3, ek_1F_3, m + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_{\mathbf{v}}(E_3, \tilde{\mathbf{v}}) = \mathbf{0}$, for which $\mathbf{w}^T\mathbf{F}_{\mathbf{v}}(E_3, \tilde{\mathbf{v}}) = \mathbf{0}$, implying $D\mathbf{F}_{\mathbf{v}}(E_3, \tilde{\mathbf{v}})\mathbf{v} = (0, 0, 0, -(m + \mu + \gamma_1 + F_3(c_1 - \alpha)))^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_{\mathbf{v}}(E_3, \tilde{\mathbf{v}})\mathbf{v}] = -(m + \mu + \gamma_1 + F_3(c_1 - \alpha))^2 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{\mathbf{v}})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mathbf{v} = \tilde{\mathbf{v}}$, between E_3 and E_4 .

Bifurcations at E₅

For E_5 the Jacobian has four explicit eigenvalues,

$$\Delta_{A_{1,2}} = \frac{r - m - 2b_1F_5 - C_5(b_2 + \alpha) - c_2C_5 \pm \sqrt{\Delta_A}}{2}$$



$$\Lambda_{B_{1,2}} = \frac{1}{2} [s - 2n - k_1 F_5 - C_5 (k_2 + \beta) \\ - v - \lambda F_5 - k_3 C_5 - \gamma_2 \pm \sqrt{\Delta_B}]$$

where

$$\Delta_{A} = [r - m - 2b_{1}F_{5} - C_{5}(b_{2} + \alpha) - c_{2}C_{5}]^{2} + 4[c_{2}C_{5}(r - m - 2b_{1}F_{5} - C_{5}(b_{2} + \alpha)] + C_{5}(\alpha - c_{1})[r - F_{5}(b_{2} + \alpha) + \gamma_{1})];$$

$$\Delta_{B} = [s - n - k_{1}F_{5} - C_{5}(k_{2} + \beta) - n - \nu - \lambda F_{5} - k_{3}C_{5} - \gamma_{2}]^{2} - 4\{[s - n - k_{1}F_{5} - C_{5}(k_{2} + \beta)][-n - \nu - \lambda F_{5} - k_{3}C_{5} - \gamma_{2}) - \beta C_{5}(s + \gamma_{2})\}.$$

Eigenvalue $\Lambda_{A_{1,2}}$

Take as bifurcation parameter *m* and getting \tilde{m} from $c_2(r - m - 2b_1F_5 - C_5(b_2 + \alpha)) + (\alpha - c_1)(r - F_5(b_2 + \alpha) + \gamma_1) = 0$, feasible for $r + \gamma_1 > F_5(b_2 + \alpha)$ with $\alpha > c_1$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (c_2, \alpha - c_1, 0, 0)^T$, $\mathbf{w} = (c_2C_5, r - F_5(b_2 + \alpha) + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_5, \tilde{m}) = (-F_5, -C_5, 0, 0)^T$, for which $\mathbf{w}^T \mathbf{F}_m(E_5, \tilde{m}) = -C_5(c_2F_5 + r - F_5(b_2 + \alpha) + \gamma_1) \neq 0$, implying $D\mathbf{F}_m(E_5, \tilde{m})\mathbf{v} = (-c_2, c_1 - \alpha, 0, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_m(E_5, \tilde{m})\mathbf{v}] = -c_2^2C_5 + (c_1 - \alpha)(r - F_5(b_2 + \alpha) + \gamma_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_5, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2c_2^2C_5(b_1c_2 + (\alpha + b_2)(\alpha - c_1)) \neq 0$. Hence a saddle-node bifurcation arises for the critical parameter value $m = \tilde{m}$.

Eigenvalue $\Lambda_{A_{1,2}}$

Take as bifurcation parameter μ and getting $\tilde{\mu}$ from $c_2(r - m - 2b_1F_5 - C_5(b_2 + \alpha)) + (\alpha - c_1)(r - F_5(b_2 + \alpha) + \gamma_1) = 0$, feasible for $r + \gamma_1 > F_5(b_2 + \alpha)$ with $\alpha > c_1$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (c_2, \alpha - c_1, 0, 0)^T$, $\mathbf{w} = (c_2C_5, r - F_5(b_2 + \alpha) + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_{\mu}(E_5, \tilde{\mu}) = (0, -C_5, 0, 0)^T$, for which $\mathbf{w}^T \mathbf{F}_{\mu}(E_5, \tilde{\mu}) = -C_5(r - F_5(b_2 + \alpha) + \gamma_1) \neq 0$, implying $D \mathbf{F}_{\mu}(E_5, \tilde{\mu}) \mathbf{v} = (0, c_1 - \alpha, 0, 0)^T$ and therefore $\mathbf{w}^T [D \mathbf{F}_{\mu}(E_5, \tilde{\mu}) \mathbf{v}] = (c_1 - \alpha)(r - F_5(b_2 + \alpha) + \gamma_1) \neq 0$. Also, $\mathbf{w}^T [D^2 \mathbf{F}(E_5, \tilde{\mu})(\mathbf{v}, \mathbf{v})] = -2c_2^2 C_5(b_1 c_2 + (\alpha + b_2)(\alpha - c_1)) \neq$ 0. Hence a saddle-node bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter *n* and getting \tilde{n} from $(s - n - k_1F_5 - C_5(k_2 + \beta))(-n - v - \lambda F_5 - k_3C_5 - \gamma_2) - \beta C_5(s + \gamma_2) = 0$, feasible for $s < n + k_1F_5 + C_5(k_2 + \beta)$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (c_2, \alpha - c_1, s + \gamma_2, \tilde{n} + k_1F_5 + C_5(k_2 + \beta) - s)^T$, $\mathbf{w} = (c_2C_5, r - F_5(b_2 + \alpha) + \gamma_1, \beta C_5, \tilde{n} + k_1F_5 + C_5(k_2 + \beta) - s)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_5, \tilde{n}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_n(E_5, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_5, \tilde{n})\mathbf{v} = (0, 0, -(s + \gamma_2), -(\tilde{n} + k_1F_5 + C_5(k_2 + \beta) - s))^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_n(E_5, \tilde{n})\mathbf{v}] = -(s + \gamma_2)\beta C_5 - (\tilde{n} + k_1F_5 + C_5(k_2 + \beta) - s)^2 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_5, \tilde{n})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_5 and E_4 .

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter \mathbf{v} and getting $\tilde{\mathbf{v}}$ from $(s-n-k_1F_5-C_5(k_2+\beta))(-n-\mathbf{v}-\lambda F_5-k_3C_5-\gamma_2)-\beta C_5(s+\gamma_2) = 0$, feasible for $s < n+k_1F_5+C_5(k_2+\beta)$. The right \mathbf{v} and left \mathbf{w} eigenvectors of the Jacobian are $\mathbf{v} = (c_2, \alpha - c_1, s+\gamma_2, n+k_1F_5+C_5(k_2+\beta)-s)^T$, $\mathbf{w} = (c_2C_5, r-F_5(b_2+\alpha)+\gamma_1, \beta C_5, n+k_1F_5+C_5(k_2+\beta)-s)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_{\mathbf{v}}(E_5, \tilde{\mathbf{v}}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_{\mathbf{v}}(E_5, \tilde{\mathbf{v}}) = 0$, implying $D\mathbf{F}_{\mathbf{v}}(E_5, \tilde{\mathbf{v}})\mathbf{v} = (0, 0, 0, -(n+k_1F_5+C_5(k_2+\beta)-s))^T$ and therefore $\mathbf{w}^T [D\mathbf{F}_{\mathbf{v}}(E_5, \tilde{\mathbf{v}})\mathbf{v}] = -(n+k_1F_5+C_5(k_2+\beta)-s)^2 \neq 0$. Now if $\mathbf{w}^T [D^2\mathbf{F}(E_5, \tilde{\mathbf{v}})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mathbf{v} = \tilde{\mathbf{v}}$, between E_5 and E_4 .

Bifurcations at E₆

For E_6 the Jacobian has four explicit eigenvalues,

$$\Lambda_{A_{1,2}} = rac{r-2m+ek_1S_6 - \lambda I_6 - \mu - \gamma_1 \pm \sqrt{\Delta_A}}{2} \ \Lambda_{B_{1,2}} = rac{s-n-2g_1S_6 - I_6(g_2+ heta) - g_4I_6 \pm \sqrt{\Delta_B}}{2}$$

where

$$\begin{split} \Delta_A &= (r - 2m + ek_1S_6 - \lambda I_6 - \mu - \gamma_1)^2 \\ -4[(r - m + ek_1S_6 - \lambda I_6)(-m - \mu - \gamma_1) \\ &-\lambda I_6(r + ek_2S_6 + ek_3I_6 + \gamma_1)] \\ \Delta_B &= (s - n - 2g_1S_6 - I_6(g_2 + \theta) - g_4I_6)^2 \\ -4\{-g_4I_6[s - n - 2g_1S_6 - I_6(g_2 + \theta)] \\ &-I_6(\theta - g_3)[s - S_6(g_2 + \theta) + \gamma_2]\} \end{split}$$

Eigenvalue Λ_{A_1} ,

Take as bifurcation parameter *m* and getting \tilde{m} from $(r-m+ek_1S_6-\lambda I_6)(m+\mu+\gamma_1)+\lambda I_6(r+ek_2S_6+ek_3I_6+\gamma_1)=0$, feasible for $r+ek_1S_6 < m+\lambda I_6$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (\tilde{m}+\mu+\gamma_1,\lambda I_6,g_4,\theta-g_3)^T$, $\mathbf{w} = (\tilde{m}+\mu+\gamma_1,r+ek_2S_6+ek_3I_6+\gamma_1,g_4I_6,s-S_6(g_2+\theta)+\gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_6,\tilde{m})=\mathbf{0}$, for which $\mathbf{w}^T\mathbf{F}_m(E_6,\tilde{m})=0$, implying $D\mathbf{F}_m(E_6,\tilde{m})\mathbf{v} = (-(\tilde{m}+\mu+\gamma_1),-\lambda I_6,0,0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_m(E_6,\tilde{m})\mathbf{v}] = -(\tilde{m}+\mu+\gamma_1)^2 - \lambda I_6(r+ek_2S_6+ek_3I_6+\gamma_1)\neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_6,\tilde{m})(\mathbf{v},\mathbf{v})]\neq 0$ a transcritical bifurcation arises for the critical parameter value $m=\tilde{m}$, between E_6 and E_4 .

Eigenvalue Λ_{A_1} ,

Take as bifurcation parameter μ and getting $\tilde{\mu}$ from $(r-m+ek_1S_6-\lambda I_6)(m+\mu+\gamma_1)+\lambda I_6(r+ek_2S_6+ek_3I_6+\gamma_1)=0$, feasible for $r+ek_1S_6 < m+\lambda I_6$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (m+\mu+\gamma_1,\lambda I_6,g_4,\theta-g_3)^T$, $\mathbf{w} = (m+\mu+\gamma_1,r+ek_2S_6+ek_3I_6+\gamma_1,g_4I_6,s-S_6(g_2+\theta)+\gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_{\mu}(E_6,\tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_{\mu}(E_6,\tilde{\mu}) = 0$, implying $D\mathbf{F}_{\mu}(E_6,\tilde{\mu})\mathbf{v} = (0,-\lambda I_6,0,0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_{\mu}(E_6,\tilde{\mu})\mathbf{v}] = -\lambda I_6(r+ek_2S_6+ek_3I_6+\gamma_1) \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_6,\tilde{\mu})(\mathbf{v},\mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_6 and E_4 .

Take as bifurcation parameter *n* and getting \tilde{n} from $g_4(s - n - 2g_1S_6 - I_6(g_2 + \theta)) + (\theta - g_3)(s - S_6(g_2 + \theta) + \gamma_2) = 0$, feasible for $s + \gamma_2 > S_6(g_2 + \theta)$ with $\theta > g_3$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (0, 0, g_4, \theta - g_3)^T$, $\mathbf{w} = (0, 0, g_4I_6, s - S_6(g_2 + \theta) + \gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_6, \tilde{n}) = (0, 0, -S_6, -I_6)^T$, for which $\mathbf{w}^T\mathbf{F}_n(E_6, \tilde{n}) = -I_6(g_4S_6 + s - S_6(g_2 + \theta) + \gamma_2) \neq 0$, implying $D\mathbf{F}_n(E_6, \tilde{n})\mathbf{v} = (0, 0, -g_4, g_3 - \theta)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_n(E_6, \tilde{n})\mathbf{v}] = -(g_4^2I_6 + (s - S_6(g_2 + \theta) + \gamma_2)(\theta - g_3)) \neq 0$. Also $\mathbf{w}^T[D^2\mathbf{F}(E_6, \tilde{n})(\mathbf{v}, \mathbf{v})] = -2g_4^2I_6(g_1g_4 + (g_2 + \theta)(\theta - g_3)) \neq 0$. Hence a saddle-node bifurcation arises for the critical parameter value $n = \tilde{n}$.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter v and getting \tilde{v} from $g_4(s - n - 2g_1S_6 - I_6(g_2 + \theta)) + (\theta - g_3)(s - S_6(g_2 + \theta) + \gamma_2) = 0$, feasible for $s + \gamma_2 > S_6(g_2 + \theta)$ with $\theta > g_3$. The right v and left w eigenvectors of the Jacobian are $v = (0, 0, g_4, \theta - g_3)^T$, $w = (0, 0, g_4I_6, s - S_6(g_2 + \theta) + \gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_v(E_6, \tilde{v}) = (0, 0, 0, -I_6)^T$, for which $w^T \mathbf{F}_v(E_6, \tilde{v}) = -I_6(s - S_6(g_2 + \theta) + \gamma_2) \neq 0$, implying $D \mathbf{F}_v(E_6, \tilde{v}) \mathbf{v} = (0, 0, 0, g_3 - \theta)^T$ and therefore $w^T [D \mathbf{F}_v(E_6, \tilde{v}) \mathbf{v}] = (g_3 - \theta)(s - S_6(g_2 + \theta) + \gamma_2) \neq 0$. Also $w^T [D^2 \mathbf{F}(E_6, \tilde{v})(\mathbf{v}, \mathbf{v})] = -2g_4^2 I_6(g_1g_4 + (g_2 + \theta)(\theta - g_3)) \neq$ 0. Hence a saddle-node bifurcation arises for the critical parameter value $v = \tilde{v}$.

Tables 4 and 5 summarize the findings respectively for saddle-node and transcritical bifurcations. Figure 2 instead shows their mutual relationships graphically.



Figure 2: Transcritical bifurcations representation of model (1); in red those numerically found.

TABLE 4: POSSIBLE SADDLE-NODE BIFURCATIONS OF MODEL

 (1).

Eq.	Eigenvalue	Threshold
E_5	$\Lambda_{A_{1,2}}=0$	$m = \tilde{m}$
	$\Lambda_{A_{1,2}}=0$	$\mu= ilde{\mu}$
E_6	$\Lambda_{B_{1,2}}=0$	$n = \tilde{n}$
	$\Lambda_{B_{1,2}}=0$	$ u = ilde{ u}$

 TABLE 5: POSSIBLE TRANSCRITICAL BIFURCATIONS OF

 MODEL (1). NA MEANS THAT SOTOMAYOR'S THEOREM IS NOT

 APPLICABLE.

Eq.	Eigenvalue	Threshold
$E_0 - E_1$	$\Lambda_1 = 0$	$m = \tilde{m}$
$E_0 - E_2$	$\Lambda_3=0$	$n = \tilde{n}$
$E_1 - E_0$	$\Lambda_1 = 0$	$m = \tilde{m}$
$E_1 - E_5$	$\Lambda_2=0$	$m = \tilde{m}$
$E_1 - E_5$	$\Lambda_2=0$	$\mu= ilde{\mu}$
$E_1(NA)$	$\Lambda_3 = 0$	$m = \tilde{m}$
$E_1 - E_3$	$\Lambda_3=0$	$n = \tilde{n}$
$E_2 - E_0$	$\Lambda_1 = 0$	$n = \tilde{n}$
$E_2 - E_6$	$\Lambda_2=0$	$n = \tilde{n}$
$E_2 - E_6$	$\Lambda_2=0$	$v = ilde{v}$
$E_2 - E_3$	$\Lambda_3=0$	$m = \tilde{m}$
$E_2 - E_3(NA)$	$\Lambda_3=0$	$n = \tilde{n}$
$E_5 - E_4(NA)$	$\Lambda_{B_{1,2}}=0$	$m = \tilde{m}$
$E_{5} - E_{4}$	$\Lambda_{B_{1,2}}=0$	$n = \tilde{n}$
$E_5 - E_4(NA)$	$\Lambda_{B_{1,2}}=0$	$\mu= ilde{\mu}$
$E_{5} - E_{4}$	$\Lambda_{B_{1,2}} = 0$	$ u = ilde{ u}$
$E_{3} - E_{4}$	$\Lambda_{B_{1,2}} = 0$	$m = \tilde{m}$
$E_{3} - E_{4}$	$\Lambda_{B_{1,2}} = 0$	$n = \tilde{n}$
$E_{3} - E_{4}$	$\Lambda_{B_{1,2}} = 0$	$\mu= ilde{\mu}$
$E_{3} - E_{4}$	$\Lambda_{B_{1,2}} = 0$	$v = ilde{v}$
$E_6 - E_4$	$\Lambda_{A_{1,2}} = 0$	$m = \tilde{m}$
$E_6 - E_4$ (NA)	$\Lambda_{A_{1,2}} = 0$	$n = \tilde{n}$
$E_{6} - E_{4}$	$\Lambda_{A_{1,2}} = 0$	$\mu= ilde{\mu}$
$E_6 - E_4$ (NA)	$\Lambda_{A_{1,2}} = 0$	$v = \tilde{v}$

Non-existence of Hopf bifurcations

The points E_0 , E_1 , E_2 have only real eigenvalues, thus Hopf bifurcations cannot arise.

