

Relaxing the Mass-Action Law

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I. INTRODUCTION

There has been a tradition, though fairly recent, of studying theoretical ecology problems using ordinary differential equations¹ or more generally simple mathematical formulations. I use the term tradition, since the use of mathematical formulations to describe natural communities dynamics is one among many methods to infer mechanisms or yield understanding on the behaviour of natural systems and in that sense the almost exclusive use of Lotka-Volterra type of systems among the theoretical ecology community can be seen as a tradition. This tradition has permitted many undeniable advances in describing biological patterns, but still has some shortcomings due to underlying assumptions of this type of models, which were both the subject of this class. For this project I decided to focus on the way space is not or not completely modelled in ODE. The huge majority of the early Lotka-Volterra type ODE systems completely ignored space using the mass-action law assumption, a principle derived from chemistry which states that under the assumption of mass-action:

the rate of a chemical reaction is directly proportional to the concentration of the reactants.

This translates for ecological systems in the following: "The rate of interactions in a given natural system are directly proportional to the density of the entities interacting, species, individuals, ...". An implication of the later is that the system and all of its entities are well mixed. This statement can be true for bacteria in a aquatic system with frequent turbulence, a system where dispersal is possible in all three dimensions and where an active redistribution of the individuals happens, but in any two dimensional environment as it is the case for most terrestrial organisms, this assumption does not hold, because of dispersal limitations. Nonetheless attempts have been made to include some spatial features deemed important into the ODE framework [Amarasekare, 2008], [McCann et al., 2005] in what is described as spatially implicit models. Spatially implicit models account for only part of a complex, real, spatial environment by abstracting a feature of this environment and linking it to the dynamics of the system modelled, but do not account for interactions happening at smaller scales and cannot explain emergent properties of a system originating in individual's behaviour as aggregation [DeAngelis and Yurek, 2017]. There is much to say about the assumptions of this protocol. First the linking itself is already an assumption on how exactly spatiality influences the system. Second, and most importantly this feature of the spatial environment is usually difficult to extract and consider independently from others that will be ignored in the process. Third, when one abstracts a spatial environment a

specific geometry is decided to represent the system, usually a grid or continuous positions, but this geometry has been showed to have an important effect on the dynamics of the system [Dieckmann Ulf, 2000]. Let's note that this last point is also of importance for what will be our next subject Individual-Based Models², since a specific representation of the spatial environment is also needed for those.

My goal for this project is to compare two frameworks: an ODE system and an IBM to understand how the assumption of mass-action law impacts the results and therefore the understanding of a natural system modelled through these different methods. This is made possible by the explicit modelling of a spatial environment in IBM where one can follow the positions of all the individuals in each population. For this purpose I made the ODE and IBM models as similar as possible, so the differences observed in the modelled system's behaviour between the two methods should only be due to the different conception of spatiality in the methods, that is, the assumption of the mass-action law or its relaxation.

In the next section, I will present the IBM used for this project.

II. INDIVIDUAL-BASED MODEL

Individual-Based Models are fairly recent in ecology and I thought that a quick overview of their development in this field would be of interest here. Individual-Based Models have become more and more popular among the ecology community over the last 20 years [Grimm, 1999], but are still overlooked by most of the theoretical ecologists because of their complexity which makes their use and the analysis of their results difficult compared to ODE systems [Evans et al., 2013]. Nonetheless, it has been argued that IBM provide an interesting method to study emergent properties in natural systems as populations patterns originating in individuals behaviour [DeAngelis and Grimm, 2014] and their are already used with much success for many applied problems: pest-control in agriculture [Van Roermund et al., 1997], [Parry et al., 2006], modelling the home-range of mobile mammals [Wang and Grimm, 2007], [Pitt et al., 2003], and conservation ecology [Letcher et al., 1998]. But an effort to integrate IBM in theoretical ecology is still lacking, this might be because of the complexity of those models and the large number of parameters they often require, also almost no consistent protocol of comparison exists between IBM and other models like ODE, but see [Siekmann, 2015]. Finally this might simply be because a traditional use of ODE is still present in theoretical ecology and reinforced by the large number of tools produced by the mathematical community to analyse such models. In our

