

A SIMPLE AND BOUNDED MODEL OF POPULATION DYNAMICS FOR MUTUALISTIC NETWORKS

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ABSTRACT. Dynamic population models are based on the Verhulst's equation (logistic equation), where the classic Malthusian growth rate is damped by intraspecific competition terms. Mainstream population models for mutualism are modifications of the logistic equation with additional terms to account for the benefits produced by the interspecies interactions. These models have shortcomings as the population divergence under some conditions (May's equations) or a mathematical complexity that difficulties their analytical treatment (Wright's type II models). In this work, we introduce a model for the population dynamics in mutualism inspired by the logistic equation but cured of divergences. The model is also mathematically more simple than the type II. We use numerical simulations to study the model stability in more general interaction scenarios. Despite its simplicity, our results suggest that the model dynamics are rich and may be used to gain further insights in the dynamics of mutualistic interactions.

1. Introduction. Dynamics of populations are modeled as classic problems in Physics. The population evolution of a biological system is determined by implicit rules, typically as differential equations. At any given time, the system state is mapped into a point of a state space. The time evolution, given a set of initial conditions, will be a trajectory in that space.

The first population model is reported by Robert Malthus [11]. In Malthus's model population growth rate is proportional to the current population:

$$\frac{dN}{dt} = r N. \quad (1)$$

where N is the number of individuals and r is the *intrinsic growth rate* (defined as the difference between birth and death rates) of N (we will assume that there are no migrations). The solution of this equation is an exponential growth that goes

2010 *Mathematics Subject Classification.* Primary: 92D25, 92C42; Secondary: 92D40.

Key words and phrases. Population dynamics, Verhulst equation, extinction, carrying capacity, mutualistic network, Type II functional.

extinct if $r < 0$ or it augments unbounded if $r > 0$ [15]. This lack of limit (when $r > 0$) in the growth process can be fixed with a friction term, as the limiting second order term introduced by Verhulst in 1838 [16] that models intra-specific competition (for one isolated population):

$$\frac{dN}{dt} = rN - aN^2 \quad (2)$$

where a is the parameter of intra-specific competition.

From the point of view of the growth rate, in Malthusian model r remains constant, independent of population, ignoring limiting factors like lack of nutrients or space, however, instead of keeping r constant, Verhulst's equation (later called *logistic equation*) assumes that this parameter decays linearly and becomes zero when environmental conditions are saturated, and the population reaches its maximum, called *carrying capacity*, K (the maximum population size that the environment can sustain indefinitely in a given conditions of water, nutrients and other necessities). The Verhulst's logistic equation is written as:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) \quad (3)$$

This equation is accepted as a basic model of population dynamics (specially after being used to fit early datasets [14, 5]) and it is a reference in textbooks in ecology or even in dynamical systems in Physics.

Notice that this differential equation (*logistic equation*) is conceptually different to the *logistic difference equation* or *logistic map* (see [7]),

$$N_{i+1} = \hat{r}N_i \left(1 - \frac{N_i}{K}\right) \quad (4)$$

where N_i is the discrete population at time step i , and \hat{r} is a dimensionless population growth factor.

Nevertheless, the logistic equation has also received many criticisms from ecologists, addressing difficulties in the interpretation of its parameters, its unrealistic form of density dependence and for internal contradictions. One of these paradoxes is the so-called Levins' paradox. This mathematical shortcoming arises when $N > K$ and $r < 0$, giving rise to an unbounded population growth. To avoid this difficulty Levins proposed that the *intrinsic growth rate*, r , should be always non-negative. However, this constraint excludes the possibility of decreasing population ([10, 6]). Gabriel *et al.* ([6]) suggested a *more sensible* resolution using the Verhulst's original formulation (2), where the *Malthusian* growth rate is separated from the friction term. The condition for a stable system is that the friction coefficient, a , must be always positive. This "constrained" model presents a difficulty in the interpretation of K , since for $r < 0$, it follows $K < 0$ and it cannot be considered as a *carrying capacity*. They redefined the *carrying capacity* as:

$$K_\infty = \lim_{t \rightarrow \infty} N(t), \text{ for } N(0) > 0, \quad (5)$$

and then

$$K_\infty = \begin{cases} a/b = K, & \text{if } a > 0, \\ 0 & \text{if } a \leq 0 \end{cases}$$

1.1. Multi-species models. These seminal models of population dynamics can only be applied to isolated species. In nature, every species interact with many other species in their environment, and these interactions are fundamental for their survival. Biological interactions in a community are a complex network where species are nodes and interactions are links.

From the mathematical point of view, population equations become coupled and the system solutions may exhibit different types of singular points.

The most usual types of interaction between species are: *predator-prey* (or *competition*), when one species population grows at the expense of the other species, i.e., when interacting species have negative effect on each other, and *mutualism*, when interaction is positive for both species.

The classic model for inter-species competition is the Lotka-Volterra's equations system for predator-prey populations [17]. In this model prey population, N , is controlled by predator population, P (with a parameter b); in the predator equation the *intrinsic* growth rate is negative but the prey population provides the positive growth rate (with a parameter c). For two species the classic Lotka-Volterra model reads:

$$\frac{dN}{dt} = N(r_N - bP) \quad (6)$$

$$\frac{dP}{dt} = P(cN - r_P) \quad (7)$$

where the parameters $r_{N,P}$, b and c are positive.

This equations system exhibits oscillatory solution for two species, however, for many species complex solutions, as chaotic regimes, can be found.

The other ubiquitous interaction between species is mutualism that results in mutual benefits. This plays a major role in the persistence of biodiversity. For example, it has been reported that mutualism is responsible of about 90% of biodiversity in tropical ecosystem [2].

Following the idea of Lotka-Volterra model the simplest model for mutualistic interaction can be written as a positive (beneficial) interaction term, proportional to both populations:

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 + a_1 N_1 N_2 \\ \frac{dN_2}{dt} &= r_2 N_2 + a_2 N_2 N_1 \end{aligned}$$

where r_1 , r_2 , a_1 , and a_2 are positive constants.

