Rethinking the logistic approach for population dynamics of mutualistic interactions

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Mutualistic communities have an internal structure that makes them resilient to external perturbations. Late research has focused on their stability and the topology of the relations between the different organisms to explain the reasons of the system robustness. Much less attention has been invested in analyzing the systems dynamics. The main population models in use are modifications of the logistic equation with additional terms to account for the benefits produced by the interspecific interactions. These models have shortcomings as the so called r - K formulation of logistic equation diverges under some conditions. In this work, we introduce a model for population dynamics under mutualism inspired by the logistic equation but avoiding singularities. The model is mathematically simpler than the widely used type II models, although it shows similar complexity in terms of fixed points and stability of the dynamics. Furthermore, each term of our model has a more direct ecological interpretation, which can facilitate the measurement of the rates involved in field campaigns. We perform an analytical stability analysis and numerical simulations to study the model behavior in more general interaction scenarios including tests of the resilience of its dynamics under external perturbations. Despite its simplicity, our results indicate that the model dynamics shows an important richness that can be used to gain further insights in the dynamics of mutualistic communities.

I. INTRODUCTION

Despite its long history, there exist still several open issues in the research of ecological population dynamics. Some of these questions were highlighted in the 125th anniversary issue of the journal Science [1–3]. For example, aspects such as the mechanisms determining species diversity in an ecosystem are under a very active scrutiny by an interdisciplinary scientific community [4–12]. Quantitative population dynamics goes back to 1202 when Leonardo Fibonacci, in his Liber Abaci, described the famous series that follows the growth of rabbit population [13]. Classical population theory began, however, in 1798 with Robert Malthus’ An Essay on the Principle of Population [14]. Malthus argued that population growth is the result of the difference between births and deaths, and that these magnitudes are proportional to the current population. Mathematically, this translates in the differential equation:

\[
\frac{dN}{dt} = r N, \tag{1}
\]

where \(N\) is the population, \(r\) is the intrinsic rate of growth of \(N\) and equals the difference between the rates of birth and death (assuming no migrations). The Malthusian model predicts an exponential variation of the population, which if \(r > 0\) translates into an unbounded growth. In this model, \(r\) remains constant along the process ignoring thus limiting factors on the population such as the lack of nutrients or space. Verhulst introduced in 1838 a friction term into the model, proposing the so-called logistic equation [15]:

\[
\frac{dN}{dt} = r N - \alpha N^2. \tag{2}
\]

The parameter \(\alpha\) represents the intra-species competition, and leads to a point of equilibrium for the dynamics in which \(\frac{dN}{dt} = 0\) with a population value approaching \(K = r/\alpha\), usually called the carrying capacity of the system.

The logistic equation is best known in the formulation that Raymond Pearl introduced in 1930 (see [16] for an excellent historical review). In this formulation, the carrying capacity appears explicitly:

\[
\frac{dN}{dt} = r N \left(1 - \frac{N}{K}\right). \tag{3}
\]

The solution of this equation is a sigmoid curve that asymptotically tends to \(K\). This formulation has some major mathematical drawbacks [17, 18]. The most important is that it is not valid when the initial population is higher than the carrying capacity and \(r\) is negative. Under those conditions, it predicts an unbounded population growth. This issue was noted by Richard Levins, and consequently is called Levins’ paradox. One simple solution consists in separating the linear and quadratic terms (as in the original Verhulst approach) ensuring that the rate \(\alpha\) is always positive. It is, however, important to stress that all mutualistic models derived from Pearl’s formula inherit its limitations in this sense.

These seminal models of population dynamics did not take into account interactions between species. When
several species co-occur in a community there can be a rich set of relationships among them that can be represented as a complex interaction network. In 1926, Vito Volterra proposed in \[19\] a two-species model to explain the behavior of some fisheries in the Adriatic sea. Volterra’s equations describe prey \( N(t) \) and predator populations \( P(t) \) in the following way:

\[
\begin{align*}
\frac{dN}{dt} &= N (a - b P), \\
\frac{dP}{dt} &= P (c N - d),
\end{align*}
\]

where \( a, b, c, \) and \( d \) are positive constants. In the Lotka-Volterra model, as is known today, the prey population growth is limited by the predator population, while the latter benefits from the prey and is bounded by its own growth. This pair of equations has an oscillatory solution in the presence of further species can even become chaotic.