For equilibrium E_3 , the trace of the first quadratic into which the characteristic equation factorizes is $b_1F_3 + g_1S_3$ which cannot vanish. The trace of the second quadratic, from (27) can be rewritten as

$$S_3(g_3-\theta) = -[m+n+\gamma_1+\gamma_2+\mu+\nu+F_3(c_1-\alpha+\lambda)]$$

and substitution into the determinant inequality, the second one in (27), produces a condition that cannot be satisfied as well:

$$-(m+\mu+F_3(c_1-\alpha)+\gamma_1)^2-\beta\lambda F_3S_3>0.$$

At E_5 again factorization occurs. It is already known that the first quadratic has a negative trace, (25), so that purely imaginary eigenvalues cannot arise. For the second one, the determinant condition, i.e. the last inequality in (26), implies

$$s-n-k_1F_5-C_5(k_2+\beta) < 0$$

and substitution into the trace inequality, the second one in (26), leads to

$$s - 2n - k_1 F_5 - C_5(k_2 + \beta) - \nu - \lambda F_5 - k_3 C_5 - \gamma_2 < 0$$

thereby preventing the trace from vanishing.

Similar considerations hold for E_6 . One trace is negative, (28). The determinant of the second quadratic, last inequality of (29), implies

$$r - m + ek_1S_6 - \lambda I_6 < 0$$

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and using this result in the trace inequality we find that the latter is strictly negative and therefore cannot vanish:

$$r-2m+ek_1S_6-\lambda I_6-\mu-\gamma_1<0.$$

STANDARD INCIDENCE MODEL

Equilibrium points

Note that for the equilibria evaluation, the standard incidences vanish when both populations vanish, as the numerators are quadratic terms, while the denominators are linear just functions.

The possible equilibria for (2) are the origin, E_0 , E_1 , E_2 and E_3 , the very same points found in the model (1). Now, their feasibility conditions are therefore (4), (5) and (6).

We now investigate the rodents-free equilibrium $E_5 = (F_5, C_5, 0, 0)$. Summing the two equilibrium equations and rearranging the second one we obtain the following two conic sections:

$$\begin{split} \Psi(C,F) &: b_1 F^2 + c_2 C^2 + (b_2 + c_1) F C + F(m-r) \\ &+ C(m+\mu-r) = 0, \\ \Phi(C,F) &: c_1 F^2 + c_2 C^2 + (c_1+c_2) F C \\ &+ (m-\alpha+\gamma_1+\mu) F + (m+\gamma_1+\mu) C = 0. \end{split}$$

Both the conics go through the origin.

The invariant $b_1c_2 - (b_2 + c_1)^2 4^{-1}$ of Ψ is not decisive to assess its nature, and thus we look for intersections with the axes,

$$O = (0,0), \quad Q_1^* = \left(0, \frac{r-m}{b_1}\right), \quad Q_2^* = \left(\frac{r-m-\mu}{c_2}, 0\right)$$

Differentiating implicitly and evaluating at the three previous points we get

$$\begin{split} F'(O) &= \frac{m+\mu-r}{r-m}, \\ F'(Q_1^*) &= -\frac{b_1(m+\mu-r)+(r-m)(b_2+c_1)}{b_1(r-m)}, \\ F'(Q_2^*) &= \frac{c_2(m+\mu-r)}{c_2(m-r)+(b_2+c_1)(r-m-\mu)}. \end{split}$$

Thus we have four cases:

• Case (A):

$$>m, m+\mu>r.$$
 (32)

 Q_1^* lies on the positive *F*-axis, Q_2^* lies on the negative *C*-axis, F'(O) > 0, $F'(Q_1^*) < 0$, $F'(Q_2^*)$ could be of either sign.

• Case (B):

$$r > m, \quad m + \mu < r.$$
 (33)

 Q_1^* lies on the positive *F*-axis, Q_2^* lies on the positive *C*-axis, F'(O) < 0.

• Case (C):

$$r < m, \quad m + \mu > r.$$
 (34)

 Q_1^* lies on the negative *F*-axis, Q_2^* lies on the negative *C*-axis and F'(O) < 0.

• Case (D):

$$r < m, \quad m + \mu < r. \tag{35}$$

 Q_1^* lies on the negative *F*-axis, Q_2^* lies on the positive *C*-axis, F'(O) > 0, $F'(Q_1^*) < 0$, $F'(Q_2^*) < 0$. However the inequalities (35) are contradictory and this situation therefore cannot arise.

This means that in Case (A) we can have either ellipses, for which there is an arc that lies in the first quadrant, or hyperbolae. In the latter situation, the origin and the two points Q_1^* and Q_2^* must all lie on the same branch. Therefore, the ellipse and hyperbola configurations are in these cases topologically equivalent. Therefore in Case (A) the arc joining the origin and Q_1^* lies in the first quadrant, independently of the type of the conic section.

In Case (B), if the three points are on the same branch of the conic, the latter can be an ellipse, and then the concave arc joining Q_1^* and Q_2^* is feasible, or a hyperbola, and the very same arc is again feasible and concave. In this case however there could be also two arcs in the first quadrant emanating respectively from each intersection Q_1^* and Q_2^* . If Q_1^* and Q_2^* lie on the same branch again the arc joining them is feasible, but convex in this case. The other possible arrangements of O, Q_1^* and Q_2^* on different branches of the hyperbola Ψ lead to impossible configurations, in view of the signs of the slopes at these points.

Case (C) gives rise to a feasible arc only in one situation. Indeed, if the three points, O, Q_1^* and Q_2^* belong to the same branch of the conic, be it an ellipse or a hyperbola, the arc on which they lie does not meet the first quadrant, but the other one is entirely feasible. If two of them lie on the same branch of the hyperbola, they must be Q_1^* and Q_2^* , because in the other two cases the slope at the origin would be positive; the arc joining Q_1^* and Q_2^* is concave and does not intersect the first quadrant.

For the second conic Φ the invariant is negative, $-(c_2 - c_1)^2 4^{-1} < 0$ showing that it is a hyperbola. Its intersections with the axes are the origin O and

$$P_1^* = \left(0, -\frac{m-\alpha+\gamma_1+\mu}{c_1}\right), \quad P_2^* = \left(-\frac{m+\gamma_1+\mu}{c_2}, 0\right)$$

Note that the abscissa of P_2^* is negative. Differentiating implicitly at the above points we find

$$F'(O) = \frac{m + \gamma_1 + \mu}{\alpha - m - \gamma_1 - \mu},$$

$$F'(P_1^*) = \frac{\alpha}{m - \alpha + \gamma_1 + \mu} - \frac{c_2}{c_1},$$

$$F'(P_2^*) = -c_2 \frac{m + \gamma_1 + \mu}{c_1(m + \gamma_1 + \mu) + c_2\alpha} < 0.$$
(36)

Thus for

1

$$\alpha > \gamma_1 + m + \mu \tag{37}$$

the height of the point P_1^* is positive, F'(O) > 0, $F'(P_1^*) < 0$ and $F'(P_2^*) < 0$. Now if the three points, O, P_1^* and P_2^* are on the same branch of the hyperbola, the arc joining O and P_1^* lies in the first quadrant. The three configurations for which two points are on the same branch, are incompatible with the sign of F'(O) or $F'(P_1^*)$. On the other hand for

$$\alpha < \gamma_1 + m + \mu \tag{38}$$

 P_1^* has negative height and F'(O) < 0. If O, P_1^* and P_2^* lie on the same branch of the hyperbola, it must be unfeasible, the remaining one lies entirely in the first quadrant. However, in this case the derivative at P_2^* would be positive, which gives a contradiction with what found above, (36). The configurations for which two points lie on the same branch are incompatible with the sign of the derivative at the origin, except when the arc joins P_1^* and P_2^* ; but in such case both branches of the hyperbola are unfeasible. In summary, thus, this situation cannot arise.

We now need to find the conditions leading to possible intersections of Ψ and Φ in the first quadrant.

For (32) and (37), the intersection depends on the combination of heights and slopes at the origin, namely it is necessary that either one of the following pairs is satisfied:

$$\frac{\alpha - m - \gamma_1 - \mu}{c_1} > \frac{r - m}{b_1}, \quad \frac{m + \gamma_1 + \mu}{\alpha - m - \gamma_1 - \mu} > \frac{m + \mu - r}{r - m}; \quad (39)$$
$$\frac{\alpha - m - \gamma_1 - \mu}{c_1} < \frac{r - m}{b_1}, \quad \frac{m + \gamma_1 + \mu}{\alpha - m - \gamma_1 - \mu} < \frac{m + \mu - r}{r - m}.$$

For (33) and (37), the intersection is always guaranteed if the heights of the points on the F axis are properly arranged, namely

$$\frac{\alpha - m - \gamma_1 - \mu}{c_1} > \frac{r - m}{b_1}.\tag{40}$$

For (34) and (37) there could be a saddle-node bifurcation leading to two intersections or none at all. But this case is rather complicated and will not be further investigated.

The analysis for the case $E_6 = (0, 0, S_6, I_6)$ parallels the one above, the details are omitted, but the results leading to sure feasible intersections are summarized here below.

We need the auxiliary conditions

$$\theta > \gamma_2 + n + \nu; \tag{41}$$

$$s > n, \quad n + v > s;$$
 (42)

$$s > n, \quad n + v < s; \tag{43}$$

For (42) and (41), the intersection depends on the combination of heights and slopes at the origin, namely it is necessary that either one of the following pairs is satisfied:

$$\frac{\theta - n - \gamma_2 - \nu}{g_3} > \frac{s - n}{g_1}, \quad \frac{n + \gamma_2 + \nu}{\theta - n - \gamma_2 - \nu} > \frac{n + \nu - s}{s - n}; \quad (44)$$
$$\frac{\theta - n - \gamma_2 - \nu}{g_3} < \frac{s - n}{g_1}, \quad \frac{n + \gamma_2 + \nu}{\theta - n - \gamma_2 - \nu} < \frac{n + \nu - s}{s - n}.$$

For (43) and (41), the intersection exists if

$$\frac{\theta - n - \gamma_2 - \nu}{g_3} > \frac{s - n}{g_1}.\tag{45}$$

 TABLE 6: POSSIBLE GUARANTEED FEASIBILITY CONDITIONS

 FOR THE EQUILIBRIA OF (2)

Equilibrium	Feasibility
$E_0 = (0, 0, 0, 0)$	-
$E_1 = \left(\frac{r-m}{b_1}, 0, 0, 0\right)$	(4)
$E_2 = \left(0, 0, \frac{s-n}{g_1}, 0\right)$	(5)
$E_3 = (F_3, 0, S_3, 0)$	(6)
$E_5 = (F_5, C_5, 0, 0)$	(32), (37), (39);
	(33), (37), (40);
$E_6 = (0, 0, S_6, I_6)$	(42), (41), (44);
	(43), (41), (45);
$E_4 = (F_4, C_4, S_4, I_4)$	numerical

Stability of the equilibrium points

The Jacobian $\widehat{J} = \widehat{J}_{i,k}$, i, k = 1, ..., 4 of the system (2) has the following entries:

$$\begin{split} \widehat{J}_{1,1} &= ek_1 S - \alpha \left(\frac{C}{F+C} - \frac{FC}{(F+C)^2} \right) - b_2 C \\ -2b_1 F - \lambda \frac{I}{S+I} - m + r, \quad \widehat{J}_{1,4} &= ek_3 C - \lambda F \frac{S}{(S+I)^2}, \\ \widehat{J}_{1,2} &= r + e(k_2 S + k_3 I) - b_2 F - \alpha F \frac{F}{(F+C)^2} + \gamma_1, \\ \widehat{J}_{1,3} &= ek_2 C + ek_1 F + \lambda F \frac{I}{(S+I)^2}, \\ \widehat{J}_{2,1} &= \alpha \left(\frac{C}{F+C} - \frac{FC}{(F+C)^2} \right) - c_1 C + \lambda \frac{I}{S+I}, \\ \widehat{J}_{2,2} &= -2c_2 C + \alpha F \frac{F}{(F+C)^2} - c_1 F - m - \mu - \gamma_1, \\ \widehat{J}_{2,3} &= -\lambda F \frac{I}{(S+I)^2}, \quad \widehat{J}_{3,1} &= -k_1 S + \beta S \frac{C}{(F+C)^2}, \\ \widehat{J}_{2,4} &= \lambda F \frac{S}{(S+I)^2}, \quad \widehat{J}_{3,2} &= -\beta S \frac{F}{(F+C)^2} - k_2 S, \\ \widehat{J}_{3,3} &= -\beta \frac{C}{F+C} - k_2 C - k_1 F - 2g_1 S - g_2 I \\ -\theta \left(\frac{I}{S+I} - \frac{SI}{(S+I)^2} \right) - n + s, \\ \widehat{J}_{3,4} &= -g_2 S - \theta S \frac{S}{(S+I)^2} + s + \gamma_2, \\ \widehat{J}_{4,1} &= -\lambda I - \beta S \frac{C}{(F+C)^2}, \quad \widehat{J}_{4,2} &= \beta S \frac{F}{(F+C)^2} - k_3 I, \\ \widehat{J}_{4,3} &= \beta \frac{C}{F+C} - g_3 I + \theta \left(\frac{I}{S+I} - \frac{SI}{(S+I)^2} \right), \\ \widehat{J}_{4,4} &= -k_3 C - \lambda F - g_3 S + \theta S \frac{S}{(S+I)^2} - 2g_4 I - n - V - \gamma_2. \end{split}$$

Recall that when each pairs F, C and S, I vanish, the corresponding fractional terms do not appear in the model, and therefore will also be omitted in the Jacobian.

At E_0 the Jacobian eigenvalues are

$$r-m$$
, $-m-\mu-\gamma_1$, $s-n$, $-n-\nu-\gamma_2$

and in view of the parameters' assumptions the stability con-



ditions become just

$$r < m, \quad s < n.$$
 (46)

At $E_1 = (F_1, 0, 0, 0)$ again the eigenvalues are explicit,

1

$$m-r, \quad -m-\mu+\alpha-\gamma_1-\frac{c_1(r-m)}{b_1},$$

$$s-n+\frac{k_1(m-r)}{b_1} \quad -n-\nu-\gamma_2+\frac{\lambda(m-r)}{b_1},$$

and stability is achieved for

$$\alpha < m + \mu + \gamma_1 + \frac{c_1(r-m)}{b_1}, \quad s + \frac{k_1(m-r)}{b_1} < n.$$
 (47)

For $E_2 = (0, 0, S_2, 0)$ we again explicitly find the eigenvalues

$$n-s, \quad -n-\gamma_2+\theta-\nu-\frac{g_3(s-n)}{g_1},$$

$$r-m+\frac{ek_1(s-n)}{g_1}, \quad -m-\mu-\gamma_1$$

and stability follows if just

$$\theta < n + \gamma_2 + \nu + \frac{g_3(s-n)}{g_1}, \quad r + \frac{ek_1(s-n)}{g_1} < m$$
 (48)

hold.

At $E_3 = (F_3, 0, S_3, 0)$ the characteristic equation factorizes into the product of two quadratic equations. Using the feasibility of E_3 the Routh-Hurwitz conditions in one case are satisfied,

$$-b_1F_3 - g_1S_3 < 0, \quad (-b_1F_3)(-g_1S_3) + ek_1^2F_3S_3 > 0$$

while the remaining ones ensure stability if satisfied:

$$\alpha + \theta < m + \mu + F_3(c_1 + \lambda) + \gamma_1 + \gamma_2 + n + \nu + g_3S_3, \quad (49)$$
$$(\alpha - m - \mu - c_1F_3 - \gamma_1)(\theta - n - \nu - \lambda F_3 - g_3S_3 - \gamma_2)$$
$$> \beta\lambda.$$

For the stability of the rodent-free and foxes-free points, we leave in the stability conditions the contributions of the fractions coming from the standard incidence terms, namely S and I for E_5 and F and C for E_6 , remarking thus that the Routh-Hurwitz conditions being satisfied depend on the relative speeds of the vanishing populations to zero, and will not be investigated any further.