However, if all parameters are positive the growth is, again, unlimited. The simplest controlled mutualistic model was proposed by May [12]. In May's model the equation for each species is a Verhulst equation plus a mutualistic interaction term. As mutualistic interaction is beneficial for both species this additive term always contributes to the total growth rate as a positive term. May's equations for two species can be written as

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1} + \beta_{12} \frac{N_2}{K_1} \right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2} + \beta_{21} \frac{N_1}{K_2} \right) \end{aligned} \quad (8)$$

where $N_1(N_2)$ is the population of the species 1(2); $r_1(r_2)$ is the intrinsic growth rate and $K_1(K_2)$ the carrying capacity of $N_1(N_2)$. Finally, β_{12} is the coefficient that weighs the benefit for N_1 of each interaction with N_2 (the reciprocal for β_{21}). Linear stability analysis can be applied to study the behavior of the system. Provided all parameters are positive four steady states can be found: total extinction ($N_1 = 0, N_2 = 0$), two partial extinctions, ($N_1 = K_1, N_2 = 0$) and ($N_1 = 0, N_2 = K_2$), and a persistence stationary solution. Extinctions are always unstable solutions and the stationary solution will exist and it will be stable when the mutualistic coefficients β_{12} and β_{21} satisfy the condition $\beta_{12}\beta_{21} < 1$ [13]. In this case population will reach a new *carrying capacity* in a finite time. Otherwise the system is unstable and it will grow in an unlimited way.

May's equations have been an inspiration for subsequent mutualist models that incorporate terms aimed at keeping populations bounded.

Few strategies have been proposed to avoid the unbounded growth of May's model. The most accepted model for mutualistic communities with limited growth is the so called *Type II* of Wright ([18]). He proposed a two-species model with an auto-limiting mutualistic term saturation (as a Type II functional response) that includes the effect of handling time T_H , which corresponds to the time needed to process resources (food) produced by the mutualistic interaction. This *Type II* model can be written as:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 - \alpha_1 N_1^2 + \frac{a b N_1 N_2}{1 + a N_2 T_H}, \\ \frac{dN_2}{dt} &= r_2 N_2 - \alpha_2 N_2^2 + \frac{a b N_1 N_2}{1 + a N_1 T_H},\end{aligned}\tag{9}$$

where a is the effective search rate and b is a coefficient that accounts for encounters between N_1 and N_2 .

Wright studied two possible cases of mutualism depending on the sign of the intrinsic growth rate, r . If r is positive the system never goes extinct because all terms in the equation are positive; that is the mutualistic is *facultative*. If r is negative the mutualistic interaction (always positive) is indispensable to subsistence (but this term does not guarantee the survival of the species), and then it is called *obligatory*. The *facultative* case has only one stable solution, the carrying capacity. When both intrinsic growth rates are negative (double *obligatory* mutualism) species can go extinct and this solution is stable. Again, the carrying capacity is also a stable solution, and a new intermediate solution appears: a manifold that separates both basins of attractions: persistence and extinction. Other works with extra features to the type II functional have been reported [9] but with similar mathematical difficulties.

The main drawbacks of the type II model are the difficulty in analytical treatment (due to the fractional nature of the mutualistic term) and the narrow range of parameters to perform numerical simulations.

After reviewing classical population dynamics equations and introducing mutualistic models, we propose a new equation that combines simplicity in its formulation with the richness of dynamical behaviors of the type II models.

The paper is organized as follows. In Section 2, we propose a bounded logistic model and its extension for mutualism, followed by its stability analysis in Section 3 and the numerical treatment of the equations in stochastic formulation in 4. In section 5 we present the numerical results of our model comparing with the other mutualistic models. Finally, we discuss the benefits of the model in Section 6.

2. A simple and robust logistic equation for mutualism. Following the original idea of Verhulst, our first step is searching a new formulation for the logistic equation that overcomes the unbounded growth solution. From the *bounded Verhulst equation* we can also rewrite May's equations to avoid the unlimited growth solutions.

2.1. A bounded Verhulst equation. The Verhulst equation can be read as:

$$\frac{dN}{dt} = r_{\text{pc}} N, \quad r_{\text{pc}} = r \left(1 - \frac{N}{K} \right) \quad (10)$$

where the *per capita* growth rate, r_{pc} , means the growth rate per population unit; in this way the *per capita* growth rate can be read as a *intrinsic* growth rate modified by one adimensional factor including competition or collaboration terms. So, in Eq 10 the adimensional factor of the *per capita* growth rate includes a negative term for intra-specific competition (for background resources (Johnson 2012)) that plays the role of *biological brake*.

However, this representation is only true for positive vegetative rates, r . Figure 1a depicts the per capita growth rate for different values of the vegetative rate r . An intra-specific competition should always decrease per capita rate with population.

The logistic equation is not valid when $r < 0$ and the population is larger than K . (The limiting factor loses its biological sense if the effective rate is negative.) For instance, if a species has reached a population size above its carrying capacity, K , and suddenly experiences high mortality (e.g. due to a severe plague), its growth rate r should drop and, consequently, the population should decay exponentially. However, the term $(1 - \frac{N}{K})$ does not guarantee this behavior.

To overcome this issue, we propose a further modification of the model based on the original idea by Verhulst. A simple way for maintaining this effect whatever the sign of the vegetative rate is including the absolute function, or the sign function,

$$\frac{dN}{dt} = N \left(r - |r| \frac{N}{K} \right) = r N \left(1 - \text{sgn}(r) \frac{N}{K} \right) \quad (11)$$

where r is the intrinsic (or *vegetative*) growth rate, defined as the difference between birth and death rates ($r = (r_b - r_d)$). Note that this mathematical artifice (the absolute value function) gives really biological sense to the limiting term because an intra-specific competition term should be always negative no matter the sign of the growth rate.

So, the population dynamics equation for a species i can be written as

$$\frac{dN_i}{dt} = (r_{b_i} - r_{d_i}) N_i - |r_{b_i} - r_{d_i}| \frac{N_i^2}{K_i} \quad (12)$$

If $r_b > r_d$, there is no difference with the classical formulation. The quadratic term is always negative, and this implies a decrease of population rate. The equation also behaves correctly when $N > K$. In this new equation, the greater the population the lower the growth rate, even for $r_b < r_d$, (the negative growth rate becomes more negative when population is greater). A comparison of per capita growth rate between the original logistic equation and the modification with the absolute intra-specific competition model of Eq. (12), can be seen in Figure 1 where the Verhulst's linear reduction is depicted. Figure 1a shows the per capita growth rate with Verhulst equation for different intrinsic growth rates, from $r = -0.8$ to $r = 0.8$.