While prey-predator and competition interactions have been approached by modelers since then, mutualistic interactions, which are beneficial for all the species involved, have not been studied in such detail. Charles Darwin noticed the importance of a mutualistic interaction between orchids and their pollinators [20]. Actually, the relations between plants and their pollinators and seed dispersers are the paradigmatic examples of mutualism. In this context, Ehrlich and Raven [21] alluded to the importance of plant-animal interactions in the generation of Earth’s biodiversity. The simplest mutualistic model without ‘an ongy of mutual benefaction’ was proposed by May [22]. Each of May’s equations for two species is a logistic model with an extra term accounting for the mutualist benefit. It is the same idea as in the Lotka-Volterra model but interactions between species always add to the resulting population. May’s equations for two species can be written as

\[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 \left( 1 - \frac{N_1}{K_1} \right) + r_1 N_1 \beta_{12} \frac{N_2}{K_1}, \\
\frac{dN_2}{dt} &= r_2 N_2 \left( 1 - \frac{N_2}{K_2} \right) + r_2 N_2 \beta_{21} \frac{N_1}{K_2},
\end{align*}
\]

where \( N_1(N_2) \) is the population of the species 1(2); \( r_1 (r_2) \) is the intrinsic growth rate of population 1(2) and \( K_1 (K_2) \) the carrying capacity. This is the maximum population that the environment can sustain indefinitely, given food, habitat, water and other supplies available in the environment. Finally, \( \beta_{12} \) is the coefficient that embodies the benefit for \( N_1 \) of each interaction with \( N_2 \). The third term has an undesirable side effect, since the population can exceed the carrying capacity. May’s equations have been an inspiration for subsequent mutualist models that incorporate terms aimed at keeping populations bounded.

Different strategies to avoid the unlimited growth have been adopted. Wright [23] proposed a two-species model with saturation as a result of restrictions on handling time, \( T_H \), which corresponds to the time needed to process resources (food) produced by the mutualistic interaction. The mutualistic term can be included as a type II functional response

\[
\begin{align*}
\frac{dN_1}{dt} &= r_1 N_1 - \alpha_1 N_1^2 + \frac{a b N_1 N_2}{1 + a N_2 T_H}, \\
\frac{dN_2}{dt} &= r_2 N_2 - \alpha_2 N_2^2 + \frac{a b N_1 N_2}{1 + a N_1 T_H},
\end{align*}
\]

where \( a \) is the effective search rate and \( b \) is a coefficient that relates encounters between individuals of species 1 and 2. Wright analyzes two possible behaviors of mutualism: facultative and obligatory. In the facultative case, \( r_{1,2} \) are positive, i.e., mutualism increases the population but it is not indispensable to species subsistence. If \( r_{1,2} \) are negative mutualism is mandatory to the species survival. This model show different dynamics depending on the parameter values, but at least for a region of parameters it shows three fixed points in the dynamics. One stable at both species extinction, other also stable at large population values and a saddle point separating both basin of attractions. Using another mutualistic model with a type II functional, Bastolla et al. [10] [24] show the importance of the structure of the interaction network to minimize competition between species and to increase biodiversity. The type II models are, however, hard to treat analytically due to the fractional nature of the mutualistic term. Other recent alternatives have been proposed as, for instance, [25]. Still, these works go in the direction of adding extra features to the type II functional rendering difficult an eventual analytical treatment.

Hitherto, the research has focused on stability looking for an explanation of the resilience of these communities in the interaction networks [9] [11] [26] [27]. The dynamics is, however, as important since changes in the parameters that govern the equations induced by external factors can lead the systems to behave differently and to modify its resilience to perturbations in the population levels. Here we revisit the basic model describing the population dynamics and propose a new equation that combines simplicity in its formulation with the richness of dynamical behaviors of the type II models.