At $E_5 = (F_5, C_5, 0, 0)$ the characteristic equation factorizes into the product of two quadratic equations, for which the Routh-Hurwitz conditions give

$$r + \frac{\alpha F_{5}^{2}}{(F_{5} + C_{5})^{2}} < 2m + 2b_{1}F_{5} + b_{2}C_{5}$$
(50)
$$+ \frac{\alpha C_{5}^{2}}{(F_{5} + C_{5})^{2}} + \mu + \gamma_{1} + c_{1}F_{5} + 2c_{2}C_{5} + \frac{\lambda I}{S + I};$$

$$\left[r - m - \frac{\alpha C_{5}^{2}}{(F_{5} + C_{5})^{2}} - 2b_{1}F_{5} - b_{2}C_{5} - \frac{\lambda I}{S + I}\right]$$

$$\times \left[\frac{\alpha F_{5}^{2}}{(F_{5} + C_{5})^{2}} - m - \mu - c_{1}F_{5} - 2c_{2}C_{5} - \gamma_{1}\right]$$

$$\geq \left[\frac{\alpha C_{5}^{2}}{(F_{5} + C_{5})^{2}} - c_{1} - \frac{\lambda I}{S + I}\right]$$

$$\times \left[r - b_{2}F_{5} - \frac{\alpha F_{5}^{2}}{(F_{5} + C_{5})^{2}} + \gamma_{1}\right],$$

as well as

$$s < \frac{\beta C_5}{F_5 + C_5} + 2n + k_1 F_5 + k_2 C_5 + v$$

$$+ \lambda F_5 + k_3 C_5 + \gamma_2 + \theta \frac{S^2 + I^2}{(S+I)^2};$$

$$\left[s - n - k_1 F_5 - k_2 C_5 - \frac{\beta C_5}{F_5 + C_5} - \frac{\theta I^2}{(S+I)^2} \right] \\\times \left[n + v + \lambda F_5 + k_3 C_5 + \gamma_2 + \frac{\theta S^2}{(S+I)^2} \right] \\+ \frac{\beta C_5}{F_5 + C_5} (s + \gamma_2) < 0.$$
(51)

Now this equilibrium can indeed be feasible and stable, as it is shown empirically in Figure 3, for the parameter values given in its caption.

The characteristic equation of $E_6 = (0, 0, S_6, I_6)$ also factorizes into the product of two quadratic equations, and the Routh-Hurwitz conditions yield

$$r + ek_{1}S_{6} < 2m + \mu + \gamma_{1} + \frac{\lambda I_{6}}{S_{6} + I_{6}} + \frac{\alpha(C^{2} - F^{2})}{(F + C)^{2}}, \quad (52)$$

$$\left[r - m + ek_{1}S_{6} - \frac{\lambda I_{6}}{S_{6} + I_{6}} - \frac{\alpha C^{2}}{(F + C)^{2}}\right]$$

$$\times \left[m + \mu + \gamma_{1} + \frac{\alpha F^{2}}{(F + C)^{2}}\right] + \left[\frac{\lambda I_{6}}{S_{6} + I_{6}} + \frac{\alpha C^{2}}{(F + C)^{2}}\right]$$

$$\times \left[r + e(k_{2}S_{6} + k_{3}I_{6}) + \gamma_{1} - \frac{\alpha F^{2}}{(F + C)^{2}}\right] < 0,$$

and

$$s + \frac{\theta S_{6}^{2}}{(S_{6} + I_{6})^{2}} < 2n + (2g_{1} + g_{3})S_{6} + g_{2}I_{6}$$
(53)
$$+ \frac{\theta I_{6}^{2}}{(S_{6} + I_{6})^{2}} + \nu + \gamma_{2} + 2g_{4}I_{6} + \frac{\beta C}{F + C},$$

$$s - n - 2g_{1}S_{6} - g_{2}I_{6} - \frac{\theta I_{6}^{2}}{(S_{6} + I_{6})^{2}} - \frac{\beta C}{F + C}]$$

$$\times \left[\frac{\theta S_{6}^{2}}{(S_{6} + I_{6})^{2}} - n - \nu - g_{3}S_{6} - 2g_{4}I_{6} - \gamma_{2} \right]$$

$$> \left[\frac{\theta I_{6}^{2}}{(S_{6} + I_{6})^{2}} - g_{3}I_{6} + \frac{\beta C}{F + C} \right]$$

$$\times \left[s - g_{2}S_{6} - \frac{\theta S_{6}^{2}}{(S_{6} + I_{6})^{2}} + \gamma_{2} \right].$$



Figure 3: Equilibrium E_5 of model (2) obtained for the parameter values (30), but for $b_1 = 0, 1, r = 2, s = 4$, and $b_2 = 0, 1, c_1 = 0, 1, c_2 = 0, 11, g_3 = 0, 11, k_2 = 0, 1, \alpha = 0, 1, \beta = 0, 2, \gamma_1 = 0, 5, \gamma_2 = 0, 1, \theta = 0, 2, \lambda = 0, 1, \mu = 5, v = 0, 1.$

This equilibrium can also be achieved, see the simulation reported in Figure 4. The parameter values are liste in the caption.

At $E_4 = (F_4, C_4, S_4, I_4)$ one must impose the Routh-Hurwitz conditions on the full matrix:

$$\operatorname{tr}(\widehat{J}(E_4)) < 0, \quad M_2 > 0, \quad M_3 < 0, \quad (54)$$
$$\operatorname{det}(\widehat{J}(E_4)) > 0, \quad \operatorname{tr}(\widehat{J}(E_4)) \cdot M_2 < M_3,$$
$$\operatorname{tr}(\widehat{J}(E_4)) \cdot M_2 \cdot M_3 > \operatorname{tr}(\widehat{J}(E_4))^2 \cdot \operatorname{det}(\widehat{J}(E_4)) + M_3^2.$$

They are complicated and do not lead to analytical expressions easy to interpret, thus they are not further explored. Table 7 summarizes our findings.

TABLE 7: STABILITY CONDITIONS FOR THE EQUILIBRIA OF (2)

Equilibrium point	Stability conditions
$E_0 = (0, 0, 0, 0)$	(46)
$E_1 = \left(\frac{r-m}{b_1}, 0, 0, 0\right)$	(47)
$E_2 = \left(0, 0, \frac{s-n}{g_1}, 0\right)$	(48)
$E_3 = (F_3, 0, S_3, 0)$	(49)
$E_5 = (F_5, C_5, 0, 0)$	(50), (51)
$E_6 = (0, 0, S_6, I_6)$	(52), (53)
$E_4 = (F_4, C_4, S_4, I_4)$	numerical

BIFURCATIONS OF MODEL (2)

Bifurcations at E_0

For E_0 the Jacobian has four explicit eigenvalues, $\Lambda_1 = r - m$, $\Lambda_2 = -m - \mu - \gamma_1$, $\Lambda_3 = s - n$, $\Lambda_4 = -n - v - \gamma_2$.

Eigenvalue Λ_1

Take as bifurcation parameter *m* and let $\tilde{m} := r$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (1,0,0,0)^T$, $\mathbf{w} = (\tilde{m} + \mu + \gamma_1, \tilde{m} + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_0, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_m(E_0, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_0, \tilde{m})\mathbf{v} = (-1,0,0,0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_m(E_0, \tilde{m})\mathbf{v}] = -(\tilde{m} + \mu + \gamma_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_0, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2b_1(\tilde{m} + \mu + \gamma_1) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_0 and E_1 .



Figure 4: Equilibrium E_6 of model (2) obtained for the parameters (30), in which however some changes occur, $b_1 = 1$, $g_1 = 1$, $g_2 = 1$, $g_4 = 0,1$, $k_1 = 1$, $k_3 = 1$, m = 1, n = 1, r = 0,2, s = 2, and the other values: $b_2 = 1$, $c_2 = 0,4$, $g_3 = 0,1$, $c_1 = 2$, $k_2 = 1$, $\theta = 3$, $\lambda = 1$, $\gamma_2 = 0,1$, $\gamma_1 = 1$, $\alpha = 1$, $\beta = 1$, v = 2, $\mu = 0,1$

Eigenvalue Λ_3

Take as bifurcation parameter *n* and let $\tilde{n} := s$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (0,0,1,0)^T$, $\mathbf{w} = (0,0,\tilde{n}+\nu+\gamma_2,\tilde{n}+\gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_0,\tilde{n}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_n(E_0,\tilde{n}) = \mathbf{0}$, implying $D\mathbf{F}_n(E_0,\tilde{n})\mathbf{v} = (0,0,-1,0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_n(E_0,\tilde{n})\mathbf{v}] = -(\tilde{n}+\nu+\gamma_2) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_0,\tilde{n})(\mathbf{v},\mathbf{v})] = -2g_1(\tilde{n}+\nu+\gamma_2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_0 and E_2 .

Bifurcations at E₁

For E_1 the Jacobian has four explicit eigenvalues,

$$\Lambda_1 = m - r, \quad \Lambda_2 = -m + \alpha - \gamma_1 - \mu - c_1 F_1,$$

$$\Lambda_3 = s - n - k_1 F_1, \quad \Lambda_4 = -n - \gamma_2 - \nu - \lambda F_1.$$

Eigenvalue Λ_1

Take as bifurcation parameter *m* and let $\tilde{m} := r$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (1,0,0,0)^T$, $\mathbf{w} = (\tilde{m} - \alpha + \gamma_1 + \mu, \tilde{m} - \alpha + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_1, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_m(E_1, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_1, \tilde{n})\mathbf{v} = (-1, 0, 0, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_m(E_1, \tilde{m})\mathbf{v}] = -(\tilde{m} - \alpha + \gamma_1 + \mu)$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_1, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2b_1(\tilde{m} - \alpha + \gamma_1 + \mu)$. Hence if $\alpha \neq \tilde{m} + \gamma_1 + \mu$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_1 and E_0 .

Eigenvalue Λ_2

Take as bifurcation parameter m and let $\tilde{m} :=$ $\frac{b_1(\mu+\gamma_1-\alpha)+c_1r}{r}$, feasible for $b_1(\mu+\gamma_1-\alpha)+c_1r>0$ $c_1 - b_1$ and $c_1 > b_1$ or $b_1(\mu + \gamma_1 - \alpha) + c_1r < 0$ and $c_1 < b_1$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (r - b_2 F_1 - \alpha + \gamma_1, b_1 F_1, 0, 0)^T$, $\mathbf{w} = (0, 1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_1, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w}^{\mathrm{T}} \mathbf{F}_m(E_1, \tilde{m}) = 0$, $D\mathbf{F}_m(E_1, \tilde{m})\mathbf{v} = (-v_1, -v_2, 0, 0)^T$ implying and $\mathbf{w}^{\mathbf{T}}[D\mathbf{F}_m(E_1,\tilde{m})\mathbf{v}] = -b_1F_1 \neq 0.$ therefore Also, $\mathbf{w}^{T}[D^{2}\mathbf{F}(E_{1},\tilde{m})(\mathbf{v},\mathbf{v})] = -2b_{1}(c_{1}(r-b_{2}F_{1}-\alpha+\gamma_{1}) + c_{2}F_{1}-\alpha+\gamma_{1}) + c_{2}F_{1}(r-\alpha+\gamma_{1}) + c_{2}F_{1}(r-\alpha+\gamma_{1}) + c_{2}F_{1}(r-\alpha+\gamma_{1}) + c_{2}F_{1}(r-\alpha+\gamma_{1}))$ $b_1c_2F_1$). Hence if $c_1(r - b_2F_1 - \alpha + \gamma_1) + b_1c_2F_1 \neq 0$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_1 and E_5 .

Eigenvalue Λ_2

Take as bifurcation parameter μ and let $\tilde{\mu} := -m - c_1 \frac{r-m}{b_1} + \alpha - \gamma_1$, feasible for $\alpha > m + c_1 \frac{r-m}{b_1} + \gamma_1$. The right **v** and left **w** eigenvectors of the Jacobian are **v** = $(r - b_2F_1 - \alpha + \gamma_1, b_1F_1, 0, 0)^T$, **w** = $(0, 1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_{\mu}(E_1, \tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w}^T\mathbf{F}_{\mu}(E_1, \tilde{\mu}) = 0$, implying $D\mathbf{F}_{\mu}(E_1, \tilde{\mu})\mathbf{v} = (0, -b_1F_1, 0, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_{\mu}(E_1, \tilde{\mu})\mathbf{v}] = -b_1F_1 \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_1, \tilde{\mu})(\mathbf{v}, \mathbf{v})] = -2b_1(c_1(r - b_2F_1 - \alpha + \gamma_1) + b_1c_2F_1)$. Hence if $c_1(r - b_2F_1 - \alpha + \gamma_1) + b_1c_2F_1 \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_1 and E_5 .



Eigenvalue Λ_3

Take as bifurcation parameter *n* and let $\tilde{n} := s - k_1 F_1$, feasible for $s > k_1 F_1$ with s > n. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_1, 0, b_1F_1, 0)^T$, $\mathbf{w} = (0, 0, n + \gamma_2 + \mathbf{v} + \lambda F_1, s + \gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_1, \tilde{n}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_n(E_1, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_1, \tilde{n})\mathbf{v} = (0, 0, -b_1F_1, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_n(E_1, \tilde{n})\mathbf{v}] = -b_1F_1(n + \gamma_2 + \mathbf{v} + \lambda F_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_1, \tilde{n})(\mathbf{v}, \mathbf{v})] = -b_1F_1(n + \gamma_2 + \mathbf{v} + \lambda F_1)(2ek_1^2F_1 + b_1k_2F_1 + b_1\beta) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_1 and E_3 .

Bifurcations at E₂

For E_2 the Jacobian has four explicit eigenvalues,

$$\Lambda_1 = n - s, \quad \Lambda_2 = -n - \gamma_2 + \theta - \nu - g_3 S_2,$$

$$\Lambda_3 = r - m + ek_1 S_2, \quad \Lambda_4 = -m - \mu - \gamma_1.$$

Eigenvalue Λ_1

Take as bifurcation parameter *n* and let $\tilde{n} := s$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (0,0,1,0)^T$, $\mathbf{w} = (0,0,\tilde{n} + \gamma_2 - \theta + \nu, s + \gamma_2 - \theta)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_2,\tilde{n}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_n(E_2,\tilde{n}) = 0$, implying $D\mathbf{F}_n(E_2,\tilde{n})\mathbf{v} = (0,0,-1,0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_n(E_2,\tilde{n})\mathbf{v}] = -(\tilde{n} + \gamma_2 - \theta + \nu)$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_2,\tilde{n})(\mathbf{v},\mathbf{v})] = -2g_1(\tilde{n} + \gamma_2 - \theta + \nu)$. Hence if $\theta \neq \tilde{n} + \gamma_2 + \nu$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_2 and E_0 .

Eigenvalue Λ_2

Take as bifurcation parameter *n* and let $\tilde{n} := \frac{g_1(\mathbf{v}+\gamma_2-\theta)+g_3s}{g_3-g_1}$, feasible for $g_1(\mathbf{v}+\gamma_2-\theta)+g_3s>0$ and $g_3 > g_1$ or $g_1(\mathbf{v}+\gamma_2-\theta)+g_3s<0$ and $g_3 < g_1$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (0,0,s-g_2S_2-\theta+\gamma_2,g_1S_2)^T$, $\mathbf{w} = (0,0,0,1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_2,\tilde{n}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_n(E_2,\tilde{n}) = \mathbf{0}$, implying $D\mathbf{F}_n(E_2,\tilde{n})\mathbf{v} = (0,0,-v_3,-v_4)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_n(E_2,\tilde{n})\mathbf{v}] = -g_1S_2 \neq 0$. Hence if $\mathbf{w}^T[D^2\mathbf{F}(E_2,\tilde{n})(\mathbf{v},\mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_2 and E_6 .

Eigenvalue Λ_2

Take as bifurcation parameter \mathbf{v} and let $\tilde{\mathbf{v}} := -n - g_3 \frac{s-n}{g_1} + \theta - \gamma_2$, feasible for $\theta > n + g_3 \frac{s-n}{g_1} + \gamma_2$. The right \mathbf{v} and left \mathbf{w} eigenvectors of the Jacobian are $\mathbf{v} = (0, 0, s - g_2 S_2 - \theta + \gamma_2, g_1 S_2)^T$, $\mathbf{w} = (0, 0, 0, 1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_v(E_2, \tilde{\mathbf{v}}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_v(E_2, \tilde{\mathbf{v}}) = 0$, implying $D\mathbf{F}_v(E_2, \tilde{\mathbf{v}})\mathbf{v} = (0, 0, -g_1 S_2, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_v(E_2, \tilde{\mathbf{v}})\mathbf{v}] = -g_1 S_2 \neq 0$. Hence if $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{\mathbf{v}})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mathbf{v} = \tilde{\mathbf{v}}$, between E_2 and E_6 .

Eigenvalue Λ_3

Take as bifurcation parameter *m* and let $\tilde{m} := r + ek_1S_2$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (g_1S_2, 0, -k_1S_2, 0)^T$, $\mathbf{w} = (\tilde{m} + \gamma_1 + \mu, r + ek_2S_2 + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_2, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_n(E_2, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_2, \tilde{m})\mathbf{v} = (-g_1S_2, 0, 0, 0)^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_m(E_2, \tilde{m})\mathbf{v}] = -g_1S_2(m + \gamma_1 + \mu) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2g_1S_2(\tilde{m} + \gamma_1 + \mu)(b_1g_1S_2 + ek_1^2S_2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_2 and E_3 .