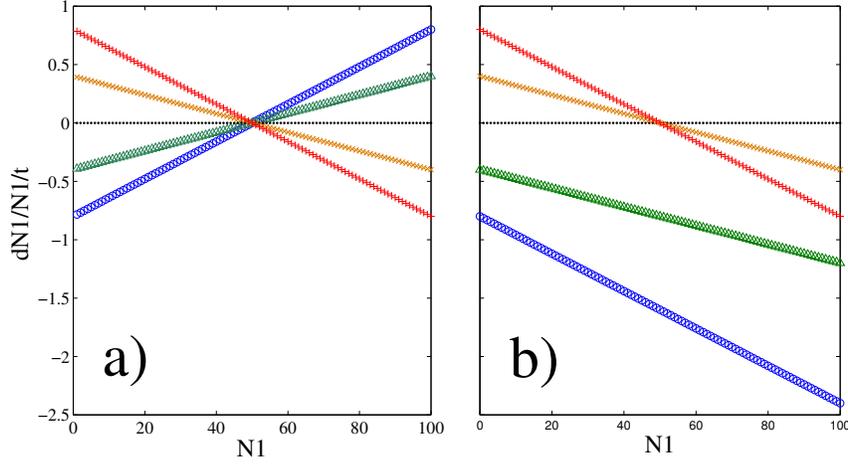


FIGURE 1. a) Per capita growth rate for logistic equation; dashed line for negative intrinsic growth rate ($r = -0.8$ black; $r = -0.4$ red), and solid line for positive intrinsic growth rate ($r = 0.4$ blue; $r = 0.8$ orange); b) The same plot for the bounded Verhulst equation.

Figure 1b shows the per capita growth rate for the *bounded* Verhulst equation, for the same intrinsic growth rate. In this case, even for negative vegetative rate, the per capita rate decreases with population.

Based on this idea for the Verhulst equation, we propose the same strategy to deal with May's model for mutualism.

2.2. A bounded population dynamic model for mutualism. In May's model it is assumed that the carrying capacity and the intrinsic rate of species i are independent of the mutualistic term. Our first key assumption is that the effect of mutualism is just as an increase of the growth rate. So, we can rewrite May's model, for 1 + 1 species, in the following way:

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 r_1 \left(1 + \beta_{12} \frac{N_2}{K_1}\right) \left(1 - \frac{N_1}{K_1}\right) \\ \frac{dN_2}{dt} &= N_2 r_2 \left(1 + \beta_{21} \frac{N_1}{K_2}\right) \left(1 - \frac{N_2}{K_2}\right)\end{aligned}\quad (13)$$

Thus the first parenthesis is a multiplicative factor for the growth rate. Now we can write the *new effective growth rates* as:

$$\begin{aligned}r_{\text{eff},1} &= r_1 + r_1 \beta_{12} \frac{N_2}{K_1} = r_1 + b_{12} N_2 \\ r_{\text{eff},2} &= r_2 + r_2 \beta_{21} \frac{N_1}{K_2} = r_2 + b_{21} N_1\end{aligned}\quad (14)$$

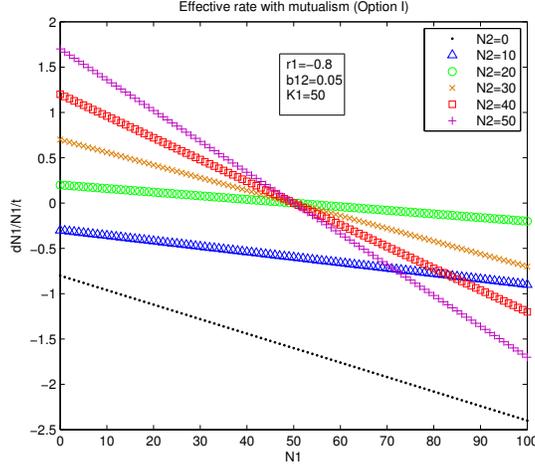


FIGURE 2. Per capita growth rate for species 1 with vegetative rate $r_1 = -0.8$, carrying capacity $K_1 = 50$, and mutualism interaction coefficient $b_{12} = 0.05$, for different values of population $N_2 = 0, 10, 20, 30, 40, 50$.

And, then, the population dynamics equations become:

$$\begin{aligned} \frac{dN_1}{dt} &= (r_1 + b_{12} N_2) N_1 \left(1 - \frac{N_1}{K_1}\right) = r_{\text{eff},1} N_1 \left(1 - \frac{N_1}{K_1}\right) \\ \frac{dN_2}{dt} &= (r_2 + b_{21} N_1) N_2 \left(1 - \frac{N_2}{K_2}\right) = r_{\text{eff},2} N_2 \left(1 - \frac{N_2}{K_2}\right) \end{aligned} \quad (15)$$

Without mutualism the model turns into classic logistic equation. The factor $\left(1 - \frac{N_1}{K_1}\right)$ limits the growth of the species 1 to the carrying capacity K_1 , (the same for species 2), no matter the strength of mutualism.

Including this modification used in 2.1, for Eqs. (15), the equations for the bounded-population mutualistic model can be written:

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 \left(r_{\text{eff},1} - |r_{\text{eff},1}| \frac{N_1}{K_1} \right) = r_{\text{eff},1} N_1 \left(1 - \text{sgn}(r_{\text{eff},1}) \frac{N_1}{K_1} \right) \\ \frac{dN_2}{dt} &= N_2 \left(r_{\text{eff},2} - |r_{\text{eff},2}| \frac{N_2}{K_2} \right) = r_{\text{eff},2} N_2 \left(1 - \text{sgn}(r_{\text{eff},2}) \frac{N_2}{K_2} \right) \end{aligned} \quad (16)$$

As we have early commented about equation 11 the function $\text{sgn}(r_{\text{eff}})$ has biological sense because the intra-specific competition should be always negative, independently of the sign of the growth rate.

To provide the most general formulation, we assume that we have a mutualistic community formed by n species of one class P (e.g. plant guild), and m species of another class A (e.g. animal guild) interacting according to a bipartite (weighted) relation network. Let us consider a species i of P with population N_i and another j of A with N_j individuals, the weights of a directed network b_{ij} account for the rate of benefit produced to the population of i by the interaction with individuals of j . Following the notation of a plant-pollinator community, P could be understood as plants and A as animals, although this choice does not reduce the generality of the

model. The set of equations for the effective growth rates of species i and j is then given by:

$$\begin{aligned} r_{\text{eff},i} &= (r_{b_i} - r_{d_i}) + \sum_{k=1}^m b_{ik} N_k \\ r_{\text{eff},j} &= (r_{b_j} - r_{d_j}) + \sum_{l=1}^n b_{jl} N_l \end{aligned} \quad (17)$$