¹For ease of lecture I will further refer to ordinary differential equations as ODE

²For ease of lecture I will further use the abbreviation IBM for Individual-Based Model

case the decision to use an IBM is a logical consequence of our problematic, but it is also an attempt to study if the comparison of two different modelling framework is possible using simple analytic tools and simulations. The IBM used here is modified from the `predatorpreywithplot.py` file of the PyCX Project (<http://pycx.sourceforge.net/>) compiled with Python 2.7. The code from the `predatorpreywithplot.py` file has been modified in several ways, but mainly to enable parallel computing of the simulations using the python multi-processing library, the structure of the model itself was mostly kept as in the original. All the scripts used to produce the data in this project are available in a github repository: https://github.com/timothevanmeter/Lotka-Volterra_IBM, the scripts to produce the different figures and the different visualisation tools are available as well.

a) *Model Structure*: The IBM uses a continuous grid on which individuals occupy positions determined by two values, x and y . The model has two species a Resource and a Predator, both species are able to disperse and reproduce. The Predator in addition is able to consume Resource individuals. The model is implemented to function with discrete time steps, for each time step the following events are resolved in the simulation in this order:

- All individuals disperse across the grid
- All possible predation events are resolved across the grid
- Dead individuals, from predation and background mortality, are removed from the grid
- All reproduction events are resolved
- New time step

Name	Category	Default Value
Width (W)	Environment	250
Height (H)	Environment	250
Maximum Time Step (T_{max})	Simulation	1000
Initial Population (I_R)	Resource	500
Population Limit (K_R)	Resource	500
Reproduction Rate (r_R)	Resource	0.3
Dispersal Ability (d_R)	Resource	8
Initial Population (I_P)	Predator	500
Population Limit (K_P)	Predator	200
Reproduction Rate (r_P)	Predator	0.3
Dispersal Ability (d_P)	Predator	8
Background Mortality (m)	Predator	0.03
Minimum Predation Distance (d_{min})	Predator	3

TABLE I: All simulation parameters are presented above with their name, category and the default value used during the simulations. For all figures and simulations only the parameters with a value differing from the default one are precised.

Table I presents all the parameters necessary for a simulation with this model.

b) *Initialisation*: All simulations are initialised by placing all initial resource and predator individuals on the grid using an uniform distribution, $\sim U^2(0, \text{Width})(0, \text{Height})$, with the width and height of the grid environment (see Table I).

c) *Dispersion of Individuals*: Every individual moves according to their Dispersal Ability. For each time step each in-

dividual moves from its current position with a value obtained from a gaussian distribution $\sim N(O, \text{Dispersal Ability})$. The borders of the grid are limiting: individuals moving beyond the maximum height and width of the grid are kept at the limits of the grid.

d) *Predation*: Predation events are defined by the variable called Minimum Predation Distance that sets the maximum distance for which a predation event can occur. If the distance between a predator and a prey is less than the square of the value of Minimum Predation Distance a predation event occurs:

$$(x_R - x_P)^2 + (y_R - y_P)^2 < (\text{Minimum Predation Distance})^2$$

It is important to note that for one time step a predator will consume all the resource individuals within its reach.

e) *Background Mortality*: Background Mortality is only included in the model for the predator with the term m . This is implemented in the model as follow: a number is drawn at random from a uniform distribution, $\sim U(0, 1)$, and compared to the value of the Background Mortality variable. Therefore a predator dies under the condition:

$$\text{Background Mortality} > U(0, 1)$$

f) *Reproduction*: The reproduction events are modelled by a random sampling between 0 and 1. The condition for a successful reproduction event is:

$$r_X(1 - \frac{X}{K_X}) > \text{random}$$

With X being either the prey or predator. For the predator there is an additional condition for a reproduction event to occur: the predator is able to reproduce only after a successful predation event. This is why the reproduction rate is scaled by the predation term, αRP , for the predator's dynamics in the ODE model (see next section). This rule corresponds to an energy limitation, there is a limited pool of energy that can be allocated to any physiological function other than survival, as reproduction, so the individuals need to have enough energy or prey biomass consumed to be able to attempt a reproduction event.