Bifurcations at E₃

For E_3 the Jacobian has four explicit eigenvalues,

$$\Lambda_{A_{1,2}} = \frac{1}{2} \left[-b_1 F_3 - g_1 S_3 \pm \sqrt{\Sigma} \right]$$
$$\Lambda_{B_{1,2}} = \frac{1}{2} (K \pm \sqrt{\Delta}),$$

where

$$\begin{split} \Sigma &= b_1^2 F_3^2 + g_1^2 S_3^2 - 2b_1 g_1 F_3 S_3 - 4ek_1^2 F_3 S_3, \\ K &= -m - n + \alpha - \gamma_1 - \gamma_2 + \theta - \mu - \nu - F_3 (c_1 + \lambda) - g_3 S_3, \\ \Delta &= [m + n - \alpha + \gamma_1 + \gamma_2 - \theta + \mu + \nu + F_3 (c_1 + \lambda) + g_3 S_3]^2 \\ -4[(-m + \alpha - \mu - \gamma_1 - c_1 F_3)(-n - \lambda F_3 - g_3 S_3 - \gamma_2 + \theta - \nu) - \beta \lambda]. \end{split}$$

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter *m* and getting \tilde{m} from $(-m + \alpha - \mu - \gamma_1 - c_1F_3)(-n - \lambda F_3 - g_3S_3 - \gamma_2 + \theta - \nu) - \beta\lambda = 0$, feasible for $(-m + \alpha - \mu - \gamma_1 - c_1F_3)(-n - \lambda F_3 - g_3S_3 - \gamma_2 + \theta - \nu) > 0$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda \frac{F_3}{S_3}, b_1F_3, \tilde{m} - \alpha + \gamma_1 + \mu + c_1F_3)^T$, $\mathbf{w} = (g_1S_3, \beta \frac{F_3}{S_3}, ek_1F_3, \tilde{m} - \alpha + \gamma_1 + \mu + c_1F_3)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_3, \tilde{m}) = (-F_3, 0, 0, 0)$, for which $\mathbf{w}^T \mathbf{F}_m(E_3, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_3, \tilde{m})\mathbf{v} = (-ek_1F_3, -\lambda \frac{F_3}{S_3}, 0, 0)^T$ and therefore $\mathbf{w}^T [D\mathbf{F}_m(E_3, \tilde{m})\mathbf{v}] = -ek_1g_1F_3S_3 - \beta\lambda \neq 0$. Now if $\mathbf{w}^T [D^2\mathbf{F}(E_3, \tilde{m})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_3 and E_4 .

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter *n* and getting \tilde{n} from $(-m + \alpha - \mu - \gamma_1 - c_1F_3)(-n - \lambda F_3 - g_3S_3 - \gamma_2 + \theta - v) - \beta\lambda = 0$, feasible for $(-m + \alpha - \mu - \gamma_1 - c_1F_3)(-n - \lambda F_3 - g_3S_3 - \gamma_2 + \theta - v) > 0$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda \frac{F_3}{S_3}, b_1F_3, m - \alpha + \gamma_1 + \mu + c_1F_3)^T$, $\mathbf{w} = (g_1S_3, \beta \frac{F_3}{S_3}, ek_1F_3, m - \alpha + \gamma_1 + \mu + c_1F_3)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_3, \tilde{n}) = (0, 0, -S_3, 0)$, for which $\mathbf{w}^T \mathbf{F}_n(E_3, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_3, \tilde{n})\mathbf{v} = (0, 0, -b_1F_3, -(m - \alpha + \gamma_1 + \mu + c_1F_3))^T$ and therefore $\mathbf{w}^T [D\mathbf{F}_n(E_3, \tilde{n})\mathbf{v}] = -eb_1k_1F_3^2 - (m - \alpha + \gamma_1 + \mu + c_1F_3)^2 \neq 0$. Now if $\mathbf{w}^T [D^2\mathbf{F}(E_3, \tilde{n})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_3 and E_4 .

Take as bifurcation parameter μ and let $\tilde{\mu} = -m + \frac{\beta\lambda}{n + \lambda F_3 + g_3 S_3 + \gamma_2 - \theta + \nu}$, feasible for $(-m + \alpha - \gamma_1 - c_1 F_3)(n + \lambda F_3 + g_3 S_3 + \gamma_2 - \theta + \nu) + \beta\lambda > 0$. The right **v** and left **w** eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda \frac{F_3}{S_3}, b_1F_3, m - \alpha + \gamma_1 + \tilde{\mu} + c_1F_3)^T$, $\mathbf{w} = (g_1S_3, \beta \frac{F_3}{S_3}, ek_1F_3, m - \alpha + \gamma_1 + \tilde{\mu} + c_1F_3)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_{\mu}(E_3, \tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w}^{\mathrm{T}}\mathbf{F}_{\mu}(E_3, \tilde{\mu}) = 0$, implying $D\mathbf{F}_{\mu}(E_3, \tilde{\mu})\mathbf{v} = (0, -\lambda \frac{F_3}{S_3}, 0, 0)^T$ and therefore $\mathbf{w}^{\mathrm{T}}[D\mathbf{F}_{\mu}(E_3, \tilde{\mu})\mathbf{v}] = -\beta\lambda \neq 0$. Now if $\mathbf{w}^{\mathrm{T}}[D^2\mathbf{F}(E_3, \tilde{\mu})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_3 and E_4 .

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter v and let

$$\tilde{\mathbf{v}} = -n - \lambda F_3 - g_3 S_3 - \gamma_2 + \boldsymbol{\theta} - \frac{\beta \lambda}{-m + \alpha - \mu - \gamma_1 - c_1 F_3},$$

feasible for

$$heta > n + \lambda F_3 + g_3 S_3 + \gamma_2 + rac{eta \lambda}{-m + lpha - \mu - \gamma_1 - c_1 F_3}$$

The right **v** and left **w** eigenvectors of the Jacobian are **v** = $(ek_1F_3, \lambda \frac{F_3}{S_3}, b_1F_3, m - \alpha + \gamma_1 + \mu + c_1F_3)^T$, **w** = $(g_1S_3, \beta \frac{F_3}{S_3}, ek_1F_3, m - \alpha + \gamma_1 + \mu + c_1F_3)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_v(E_3, \tilde{v}) = \mathbf{0}$, for which $\mathbf{w}^T \mathbf{F}_v(E_3, \tilde{v}) = \mathbf{0}$, implying $D\mathbf{F}_v(E_3, \tilde{v})\mathbf{v} = (0, 0, 0, -(m - \alpha + \gamma_1 + \mu + c_1F_3))^T$ and therefore $\mathbf{w}^T[D\mathbf{F}_v(E_3, \tilde{v})\mathbf{v}] = -(m - \alpha + \gamma_1 + \mu + c_1F_3)^2 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{v})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mathbf{v} = \tilde{\mathbf{v}}$, between E_3 and E_4 .

Numerically, we have also determined other transcritical bifurcations, reported in Figures 5-6 as well as a sequence of transitions, Figure 7. Finally, Figure 8 summarizes the mutual relationships among the equilibria of (2) via transcritical bifurcations.



Figure 5: Transcritical bifurcation $E_4 - E_6$ in terms of the bifurcation parameter *m*. Note that in the bottom two frames the vertical axis starts from a positive value.



Figure 6: Transcritical bifurcation $E_6 - E_4$ in terms of the bifurcation parameter μ . Note that in the bottom two frames the vertical axis starts from a positive value.



Figure 7: The sequence of transcritical bifurcations $E_4 - E_3 - E_2 - E_0$ in terms of the bifurcation parameter *n*.

Non-existence of Hopf bifurcations

We consider here only E_3 . Again the Jacobian factorizes into the product of two quadratic equations, the first one of which has the strictly positive trace $b_1F_3 + g_1S_3$, so that the Hopf bifurcation cannot arise. Annihilating the trace of the other one, i.e. making the first inequality of (49) an equality, we obtain

$$-m+\alpha-\mu-c_1F_3-\gamma_1=n+\nu+\lambda F_3+g_3S_3+\gamma_2-\theta$$

and substituting it into the determinant inequality, the second one in (49), we find

$$-(-m+\alpha-\mu-c_1F_3-\gamma_1)^2-\beta\lambda>0$$

which of course cannot be satisfied.

For E_5 again there are two minors of order two to be considered. From the Routh-Hurwitz conditions for the first one, annihilating the trace gives

$$-\beta \frac{C}{F+C} - k_2C - k_1F - n + s = k_3C + \lambda F + n + \nu + \gamma_2$$

and substitution into the determinant condition leads to the inconsistency

$$-(k_3C+\lambda F+n+\nu+\gamma_2)^2-(s+\gamma_2)\beta\frac{C}{F+C}>0$$

At E_6 a similar situation occurs, from the trace we get

$$ek_1S - \lambda \frac{I}{S+I} - m + r = m + \mu + \gamma_1$$





Figure 8: Transcritical bifurcations representation of model (2); in red those numerically found.

so that from substitution into the determinant, once again a contradiction arises,

$$-(m+\mu+\gamma_1)^2-\lambda\frac{I}{S+I}(r+e(k_2S+k_3I)+\gamma_1)>0.$$

We have not analysed any further the two remaining minors.

DISCUSSION

The two proposed models differ only in the way the parasite is transmitted. In view of this remark, the disease-free equilibria of the two models, namely E_0 , E_1 , E_2 , E_3 , are identical both in feasibility as well as stability conditions, at least for the first three points, as for the latter the conditions are more involved and even substituting explicitly the population equilibrium values does not allow a comparison.

There are however differences in the remaining equilibria that do not contain all the populations.

The feasibility of rodents-free point E_5 in both models has been investigated through the intersection of suitable lines in the C - F plane. There are several sets of possible conditions leading to feasible points in both models, therefore a direct comparison it not possible. They have been shown in both cases not to be empty, through numerical simulations, that of course show also these equilibria to be stable. The analytical stability conditions in case of model (1) are explicit, since one of the Routh-Hurwitz conditions is satisfied, for (2) all of them must be taken into account. In addition, in case of (2) the satisfaction of the inequalities is more complicated, as it depends on the speed at which both rodents subpopulations vanish. This element may make the stability more difficult to be achieved.

For the foxes-free point E_6 similar considerations hold. Coexistence in both cases has been obtained through simulations.

We have also provided two graphs that link together the various equilibria, via transcritical bifurcations. The structure is the same for both models. The two transitions from the origin to either the healthy foxes-only point E_1 or the healthy

rodents-only equilibrium E_2 are obtained if the respectives mortality rates of the species that disappears is low enough. From these points, the disease can appear in the thriving population if its mortality is low, this being either the natural or the disease-related one. Thus, to be specific, from E_1 we can obtain E_5 by acting either on m or μ , and a similar situation involving n and v exists between E_2 and E_6 . Another possibility exists here as well, namely the disease-free point E_3 can be reached from either E_1 or E_2 . It is necessary in both cases to act on the mortality of the species that is absent in the original equilibrium, suitably reducing it.

In model (2), coexistence has been shown that it can be achieved from the disease-free point E_3 by acting on the combined mortalities of both species, either natural or diseaserelated, or also from the foxes-free point, if their mortalities are lowered enough. For system (1), coexistence can similarly be attained also from E_6 , where foxes are absent, if their mortalities are low enough. In the same way from E_5 the mortalities of the rodents should be low to achieve coexistence. Numerically however, this has been seen to occur also if both foxes mortalities increase, see Figures 9, 10.

In addition, at least for model (1), saddle-node bifurcations could occur generating pairs of equilibria. This has been seen in the feasibility analysis, in the cases when the intersection of the curves leading to the equilibrium could be double, and vanish if the curves are slightly shifted. We gave a hint to this phenomenon, without deepening its analysis. On the other hand, the investigation of the bifurcations through Sotomayor's theorem indicates that they are indeed possible, for the points E_5 and E_6 where only one species survives, with the parasite endemic in it.



Figure 9: Transcritical bifurcations $E_5 - E_4$ for model (1) in terms of the foxes natural mortality *m*. Parameter values in addition to those listed in (30): $b_2 = 0,2, c_1 = 0,22, c_2 = 0,21, g_3 = 0,11, k_2 = 0,1, \alpha = 4, \beta = 0,2, \gamma_1 = 0,1, \gamma_2 = 3, \theta = 0,2, \lambda = 15, \mu = 0,22, \nu = 5$

We have also addressed the question whether persistent oscillations can be found in these models. Their onset through a Hopf bifurcation is immediately seen to be impossible at the origin and at the healthy species-only points E_1 and E_2 , because in such cases the eigenvalues are all real. For the equilibria that involve more populations, a nonexistence proof has also been provided in some cases.

From the ecological and conservationist point of view, the aim of the biologist would be the achievement of the disease-free environment, which is attained at equilibrium E_3 where *Echinococcus* is eradicated. Of course also E_1 and E_2 , apart from the ecosystem collapse at E_0 , do not harbor the parasite,


Figure 10: Transcritical bifurcations $E_5 - E_4$ for model (1) in terms of the foxes natural mortality μ . Parameter values other than the reference ones (30): $b_2 = 0,2, c_1 = 0,22, c_2 = 0,21, g_3 = 0,11, k_2 = 0,1, \alpha = 4, \beta = 0,2, \gamma_1 = 0,1, \gamma_2 = 3, \theta = 0,2, \lambda = 15, v = 5$

but at the expense of having one species eradicated, which in general is not a good situation. This except for the case in which they are the rodents, and in particular if they are considered pests, e.g. mouses. Note that even removing their main prey, the foxes can survive. Indeed they are generalist predators. Other food sources are present in the environment, and suitably accounted for in both models via the inclusion of the logistic-like terms, or, with a different terminology, by using the concept of emerging carrying capacities Sieber et al. (2014).

For the ecosystem to attain stably the desired situations, the bifurcation maps of Figures 2 and 8 turn out to be rather useful. Figure 7 shows for instance one possible such path, for which as *n* increases, the system moves away from coexistence of all the populations to the disease-free point, and eventually, if the rodents mortality keeps on increasing, to the healthy rodents-only state and eventually to extinction of all species. This appears counterintuitive, but a high rodents mortality may indeed deplete their predators, and if the latter cannot find suitably sizeable alternative food source, they may suffer more than their prey. Given any state in which the system is found, these maps indicate to the ecologist the possible ways to achieve the parasite-free equilibrium E_3 . But above all they also provide the parameters on which it is necessary to operate in order to reach the desired outcome.

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The big ifs in the outcomes of species interactions: review and insights from the *Interaction Function (IF)* model

Desenlaces condicionales en interacciones entre especies: revisión y perspectiva del modelo *Función de Interacción (FI)*

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Abstract— The conceptual framework for species interactions calls for a new perspective: conditional outcomes are not rare; but, rather, closer to the norm. Interactions may shift or switch between beneficial and detrimental following variations in the (context-dependent) balance of costs and benefits involved for each species. A classic (simple) model such as a Lotka-Volterra can be adjusted to represent these (complex) dynamics by introducing the appropriate nonlinearities in the interspecific terms. The Interaction Function (IF) model introduces a density-dependent function that takes values along the negative to positive continuum; a change in sign denotes a shift in the effect of one species on the other. In this paper I discuss the foundations and development of the IF model, along with other models and conceptual bodies that have emerged on the topic. A brief advance on the central results: (i) the systems present multiple stable equilibria where species may coexist at any combination of interaction outcomes (+ , – , 0), or one be excluded, (ii) transitions between outcomes occur either gradually (environmental conditions vary) or abruptly (drastic change in population abundances leads to another domain of attraction); catastrophic jumps are also possibilities, (iii) fragmentation of space and dispersal trigger source-sink dynamics that cause further variation in the outcomes at local and regional levels, and, remarkably, dynamic variations in the sink or source roles of localities and populations also occur. The fundamental conclusion is that the beneficial or detrimental role of a species in an association is a spatiotemporal dynamic quality, determined by the balance of many concurrent density-dependent effects, some reinforcing, some counteracting, one another.

Keywords—context-dependent, alternative stable states, conditional outcomes, spatiotemporal dynamics, density-dependence, costbenefit, theoretical ecology, mutualism, antagonism, exploiter

Resumen— El marco conceptual de interacciones entre especies requiere una nueva perspectiva: los desenlaces variables (condicionados) no son raros; están más bien cerca de ser la norma. Las interacciones pueden cambiar entre beneficiosas y perjudiciales debido a variaciones en el balance (contexto-dependiente) de los costos y beneficios involucrados para cada especie. Un modelo clásico (simple), como Lotka-Volterra, se puede ajustar para representar estas dinámicas (complejas) introduciendo las no linealidades apropiadas en los términos interespecíficos. El modelo de Función de Interacción (FI) para desenlaces condicionales introduce una función denso-dependiente que toma valores a lo largo del continuo negativo a positivo; un cambio de signo denota un cambio en el efecto (denso-dependiente) de una especie sobre la otra. En este artículo analizo los fundamentos y desarrollo del modelo FI, junto con otros modelos y marcos conceptuales que han surgido en el tema. Un breve avance de los resultados centrales: (i) los sistemas presentan múltiples equilibrios estables donde las especies pueden coexistir, en cualquier combinación de desenlaces de interacción (+, -, 0), o una especie puede ser excluida, (ii) ocurren transiciones entre desenlaces, ya sea gradualmente (condiciones ambientales varían) o abruptamente (cambio drástico en abundancias poblacionales conduce a otro dominio de atracción); saltos catastróficos también son posibilidades, (iii) la fragmentación del espacio y la dispersión, desencadenan dinámicas fuente-sumidero que causan mayor variación en los desenlaces a nivel local y regional y, notablemente, también ocurren variaciones dinámicas en los roles de fuente y sumidero de las localidades y regiones. La conclusión fundamental es que el papel beneficioso o perjudicial de una especie en una asociación es una cualidad espacio-temporal dinámica, determinada por el balance de múltiples efectos denso-dependientes concurrentes, algunos que se refuerzan, otros se contrarrestan, entre sí.

Palabras clave—contexto-dependiente, estados estables alternativos, transiciones en desenlaces variables, dinámica espacio-temporal, denso-dependencia, costo-beneficio, ecología teórica, mutualismo, antagonismo, explotador

Two monks were arguing about a flag. One said: 'The flag is moving'. The other said: 'The wind is moving'. The sixth patriarch happened to be passing by. He told them: 'Not the wind, not the flag; mind is moving'.