Thus, the final population dynamics equations are:

$$\begin{aligned} \frac{dN_i}{dt} &= r_{\text{eff},i} N_i - |r_{\text{eff},i}| \frac{N_i^2}{K_i} \\ \frac{dN_j}{dt} &= r_{\text{eff},j} N_j - |r_{\text{eff},j}| \frac{N_j^2}{K_j} \end{aligned} \quad (18)$$

where the subscript i runs for species of class P and j for species of class A . The term $(r_{\text{eff},i} - |r_{\text{eff},i}| \frac{N_i}{K_i})$ becomes the new per capita rate of species i , including the mutualism and the intra-specific competition. Figure 2 depicts the per capita rate for the 1-species (in a mutualistic system of 1 + 1 species), with negative vegetative rate, $r_1 = -0.8$, and mutualistic interaction coefficient, $b_{12} = 0.05$ and $K_1 = 50$, for different values of population of species 2, $N_2 = 0, 10, 20, 30, 40, 50$. For $N_2 = 20$ the per capita rate is still negative, so the system will go to extinction; however, for $N_2 = 30$ the per capita rate becomes positive and the populations will reach the carrying capacity, K_1 .

3. Stability analysis. For the sake of mathematical simplicity, we start the stability analysis of the 2-species model equation.

3.1. 2-species model analysis. The equations for a system composed of species 1 (e.g. a plant) and species 2 (e.g. a animal) can be written as

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 \left(r_{\text{eff},1} - |r_{\text{eff},1}| \frac{N_1}{K_1} \right) \\ \frac{dN_2}{dt} &= N_2 \left(r_{\text{eff},2} - |r_{\text{eff},2}| \frac{N_2}{K_2} \right) \end{aligned} \quad (19)$$

where K_1 and K_2 are the carrying capacities. The corresponding effective growth rates are

$$\begin{aligned} r_{\text{eff},1} &= r_1 + b_{12} N_2 \\ r_{\text{eff},2} &= r_2 + b_{21} N_1 \end{aligned} \quad (20)$$

From equations 19 five steady-state points are identified: the trivial solution ($N_1 = 0, N_2 = 0$), i.e. total extinction, present for all the values of the parameters r_1 and r_2 ; the fixed point ($N_1 = K_1, N_2 = K_2$) is obtained for $r_2 > 0$ and $r_1 > 0$ simultaneously (because b_{12} and b_{21} are positives), i.e. *facultative* mutualism for the two species; and partial extinctions, ($N_1 = 0, N_2 = K_2$) and ($N_1 = K_1, N_2 = 0$) exist for $r_2 > 0$ and $r_1 > 0$, respectively *facultative* mutualism for the surviving species). All these four solutions are equivalent to those of the classic Verlhust model. A new fixed point is obtained for obligated mutualism, $r_2 < 0$ and $r_1 < 0$, when $r_{\text{eff},1} = r_{\text{eff},2} = 0$ and it corresponds to the population values ($N_1 = -r_2/b_{21}$, $N_2 = -r_1/b_{12}$).

The linear stability analysis of the first four fixed points can be done from the Jacobian matrix, \mathbf{J} , defined from the population equations system:

$$\begin{aligned}\frac{dN_1}{dt} &= f_1(N_1, N_2) \\ \frac{dN_2}{dt} &= f_2(N_1, N_2)\end{aligned}\quad (21)$$

as

$$\mathbf{J}_{(N_1^*, N_2^*)} = \begin{pmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{pmatrix} \Big|_{N_1^*, N_2^*} \quad (22)$$

At the trivial solution the Jacobian matrix is

$$\mathbf{J}_{(0,0)} = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix} \quad (23)$$

Total extinction has the intrinsic growth rates, r_1 and r_2 , as eigenvalues, so it is a stable solution only for obligated mutualism ($r_1 < 0$ and $r_2 < 0$) and unstable otherwise.

At $(0, K_2)$ the Jacobian matrix is

$$\mathbf{J}_{(0, K_2)} = \begin{pmatrix} r_1 + b_{12}K_2 & 0 \\ 0 & -r_2 \end{pmatrix} \quad (24)$$

The two eigenvalues are $\lambda_1 = r_1 + b_{12}K_2 < 0$ and $\lambda_2 = -r_2$. The stability condition ($\lambda_1 < 0$ and $\lambda_2 < 0$) requires that $r_2 > 0$ and that $r_1 < -b_{12}K_2 < 0$. Equivalent results are obtained for the point $(K_1, 0)$, with the conditions: $r_1 > 0$ and that $r_2 < -b_{21}K_1 < 0$.

The persistence solution at (K_1, K_2) has the Jacobian matrix

$$\mathbf{J}_{(K_1, K_2)} = \begin{pmatrix} -r_1 - b_{12}K_2 & 0 \\ 0 & -r_2 - b_{21}K_1 \end{pmatrix} \quad (25)$$

And then there is one stable fixed point when the following conditions are fulfilled

$$\begin{aligned}r_{\text{eff},1}^* &= r_1 + b_{12}K_2 > 0 \\ r_{\text{eff},2}^* &= r_2 + b_{21}K_1 > 0\end{aligned}\quad (26)$$

These conditions yield one stable solution at maximum population (carrying capacities) when both *effective* rates are positive.

The last fixed point at $(-r_2/b_{21}, -r_1/b_{12})$ satisfies $r_{\text{eff},1} = 0$ and $r_{\text{eff},2} = 0$, and it only appears for $r_1 < 0$ and $r_2 < 0$. In this case the Jacobian matrix is not defined because the absolute value function is not differentiable at $x = 0$. However, one can study the linear stability at the vicinity of that point under the two assumptions: $r_{\text{eff}} > 0$ and $r_{\text{eff}} < 0$. We can define four Jacobian matrices depending on the *sign* of $r_{\text{eff},1}$ and $r_{\text{eff},2}$. So, at the vicinity of the fixed point we can write the derivatives

$$\begin{aligned}\frac{\partial f_1}{\partial N_2} &= -\frac{b_{12}}{b_{21}}r_2 \left(1 - \text{sgn}(r_{\text{eff},1}) \frac{r_2}{b_{21}K_1} \right) \\ \frac{\partial f_2}{\partial N_1} &= -\frac{b_{21}}{b_{12}}r_1 \left(1 - \text{sgn}(r_{\text{eff},2}) \frac{r_1}{b_{12}K_2} \right)\end{aligned}\quad (27)$$