Once introduced the classical population dynamics equations and the review of mutualistic models, the paper is organized as follows. In Section [III] we propose a modified logistic model for mutualism, followed by its stability analysis in [IV] [V]. In section [VI] we present the numerical results of our model comparing with the other mutualistic models. Finally, we discuss the benefits of the model in Section [VII] [A] introduces the data tables used in the experiments and [B] describes the numerical treatment of the equations in stochastic formulation.
due to a severe plague, its growth rate slightly decreased with populations larger than $K$ and suddenly experiences high mortality when $r < 0$ and if the population is larger than $K$, the limiting factor of Eq. (3) loses its biological sense. For instance, if a species has reached population size close to $K$ and suddenly experiences high mortality due to a severe plague, its growth rate $r$ should drop and, consequently, the population should decay exponentially. However, the term $(1 - \frac{N}{K})$ acts in the opposite direction. To overcome this issue, we propose a simple modification of the model inspired in Verhulst’s original idea

$$\frac{1}{N} \frac{dN}{dt} = (r - |r|) \frac{N}{K} = r \left(1 - \frac{N}{K}\right) \quad (7)$$

where the terms on the right hand side of the equation can be seen as a de-facto per capita growth rate, including the negative density-dependence as intra-specific competition for background resources. The growth rate $r$ is a combination of the birth ($r_b$) and death ($r_d$) rates $r = (r_b - r_d)$. If $r_b > r_d$, there is no difference between Eq. (7) and the classical Pearl’s formulation. Otherwise, the quadratic term is always negative which leads to a quick decay of the population. A comparison between the original logistic equation and the modification of Eq. (7) can be seen in Figure 1 (logistic) and 1b (modification). In the new equation, the de-facto growth rates decrease with populations larger than $K$ even for $r < 0$.

If we assume that the carrying capacity and the intrinsic growth rate of a species are independent of the presence of mutualism, the effect of mutualistic interactions should appear as a modulating factor on an new effective growth rate for the species. Taking this into account, we can write a new set of equations for a mutualistic community including, besides, the correction that led to Eq. (7) to control Levin’s paradox. Let us consider in a general scenario with a mutualistic community formed by $n$ species of class $a$ and $m$ species of class $p$ interacting according to a bipartite (weighted) relation network. A generic species $i$ of $a$ will have a population $N_i^a$ and other $j$ of $p$, $N_j^p$. Following the notation of a plan-pollinator community, $a$ might be seen as animals and $p$ as plants. The weights of the directed interaction network $b_{ij}$ account for the rate of benefit produced to the population of $i$ by the interaction with individuals of $j$. In the simplest linear model, the equations for the effective growth rates of species $i$ and $j$ could be written as

$$r_{ef_i} = r_{b_{ij}}^a - r_{d_{ij}}^a + \sum_{k=1}^{m} b_{ik} N_k^p,$$

$$r_{ef_j} = r_{b_{ij}}^p - r_{d_{ij}}^p + \sum_{s=1}^{n} b_{js} N_s^a, \quad (8)$$

where $r_{b_{ij}}^a$ and $r_{d_{ij}}^a$ are, respectively, the birth and death rates of the population of each species. Introducing these growth rates into the modified logistic model of Eq. (7), we obtain the following equations for the population dynamics with mutualism:

$$\frac{1}{N_i^a} \frac{dN_i^a}{dt} = r_{ef_i} - |r_{ef_i}| \frac{N_i^a}{K_i^a} \quad (9)$$

$$\frac{1}{N_j^p} \frac{dN_j^p}{dt} = r_{ef_j} - |r_{ef_j}| \frac{N_j^p}{K_j^p} \quad (10)$$

Note that the right hand terms are now the new per capita de-facto rates of species $i$ and $j$, including mutualism and intra-specific competition. In this new model, the mutualistic interaction is part of the growth rate as a positive factor, in such a way that for a given vegetative growth rate (positive or negative) an increase in mutualism means always higher effective growth rates. Moreover, the population remains in the vicinity of the carrying capacity even in the case of obligatory mutualism with negative signs of the growth rates $r_{ef_i}$, $r_{ef_j}$ or of the effective rates $r_{ef_i}$ and $r_{ef_j}$.