- Mumon Ekai (1228) The Gateless Gate

PRELUDE

Interactions with conditional outcomes, or contextdependent interactions, have received extensive attention over the past years. One foot in front of the other, a vast body of empirical and theoretical knowledge (observations, field and lab experiments, conceptualization, mathematical models) has been built on the dynamic nature of the outcomes in population associations. This has come hand in hand with the trending interest in promoting mutualism as a relevant interaction in the structuring of natural communities, as are competition and predation. And this is because mutualism happens to be one of the strongest representative of a conditional interaction.

The beginnings. In 1988, J. N. Thompson wrote, 'Just as variation in traits in populations is the raw material for the evolution of species, variation in outcome is the raw material for the evolution of interactions'; he was introducing his exhaustive review on the evolution of interspecific interactions. In 1994, J. L. Bronstein published an insightful review on conditional outcomes in mutualistic interactions based on empirical data and observations. It stated clearly the importance of considering a different perspective: 'any interaction might be considered to occupy a potentially dynamic position along a continuum of possible outcomes, ranging from beneficial to progressively more antagonistic' as a result of the balance of costs and benefits involved for each partner species. She referred mainly to those interactions that involve both mutualistic and antagonistic effects from one species to the other and vice versa. This is the case, for instance, of the association between plants and insect pollinators: plants receive the benefit of pollination from the insects, but these eat their fruits, or may demand high production of flowers and nectar; in turn, pollinators get food and nests, but plants may abort the fruits carrying their eggs and larvae. Thus, this interaction may shift between mutualism and parasitism (either way) depending on the net balance of costs and benefits for each species, which in turn depends on the relative abundances of the two species and on general environmental conditions (this is a widely reported case in the literature, see e.g., Herre and West, 1997; Addicott and Bao, 1999; Van Der Kooi et al., 2021).

A lot has happened since. The new perspective of conditionality in the outcomes has triggered the revision of many other (or all) species associations (e.g., Agrawal et al. 2007; Chamberlain et al. 2014; Hoeksema and Bruna 2015; Messan-Rodriguez et al. 2018; Song et al. 2020), and has demanded a solid new conceptual framework beyond just conditional mutualism; one that defines the outcome of any population interaction as a dynamical entity, subject to variations conditioned by demographic or environmental conditions, not only in intensity, but more importantly, in its beneficial or detrimental nature.

In this article I explore, first, the empirical and natural framework, some representative cases of pairwise interactions with conditional outcomes, with the aim of finding common (or distinct) features and mechanisms that allows some categorization. Second, I present and discuss analyses and insights drawn from theoretical models. I do this by following the trail of a model I have developed over some years, the *Interaction Function (IF)* model (Hernandez, 1998, 2008, 2009, 2015, 2021; Hernandez and Barradas, 2003), discussing, comparing and complementing relevant results and contributions, along with other models and conceptual bodies that have emerged on the issue of conditional or context-dependent interactions.

On the whole, this paper aims to present a fluid narrative on the subject of the conditional nature of some species interactions, supported by theoretical models and concepts, but avoiding the most formal (mathematical) details, which can be found in the original articles and references.

ON BEING CONDITIONAL IN NATURE

Interactions between populations have been categorized from many angles, both empirically and theoretically. There are the definite (static) labels of parasitism, predator-prey, competition, mutualism, commensalism, etc., where a victim is always a victim, a competitor is always a competitor, and so on. And there are those cases where the beneficial presence of one species may become detrimental, or vice versa; that is, when a victim becomes an exploiter, or a mutualist becomes a parasite or a predator, and so forth. Nature provides examples to fit all the possibilities we could think of. The point is that after years of trying to build robust categorizations we end up with more exceptions than rules. That is the nature of nature.

In this section I look at the empirical or natural angle, those features that we observe in nature, in interactions between two populations in which the outcome is conditional. By *outcome* I mean the beneficial or detrimental effect of one species on the other (formalities on this issue will come later), by *conditional* I mean that it may change according to some circumstances related, or not, to the interacting species.

I present now brief recounts of some typical cases of conditional interactions, highlighting: benefits and costs for each species, their causes of variation, possible outcomes for the interaction, conditions that trigger changes in the outcomes (for one or both species), and provide some references for more detailed information.

1. *Plant, insect and pollination.* Adult insects oviposit on the plant and its larvae feed on the seeds and fruits; this is the benefit for the insect, but it also represents a cost for the plant. The plant can abort some of the fruits selectively: those that contain more insect eggs and larvae; this is a cost to the pollinator. The benefit for the plant is clearly pollination, but there is a cost involved in the production of flowers and nectar, also, if there are few



pollinators this benefit is low, and if there are many, the cost of feeding the larvae is high. Then, this interaction can result in a mutualism or a parasitism, where the parasitized species can be either the insect or the plant. The outcome depends on the net balance of benefits and costs, which in turn depend on the relative abundances of the species and on general environmental conditions (e.g., Herre and West 1997; Addicott and Bao 1999; Holland et al. 2002).

- 2. Epibiont and host. Epibionts (anemones, sponges, algae) live and grow on the surface of hosts (crabs, insects, algae, etc.). Hosts benefit from the protection from predators by the epibionts (camouflage, active defence), however, it may involve costs due to surface harm or mobility impairment. Both, the degree of protection and of harm caused, largely depend on the proportion of host surface covered by the epibiont. Epibionts benefit from substrate and mobility (greater access to nutrients) provided by the host; however, hosts can lead them to unfavourable environments. Predators may reject or attack the epibiont-host symbiont depending on the epibionts being unpalatable or a preferred prey, thus, the predator species present in the environment also affect the outcome of the association. The interaction can be mutualism or parasitism, where the parasitized species can be either the epibiont or the host (Vance, 1978; Duffy, 1990; Threlkeld et al., 1993; Wahl and Hay, 1995).
- 3. *Mycorrhizae: plant and fungus.* Mycorrhizae are fungus-plant associations that involve transfer of nutrients from the soil. The fungus, attached to the roots, provides the plant with the phosphorus it needs. This is beneficial for plants in soils with low nutrient availability, however, in fertile soils the action of the fungus with carbon compounds that it withdraws from its own organism, thus the net balance of costs and benefits may be negative for the plant, particularly if the densities of fungi are high. Thus, in this interaction the role of the fungus can vary between mutualistic and parasitic, depending on environmental conditions and abundances (Johnson et al., 1997; Gange and Ayres, 1999).
- 4. *Mullerian mimics.* At low densities, interactions between Mullerian mimics are mutualistic as they facilitate the training of predators in recognizing unpalatable prey. At higher densities they become competitors because they share resources(Gilbert, 1983).
- 5. *Whelks and lobsters.* In South Africa, at Malgas Island whelks are the favourite prey of an abundant population of rock lobsters; at Marcus Island, 4 Kms apart, same environmental conditions, rock lobsters are completely absent, whereas very high densities of whelks are present. According to local reports, the situation in Marcus Island occurred after a temporary environmental disturbance that caused the extinction of lobsters, allowing the considerable increase in the whelk population. When a thousand lobsters were introduced in an attempt to recolonize the region, they were overwhelmed and consumed until complete extinction by whelks within a week.

The interchange of roles between prey and predators prevents the reinvasion of lobsters on this island (Barkai and McQuaid, 1988).

- 6. Ants and aphids. Ants benefit from their association with aphids because they provide excretions or secretions (honeydew) rich in sugars and amino acids. Aphids are tended by ants (cleaning, transport, shelter) and get protection against natural predators, however, benefits for aphids may be low or even negative if aphid densities are high, or if predator densities are low. Thus, the mutualistic ant may become a parasite (exploiter). On the other hand, the higher the quality of the host plant fluids, the higher the quality of the honeydew produced by the aphids, thus, more ants are attracted, which is beneficial for the aphids; however, when the quality of the honeydew produced is low, and/or the ants have another source of food (e.g. flowers), the ants may predate on the aphids, given there is a high density of aphids per ant. Thus, the mutualistic ant becomes a predator. Ants need protein food (insect prey) for larvae growth and egg production by the queen, and sugary food as energy source for workers; then, the different ant roles respond to different nutritional demands of the ant colony (Addicott, 1979, 1981; Cushman, 1991; Cushman and Addicott, 1991; Sakata, 1994, 1995; Stadler and Dixon, 1998; Del-Claro and Oliveira, 2000; Offenberg, 2001; Stadler et al., 2002; Revilla and Encinas-Viso, 2015).
- 7. Seeds and rodent seed dispersers. Rodents consume seeds, but also provide seed dispersal (scatter, hoarding, caching) which has a beneficial effect on the growth rate of plant populations, however, this effect can be low at low rodent densities. Each rodent may: eat the seed in situ, or remove it (e.g. bury it, scatter), in which case the seed may: germinate, or be eaten by the rodent later. The seed–rodent interaction switches from mutualism to predation with the increase of rodent abundance per seed (Zeng et al., 2021; Zhang et al., 2021).

From the cases described above some features emerge on how the variations in the outcomes occur, or what are the conditions that trigger, or allow, a variation in the outcome. First, note that, in all cases, for a variation in outcome to occur, there has to be an appropriate relative abundance of the two species; and secondly, some other general environmental conditions, particular to each case, favour one outcome or the other. Additionally, we observe that variations in the outcomes may be gradual or sudden, reversible or irreversible, part of a life cycle or phenology of the species, and they may occur in both species or only in one. From this, I recognize two general trends in the variation in the outcome of the interactions:

(i) Those that shift – from mutualism to parasitism or competition – and may swing back

Cases 1 to 5: plant-pollinator, epibiont-host, plant-fungus (mycorrhiza), mimic-mimetized, whelks-lobsters.

These cases show how the outcome of the interaction depends on the net balance of benefits and costs for each species, which in turn depend on species densities and some environmental conditions. Then, depending on the particular form of these relationships the balance for each species may vary, not only in intensity, but may go through negative (detrimental), neutral and positive (beneficial) values. Therefore, the pairwise interaction may go, as in a sort of swing process, through the different possibilities: from mutualism to parasitism (either way), or to competition, or amensalism, etc., following the variation of conditions.

(ii) Those that switch – be a mutualist or be a predator – choose every time

Cases 6 and 7: ants-aphids, rodents-seeds.

In these cases the outcome of the interaction depends not only on the net balance of costs and benefits for each species, but also on the different demands of the species life cycle or population structure. The key feature in this category is that each individual can play the two roles (e.g. predator and mutualist) and will act as one or the other depending on relative densities and environmental conditions at that moment. Therefore, the two possible interactions are occurring simultaneously in the system.

About (i) and (ii) – to shift and swing or to switch

Note that in the cases of ant-aphid and seed dispersers, both *shift* and *switch* situations occur: there is a *shift* situation between mutualism and parasitism, and it is from either of these that the *switch* to predation occurs. That is, every ant, at every moment, when facing an aphid makes the decision (there are chemical and environmental cues to help) of either tending or eating it, depending on the nutritional demand of the ant colony. Ants only choose to predate if there are enough aphids to provide honeydew, and/or there are other sources of nectar, otherwise, the ant will not eat the aphid and will look for proteins (if needed) in other insect species. Then, it will tend the aphid, under a mutualistic or exploitative role, context-depending. Similarly, seed dispersers will choose between eating or not a seed; if not eaten, the seed may be taken somewhere else (scattered, buried, etc.), where it can germinate.

In the (only) *shift* situation there is no decision making, nor simultaneous roles of the species, rather, the whole two-species system would be in one type of interaction at a time, be it a mutualism, parasitism, or competition, etc., depending on the beneficial or detrimental outcome of the benefits and costs balance for each species at that moment and circumstance.

ON MODELLING THE DYNAMICS OF CONDI-TIONAL OUTCOMES

The classical Lotka-Volterra (*LV*) model expresses the dynamics of interacting species in terms of the sum of the effects that each species has on the per capita growth rate of every other; these effects are linear functions of densities. For two interacting populations with densities N_1 , N_2 , the model

can be written as,

$$\frac{dN_i}{dt} = r_i N_i \left(1 + \alpha_{ii} \frac{N_i}{K_i} + \alpha_{ij} \frac{N_j}{K_i} \right) \quad i, j = 1, 2$$
(1)

where r_i is the intrinsic rate of increase of species *i*, K_i is the carrying capacity, and α_{ii} and α_{ij} are the intraspecific and interspecific interaction coefficients, respectively. Note that the positive or negative effect of one population on the growth rate of the other is determined by the signs of the α_{12} and α_{21} coefficients: both positive for mutualism, both negative for competition, one positive and one negative for a victim–exploiter (consumer–resource) interaction, null and positive for commensalism, and null and negative for amensalism. Also note that this form of the model corresponds to facultative interactions (the species reach their carrying capacities when the other species is not present), for obligate interactions some adjustments can be made; will not be considered here, though. See Appendix A for more details on the Lotka–Volterra model.

The Interaction Function (*IF*) model (Hernandez, 1998, 2008, 2009; Hernandez and Barradas, 2003) follows the general reasoning of the *LV* model but introduces a notion that allows the study of the dynamics of interactions with conditional outcomes: interaction coefficients α_{ij} , are not constant but density-dependent functions $\alpha_{ij} \equiv \alpha_{ij}(N_i, N_j)$ that can take both positive and negative values at certain density ranges. That is, the effect of species *j* on species *i* can be either beneficial ($\alpha_{ij} > 0$) or detrimental ($\alpha_{ij} < 0$) depending on population densities (and some parameters included in its formulation to represent environmental conditions). Then, for a two-species system the model can be written as,

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} + \alpha_{12} \left(N_1, N_2 \right) \frac{N_2}{K_1} \right]$$
$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} + \alpha_{21} \left(N_1, N_2 \right) \frac{N_1}{K_2} \right]$$
(2)

where $\alpha_{ij}(N_i, N_j)$ measures the per capita effect of species *j* on the population growth rate of species *i* at given N_1, N_2 densities, and $\alpha_{ii} = -1$, which is a common assumption for this kind of model, meaning that the intraspecific interaction remains linear.

What's in the shape of the interaction functions $\alpha_{ij}(N_i, N_j)$

The concept behind the density-dependent interaction function $\alpha_{ij} \equiv \alpha_{ij}(N_i, N_j)$ is that it represents the net balance of the benefits and costs involved for species *i* due to the presence of species *j*, which, as exposed in the natural cases above, are in turn density-dependent. Then, the actual form of the function comes from $\alpha_{ij}(N_i, N_j) = Benefits(N_i, N_j) - Costs(N_i, N_j)$, and depending on the particular shapes of these, at given density ranges, the interaction can be beneficial $(\alpha_{ij} > 0)$ or detrimental $(\alpha_{ij} < 0)$. Figure 1 depicts two basic examples, in both benefits are greater than costs at lower N_j , but costs grow faster, thus, at higher N_j costs are higher than benefits; hence the shift in sign in the net balance.

To explore the general features (mechanisms, processes, patterns) of the *IF* model, there is no need to express the





Figure 1: $\alpha_{ij}(N_i, N_j)$ functions resulting from density-dependent (Benefits-Costs) functions, with specific formulations (a) B = bN/(d+N) and C = cN/(f+N), (b) B = b + dN and C = c + fN. In both cases curves cross at an intermediate density, thus the sum is positive at low densities, negative at higher densities. The general shapes of the resulting $\alpha_{ij}(N_i, N_j)$ functions can be expressed directly as a (a) quadratic ratio $\alpha = (bN - N^2) / (1 + cN^2)$ and (b) linear $\alpha = b - cN$.

costs and benefits formulations explicitly, only generic forms of the α_{ij} 's are needed, as long as these comply with the condition that it shifts in sign with density. To make the point clearer, we could assemble a hypothetical model as follows,

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} + \left(\frac{b_1 N_2 - N_2^2}{1 + c_1 N_2^2} \right) \frac{N_2}{K_1} \right]$$
$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} + (b_2 - c_2 N_1) \frac{N_1}{K_2} \right]$$
(3)

Equations (3) depict the *IF* model with the two general functional forms of $\alpha_{ij}(N_i, N_j)$ presented in Figures 1(a,b), i.e., a quadratic ratio in $\alpha_{12}(N_2)$ and a linear form in $\alpha_{21}(N_1)$. Parameters b_i, c_i , give the actual shape to the curves, they represent the way in which general (biotic or abiotic) conditions are reflected on the interactions intrinsic features, e.g., saturation values, sensitivity of the interaction to changes in the partner's density, thresholds between positive and negative interactions, etc. Note that in model (3) both $\alpha_{12}(N_2)$ and $\alpha_{21}(N_1)$ functions take positive values at low partner's density and become negative at higher densities; thus, this model could correspond to the situations of the *shift* case (i) defined in the section above.

A quick look at model (3) allows a first outline of the stability properties; it shows that at non-trivial equilibrium $(dN_1/dt = dN_2/dt = 0)$ populations may coexist, (say at N_1^*, N_2^*), or one species may be excluded, the other at its carrying capacity, $(N_i^* = K_i, N_j^* = 0)$. However, the specific nonlinearity introduced by the $\alpha_{ij}(N_i, N_j)$ interaction functions will provide a remarkable spectrum of possibilities.