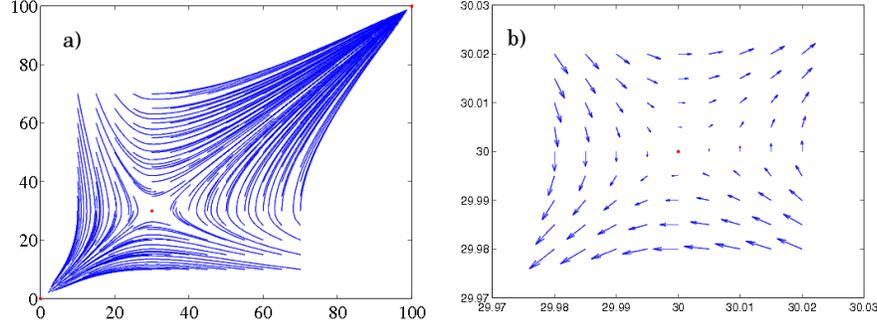


FIGURE 3. a) Solutions of Eq. 16 for $r_1 = r_2 = -0.9$, $b_{12} = b_{21} = 0.03$ and $K_1 = K_2 = 100$ starting at a meshgrid from 10 to 70. b) Flow diagram around the *saddle* point (30,30). Red points are fixed points.

So, for example, the Jacobian matrix \mathbf{J}^{+-} with $\text{sgn}(r_{eff}, 1) = +1$ and $\text{sgn}(r_{eff}, 2) = -1$ is

$$\mathbf{J}^{+-} = \begin{pmatrix} 0 & -\frac{b_{12}}{b_{21}} r_2 \left(1 - \frac{r_2}{b_{21} K_1}\right) \\ -\frac{b_{21}}{b_{12}} r_1 \left(1 + \frac{r_1}{b_{12} K_2}\right) & 0 \end{pmatrix} \quad (28)$$

The eigenvalues obtained from $|\mathbf{J}^{\pm, \mp} - \lambda \mathbb{I}| = 0$ are

$$\lambda_{1,2}^{\pm, \mp} = \pm \sqrt{r_1 r_2 \left(1 \pm \frac{r_2}{b_{21}} K_1\right) \left(1 \mp \frac{r_1}{b_{12}} K_2\right)}$$

From any definition of $\text{sgn}(r_{eff}, 1)$ and $\text{sgn}(r_{eff}, 2)$ all factors inside the square root are positive, then there are always one eigenvalue positive and the other one negative. This means that for any vicinity of this fixed point there exist an attractive basin and a repulsive basin, so it is a *saddle* point.

Even though the Jacobian matrix is not well defined at this fixed point the flow diagram can be obtained and only one flow line passes through each point.

This saddle point regulates the boundary between the basin of attraction of the other stable fixed points and, therefore, controls the resilience of the full system to external perturbations. If it lays close to the extinction values ($N_1 = 0, N_2 = 0$), the system as whole is more stable to external perturbations because the basin of attraction of (K_1, K_2) is more extense. The opposite occurs when it lays closer to the nominal capacity of the system. Figure 3a shows the solutions of initial value problems for Eq. 16 for two species in *obligated* mutualism ($r_1 < 0$ and $r_2 < 0$), with starting points at the meshgrid points from 10 to 70; Figure 3b shows a flow diagram around the *saddle* point (30,30). The greater the mutualistic coefficient the closer the saddle point to the origin (0,0).

3.2. N-species model analysis. For a full network with multiple species as plants or animals, the expressions to consider are Eqs. (18). The steady states solutions are, again, total extinction ($N_i = 0$, for all i), total survival of all species at their carrying capacities ($N_i = K_i$, for all i), and any combinations of the trivial solution,

$N_i = 0$, and the carrying capacities $N_j = K_j$, with the constraint for the surviving species:

$$r_{\text{eff},j}^* = r_j + \sum_l b_{jl} K_l > 0, \quad (29)$$

where l runs over all species of different class from j that reach the carrying capacity at the steady state ($N_l = K_l$).

The Jacobian matrix for total extinction is like Eq. 23, with the intrinsic growth rates at the diagonal, so it is a stable solution only for obligated mutualism ($r_i < 0$ for all i) and unstable otherwise.

For maximum population the Jacobian matrix is, like Eq.30,

$$\mathbf{J}_{(N_i=K_i, N_j=K_j)} = \begin{pmatrix} -r_{\text{eff},i} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & -r_{\text{eff},j} \end{pmatrix} \quad (30)$$

Then this solution is intrinsically stable because all the eigenvalues $\lambda_i = -r_{\text{eff},i}^*$ are negative (following Eq.29).

The stability of the solutions of partial extinction for $N_k = 0$ and $N_l = K_l$, with k running for species going into extinction and l for species reaching their carrying capacity, respectively, can be determined from the generic Jacobian entries:

$$\begin{aligned} \frac{\partial f_i}{\partial N_i} &= r_{\text{eff},i} - 2|r_{\text{eff},i}| \frac{N_i}{K_i} \\ \frac{\partial f_i}{\partial N_j} &= N_i b_{ij} - \text{sgn}(r_{\text{eff},i}) b_{ij} \frac{N_i^2}{K_j} \end{aligned} \quad (31)$$

The Jacobian matrix is diagonal with entries

$$\mathbf{J}_{(N_k=0, N_l=K_l)} = \begin{pmatrix} r_{\text{eff},k} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & -r_{\text{eff},l} \end{pmatrix} \quad (32)$$

where the diagonal entries, $r_{\text{eff},k}$, are positive because

$$\left. \frac{\partial f_k}{\partial N_k} \right|_{N_k=0} = r_k + \sum_l b_{kl} K_l \quad (33)$$

and $r_{\text{eff},l}$ are negative because

$$\left. \frac{\partial f_l}{\partial N_l} \right|_{N_l=K_l} = r_{\text{eff},l} - 2|r_{\text{eff},l}| \frac{K_l}{K_l} \quad (34)$$

and $r_{\text{eff},l} > 0$.

Then, the condition for partial extinction to be stable is $r_k < -\sum_s b_{ks} K_s$, that is, the intrinsic growth rate of species going to extinction is more negative than minus the mutualistic contribution of its alive partners; and $r_l > -\sum_s b_{ls} K_s$, that is, the intrinsic growth rate of surviving species is greater than minus the mutualistic contribution of its alive partners.