### III. STABILITY ANALYSIS

For the sake of simplicity, we start the stability analysis considering the 2-species model equation. The equations for a system composed of an animal 1 and a plant 2 can be written as

$$\frac{dN_1^a}{dt} = r_{ef_1}^a N_1^a - |r_{ef_1}^a| \frac{N_1^a}{K_1^a}$$

$$\frac{dN_2^p}{dt} = r_{ef_2}^p N_2^p - |r_{ef_2}^p| \frac{N_2^p}{K_2^p} \quad (11)$$

Figure 1: a) Per capita growth rate for logistic equation; dashed line for negative vegetative growth rate ($r_1 = -0.8$ black, $r_1 = -0.4$ red), and solid line for $r > 0$ ($r_1 = 0.4$ blue, $r_1 = 0.8$ orange); b) The same plot for the modified logistic equation (7).
Equation (11) with Figure 2: Flux diagrams for the dynamics of a) our model of Equation (11) with $r_1^p = r_2^p = -2.5$, $b_{12} = b_{21} = 0.05$ and $K_1^p = K_2^p = 100$, and b) of the type II model of Equation (10) with $r_1 = r_2 = -0.1$, $\alpha = 1/100$, $\alpha = 1/3$, $T_H = 1/5$ and $b = 1/25$. The fixed points of the dynamics are displayed as red circles, the arrows correspond to the vectors $(dN_1^p/dt, dN_2^p/dt)$ and their colors and lengths are related to the vector norm. Note that in both cases two fixed points: one at $(0, 0)$ and the other on the top-right side of the diagrams are stable, while the one in the middle is a saddle point.

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

$$r_{ef1}^p = r_1^p + b_{12} N_2^p,$$
$$r_{ef2}^p = r_2^p + b_{21} N_1^p.$$  \hspace{1cm} (12)

These equations have five fixed points for the dynamics (stationary states). The first four are equivalent to those of the classic Verhulst model. The first, without population $(N_1^p, N_2^p) = (0, 0)$, is present for all the values of the parameters $r_1^p$ and $r_2^p$. The fixed points at $(N_1^p, N_2^p) = (K_1^p, 0)$ and at $(0, K_2^p)$ are possible only for facultative mutualism of any of the two species and either $r_1^p > 0$ or $r_2^p > 0$. The fixed point at $(N_1^p, N_2^p) = (0, 0)$ is obtained for $r_1^p > 0$ and $r_2^p > 0$ simultaneously and under obligate mutualism when the mutualistic interactions are able to overcome the negative vegetative growth of the species populations. The fifth fixed point is obtained only for obligate mutualism, $r_1^p < 0$ and $r_2^p < 0$, and corresponds to the point at which $r_{ef1}^p = r_{ef2}^p = 0$, which means at population values $(N_1^p, N_2^p) = (-\frac{r_1^p}{b_{12}}, -\frac{r_2^p}{b_{21}})$.

Regarding stability, the first fixed point at zero population is stable for obligate mutualism ($r_1^p < 0$ and $r_2^p < 0$) and unstable otherwise. The fixed point at $(0, K_2^p)$ has two eigenvalues: $\lambda_1 = -r_2^p$ and $\lambda_2 = r_1^p + b_{12} K_2^p < 0$. The stability condition ($\lambda_1 < 0$ and $\lambda_2 < 0$) requires $r_2^p > 0$ and $r_1^p < -b_{12} K_2^p < 0$. Equivalent results are obtained for the point $(K_1^p, 0)$. The next fixed point, the one at $(K_1^p, K_2^p)$, is stable when the following conditions are fulfilled:

$$r_1^p + b_{12} K_2^p > 0,$$
$$r_2^p + b_{21} K_1^p > 0.$$  \hspace{1cm} (13)

These conditions yield a stable solution at maximum population (carrying capacities) only when both effective rates are positive. The last fixed point at $(-\frac{r_1^p}{b_{12}}, -\frac{r_2^p}{b_{21}})$, only appearing for obligate mutualism, is a saddle point. This point is important because it marks the boundary between the basin of attraction of the other stable fixed points and, therefore, controls the resilience of the system to external perturbations. If it lays close to the extinction values $(N_1^p, N_2^p) = (0, 0)$, the system is more stable to perturbations because the basin of attraction of $(K_1^p, K_2^p)$ is vaster. The opposite occurs when it gets closer to the nominal capacity of the system.