Spoiler alert: the model presents multiple stable equilibria – at different interaction outcomes

Now I look into the graphical stability analysis of the *IF* model, that is, the nullclines (or zero-growth isoclines) for N_1 and N_2 , and equilibria solutions, for different sets of parameters in phase-plane. This kind of analysis has the virtue of conveying all needed (global) information about the system. To perform it we use explicit formulations for the $\alpha_{ij} \equiv \alpha_{ij}(N_i, N_j)$ interaction functions; figure 2 shows some of the patterns obtained when two linear $\alpha_{ij}(N_i, N_j)$ interaction functions, i, j = 1, 2, are used

in model (2). In this figure we can observe graphically the results that the quick look at the model above already told us: that the system may present a single stable solution (figures 2a and 2b), or multiple solutions at stable equilibria (alternative stable states), where species may coexist (figure 2c), or one species may be excluded, the other is at its carrying capacity (figure 2d).

I must add a comment here. The shape of the nullclines: humped closed crossing both axes, which ultimately is responsible for the appearance of multiple equilibria, occur for any interaction function α_{ij} chosen, as long as it complies with the condition that it takes values along the positive to negative continuum as density increases; the hump occurs at the change in sign of the α_{ij} function (details in Hernandez, 1998; Hernandez and Barradas, 2003).

The next pertinent step is to determine whether these solutions correspond to different outcomes in the nature of the interaction. The proper (formal) characterization of the outcomes in the interactions is not a trivial issue, and there is hardly a consensus among authors. I discuss this fully in Hernandez (2009), and present here the main ideas in Appendix B. For now, suffice it to say that I regard the outcome of an interaction in terms of its beneficial or detrimental nature towards the other species, and this is defined by comparing the performances of the species alone and when the other species is present. In more formal terms, an interaction is *beneficial, neutral or detrimental* for a *species i*, if when associated with a *species j* it reaches an equilibrium density N_i^* that is *greater, equal or smaller* than its carrying capacity K_i , respectively.

Note that the graphs in figure 2 allow for a representation of these ranges as quadrants in phase space where equilibria solutions lie. I use the classic symbols (+ +), (--), (+-), (- +), to denote types of interaction: mutualism, competition, and victim-exploiter (either way), respectively. Neutral interactions: commensalism and amensalism, are obviously also present, sort of midway between the others, however, I will not mention them explicitly, just to keep things simple. Note that the order in the signs in this nomenclature corresponds to the signs in $(\alpha_{21} \alpha_{12})$, at a given point in the plane. A comment aside: sometimes the signs of the jacobians are used to categorize types of interactions, however, this is misleading, their signs refer to stability properties only (see Appendix B).

Thus, we definitely show that the outcome in the interactions may be different for different sets of parameters. That is to say, the concept introduced in the *IF* model allows the representation of variable outcomes in the interaction for the same two species, depending on relative densities and general environmental conditions. Now, what about the dynamics of these variations?

The outcomes of interactions are dynamic – they transit in gradual, abrupt or catastrophic manner

From the patterns shown in figure 2 we see that as parameters change, the relative positions of the nullclines change,



Figure 2: Nullcline graphics in phase plane for *Interaction Function* model (2) with linear $\alpha_{ij} = b_j - c_j N_i$, for i, j = 1, 2, for four sets of parameters. N_1 nullcline (light curve), N_2 nullcline (dark curve), stable equilibria (N_1^*, N_2^*) (dark dots), dashed lines at K_1 and K_2 define quadrants for outcomes of interaction (legend upper corner). Formal stability analyses in Hernandez (1998, 2008); Hernandez and Barradas (2003).

causing equilibrium solutions to appear and disappear by processes of bifurcations and annihilations of the stationary states. In so doing, there are also changes in their stability properties. The appropriate way to present and analyse these is in a bifurcation diagram, which displays equilibrium solutions with respect to parameter values. Figure 3 shows the bifurcation diagram for N_1^* vs K_1 for the *IF* model, that is, the equilibrium density that species 1 would reach at different carrying capacity values (all other parameters are kept constant and equilibrium densities N_2^* vary along with N_1^* according to the model dynamics, but are not shown in the figure). The S shape of the diagram is typical of the hysteresis phenomenon (Thom, 1972; Zeeman, 1977). The solid upper and lower branches contain the stable equilibrium values and the dark dashed line that joins them contain the unstable equilibria. Observe that for low K_1 values there is only one corresponding N_1^* (e.g., dots at A), at higher K_1 there are two (one on each branch, e.g., dots at B, C and D), and at very high K_1 the system reaches a unique fixed stable equilibrium at $N_1^* = K_1$ (i.e., species 2 is excluded; off the graph borders). Note that these situations correspond to cases (a) to (d) in figure 2. Bifurcation diagrams can be (and were) constructed for any of the two equilibrium densities, N_1^* or N_2^* , with respect to any of the model parameters: K_i and those in the α_{ii} functions (parameter r_i was kept constant along all studies). For the IF model all combinations yielded hysteresis behaviour.

The diagram in figure 3 also allows the delimitation of sections for the different outcomes of the interaction: (+ +), (--), (+ -), (- +); these correspond to the quadrants defined in figure 2. Therefore, it shows remarkably clear the ways in which the system may transit along the different outcomes as the parameter varies. This is illustrated at some locations in the diagram. At (A) a transition between (+ +) and (+ -) happens by gradually increasing parameter K_1 , and vice versa. At (B) the system might be either on the upper branch, at a (- +), or the lower, at a (+ -), transitions between the two situations may occur if the population densities change, so that they move between domains of attraction; note that this happens at a constant K_1 value, i.e., same environment. An equivalent situation occurs at point (C) between an exclusion of species 2, species 1 at carrying capacity, i.e., $(K_1,0)$, and



Figure 3: A typical bifurcation diagram for the *IF* model. Equilibrium density for species $1,N_1^*$, vs. its carrying capacity, K_1 ; other parameters constant. Equilibrium densities for species $2, N_2^*$, vary according to the model dynamics (not shown). Solid dark (upper and lower branches) contain stable N_1^* , intermediate dark dashed line contain unstable N_1^* . Straight light dashed lines define sections for the type of interaction (see text and figure 2).

a (+ –). The transition at (D) shows a catastrophic event, a typical hysteresis performance that occurs at a turning point: say that the system is at the upper branch in the (– +) region, then K_1 starts decreasing gradually and so follows N_1^* ; when the border of the branch ends (the turning point) the system drops to the stable equilibrium in the lower branch. Thus, the system undergoes an abrupt decrease in the N_1^* equilibrium density due to a minute variation of the K_1 parameter. This is called a cusp catastrophe (Thom, 1972; Zeeman, 1977).

We gather then, according to the model, that there are two basic modes of transitions in the outcomes of interactions: (i) gradual, smooth, driven by monotonic variation of parameters, that is, by changes in the environment that induce changes on intrinsic properties of the interactions (sensitivi-



ties in the effect of one species on the other, saturation values, etc.); and (ii) abrupt, driven by drastic changes in (relative) densities, between alternative stable states, that is, they occur under the same environmental conditions. The catastrophic jumps are threshold situations, sort of midway between the two modes because they are abrupt, between alternative stable states, however, they are triggered by a (minute) change in a parameter. So, voila! a mechanism for the variation in the outcomes of conditional interactions has been described.

An appealing speculation on lobsters and whelks

As a speculative reflection, note that the diagram in figure 3 suggests a possible explanation for the lobsters and whelks case in South Africa (mentioned above). Say the situation in Malgas Island corresponds to coexistence at point C, where the interaction is (+ -), that is, whelks (N_1) are the prey of lobsters (N_2) ; and, as reported, this was also the original situation for Marcus Island. Then, a huge (but temporary) perturbation extinguished all lobsters at Marcus, taking the system to the upper branch, at $(K_1, 0)$, i.e., whelks reach their carrying capacity after the removal of their main predators. The attempted reintroduction of lobsters failed because the relative densities were not enough to bring the system to the lower branch again. This could also be visualized as a catastrophic jump at the turning point at the right end of the lower branch.

Are there bifurcations and catastrophes everywhere?

The phenomenon of hysteresis is receiving particular attention in recent years in the field of ecological studies, in particular, as very small variations in the environment can cause drastic changes in the systems, is a matter of great interest in subjects related to climatic changes. One of the most relevant (worrying) issues in a hysteretic regime is that once a catastrophic jump has occurred, reversing the conditions that caused it does not ensure going back to the same place, it has to go all the way along the curve and jump again at next turning point. Therefore, it is crucial to determine if the occurrence of a drastic change in a system is due to the presence of a hysteresis phenomenon, or is just a response to some drastic environmental change; it is also fundamental to have the possibility of interpreting early signals to anticipate critical situations (Scheffer and Carpenter, 2003; Schröder et al., 2005; Dakos et al., 2015).

AN *IF* MODEL FOR MYCORRHIZAE – A FORE-TASTE

One of the population associations that has shed more light into the understanding of conditional interactions is mutualism (cooperation, facilitation). This is because the more one looks into the mutualistic natural situations the more one gets the idea that the balance of costs and benefits involved for the mutualistic species is not always positive, rather, it very easily shifts towards the antagonistic sides, for either species.

As mentioned above, mycorrhizae are associations of fungal species attached to the roots of plants. Traditionally, this interaction has been classified as mutualistic due to the mu-



Figure 4: Experimental results and fitted curve, of the net benefit received by plants with mycorrhizae as a function of their density (modified from Gange and Ayres, 1999).

tual exchange of nutrients between species; however, the net balance of benefits and costs can be negative for the plant in fertile soils and/or at high fungi densities, in which case the fungus becomes a parasite (exploiter) of the plant.

I want to introduce here a succinct preview of an Interaction Function model for mycorrhizas (not out yet, coming soon, with an appealing evolutionary twist) mainly to raise two particular issues: experimental data used as an input for the costs-benefits interaction function, and the case where no alternative stable states are possible.

Gange and Ayres (1999), with experimental data from Gange and Nice (1997), estimated the net 'benefits' (their marks, meaning that it is the net balance after taking out costs) that the plant receives at different densities of fungal colonization; they fit a second-order polynomial curve (see figure 4). Their results indicate that at high fungus densities the net effect to the plant becomes negative; that is, the costs outweigh the gross benefits.

The function fitted to the data is a parabola and represents the density-dependent effect of the fungus on the plant, i.e., it provides an explicit formulation for the fungus interaction function, α_{21} , for a model in equation (2),

$$\alpha_{21}(N_1) = b_2 N_1 - c_2 N_1^2 \tag{4}$$

where N_1 and N_2 represent the fungus and plant abundances, respectively, b_2 and c_2 are parameters that shape the curve. On the other hand, I can assume that the net effect of the plant on the fungus is always positive, with saturation, thus, we can use the hyperbolic benefits curve shown in figure 1(a) for the plant interaction function, α_{12} ,

$$\alpha_{12}(N_2) = \frac{b_1 N_2}{1 + c_1 N_2} \tag{5}$$

where b_1 and c_1 are the shape parameters. Introducing these formulations in model (2) we get,

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} + \left(\frac{b_1 N_2}{1 + c_1 N_2} \right) \frac{N_2}{K_1} \right]$$
$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} + \left(b_2 N_1 - c_2 N_1^2 \right) \frac{N_1}{K_2} \right]$$
(6)

Figure 5 shows some representative patterns of the graphical stability analysis obtained for model (6). In figure 5(a) the parameters are such that the outcome of the interaction, at stable coexistence (crossing of nullclines), is mutualistic, i.e. both equilibrium densities N_1^* and N_2^* , are greater than their corresponding carrying capacities, K_1 and K_2 , meaning that each species causes a positive effect on the population growth on the other. Figure 5(b) shows a transit to a parasitism (fungus as exploiter) when parameters of the interaction functions, α_{12} or α_{21} , are varied; this may be caused by intrinsic changes in the way each species has effects on the other, e.g. sensitivity, or saturation values, caused, in turn, by variations in some biotic or abiotic environmental conditions. Figure 5(c) shows a transition to parasitism when the carrying capacity of the plant, K_2 , is higher. This may illustrate the situation of a fertile soil for the plant, that is, the plant on its own would reach a higher equilibrium density than in association; the help of the fungus is not needed, on the contrary, depletes the plant's performance.

The fungus nullcline has no hump

It is important to comment here significant differences between the nullclines in figure 2 and those in figure 5. Specifically, observe that the nullcline for the fungus in figure 5 is not closed, it has no hump shape. This is because the fungus always receives benefits from the plant, that is, the interaction function α_{12} (equation 5), although non-linear, is always positive. Also note that, looking at the patterns in figure 5, the fungus nullcline will never go to the (+ –) quadrant (which would mean that the plant is the exploiter), it just moves along the quadrants on the right hand side (fungus always wins). And a relevant consequence in this case is that there are no multiple stable equilibria situations. That is, there are no abrupt or catastrophic transitions between outcomes, only gradual.

FRAGMENTATION OF SPACE TRIGGERS SOURCE-SINK DYNAMICS – AND FURTHER VARIATION IN THE OUTCOMES

Now I want to introduce the effects of spatial heterogeneity, that is, the dynamics of conditional outcomes when the interacting species are allowed to disperse along patches. This is done in a two-patch model of explicit local dynamics, using the general Interaction Function model (2), with linear $\alpha_{ij}(N_i, N_j)$ in both equations, performing within each patch. Dispersal between patches is included in the model through parameters γ_i and δ_i , which are fractions of the respective population densities. The model for two species i, j = 1, 2becomes,

$$\frac{dN_i}{dt} = r_i N_i \left[1 - \frac{N_i}{K_i} + (b_i - c_i N_j) \frac{N_j}{K_i} \right] - \gamma_i N_i + \delta_i M_i$$
$$\frac{dM_i}{dt} = s_i M_i \left[1 - \frac{M_i}{L_i} + (g_i - h_i M_j) \frac{M_j}{L_i} \right] - \delta_i M_i + \gamma_i N_i \quad (7)$$

The first equation in (7) represents the local dynamics in patch 1, with population densities N_1 and N_2 ; the second equation represents the local dynamics in patch 2, with the same two species, densities M_1 and M_2 . Parameter γ_i , i = 1, 2, represents the (constant) fraction of species 1 or

species 2 that migrates from patch 1 to patch 2; parameter δ_i , i = 1, 2, the fraction from patch 2 to patch 1, accordingly. The rest of the parameters denote the pairwise interaction performances and general environmental conditions, for each patch (as defined in sections above).

A variety of different situations can be explored: patches with same or different environments, single or multiple solutions before migration starts, in different outcome regimes, in coexistence or exclusion, and all combinations of these. Figures 6 and 7 display two particular cases on phase plane graphs.

The main result gathered from the spatial *IF* model (7) is that the fragmentation of space (spatial heterogeneity) with migrations between patches, do promote further variations in, first, the outcome of interactions, both at the regional and local scales; and second, in the number of stable solutions (produced by bifurcations or annihilations of equilibria). Significant trends in these dynamics can be summarized after exploring several different situations (Hernandez, 2008):

(i) The variation in the outcome for a given species is favourable when migrations (emigration, immigration, or both) imply a proportional increase in individuals of that species within the patch. Thus, a victim can become a mutualist or an exploiter, an excluded species can invade, and a good competitor can exceed its own carrying capacity. And of course, vice versa, dispersal is detrimental for a species when it involves a proportional decrease in its local density. This I labelled as the '*enhancement effect of dispersal*'.

(ii) Regardless of which species migrates, bifurcations of equilibrium points occur in the patches that receive the migrations, and annihilations occur in the patches that provide the migrations. Thus, the number of equilibrium solutions, at each patch, increase or decrease correspondingly, when dispersal of individuals is allowed. In addition, the bifurcations and annihilations of equilibria only occur within a range of intermediate migration rates, that is, they do not occur if the rates are very low or very high. Similar results of this phenomenon are in Gyllenberg and Hanski, 1992; Hanski and Zhang, 1993; Hanski et al., 1995; Shurin et al., 2004.

Sources or sinks? – whatever, they also shift and swing

The results of the *IF* models acknowledge that both positive and negative density dependence processes drive the dynamics of interactions with variable outcomes, depending on density ranges; and these occur at both local and regional dynamics, adding up with reinforcing or contrasting effects. Source-sink dynamics is the appropriate framework for discussion of these issues, and provides fascinating inferences and insights. Some hints: Although in the model migration is considered density-independent (i.e., migration rates are constant) there are density-dependent effects associated with dispersion *per se* (Amarasekare and Nisbet, 2001; Amarasekare, 2004). For sink populations with low local abundance, it is beneficial to receive individuals because it increases their growth rates (*rescue effect*); however, this represents costs for the source populations, due to the loss





Figure 5: Graphical stability analysis of the *IF* model for a mycorrhiza association: fungus (species 1), plant (species 2), nullclines for fungus (light line) and plants (dark line), for given sets of parameters, stable equilibria at crossing nullclines (dark dot), outcomes of the interactions shown in quadrants defined by carrying capacities, K_1 and K_2 , (a) mutualism, (b) transit to parasitism (lower b_1 or b_2 , or higher c_1 or c_2), (c) transit to parasitism (higher K_2).



Figure 6: Effect of migration on outcome of interaction between species 1 (*sp1*) and species 2 (*sp2*) from patch 1 (P1) to patch 2 (P2); quadrants at carrying capacities define outcome of interaction (see figure 2); stable equilibria (black dots), unstable equilibria (white dots), (a) In isolated patches: single stable solutions; in P1: victim-exploiter; in P2: *sp1* excluded, *sp2* at carrying capacity, (b) Migration of *sp2* from P1 to P2 causes variations in outcomes; in P1: to mutualism; in P2: still exclusion of *sp1*, but *sp2* reaches equilibrium density higher than carrying capacity (modified from Hernandez, 2008).