Other fixed points can be obtained from the condition $r_{\text{eff},i} = 0$, for all i . As it was commented in the case of 1+1 species, the absolute function is not differentiable at $x = 0$. However, we can define the derivatives at the vicinity of that fixed point

(Eq.27). Assuming $r_{\text{eff},i} > 0$ the Jacobian matrix entries are:

$$\begin{aligned} \left. \frac{\partial f_i}{\partial N_i} \right|_{r_{\text{eff},i}=0^+} &= 0 \\ \left. \frac{\partial f_i}{\partial N_j} \right|_{r_{\text{eff},i}=0^+} &= N_i b_{ij} \left(1 - \frac{N_i}{K_i} \right) \equiv J_{ij} > 0 \end{aligned} \quad (35)$$

is a *non-negative* matrix. This fixed point cannot be a stable node because all eigenvalues cannot be negative:

$$\sum_i \lambda_i = \text{Tr}(\mathbf{J}) \quad (36)$$

Then this intermediate solution, between total extinction and maximum population, if it exists, it will always be an unstable node.

4. Numerical treatment of the equations. Population dynamics equations deal with discrete variables: animal or plant population is an integer variable that increases or decreases in discrete units. Although mathematical models are expressed as continuum equations, fluctuations and stochasticity of reality make discrete numerical simulations a good approach.

The method for discrete simulations used in this work is the Discrete Stochastic Simulation (Binomial Simulations) rather than Markov models because in moderate size problems is much faster [8, 1]. This technique is a reasonable choice when the outcome of the stochastic process over a finite time interval has only two values: breeding or not; when time interval is short enough breeding can be described by a Bernoulli trial. A similar technique has been applied before to epidemiologic studies (see, for instance, [1]).

In a general Malthusian model, with intrinsic growth r , the probability of breeding over a time interval ΔT can be described by an exponential distribution with average value $1/r$. So, the probability of reproduction is:

$$P = \int_0^{\Delta T} r e^{-r t} dt = 1 - e^{-r \Delta T} \quad (37)$$

The increase in population of one species with N individuals at time t , with exponential growth, in an interval ΔT , will be

$$N(t + \Delta T) = N(t) + \text{sgn}(r) \text{Binomial}(N(t), P) \quad (38)$$

Then, the equations system 16 can be written in stochastic form as:

$$\begin{aligned} N_i(t + \Delta T) &= N_i(t) + \text{sgn}(\hat{r}_{\text{eff},i}) \text{Binomial}(N_i(t), P_i), \\ N_j(t + \Delta T) &= N_j(t) + \text{sgn}(\hat{r}_{\text{eff},j}) \text{Binomial}(N_j(t), P_j), \end{aligned} \quad (39)$$

where the subscript i runs for species of one class, A , and j runs for species of the other class P ; $\hat{r}_{\text{eff},i}$ i th-species effective growth rate in the simulation period, and P_i is the probability of growth according to equation 37. Although ecological parameters are yearly our time step is one day, so we have to rescale the *effective* growth rate:

$$\hat{r}_{ef} = (1 + r_{ef})^{1/365} - 1 \quad (40)$$

5. **Numerical results.** It is hard to obtain analytical results for a general community because the interactions form a complex bipartite graph [4, 3]. In this section, we show the results of numerical simulations performed to explore the stability of the model solutions. Indeed, we have performed simulations within the three basins of attraction, namely, total extinction, partial extinction and survival at carrying capacity. All simulation parameters are listed in Section 7.

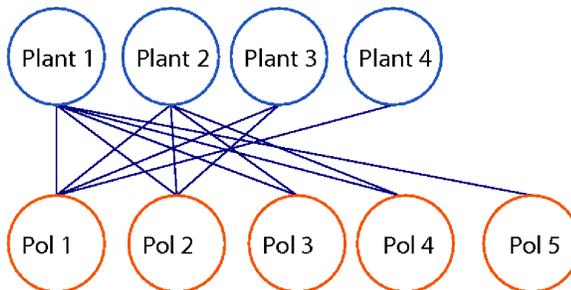


FIGURE 4. Mutualistic community with five species of plants and four species of pollinators.

Figure 4 shows a small mutualistic community created for our experiments. In empirical studies, the number of interacting species in each class is of the order of tens, but this simplified example already displays the characteristic behaviors of larger communities.

In the first experiment, the system starts with all effective rates below zero, except for that of pollinator number 4. We are assuming a case of obligated mutualism. Under these circumstances, it is easy to find the minimum initial population sizes for the survival of the nine species mutualistic community, solving $r_{\text{eff},i} = 0$ in (17), for all i . Effective rates only become positive due to mutualistic benefit. Initial populations are not high enough to make positive the effective rates $r_{\text{eff},i}^{\text{class}}$, except for the aforementioned pollinator. Plant species 1 and 2 start with populations above their carrying capacities. This example shows the *extinction attractor* where all populations eventually tend to zero.

Figure 6 depicts a simulation with the same network but some different parameter values (see Table 2). Plant populations start below carrying capacity but positive *effective* growth rates lead the population to maximum values. Note that population of pollinator 5 starts above its carrying capacity but the initial negative *effective* growth rate decreases the number of individuals. On the other hand, pollinator 4 starts with very low population and the mutualistic term produces a high *effective* growth rate that increases population towards carrying capacity (*effective* growth rate are shown in the lower charts). The evolution of *effective* growth rates graph shows how they evolve towards equilibrium as populations are closer to *maxima*.

In the third simulation we explore partial extinctions (Figure 7). Again, all intrinsic rates are negative but mutualistic link weights and initial populations have been slightly modified to make positive several per capita rates (see Table 3).

In this experiment all populations start below carrying capacities. Species of both classes grow towards the *maximum* except pollinator 4 and plant 4 that become extinct. Note that plant 2 starts with a negative per capita rate that decreases

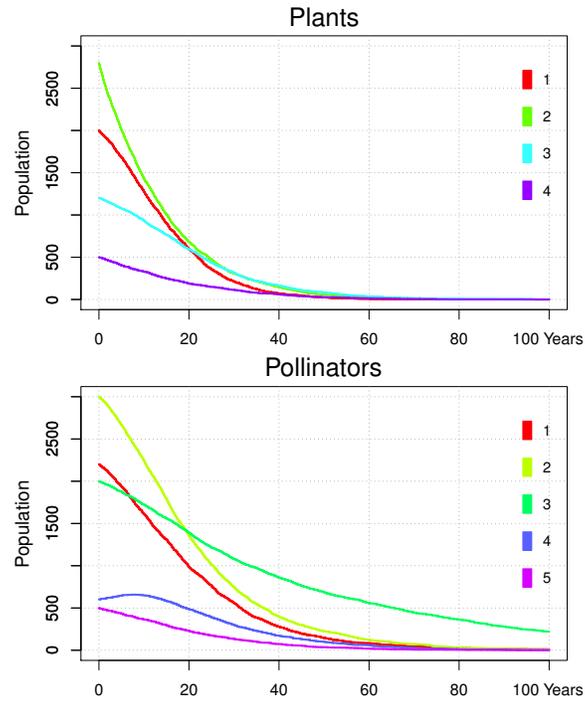


FIGURE 5. Population dynamics for 4 + 5 species evolving towards total extinction (each species is color-coded).