We graphically show the flux diagram and fixed points of our model under obligatory mutualism in Figure 2b. In this case, there are three fixed points: two stable at $(0, 0)$ and $(K_1^p, K_2^p) = (100, 100)$ and the saddle point at $(50, 50)$. Also, and to compare the dynamics of our model and of a type II model, we have depicted the flux diagram of Eq. (6) in Figure 2b. Selecting suitable parameters, it is possible to find a similar configuration with three fixed points: two stable and a saddle point. However, the complexity of the type II equations renders much harder the search for the region of parameters where this configuration occurs. Besides, the ecological interpretation of the parameters in this region is less direct than in our model and much more difficult to estimate in a field study.

For a full network with multiple species of plants and animals, the model to consider is expressed in Equations (10). Some of the steady states are the combinations of the trivial solution, $N_{i,j}^p = 0$, and the carrying capacities...
where the index \( k \) runs over all species of type different from \( i \) whose populations reach the carrying capacity at the steady state (\( N_k = K_k \)). Under this condition, the Jacobian matrix at the steady state is diagonal with elements \( -r_{\text{ef}i}^* \). This means that all these steady states are intrinsically stable.

The condition for the non-trivial stationary states (\( r_{\text{ef}i}^* > 0 \)) can be regarded as a lower limit for the vegetative growth rate:

\[
r_i > -\sum_k b_{ik} K_k.
\]

Depending on \( b_{ik} \) this relation can be fulfilled for positive vegetative growth rates (\( r_i > 0 \)) as well as for negative ones as long as they are larger in modulus than the mutualistic contribution. If \( b_{ik} \geq 0 \), the more rewarding the mutualistic interactions are, the lower the limit for the vegetative growth rate condition to reach the carrying capacity. Finally, as before, the position of the saddle point in the presence of two stable fixed points can be derived from the equation system

\[
r_i + \sum_k b_{ik} N_k = 0.
\]

IV. NUMERICAL RESULTS

It is hard to obtain analytical results for a general community due to the intricacy of mutualistic interactions that may form a complex bipartite graph. Only some approximate results have been obtained for a type II model in [10, 24]. This is the reason why we opt here for performing a numerical exploration of the stability and resilience of the model in a more general network. Since the number of individuals in a population is a discrete variable, we have integrated the model using a stochastic and discrete approach. A similar technique has been applied before to epidemiologic studies (see, for instance, [28]). Details on the model implementation are given in \[A\].

Figure 3 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 main behaviors of larger communities. In the first experiment, the system starts with the effective rates of all species below zero, except for that of pollinator number 4 (see numerical configuration of the experiment in \[A\], table \[I\]). We are essentially assuming a case of obligatory mutualism. Under these circumstances, it is easy to find the minimum initial population sizes for the survival of the nine-species mutualistic community, solving \( r_{\text{ef}i}^* = 0 \) in

\( N_{ij}^* = K_{ij} \), with the constraint

\[
r_{\text{ef}i} = r_i + \sum_k b_{ik} K_k > 0,
\]

Figure 4: First experiment results, population dynamics for the different species (each species is color-coded). Numerical configuration of the experiment, \[A\] table \[I\]. Equivalent rates only become positive due to mutualistic benefit. Initial populations are not high enough to make positive the effective rates \( r_{\text{ef}i} \), except for the aforementioned pollinator. Plant species 1 and 2 start with populations above their carrying capacities. This example shows the extinction attractor of dynamics where all populations eventually tend to zero.

The next simulation shown in figure 5 explores the other stable points of the two species analysis: the ones equivalent to \( (0, K_p^2) \), \( (K_a^1, 0) \) and \( (K_a^1, K_p^2) \). Again, all intrinsic rates are negative but mutualistic link weights and initial populations have been slightly modified to make positive several effective rates (see Table B.2). This time all populations start below carrying capacities. Species of both classes grow towards the carrying capacity except pollinator 4 that becomes extinct and plant 4...
that ends the simulation close to extinction. These two species start with negative effective growth rates that are maintained during the simulation. In contrast, plant 2 starts with a negative effective rate that turns positive as the simulation progresses due to the growth of the pollinator population. The evolution of effective rates graph shows how they evolve towards equilibrium as populations are closer to the carrying capacity.