III. ORDINARY DIFFERENTIAL EQUATIONS SYSTEM

In this section I *translate* the previous IBM model into an ODE formulation. As previously mentioned this formulation needs to be as similar to the IBM's functioning as possible so that the differences in behaviour of the two methods can be entirely attributed to the way the spatiality of the environment is modelled. The following ODE system was used:

$$\begin{aligned} \dot{R}(t) &= r_R(1 - \frac{R}{K_R}) - \alpha RP & (\text{System S}) \\ \dot{P}(t) &= r_P \alpha RP(1 - \frac{P}{K_P}) - mP \end{aligned}$$

The *translation* of the *per capita* growth rate for the Resource and the reproduction rate for the Predator from the IBM are straightforward, since the IBM already uses a mathematical formulation to model reproduction (see Reproduction). The mortality for the Predator also does not cause any problem

and can be simply added as a constant, m . The way to model the consumption rate yields more problems. I decided to incorporate a single term summarising the predation, α . This term is used in the Resource's dynamics as $-\alpha RP$, modelling the consumption of the Resource by the Predator, and is also combined to the reproduction rate of the Predator as $r_P(1 - \frac{P}{K_P}) \cdot \alpha RP$, modelling the energy limitation previously mentioned (see Reproduction). The obvious problem of this formulation is that by summarising predation in a single term we ignore the spatial constraints of predation, but since our aim is to compare the behaviour of models relaxing or not the assumption of mass-action law this formulation suits our purpose. I should note that if there was any other conceptual differences than the assumption of mass-action law, hiding inside the predation term, α , our comparison would have to be corrected if possible or dismissed in the worst case.

A. Isocline Analysis

From the System S the isoclines for the resource, R , and the predator, P are derived below for $\dot{R}(t) = 0$ and $\dot{P}(t) = 0$.

$$\begin{aligned} \dot{R}(t) = 0 &\Leftrightarrow \alpha RP = r_R(1 - \frac{R}{K_R}) \\ &\Leftrightarrow P = \frac{1}{R} \cdot \frac{r_R}{\alpha} - \frac{r_R}{\alpha K_R} \end{aligned} \quad (R^*)$$

$$\begin{aligned} \dot{P}(t) = 0 &\Leftrightarrow mP = r_P \alpha RP(1 - \frac{P}{K_P}) \\ &\Leftrightarrow m = r_P \alpha R - \frac{r_P \alpha R}{K_P} \cdot P \\ &\Leftrightarrow P = K_P - \frac{1}{R} \cdot \frac{m}{r_P \alpha} \end{aligned} \quad (P^*)$$

We can see that R 's isocline (R^*) is a curve in \mathbb{R}^+ , as P 's isocline (P^*) is a curve in \mathbb{R} . As seen in Figure 1 for the Resource to maintain itself in the system there is a continuous gradient between two extreme situations where the Predator, P , is very abundant and the Resource, R , is rare and another extreme where it is the Resource, R , that dominates the system and the Predator, P , that is rare. The Predator's isocline form is presented in Figure 7. When $R \rightarrow 0$, P^* is superposed with y axis, as when Resource are increased the value of P^* increases rapidly towards the value of its population limit, K_P until it reach it and then remains constant, more formally $R \rightarrow \infty \Leftrightarrow P^* = K_P$. If we are now to imagine the intersections of R 's isocline (Figure 1) and P 's isocline (Figure 2) we see that the only possible equilibrium points are all along the Predator axis, on the left hand side in Figures 1 and 2 and that the position of the possible equilibrium points depends on the form of both isoclines: how close to the y axis they intersect and therefore how close to extinction is the Resource. Figure 3 synthesizes this with both isoclines on the R, P domain and the associated vector field. We can observe that there is a stable solution where R 's and P 's isoclines intersect which is attractive from any point in the phase plane. Indeed, all the trajectories gather at this point equilibrium. This point equilibrium is very close to the y axis and as we mentioned earlier because of the respective