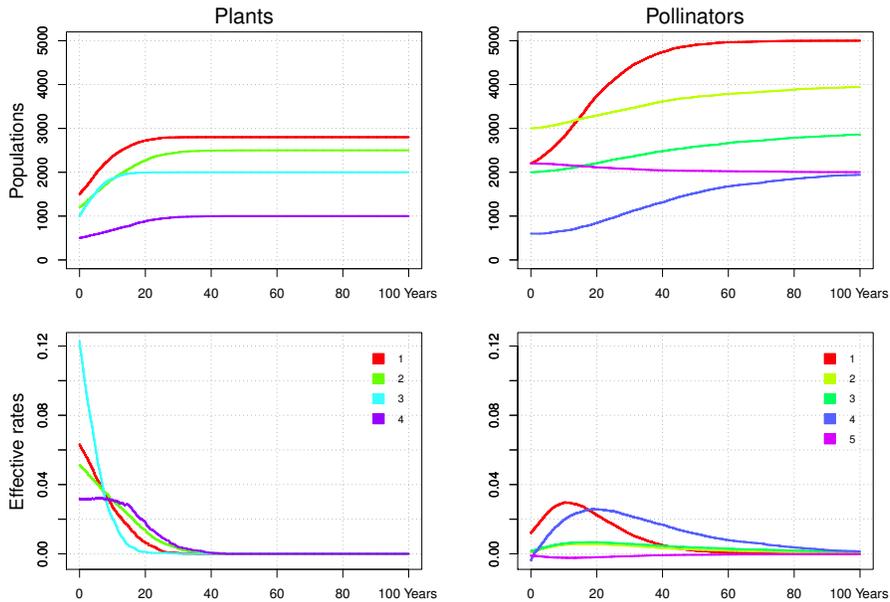


FIGURE 6. Population size (up) and *effective* growth rate (down) of the same 4+5 species (Figure 4), over time evolving towards carrying capacity (each species is color-coded).

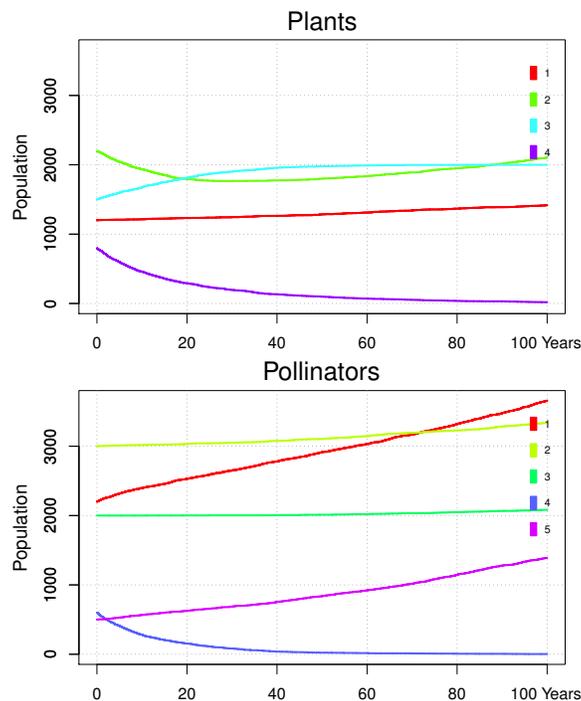


FIGURE 7. Third experiment results, population dynamics over time for the different species. Pollinator 4 and plant 4 go to extinction (each species is color-coded).

its initial population but it turns positive along the simulation by the effect of pollinators growth.

6. Conclusions. In this work, our aim is to build a simple and bounded model derived from the logistic approach to simulate mutualistic dynamics. The introduced equations overcome the unlimited growth of the logistic equation and May's model. Although there are other specific models trying to solve this drawback, like type II models, the complexity of their equations makes them difficult to use. Our model allows linear stability analysis, and it shows similar fixed point structure and it is as rich in dynamic behaviors as the type II models. In addition, the nonlinearities are simpler than those of the type II models and with fewer parameters, which allows to assign them an ecological interpretation.

We have studied the dynamics of the simple 2-species model finding the fixed points and their stability analytically. In the important case of *obligated* mutualism the *saddle* point can be established, and from it one can find the basins to extinction or to survival. Analytical extensions for $n + m$ species have also been made. Finally, we have performed numerical simulation for a $(5 + 4)$ -species community and we have found a rich dynamics with some variations of the parameters, from persistence of all species to partial or total extinction.

Comparing the linear stability analysis and the wider range of parameters suitable for numerical simulations we concluded that this model is simpler than Wright's Type II and exhibits similar dynamic richness.

The simplicity of the numerical model will allow to study resilience of a community to external perturbations introducing the perturbation in a simple way. Work in this line is in progress.

7. Data tables. The parameters used in the three simulations are listed in the following tables.

	Plant 1	Plant 2	Plant 3	Plant 4
b_{pol1j} (10^{-6})	1	12	12	16
b_{pol2j} (10^{-6})	20	4	11	0
b_{pol3j} (10^{-6})	20	10	0	0
b_{pol4j} (10^{-6})	10	0.1	0	0
b_{pol5j} (10^{-6})	10	0	0	0
$N_{init j}$	2000	2800	1200	500
K_j	1500	2500	2000	1000
$r_{birth j}$	0.004	0.01	0.01	0.005
$r_{death j}$	0.13	0.10	0.08	0.065

	Pol 1	Pol 2	Pol 3	Pol 4	Pol 5
b_{pl1m} (10^{-6})	4	13	5	30	20
b_{pl2m} (10^{-6})	12	6	10	0.1	0
b_{pl3m} (10^{-6})	2	5	0	0	0
b_{pl4m} (10^{-6})	10	0	0	0	0
$N_{init m}$	3000	3000	2000	600	500
K_m	5000	4000	3000	2000	2000
$r_{b m}$	0.08	0.02	0.05	0.08	0.02
$r_{d m}$	0.14	0.078	0.07	0.14	0.08

TABLE 1. Mutualistic coefficients and conditions for the first experiment (fig. 5), with the network of fig. 4. Top, pollinator-plant interaction matrix; bottom, plant-pollinator matrix

Acknowledgments. JMP thanks A. Alonso for mathematical support in stability analysis. We have received partial financial support from the Spanish Ministry of Economy (MINECO) under projects MTM2012-39101, MODASS (FIS2011-24785) and ADAPTA (CGL2012-33528); from the project PGUI of Comunidad de Madrid MODELICO-CM/S2009ESP-1691 and from the EU Commission through projects EUNOIA and LASAGNE. JJR acknowledges funding from the Ramón y Cajal program of MINECO.