The stability analysis performed in the previous section assumes constant conditions in the rates of the equations. Actually, these rates may vary in more realistic scenarios due to different environmental perturbations. We investigate next the resilience of the system to external perturbations by including temporal sharp increases in the mortality rates for to simulate droughts or plagues.

Literature claims that nestedness is a network property that provides resilience to mutualistic communities [29]. In interaction networks, two types of species can be found: generalists, linked to many instances of the other class; and specialists, tied only to a small number of them. In nested patterns there is a core of generalist species that are highly coupled, whereas specialists are much more likely to be connected to generalists than to other specialists. Researchers have devoted many efforts to find a formal definition and metrics to characterize nestedness, but its influence on system dynamics is not well described. Here, we show two examples to get a glimpse of the role of nestedness in species survival. In the next numerical experiment, we use a network with seven species of plants and five of pollinators [Fig. 6]. We are not going to develop a formal justification, but this network is strongly nested with an easy to identify core of generalist species and specialists tied to generalists of the other class. Initial populations have been chosen to be above the survival threshold.

The system would grow up to reach its overall carrying capacity in the absence of external events, as it happens in Fig. 7. The extinction of plant species 7, which is only linked to pollinator species 1, the most specialist of its class, suffers an additional 0.4 yearly death rate and it becomes extinct. Plant species 7 is only linked to pollinator species 1, the most specialist of its class. Initially, populations have been chosen to be above the survival threshold, and the system is strongly nested with an easy to identify core of generalist species. Initial populations have been chosen to be above the survival threshold.

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network (Fig. 8), that breaks the strong nestedness of previous example. This time plant species 6 is linked to pollinator species 5, an specialist. We also remove the link connecting plant 1 and pollinator 5 and replace it with a link between plant 7 and pollinator 1. Numerical values of the rates for the interaction network are described in Table IV.

Survival chances of a new species that arrives to the community are greater if it is linked to a generalist. This well known property is not only due to the fact that generalists are less prone to extinction because the higher number of links provide them more mutualistic benefit. Linking to an specialist of the the other class exposes to destruction by dragging.

We repeat the simulation but this time with the weaker nested network. The plant species 6 starts with a negative effective rate, that slowly turns positive by the growth of the system. Other species populations move toward carrying capacities slowly from the beginning of the simulation. At time 25000, plant species 7 suffers the same attack as before, and additional 0.40 yearly death rate, that triggers its extinction. However, the effect this time is different. Pollinator species 5 depends for its survival on plant species 7, so the slope of its population becomes negative and will eventually vanish. Plant 6, just connected to specialist pollinator 5, also loses its unique source of mutualistic benefit. So, an external event on plant 7 has dragged plant 6 to destruction because they were indirectly linked by specialist pollinator 5. If both plant species share links with a generalist pollinator this cascade effect is much more unlikely, since generalists are very robust when facing the loss of just one link.

V. CONCLUSIONS

In this work, we have introduced a model derived from the logistic approach to study population dynamics under mutualistic interactions. The proposed equations overcome the drawbacks of the logistic and May’s model when dealing with negative growth rates, an important issue when the system is far from equilibrium and mutualism is obligate. Our model also allows for an easier analytical treatment since the nonlinearities are simpler than for instance those of the type II models. This simplicity makes it also easier to estimate from empirical data the different rates involved in the equations or to assign them an ecological interpretation. This is a key point because mutualism observed dataset are scarce since its compilation is a painstaking task.

We have studied the dynamics of the model finding the dynamics fixed points and their stability analytically for a simple case, and numerically for a more involved community. Our model shows the fixed point structure of May’s model with the notable addition of a saddle point that controls the stability of the whole system. In this regard the model is as rich in dynamic behaviors as the type II models but with a much simpler mathematical structure. We have analyzed numerically the resilience of our model to external perturbations introducing perturbations in a simple but relatively involved mutualistic network. As in other communities described in the literature, the system resilience is a function of the structure of the network. We hope that this new model can be used to gain further insights in the mutualistic communities due to its rich dynamics and simplicity.