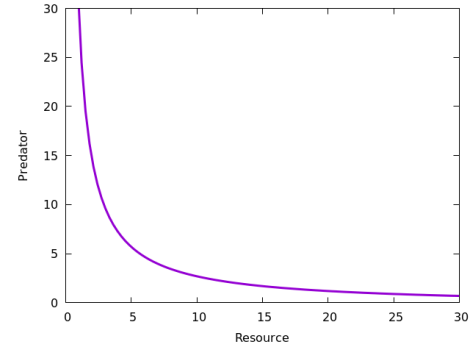


Figure 1: Isocline curve, R^* , for the Resource, R , in the R, P domain.

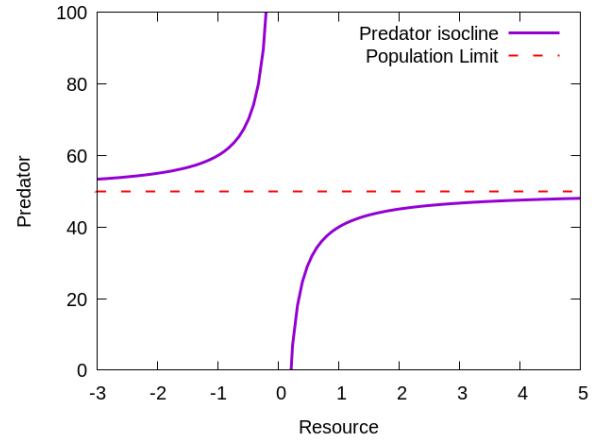


Figure 2: Zoom of the Figure 7 (see Appendix 1) near the population limit, K_P .

forms of the isoclines this is always the case. Analytically, this is not a concern since the equilibrium point is attractive from anywhere in the phase plane, but the system is likely to collapse once stochasticity is included: the Resource being so close to extinction. To add to this last point, the predation parameter, α , is likely to ensure more stability in the system when small, because it controls the shape of both isoclines: $R^* \approx \frac{1}{x \cdot \alpha}$, $P^* \approx K_P - \frac{1}{x \cdot \alpha}$ indeed when α is small both $\frac{\partial R^*}{\partial t}$ and $\frac{\partial P^*}{\partial t}$ have smaller values, the isoclines reach their respective asymptotic limits slower which makes possible the existence of equilibrium points further away from the y axis.

B. Invasibility of the System

To assess if invasion is possible for R and P when the other species is dominant in the system I first formulate the isoclines for R and P when the other species is absent.

$$\begin{aligned} \dot{R}(t) &= r_R(1 - \frac{R}{K_R}) \\ &\Leftrightarrow R_{I^*} = K_R \end{aligned}$$

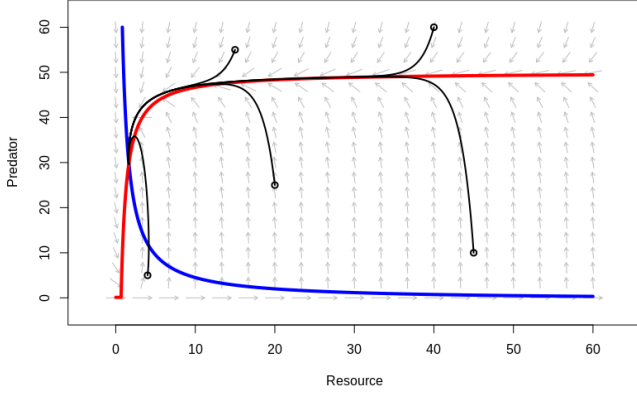


Figure 3: The R, P phase plane with in red the **Predator's isocline** and in blue the **Resource's isocline**. The black lines represent trajectories of the system taken for the initial positions symbolized by a black circle, \odot . The parameters used for this figure are $r_R = 0.5$, $K_R = 100$, $r_P = 0.3$, $K_P = 50$, $\alpha = 0.01$, $m = 0.2$

$$\begin{aligned}\dot{P}(t) &= r_P \alpha R P \left(1 - \frac{P}{K_P}\right) - mP \\ \Leftrightarrow P_I^* &= \frac{r_P}{m + \frac{r_P}{K_P}}\end{aligned}$$