REFERENCES

- [1] D. Balcan, V. Colizza, B. Gonçalves, H. Hu, J. J. Ramasco and A. Vespignani, [Multiscale mobility networks and the spatial spreading of infectious diseases](#), *Proceedings of the National Academy of Sciences USA*, **106** (2009), 21484–21489.
- [2] J. Bascompte and P. Jordano, [Plant-animal mutualistic networks: The architecture of biodiversity](#), *The Annual Review of Ecology, Evolution, and Systematics*, **38** (2007), 567–593.
- [3] U. Bastolla, M. A. Fortuna, A. Pascual-García, A. Ferrera, B. Luque and J. Bascompte, [The architecture of mutualistic networks minimizes competition and increases biodiversity](#), *Nature*, **458** (2009), 1018–1020.
- [4] U. Bastolla, M. Lässig, S. C. Manrubia and A. Valleriani, [Biodiversity in model ecosystems, II: Species assembly and food web structure](#), *Journal of Theoretical Biology*, **235** (2005), 531–539.

	Plant 1	Plant 2	Plant 3	Plant 4
b_{pol1j} (10^{-6})	50	22	42	56
b_{pol2j} (10^{-6})	20	40	81	0
b_{pol3j} (10^{-6})	20	10	0	0
b_{pol4j} (10^{-6})	50	0.1	0	0
b_{pol5j} (10^{-6})	10	0	0	0
$N_{init j}$	1500	1200	1000	500
K_j	2800	2500	2000	1000

	Pol 1	Pol 2	Pol 3	Pol 4	Pol 5
b_{pl1m} (10^{-6})	40	13	15	30	20
b_{pl2m} (10^{-6})	12	6	1	1	0
b_{pl3m} (10^{-6})	2	5	0.1	0	0
b_{pl4m} (10^{-6})	1	1	0	0	0
$N_{init m}$	2200	3000	2000	600	2200
K_m	5000	4000	3000	2000	2000

TABLE 2. Mutualistic coefficients and conditions for the second experiment (fig. 7) with the same interaction network. Top, pollinator-plant interaction matrix; bottom, plant-pollinator matrix. Birth and death rates are the same as in Table1 except $r_{d,pl3} = 0.1$, $r_{d,pol2} = 0.048$, and $r_{d,pol5} = 0.04$

	Plant 1	Plant 2	Plant 3	Plant 4
b_{pol1j} (10^{-6})	10	22	42	6
b_{pol2j} (10^{-6})	20	4	11	0
b_{pol3j} (10^{-6})	20	10	0	0
b_{pol4j} (10^{-6})	1	0.1	0	0
b_{pol5j} (10^{-6})	1	0	0	0
$N_{init j}$	1200	2200	1500	800
K_j	1500	2500	2000	1000

	Pol 1	Pol 2	Pol 3	Pol 4	Pol 5
b_{pl1m} (10^{-6})	34	33	15	20	60
b_{pl2m} (10^{-6})	12	6	1	0.1	0
b_{pl3m} (10^{-6})	2	5	0	0	0
b_{pl4m} (10^{-6})	1	0.1	0	0	0
$N_{init m}$	2200	3000	2000	600	2200
K_m	5000	4000	3000	2000	2000

TABLE 3. Mutualistic coefficients and conditions for the third experiment (fig. 7) with the same interaction network. Top, pollinator-plant interaction matrix; bottom, plant-pollinator matrix. Birth and death rates are the same as in Table1 except $r_{d,pl4} = 0.053$, $r_{d,pol4} = 0.09$, and $r_{b,pol4} = 0.01$

[5] W. Feller, [On the logistic law of growth and its empirical verifications in biology](#), *Acta Biotheoretica*, **5** (1940), 51–66.

[6] J. P. Gabriel, F. Saucy and L. F. Bersier, [Paradoxes in the logistic equation?](#), *Ecological Modelling*, **185** (2005), 147–151.

[7] J. R. Groff, [Exploring dynamical systems and chaos using the logistic map model of population change](#), *American Journal of Physics*, **81** (2013), 725–732.

- [8] L. Gustafsson and M. Sternad, [Bringing consistency to simulation of population models–Poisson simulation as a bridge between micro and macro simulation](#), *Mathematical Biosciences*, **209** (2007), 361–385.
- [9] C. A. Johnson and P. Amarasekare, [Competition for benefits can promote the persistence of mutualistic interactions](#), *Journal of Theoretical Biology*, **328** (2013), 54–64.
- [10] E. Kuno, Some strange properties of the logistic equation defined with r and k : Inherent defects or artifacts?, *Researches on population ecology*, **14** (1991), 33–39.
- [11] T. R. Malthus, *An Essay on the Principle of Population or a View of Its Past and Present Effects on Human Happiness; with an Inquiry into Our Prospects Respecting the Future Removal or Mitigation of the Evils which It Occasions*, 1st edition, Roger Chew Weightman, Washington, 1798. Available from: <http://opac.newsbank.com/select/shaw/17975>.
- [12] R. May, Models for two interacting populations, in *Theoretical Ecology. Principles and Applications*, 2nd edition (ed. R. May), 1981, 78–104.
- [13] J. D. Murray, *Mathematical Biology I: An Introduction*, 3rd edition, Springer-Verlag, New York, 2002.
- [14] R. Pearl, [The biology of population growth](#), *Zeitschrift für Induktive Abstammungs- und Vererbungslehre*, **49** (1929), 336–338.
- [15] E. Stokstad, [Will malthus continue to be wrong?](#), *Science*, **309** (2005), p102.
- [16] P. F. Verhulst, Recherches mathématiques sur la loi d'accroissement de la population [Mathematical researches into the law of population growth increase], *Nouveaux Memoires de l'Academie Royale des Sciences et Belles-Lettres de Bruxelles*, **18** (1845), 1–42.
- [17] V. Volterra, [Fluctuations in the abundance of a species considered mathematically](#), *Nature*, **118** (1926), 558–560.
- [18] D. H. Wright, [A simple, stable model of mutualism incorporating handling time](#), *The American Naturalist*, **134** (1989), 664–667.

Received July 2014; revised November 2014.

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