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much faster. Poisson Simulation aggregate state variables make them els, the set of states may be huge, while Binomial or Binomial Simulations). In moderate size Markov approach has a number of disadvantages compared with quently used for this kind of simulation, but this ap- sometimes is a non trivial challenge.

Appendix A: Data tables

Data used as input in the experiments are presented in Tables A1, A2, A3 and A4.

| Pl 1 | Pl 2 | Pl 3 | Pl 4 |
|------|------|------|------|
| \( b_{pol1j}(10^{-6}) \) | 1    | 12   | 12   | 16   |
| \( b_{pol2j}(10^{-6}) \) | 20   | 4    | 11   | 0    |
| \( b_{pol3j}(10^{-6}) \) | 10   | 0    | 0    | 0    |
| \( N_{init \ j} \) | 2000 | 2800 | 1200 | 500  |
| \( K_j \) | 1500 | 2500 | 2000 | 1000 |
| \( r_{birth \ j} \) | 0.04 | 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 |
|------|------|------|------|------|
| \( b_{pol1m}(10^{-6}) \) | 4    | 13   | 5    | 3020 |
| \( b_{pol2m}(10^{-6}) \) | 12   | 6    | 1    | 0    |
| \( b_{pol3m}(10^{-6}) \) | 2    | 5    | 0    | 0    |
| \( b_{pol4m}(10^{-6}) \) | 10   | 0    | 0    | 0    |
| \( N_{init \ m} \) | 3000 | 3000 | 2000 | 600  |
| \( K_m \) | 5000 | 4000 | 3000 | 2000 |
| \( r_{birth \ m} \) | 0.08 | 0.02 | 0.05 | 0.025|
| \( r_{death \ m} \) | 0.14 | 0.078| 0.07 | 0.14 | 0.08 |

Table I: Mutualistic coefficients and conditions for the first experiment (fig. 3). Top, pollinator-plant interaction matrix; bottom, plant-pollinator matrix

Appendix B: Numerical treatment of the equations

Population models deal with sets of discrete entities such as animals or plants and computer simulation is a powerful tool to describe the dynamics and stochastic behavior. The choice of a specific simulation method depends on its accuracy and computational efficiency, and sometimes is a non trivial challenge.

For instance, Discrete Markov models have been frequently used for this kind of simulation, but this approach has a number of disadvantages compared with Discrete Stochastic Simulation (Poisson simulations or Binomial Simulations). In moderate size Markov models, the set of states may be huge, while Binomial or Poisson Simulation aggregate state variables make them much faster. For instance, Discrete Markov models have been frequently used for this kind of simulation, but this approach has a number of disadvantages compared with Discrete Stochastic Simulation (Poisson simulations or Binomial Simulations). In moderate size Markov models, the set of states may be huge, while Binomial or Poisson Simulation aggregate state variables make them much faster. 28 30.

| Pol 1 | Pol 2 | Pol 3 | Pol 4 | Pol 5 |
|------|------|------|------|------|
| \( b_{pol1j}(10^{-6}) \) | 10   | 22   | 426  |      |
| \( b_{pol2j}(10^{-6}) \) | 20   | 4    | 11   | 0    |
| \( b_{pol3j}(10^{-6}) \) | 20   | 10   | 0    | 0    |
| \( b_{pol4j}(10^{-6}) \) | 10   | 0    | 0    | 0    |
| \( b_{pol5j}(10^{-6}) \) | 10   | 0    | 0    | 0    |
| \( N_{init \ j} \) | 1200 | 2200 | 1500 | 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 | 0.053|

| Pol 1 | Pol 2 | Pol 3 | Pol 4 | Pol 5 |
|------|------|------|------|------|
| \( b_{pol1m}(10^{-6}) \) | 34   | 33   | 15   | 20   | 60   |
| \( b_{pol2m}(10^{-6}) \) | 12   | 6    | 1    | 0    | 0    |
| \( b_{pol3m}(10^{-6}) \) | 2    | 5    | 0    | 0    | 0    |
| \( b_{pol4m}(10^{-6}) \) | 10   | 0    | 0    | 0    | 0    |
| \( N_{init \ m} \) | 2200 | 3000 | 2000 | 600  | 500  |
| \( K_m \) | 5000 | 4000 | 3000 | 2000 | 2000 |
| \( r_{birth \ m} \) | 0.08 | 0.02 | 0.05 | 0.08 | 0.02 |
| \( r_{death \ m} \) | 0.14 | 0.078| 0.07 | 0.09 | 0.08 |