Figure 7: As in figure 6, but effect on multiple stable states situation (a) In isolated patches: alternative stable states; in P1: both victim-exploiter situations, but with role reversal; in P2: one exclusion-carrying capacity situation, and one victim-exploiter, (b) Migration of *sp2* from P2 to P1 causes variation; in P1: number of equilibria increase (clouds of points), each original stable solution bifurcates, top: into one exclusion, one victim-exploiter, lower: into two victim-exploiter; in P2: *sp1* invades where it was excluded, in competition with *sp2*, lower: still victim-exploiter (modified from Hernandez, 2008).



Figure 8: Metacommunitarian setting of the experiments; example of three communities with ten species per community (from Griffon and Hernandez, 2019).

of reproductive individuals. Then, at the regional level, dispersion incorporates cost-benefit relationships on growth rates, which can reinforce or counteract the cost-benefit balance that occurs at the local level. Therefore, the model shows not only the dynamics of variation of outcomes in the interactions (in the roles of victim, exploiter, mutualist, etc.), but also, that the roles of source or sink of the populations are dynamic and may vary at the regional level. Finally, just as environmental parameters at the local level can cause catastrophic jumps between outcomes in the interaction, the spatial model predicts that migrations promote jumps between outcomes at the regional level, which may or may not act in accordance with the local effects. More discussion on this in Hernandez (2008) and at a wider revision on density-dependence and spatial heterogeneity in Hernandez (2015).

A round-up finale, so far. In the context of variable or conditional population interactions, the concept of the *role of a species* does not make sense on its own; rather, it becomes a *spatiotemporal dynamic quality*.

THE SPATIAL *IF* MODEL, THE ECOLOGICAL NETWORK AND THE AGROECOSYSTEM

The spatial *IF* model (7) has been used as a framework to explore the dynamics of networks of ecological interactions. I briefly present here two particular cases: randomly constructed networks and real networks associated to specific agroecosystems (complete studies in Griffon and Hernandez, 2014, 2019; Griffon and Rodríguez, 2017).

The random ecological networks include all possible types of interactions (+, -, 0,and conditional outcomes); the proportions of each are defined by a random process. The systems were evaluated at community and metacommunity levels (3 to 80 nodes, 1 to 3 networks); see figure 8.

The model used for the community dynamics (Lotka-Volterra) included interaction functions $\alpha_{ij}(N_i, N_j)$ in the equations, *sensu IF* models. The dynamics were numerically explored, with different initial proportions of all interactions, until extinction or persistence of the networks. The experiments show a vast number of extinctions (after just



Figure 9: Ecological networks and population dynamics in (a) Monoculture and (b) Conuco, with fixed interactions; (c) Monoculture and (d) Conuco, with conditional interactions.
Colours in network links represent different types of interaction: victim-exploiter (red), competition (yellow), mutualism (dark blue), amensalism (pink), commensalism (light blue), conditional interaction (purple). Colours in the dynamics represent densities of different species (from Griffon and Hernandez, 2014; Griffon and Rodríguez, 2017).

a few iterations), and the persistent communities present low percentages of surviving species. The most notable results are that spatial heterogeneity significatively reduces species loss; that persistent communities show an increase in the proportion of positive and nonreciprocal interactions (commensalism and amensalism) with respect to the initial network, and that the systems are locally stable (Griffon and Hernandez, 2019).

The real ecological networks associated to agroecosystems were constructed to study relevant properties that may lead in the decision making of agricultural practices, and obtain practical clues for farmers. Two particular agroecosystems were studied: a corn monoculture and a multi-species ancestral crop system (Conuco); the latter presents a greater number of interactions and interaction types. The LV equations included either fixed α_{ij} values, or interaction functions $\alpha_{ii}(N_i, N_i)$, so that systems without and with conditional interactions were explored. The numerical simulations were performed with parameters taken from field data and (experienced) knowledge of local farmers (Griffon and Hernandez, 2014; Griffon and Rodríguez, 2017). The typical longterm dynamics obtained for each topology are displayed in Figure 9. The fix interactions situations (figures 9a and 9b) show non-persistent dynamics, and so does the monoculture network topology with conditional interactions (figure 9c); whereas the Conuco system shows persistent dynamics in all cases (figure 9d).

One crucial result is that the presence of conditional interactions generates persistence (in the Conuco system). However, it was also found that spatial heterogeneity and dispersal (the metacommunity) increases the probability of persistence (rescue effect). As a matter of fact, in some cases the persis-



tence is only ensured if there are several ecosystems connected; this situation points to the necessity of the coordinated participation of more than one farm in the implementation of ecological management programs (e.g., pest control), which involves additional social human issues to consider.

Metaphorically speaking

The ecological network model with conditional outcomes was also used to investigate the dynamics of the transitions between the monoculture and the agroecological (Conuco) systems (Griffon et al., 2021). This was performed by modifying the architecture of the networks (increase / decrease the number of interactions) along the transitions. One interesting result is that the topological features that confer persistence to the agroecological (multi-species) system, prevail even when the number of interactions are considerably reduced; not so in the networks generated from the monoculture. In general, the resulting paths to transit from one system to the other, or the reverse, bring to mind the graphic representation of a cusp catastrophe surface (similar in shape to figure 3), in which divergent trajectories can lead to alternative states (the monoculture and the agroecological systems) and can shift from one to the other abruptly (catastrophe) or smoothly (along the surface). This metaphorical representation reduces the complexity of the system and facilitates its interpretation, i.e., we can study the action of the Lotka-Volterra dynamics on the system (which is the ultimate responsible for any outcome, but has too many parameters to look at) by exploring the general patterns that emerge from large-scale properties that can be grasped more easily.

When looking at the results of the long-term persistent dynamics, with interactions that end up sometimes with stationary values, some other times oscillatory, but that were all generated from conditional interaction functions $\alpha_{ij}(N_i, N_j)$, one cannot avoid thinking that all interactions in nature, no matter how rigid they seem, are intrinsically variable.

WRAPPING UP - MODELS FROM AND FOR EVERYONE – TAKE YOUR PICK

There are extensive reviews in the literature on a variety of topics on population interactions: about categorizations; about the classic pillars competition and predation, and lately, mutualism, being promoted to a third pillar; and about many other related issues, you name it. In this paper I deal with the particular topic of population interactions with conditional outcomes, or context-dependent interactions, but I do not intend to provide a full revision on the subject. Rather I aim to address very specific issues using the framework of the Interaction Function (*IF*) model; and with this set a ground to comment on other related works and insights, and hopefully induce some debate of ideas in the minds of those reading this.

It is undeniable the impact of the Lotka-Volterra model in setting the basic principles for the study of the dynamics of population interactions. I find that one of the most relevant features is that it sets a link between scales and levels, that is, the quantification of the effects of individual features that may or may not have impact at the population level, all the *per capitas*. From this, models have expanded in many directions: to the community level, where they meet the ecological networks approach; to evolutionary issues, where fitness finds a proxy in terms of population growth rates; to spatial issues and the metacommunity level, where migrations make all the difference; and all these go from the in-depth mathematical studies, with all the dancing of variables, corollaries and parameter thresholds, to the downto-earth application of results to very specific ecological problems.

Along the narrative of this paper I have dropped references, here and there, when writing about specific issues; now I want to comment on some other references to complement on knowledge and viewpoints. I must add here a very personal worry (which has been addressed lately by other authors, though). Sometimes the access to the scientific production of papers is biased to only some regions of the world and some languages; I am aware that there is a huge production going on in the other regions and the other languages, but (for reasons I will not debate here) there is very limited access to that and, therefore, no cross-references from other papers. I honestly would have loved to find and discuss here those papers with top scientific standard contents and original ideas, but which have received no citations due to limited access to them. Thus, I already apologize if this bias is also present in the set of works discussed here.

The fundamental results occur because the nonlinear term can shift in sign - maths talking

I want to single out the central results drawn from the Interaction Function (*IF*) model on the dynamics of conditional interactions, explored along the previous sections, and proceed from there,

1. The model presents either unique or multiple stable equilibria (alternative stable states) where species may coexist at any combination of interaction outcomes: (+ +), (--), (+-), (- +), and corresponding neutrals, or one species may be excluded, the other at its carrying capacity, or both may be excluded; for given sets of densities and parameters.

2. Transitions between interaction outcomes can occur in two modes: (i) by variation of the parameters, which reflect intrinsic features of the interaction itself and/or extrinsic general environmental conditions; (ii) by the variation of population densities, which brings the system to a different domain of attraction (in the multiple stable equilibria situation). The transitions may occur gradually or abruptly (including cusp catastrophes).

3. When spatial heterogeneity and migrations are included, negative and positive density-dependent processes, at local and regional levels, act in reinforcing or contrasting manner, causing further variation in the outcomes of the interactions and, more importantly, inducing the populations to perform as sources or sinks, and this occurs in a dynamical fashion, that is, the source and sink roles also shift in a conditional, context dependent, manner.

A crucial statement comes out from results 1 and 2 – and 3 follows

The key factor responsible for the performance described in the results is the specific nonlinearity introduced in the interspecific term of the model, that is, the effect of one species on the *per capita* growth of the other is a density-dependent function that can take values along the negative-positive continuum. This is the attribute that produces the humped, closed crossing both axes, shapes of the nullclines (the hump occurs at the change in sign of the function), which in turn produce the equilibria patterns observed, and hence, the results mentioned above.

As commented previously, the *IF* model produces these same patterns and results for any formulation of the interaction function $\alpha_{ij}(N_i, N_j)$, as long as it takes positive and negative values as density varies (details in Hernandez, 1998; Hernandez and Barradas, 2003). In contrast, but reinforcing the argument, the always positive α_{ij} interaction function in the model for mycorrhizas depicted above produces an open nullcline, with no humps, crossing only N_1 -axis, which excludes the possibility of multiple stable equilibria (gradual transitions between outcomes can occur, though).

Hence, these results are of a mathematical (almost geometrical) nature. And this is a precious value of the theoretical work, it can lead to features not easily observed otherwise. However, it is imperative now to look into the way the functional forms were originally conceived, the biological facts that prompt them, and then, we get ecological relevant information. Maths is not alone.

Maths talks but ecology matters

In the case of the *IF* model the reason behind the formulation of the interaction function is related to the forms of the costs and benefits involved in the association. For instance, it is biologically sound to consider that both benefits and costs for each species grow with the partner's density up to a saturation level; or other forms can be explored, also sound. Thus, one way or the other this provides the mechanism that promotes the behaviours observed.

Therefore, it is interesting to look into other models that ended up with the same results as the *IF* model but starting from different ecological principles. This is the case, for instance, of the consumer-resource model, which was also developed to study the dynamics of transitions between outcomes of conditional interactions, and arrived at the same results, 1 and 2, stated above (Holland and DeAngelis, 2009, 2010). The model (also based on Lotka-Volterra dynamics) considers that each species in a bi-directional interaction acts as both a consumer and resource of the other. This is included in the interspecific term of the population growth equations, for each species, as the sum of two density-dependent, saturating, functional responses (inspired by classical predator-prey models). For some parameters this sum takes values in the positive to negative continuum, hence, the model reaches the same central results (1 and 2) as the *IF* model. No surprise at all there; however, the valuable fact is that the model provides a different ecological route or mechanism to understand the dynamics of conditional interactions. And no doubt, there will be more to come.

General revisions on population interactions with conditional outcomes are abundant, some with an empirical approach, some that include models (e.g., Bronstein, 1994; Chamberlain et al., 2014; Messan-Rodriguez et al., 2018; Song et al., 2020); many are focused on the mutualismantagonism situation, which also sheds light on the broader topic (e.g., Herre et al., 1999; Hale and Valdovinos, 2021; Zhang et al., 2020), or on particular biological systems that present variable outcomes (e.g. Agrawal et al., 2007; Baraza et al., 2006; Norkko et al., 2006; Lee et al., 2009; Hoeksema and Bruna, 2015).

A large body of work on the dynamics of interactions with conditional outcome focus on further rigorous theoretical analyses of these strongly nonlinear systems. In-depth mathematical analyses provides additional knowledge into mechanisms, patterns, predictions, etc., see e.g. González-Guzmán (2006); Graves et al. (2006); Lara and Rebaza (2012). Messan-Rodriguez et al. (2018) develop a model to investigate the dynamics of bi-directional resource exchange between two local ecosystems in a metaecosystem framework; they show that the outcomes of the interactions and the persistence of the ecosystems depend on the relative cost and benefit of resource exchange. They perform a thorough mathematically oriented analysis (bifurcation analysis), but always keeping in mind the biological meaning of their results and conclusions. This article provides an excellent vast and explanatory account of models on the dynamics of pairwise conditional interactions in the literature.

In the mutualism-antagonism spectrum there are abundant models, especially in the past years. Hale and Valdovinos (2021) provide a constructive review on many of these models, with a historical approach, and categorize them according to specific features (e.g., mechanisms, assumptions, predictions); Hale et al. (2020) developed a general model for mutualism under the assumption that costs associated with rewards are negligible at the population level (or can otherwise be accounted for in parameter values). This provides a proper framework to study mutualism in cases where these conditions apply. Thompson et al. (2006) find that immigration and emigration of mutualistic partners have different effects on the interaction outcomes if the effects of the mutualism acts differently on the demographic rates (reproduction and mortality) of the populations.

Revilla and Encinas-Viso (2015) study transitions between mutualism and antagonism in the herbivory-pollination situation with a phenological approach; different stages of the insect life cycle have effect on different parts of the plant, that is, adult insects interact with flowers in a mutualistic way (pollination), but larvae consume the leaves, acting as



exploiters (herbivory). Thus, the balance of costs and benefits come from consumer-resource dynamics. They build a model of ordinary differential equations for the growth rates of plants, flowers, adult insects, and larvae, which include intra- and inter-specific terms, the latter as saturating functional responses. The synchrony of events and the rates of development along the insect life cycle are determinant on the outcome of the interaction, e.g. time spent as antagonist (larva) with respect as mutualist (adult). They discuss the external drives that may cause changes in the insect life cycle (temperature, plant nutrients, pesticides) hence acting on the balance between mutualism and antagonism. Models on evolutionary issues in Revilla and Křivan (2018); Křivan and Revilla (2019), complement these ideas. This approach to modelling might be appropriate to study the switch situations described in the case (ii) in the second section above.

Zhang (2003) develops a model to study interactions that go from competition to mutualism between low and high population densities, which promotes coexistence; Zhang et al. (2007), following the *IF* model and Zhang (2003), study stability properties of transitions between outcomes, very mathematically oriented. Zhang et al. (2020), study the role of mutualism between antagonists in regulating ecological and evolutionary processes, density-dependent transition between mutualism and antagonism which should be favoured by natural selection (in a coevolutionary process), includes also an extensive review of other models and empirical work on rodents.

Some models study particular biological systems with variable interaction outcomes, using the LV model, or IF model approach. Neuhauser and Fargione (2004) model the mycorrhiza-plant interaction; the outcome between mutualism and parasitism is defined by population densities and environmental conditions. Sánchez-Garduño et al. (2014) build a mathematical model, based on a LV model, to study the main phenomenological features of the case of role reversal in the predator-prey interaction between whelks and lobsters in South Africa (mentioned above); they present results for both the temporal and spatiotemporal cases. Momo et al. (2006) modelled the dynamics of a marine plankton community to study the effect of UVB radiation on the community. They used four coupled ODE's of population growth rates and experimental data. Among other results, they found that if UVBR decreases predation all population abundances change and the community is driven to a new equilibrium. If nutrients supply is very large an indirect interaction of apparent competition emerges in the community, if there is an increase in the common predator population, whereas in conditions of nutrient depletion an apparent mutualistic interaction is expected. This provides an interesting situation of conditional apparent interactions.

I already commented, in section 5 above, on the series of papers by Griffon and Hernandez (2014, 2019); Griffon and Rodríguez (2017); Griffon et al. (2021), in which the spatial *IF* model is used to build ecological networks aiming to find results that can be applied in the agroecological field. I want to comment on two works that share two separate lines with the Griffon et al., papers: one theoretical, related to the

model development; the other applied, in the agroecological field.

Regarding the development of ecological networks, Yan and Zhang (2014) developed a model which share the structure and approach of Griffon and Hernandez (2014), that is, based on *LV* equations for many species, build ecological networks that include all types of interactions, with the possibility of changing sign, i.e., variable outcomes (the difference in the formulations is that Griffon and Hernandez use difference equations whereas Yan and Zhang use differential equations, also they do not do spatial analysis). The relevant issue is that Yan and Zhang (2014) also found that the persistence of complex networks is highly influenced by interactions that can shift sign; according to their results, the persistence increases or decreases depending on shifts occurring from positive, or to negative, or neutral, and at given density ranges.

With respect to applications on the agroecological field, the work of Bageta et al. (2018) studies the interaction between vine (*Vitis vinifera* L.) and cover crop, using a model also based on the *IF* model. They first explore the interactions with field experiments, and use these data to feed the model. They conclude that the interactions between the vine plant and the cover crop can shift between commensalism and amensalism, which means that the cover crop does not have a detrimental effect on vine growth.