We now substitute the equilibrium density for P when R is absent into $\dot{R}(t)$ to determine if R is able to invade the system.

$$\dot{R}(t) = r_R \left(1 - \frac{R}{K_R}\right) - \alpha R \frac{r_P}{m + \frac{r_P}{K_P}}$$

Since when invading $R \rightarrow 0$

$$\Leftrightarrow \dot{R}(t) = r_R - \alpha R \frac{r_P}{m + \frac{r_P}{K_P}}$$

For the invasion to be successful we need $\dot{R}(t) > 0$

$$\Leftrightarrow r_R > \alpha R \frac{r_P}{m + \frac{r_P}{K_P}}$$

This can be simplified because usually $K_P \gg r_P$ which yields the following:

$$r_R > \alpha R \frac{r_P}{m} \quad (C1)$$

This shows that the Resource can invade the system when its reproduction rate exceeds the impact of predation of the Predator's population, $\frac{r_P}{m}$ is simply the growth rate of the Predator's population.

As above, we can substitute the equilibrium density for R when P is absent into $\dot{P}(t)$ to determine if P is able to invade the system.

$$\dot{P}(t) = r_P \left(1 - \frac{P}{K_P}\right) \alpha P K_R - mP$$

Since when invading $P \rightarrow 0$

$$\Leftrightarrow \dot{P}(t) = r_P \alpha P K_R - mP$$

For the invasion to be successful we need $\dot{P}(t) > 0$

$$\Leftrightarrow r_P \alpha K_R > m \quad (C2)$$

Here condition C2 is straightforward: for the Predator to invade the system its reproduction rate combined to the expected consumption rate of the Resource needs to exceed its mortality rate. We will note the presence of the Resource's population limit, K_R , in the consumption term. Effectively, the absolute presence of the Resource is necessary but not sufficient to permit the Predator to invade. This is because of the Predator's energy limitation modelled within its reproduction rate.

C. Eigenvalues Analysis

Using our equation System S we can derive the jacobian matrix \mathbb{J}_S :

$$\mathbb{J}_S = \begin{pmatrix} -(\frac{r_R}{K_R} + \alpha P) & -\alpha R \\ r_P \alpha P (1 - \frac{P}{K_P}) & r_P \alpha R (\frac{K_P - 2P}{K_P}) \end{pmatrix}$$

The characteristic eigenvalues have the form:

$$\begin{aligned}\lambda_1 &= \frac{1}{2} \cdot (-\sqrt{a^2 - 2ad + 4bc + d^2} + a + d) \\ \lambda_2 &= \frac{1}{2} \cdot (\sqrt{a^2 - 2ad + 4bc + d^2} + a + d)\end{aligned}$$

After substituting the terms of the matrix \mathbb{J}_S in λ_1 and λ_2 , I was not able to obtain a simplified mathematical expression that had an obvious biological meaning and therefore did not further pursue this method.

IV. COMPARISON

Using the IBM described previously (see IBM section) I was able to run exploratory simulations to characterise the behaviour of the system. Figure 5 presents an equivalent of the invasibility criteria of the system for the IBM. For any initial population number of Predator we see an average invasion of the system with both Resource and Predator coexisting for long period of time in the system, it might be useful to remind that the minimum number of individuals presented on the y axis is obtained for simulations with 1000 time steps, showing that the system is relatively stable. We can try to compare with the condition for invasion in the ODE model:

$$\begin{aligned}r_P K_R \alpha &> m \\ 0.3 \cdot 500 \cdot \alpha &> 0.03 \\ \alpha &> 2 \cdot 10^{-4}\end{aligned}$$