Table II: Mutualistic coefficients and conditions for the second experiment (fig. 5). Top, pollinator-plant interaction matrix; bottom, plant-pollinator matrix

| Pol 1 | Pol 2 | Pol 3 | Pol 4 | Pol 5 | Pol 6 | Pol 7 |
|------|------|------|------|------|------|------|
| \( b_{pol1j}(10^{-6}) \) | 20   | 12   | 16   | 19   | 16   | 35   |
| \( b_{pol2j}(10^{-6}) \) | 12   | 14   | 4.1  | 2    | 22   | 0    |
| \( b_{pol3j}(10^{-6}) \) | 20   | 11   | 3.1  | 20   | 0    | 0    |
| \( b_{pol4j}(10^{-6}) \) | 11   | 24   | 0    | 0    | 0    | 0    |
| \( b_{pol5j}(10^{-6}) \) | 1    | 0    | 0    | 0    | 0    | 0    |
| \( N_{init \ j} \) | 1200 | 1500 | 800  | 770  | 700  | 400  | 200  |
| \( K_j \) | 2000 | 1800 | 1500 | 1200 | 1000 | 900  | 700  |
| \( r_{birth \ j} \) | 0.004| 0.01 | 0.02 | 0.005| 0.004| 0.025|
| \( r_{death \ j} \) | 0.03 | 0.04 | 0.04 | 0.055| 0.03 | 0.04 | 0.05 |

Table III: Mutualistic coefficients and conditions for the experiment of strongly nested network (fig. 6). Top, pollinator-plant interaction matrix; bottom, plant-pollinator matrix.
We have chosen Binomial Simulation to solve the equations of our mutualistic population model. This technique is a stochastic extension of Continuous System Simulation and a reasonable choice when the outcome of the random process has only two values. For instance, survival over a finite time interval is a Bernoulli process, the individual either lives or dies. Breeding may also be described by a Bernoulli trial if time interval is small. However, in general the number of offspring that become independent of their parents is the product of a number of stochastic processes, and the resulting probability distribution of reproductive success may be quite complex.

For a species with intrinsic growth rate \( r \), we can assume that probability of breeding over an interval \( \Delta T \) is exponentially distributed with an average value \( 1/r \). So, the probability of reproduction is:

\[
P = \int_0^{\Delta T} e^{-rT} \, dt = 1 - e^{-r \Delta T} \quad (B1)
\]

In particular, a population of \( N \) individuals in time \( t \), with pure exponential growth, will be in \( t + \Delta T \):

\[
N(t + \Delta T) = N(t) + \text{sgn} (r) \text{ Binomial} (N(t), P) \quad (B2)
\]

The set of equations \( \{10\} \) becomes in binomial stochastic form:

\[
N_j^a(t + \Delta T) = N_j^a(t) + \text{sgn} \left( \hat{r}_{eq} \right) \text{ Binomial} \left( N_j^a(t), P_j^a \right)
N_j^p(t + \Delta T) = N_j^p(t) + \text{sgn} \left( \hat{r}_{eq} \right) \text{ Binomial} \left( N_j^p(t), P_j^p \right) \quad (B3)
\]

where \( \hat{r}_{eq} \) is the class \( a \) j-species equivalent growth rate in the simulation period, and \( P_j^a \), \( P_j^p \), the probabilities of growth according to equation \( \{10\} \). In particular, working with one day steps, as we do:

\[
\hat{r}_{eq} = e^{e_{eq}/365} - 1 \quad (B4)
\]
on the Good Effects of Intercrossing (Murray, London, 1862).

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