What if theoretical interpretations do not feel natural

When, from a theoretical stand, we are trying to interpret and represent an observation of nature, we should aim for consistency. In the topic of the characterisation of interaction outcomes there are theoretical discrepancies (among them, and with natural observations), and as usually happens, all sides pose their arguments and proofs. In particular, I want to comment on the use of the jacobians of the community matrix to characterise population interactions (see Appendices A and B for some details, and Hernandez, 2009, for thorough elaboration and discussion). The rationale behind the use of the jacobians comes in terms of the responses of interacting populations to small perturbations at equilibrium, e.g., if a small increment in the equilibrium density of one species causes an increase in the other's, then the outcome is considered as beneficial (from the former to the latter), and so on for all combinations (increases and decreases, actions and responses). These are interpreted as representing the general effects of one species on the other, hence, pairs of responses end up categorising the interactions as mutualism, competition, victim-exploiter, etc. However, when applied to some models (see e.g., Zhang, 2003; Neuhauser and Fargione, 2004; Zhang et al., 2007, 2020; Lara and Rebaza, 2012), sometimes the results show, for instance, a victim-exploiter outcome assigned to a situation in which both populations reach higher densities than their corresponding carrying capacities. According to the rationale used along this article, this situation should correspond to a mutualism because both populations show a better performance in association than they would alone. As discussed in Appendix B and Hernandez (2009), the jacobians evaluate shifts between

stability modes (nodes and focus) in the dynamics near equilibrium, not shifts in the outcomes of interactions (sometimes they coincide, mathematically).

Having said this, the question is, is it ecologically appropriate to consider an interaction as victim-exploiter when it is observed that the two populations reach higher densities in association than alone? I say no, they should be characterised as mutualists. The debate, however, has more angles and edges. I personally consider that theoretical frameworks should be consistent and formally correct because they are meant to provide the guidelines to explore and understand the natural world. However, I also acknowledge that sometimes the empirical realities are far from the theoretical conditions. For instance, not always (to say the least) we can tell if a real system is at, or even close to, a stable equilibrium, or we do not know, neither have the means to measure, the carrying capacities, or maybe to know about those small effects after perturbations is what we need for a management program; and so on. All these considerations have a proper place in the discussion. Nonetheless, my stand is that theoretical research must be pristine, although some rough corners and dirty shoes will have to be agreed for the field setting.

After maths and after thoughts

What have we learned? ... have we?

Nature is ambiguous, variation is the rule, diversity is the rule. The ineffable nature of nature.

Scientists do not make the rules, they just try to understand; some for the sake of curiosity, the nature of humans, others to take control, the nature of humans. The human condition.

Labels and structures are deeply embedded in the minds. That's what we think we need to do to understand. Maybe, as understanding makes its way through, we will learn to perceive the lines more than the dots; hopefully in our way to transcending the lines too.

A monk asked Fuketsu: 'Without speaking, without silence, how can you express the truth?'. Fuketsu observed: 'I always remember springtime in southern China. The birds sing among innumerable kinds of fragrant flowers'.

- Mumon Ekai (1228) The Gateless Gate

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APPENDIX A. THE LOTKA–VOLTERRA MO-DEL AND LEVIN'S COMMUNITY MATRIX

(Excerpts from Hernandez, 2009)

The dynamics of two interacting populations with densities N_1 and N_2 can be modelled by the system

$$\frac{dN_i}{dt} = F_i(N_i, N_j) \equiv N_i f_i(N_i, N_j) \quad i, j = 1, 2$$
(A.1)

 F_i is the total population growth rate of species *i*, and f_i the *per capita* growth rate, as a function of population abundances. When $dN_1/dt = dN_2/dt = 0$, the system is at equilibrium $N^* = (N_1^*, N_2^*)$.

The generalised Lotka–Volterra model expresses the *per* capita growth rates of each interacting species as linear functions of the densities of other species (see e.g., Case, 2000). For a community of n interacting species the model can be written as

$$\frac{dN_i}{dt} = N_i \left(r_i + \sum_{j=1}^n a_{ij} N_j \right) \quad i, j = 1, 2$$
 (A.2)

where r_i and a_{ij} are constant parameters; r_i is the intrinsic growth rate of species *i* and the a_{ij} are interaction coefficients that express the effect of a species *j* on a species *i*. For an equivalent model,Levins (1968) defined the *community matrix* **A** as the square matrix containing all a_{ij} coefficients. The signs of a_{ij} and a_{ji} pairs denote the type of interaction between species *i* and *j*: both signs equal for competitors, opposite signs for predator–prey (Levins, 1968).

For a two-species system the *per capita* expression of model (A.2), in matrix form, is

$$\begin{pmatrix} \frac{1}{N_1} \frac{dN_1}{dt} \\ \frac{1}{N_2} \frac{dN_2}{dt} \end{pmatrix} = \begin{pmatrix} r_1 \\ r_2 \end{pmatrix} + \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \end{pmatrix}$$
(A.3)

which shows clearly the 2-by-2 *community matrix* A of elements a_{ij} .

A generic Lotka–Volterra (LV) model for two interacting populations, with explicit carrying capacities K_i , is commonly written as

$$\frac{dN_i}{dt} = N_i r_i \left(1 + \alpha_{ii} \frac{N_i}{K_i} + \alpha_{ij} \frac{N_j}{K_i} \right) \quad i, j = 1, 2$$
 (A.4)



where α_{ii} is the intraspecific interaction coefficient (usually considered = -1, for linear intraspecific competition), and α_{ij} is the interaction coefficient between the two populations; the interactions are facultative for both populations, they reach carrying capacity K_i in the absence of species *j*.

Interaction coefficients α_{ij} play a crucial role in the representation and categorization of the types of interactions involved in the system. In plain terms it expresses how an individual of one species experiences the presence of the other species, both in strength (magnitude) and regarding its beneficial or detrimental nature (positive or negative); it accounts for how much one individual is worth in terms of an individual of the other species. Thus, it is a parameter related to the individual level that has an effect on the population level, that is, on the *per capita* (and hence, on the total) population growth of the other species.

If interaction coefficients α_{ij} are constant, model (A.4) allows for linear representations of the dynamics of all basic population interactions. The positive or negative effect of one population on the growth rate of the other is defined by the signs of α_{12} and α_{21} coefficients: both positive, or both negative, for mutualism and competition, respectively; one positive and one negative for a victim–exploiter (consumer–resource) interaction; for commensalism and amensalism, one coefficient is null and the other positive or negative, respectively.

In matrix notation, model (A.4) can be written as

$$\begin{pmatrix} \frac{1}{N_1} \frac{dN_1}{dt} \\ \frac{1}{N_2} \frac{dN_2}{dt} \end{pmatrix} = \begin{pmatrix} r_1 \\ r_2 \end{pmatrix} + \begin{pmatrix} \alpha_{11} \frac{r_1}{K_1} & \alpha_{12} \frac{r_1}{K_1} \\ \alpha_{21} \frac{r_2}{K_2} & \alpha_{22} \frac{r_2}{K_2} \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \end{pmatrix}$$
(A.5)

which shows clearly that elements $\alpha_{ij}r_i/K_i$ correspond to the interaction coefficients a_{ij} in (A.3); thus, Levins' *community matrix* **A** (A.3) for the generic *LV* model (A.4) is

$$A = \begin{pmatrix} \alpha_{11} \frac{r_1}{K_1} & \alpha_{12} \frac{r_1}{K_1} \\ \alpha_{21} \frac{r_2}{K_2} & \alpha_{22} \frac{r_2}{K_2} \end{pmatrix}$$
(A.6)

Therefore, according to the Levins' *community matrix* approach, the signs of the α_{ij} coefficients in model (A.4) uniquely determine the nature of the interactions, as expected. That is, the sign patterns of pairs ($\alpha_{21} \alpha_{12}$), written as (+ +), (--), (+-), (+ 0), (- 0), (0 0), correspond to mutualism, competition, victim–exploiter, commensalism, amensalism and neutral, respectively.

APPENDIX B. ON THE (DEBATED) APPROACH TO DEFINE THE NATURE OF POPULATION IN-TERACTIONS

(Abridged from Hernandez, 2009)

In the literature we find a variety of criteria on the appropriate way to cathegorize the *types* of interactions between populations (see e.g. Berlow et al., 1999, 2004); the term *type* may refer to the *strength* (magnitude), to the *nature* (beneficial or detrimental), or both. In this Appendix I discuss some formalities on the appropriate caracterisation of the *nature* of population interactions, with emphasis on the appopriateness of different approaches. I will be referring to some expressions of Appendix A above.

The relative performance approach

A widely common approach to characterise types of interaction is by comparing its performance alone with that in association (e.g. May, 1981; Berlow et al., 1999, 2004; Thompson et al., 2006; Holland and DeAngelis, 2009; Revilla and Encinas-Viso, 2015; Messan-Rodriguez et al., 2018). An interaction is *beneficial* if the population reaches a higher equilibrium density in the presence of the other species than in its absence; if it is lower, the association is considered *detrimental*.

We can quantify this statement using a Lotka-Volterra model as in (A.4) above. If N_i^* is the equilibrium density of species *i* when it grows in association with species *j*, and K_i is the carrying capacity K_i , then the difference $(N_i^* - K_i)$ measures the beneficial or detrimental effect of species *j* on species *i*. This expression divided by the carrying capacity K_i provides an appropriate *per capita* measurement of the intensity and sign of the interaction as experienced by each species. This can be formally expressed as

$$\Delta K_i^* = \frac{N_i^* - K_i}{K_i} \tag{B.1}$$

Hence, the *nature* of the interaction from a comparative or *relative performance approach* is characterised by the signs of

$$\Delta_K^* = \begin{pmatrix} \Delta K_2^* & \Delta K_1^* \end{pmatrix} \tag{B.2}$$

so that, mutualism (+ +) corresponds to $N_2^* > K_2$ and $N_1^* > K_1$, victim-exploiter or consumer-resource (+ -) to $N_2^* > K_2$ and $N_1^* < K_1$, and competition (- -) to $N_2^* < K_2$ and $N_1^* < K_1$. When $N_i^* = K_i$, then $\Delta K_i^* = 0$, thus the interaction is neutral. For obligate interactions it is assumed that $K_i = 0$.

When K_i is not an explicit parameter in the model, the corresponding value can be calculated; it is the magnitude of N_i^* evaluated at $N_j = 0$; that is, the value of N_i that satisfies $F_i(N_i, 0) = 0$ in equation (A.1) above.

For the Lotka-Volterra model (A.4), with linear intraspecific coefficients $\alpha_{ii} = -1$ and $\alpha_{ij}\alpha_{ji} < 1$, the stable equilibrium solutions can be expressed as

$$N_i^* = K_i + \alpha_{ij} N_j^* \tag{B.3}$$

from which is easy to show that (B.1) becomes

$$\Delta K_i^* = \frac{\alpha_{ij} N_j^*}{K_i} \tag{B.4}$$

Thus, the signs of $\Delta_K^* = (\Delta K_2^* \quad \Delta K_1^*)$ in (B.2) are given by the signs of $(\alpha_{21} \ \alpha_{12})$: (+ +) mutualism, (- –) competition, (+ –) or (+ –) victim-exploiter, (+ 0) commensalism, (– 0) amensalism, (0 0) neutral. Therefore, the resulting types of interaction for model (A.4) from the *relative performance* approach, Δ_K^* are consistent with the Levins' *community* matrix A (A.6) above.

The *Interaction Function (IF)* model for the dynamics of interactions with variable outcomes is expressed as (equation 2, in main text)

$$\frac{dN_i}{dt} = N_i r_i \left[1 + \alpha_{ii} \frac{N_i}{K_i} + \alpha_{ij} (N_i, N_j) \frac{N_j}{K_i} \right]$$
(B.5)

where $\alpha_{ij}(N_i, N_j)$ is the interaction function that accounts for the balance of density-dependent costs and benefits involved in the association for species *i*; this function can take values in the negative and positive continuum.

By symmetry with (A.6) we can compute the *community matrix* **A** for the *IF* model as

$$A = \begin{pmatrix} \alpha_{11} \frac{r_1}{K_1} & \alpha_{12} (N_1, N_2) \frac{r_1}{K_1} \\ \alpha_{21} (N_1, N_2) \frac{r_2}{K_2} & \alpha_{22} \frac{r_2}{K_2} \end{pmatrix}$$
(B.6)

That is, as the interaction functions, $\alpha_{ij}(N_i, N_j)$, are density dependent, so is the *community matrix*, $A \equiv A(N_i, N_j)$, and it is clear that the signs of the elements of A evaluated at any (N_i, N_j) are again the signs of the corresponding $\alpha_{ij}(N_i, N_j)$; hence, at equilibrium these correspond to the signs of $(\alpha_{12}^* \alpha_{21}^*)$.

By symmetry with (B.3), the equilibrium solution for the *Interaction Function* model (B.5) is

$$N_{i}^{*} = K_{i} + \alpha_{ij}^{*} \left(N_{i}^{*}, N_{j}^{*} \right) N_{j}^{*}$$
(B.7)

thus, as in (B.4), we get

$$\Delta K_i^* = \frac{\alpha_{ij}^* \left(N_i^*, N_j^* \right) N_j^*}{K_i} \tag{B.8}$$

Therefore, the signs of ΔK_i^* and of α_{ij}^* are always the same, hence, the outcomes from the *relative performance* approach and Levins' (1968) *community matrix* are consistent.

Note that these characterisations also correspond to the graphical representation within quadrants in the N_i , N_j phase plane defined by straight lines drawn at K_i and K_j (see e.g., figure 2, in main text).

The misleading use of the jacobian

The jacobian matrix is the essential tool for stability analysis in the systems examined here. However, sometimes it is also used to categorize types of interactions. This ambivalence in the usage of the jacobians has led to confusion and misconceptions in the characterisation of population interactions. Let's elaborate.

The jacobian matrix *J* for the dynamical system defined in (A.1) is obtained by taking partial derivatives with respect to population densities, that is, a matrix with elements $J_{ij} = \frac{\partial}{\partial N_j} \left(\frac{dN_i}{dt} \right)$, for i, j = 1, 2. This means linearizing the system, thus, if it is evaluated at a given point we can study the dynamics of small perturbations in the neighbourhood of that point. The off-diagonal elements of J^* evaluated at equilibrium, say $(J_{21} J_{12})^*$ or $(J_{21}^* J_{12}^*)$, assess the response of the growth rate of species i to small changes in the density of species j at equilibrium. For instance, a positive J_{21}^* means that a small increment in N_1 at equilibrium causes an increase in the growth rate of species 2, hence N_2 increases, whereas if negative, a small increment in N_1 at equilibrium causes N_2 to decrease. These responses were interpreted as representing the effects of one species on the other, that is, the signs of the $(J_{21} J_{12})^*$ pairs were matched to the types of population interactions: (+ +) for mutualism, (--) for competition, (+-) for predator-prey, etc. In other words, the jacobian matrix was considered as an extension of Levins' community matrix (May, 1973).

On the other hand, the stability properties of these dynamical systems can also be inferred from the jacobian matrix evaluated at equilibrium, in particular, from its eigenvalues. The equilibrium is stable, if and only if the real parts of all the eigenvalues are negative, otherwise it is unstable (or a saddle point). If the eigenvalues have no imaginary parts, the perturbed system moves monotonically to, or away from, equilibria (a node), if the imaginary parts are non-zero, the movement is oscillatory (a focus); also May (1973).

And, this is where metrics collide and disentangling is required. Some evaluations and comparisons can be performed on different systems and get some answers; this was done in Hernandez (2009), I present here a succinct recount.

The jacobians were analytically and numerically evaluated in well-known classical linear and nonlinear models of population interactions (e.g. Lotka–Volterra competition, Rosenzweig–MacArthur predator-prey, etc.). The results show that in all these cases the signs of $(J_{21} J_{12})^*$ are uniquely determined, either positive or negative, and they correspond exactly to the signs of elements $(\alpha_{21}, \alpha_{12})^*$ of the community matrix A (A.6); it is also shown that they correspond to the signs in ΔK_i^* (equation B.2), i.e., to the relative performance approach. Therefore, all types: (+ +), (--), (+-), etc., obtained from the three approaches are coincident in these systems.

The inconsistencies arise when interactions with variable outcome are evaluated. In these models (e.g. IF models in Hernandez 1998, 2008, competition-cooperation model in Zhang, 2003, mutualism-parasitism model in Neuhauser and Fargione, 2004) the signs of $(J_{21} J_{12})^*$ are not univocally determined, they are defined as a subtraction of terms, thus they can take negative or positive values (depending on densities and parameters). The same models were evaluated with the relative performance approach; the results show that the signs of $(\Delta K_2^* \Delta K_1^*)$ also vary for different sets of parameters. The assessment of both sets reveals that in some cases the results from the two approaches agree, in some others they do not. On the other hand, as expected from statements made above, the outcomes from the relative performance approach and those from the community matrix A, do agree, in all cases, that is, signs of $(\Delta K_2^* \Delta K_1^*)$ are always the same as signs of



$(\alpha_{21}, \alpha_{12}).$

The disentangling

When the elements of the jacobian, $(J_{21} J_{12})^*$, are evaluated in models for interactions with variable outcomes, and these present the possibility of different signs for different sets of parameters (as described above), one might be tempted to interpret this as representing the shifts in the outcomes of interactions. It is not so; it is nothing more than shifts between stability modes: from node to focus, or vice versa. This can be analytically proven from the formal expression of the eigenvalues of a 2-by-2 matrix, from which the thresholds between focus and nodes can be easily computed and seen to correspond to the shifts (details in Hernandez, 2009). This can also be easily observed graphically in a phase plane representation (e.g. figure 2 and 5, in main text). The jacobians are the slopes on the nullclines at equilibrium (linearization at equilibria), the shifts in sign correspond to the changes of slopes, hence, changes in the eigenvalue conditions between focus and node.

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