Since we cannot have an estimation of α for the IBM model the stability and long-term coexistence observed in the simulations of Figure 5, might be simply caused by a too important predation level in our simulations. To test this hypothesis I looked at the system's stability for different values of the Minimum Predation Distance, d_{min} . This decision is based on the behaviour of the IBM that seems to be very sensitive to variation in the d_{min} parameter and intuitively is the closest conceptually to the predation term, α , in the ODE. The results are presented in Figure 6. We can observe that for values of d_{min} under 3.0 the Predator is not able to maintain itself in the environment, this is caused by the energy limitation: when

this value is too low the Predators are not able to consume enough Resource to both survive and reproduce. Also, when increasing d_{min} for values greater than 3.0 we can see a steady decrease in the minimum number of Resource individuals and for values of d_{min} greater than 7.0 the Resource population cannot maintain itself in the system. This extinction of the Resource for large values of d_{min} , can be due to two distinct causes:

- First, when the value of d_{min} is larger than that of the Resource's Dispersal Ability the Resource individuals cannot escape predation by dispersion and the impact of predation is thus too important for the system to foster coexistence.
- Second, as mentioned previously (see Isoclines section) for large values of α the both isoclines steepened towards their asymptotic limits making the possible equilibrium point closer to the y axis and the Resource to extinction. Which correspond very well to the increasing *stochastic-like* behaviour of the model for larger values of α . This can be seen in Figure 6, where for high values of d_{min} the variance in the minimum number of individuals increases and even though there is very few extinctions of the Resource the system is less stable. This pattern is also visible in Figure 4, where there is progressive increase in the variance of the minimum number of individuals without any extinction.

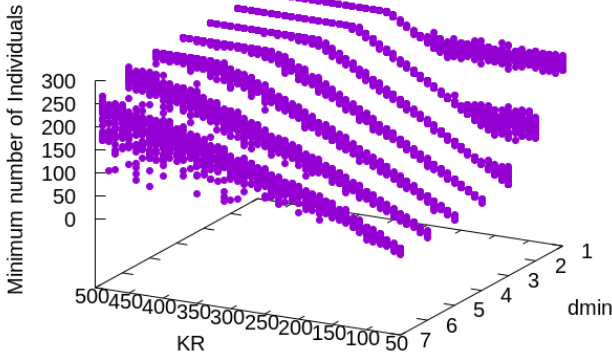


Figure 4: Each dot, \bullet , represents the minimum number of Resource individuals for one simulation. The x axis corresponds to the population limit for the Resource, K_R . The y axis corresponds to the minimum predation distance, d_{min} . The parameters used for this figure are $I_P = 100$, $K_P = 100$. For each combination of parameters 30 simulations were performed.

V. DISCUSSION

The comparison between our two models is sadly limited by our ability to estimate an equivalent of the ODE's term α and by the time required to adequately explore the parameter space for the IBM model. Both models show remarkably

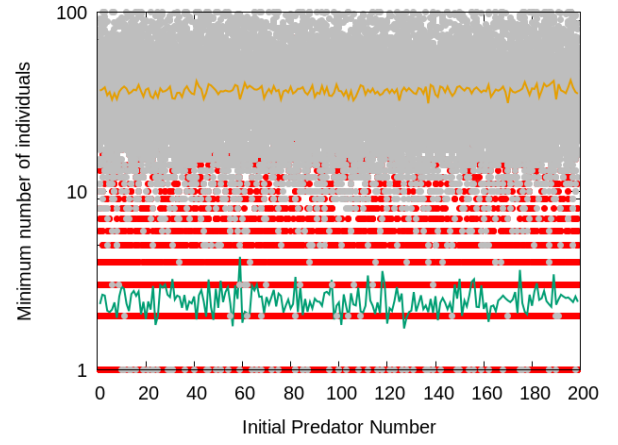


Figure 5: Each dot represents the minimum number of individuals, Resource in red \bullet , Predator in gray \bullet , for one simulation with a initial number of Predator, on the x axis, corresponding to the parameter Initial Population of the Predator. The lines are the running means of minimum number of individuals, the Resource is represented by the green line $-$, and the Predator by the gold line $-$. The parameters used for this figure are $I_R = 300$, $d_R = 4$, $d_{min} = 8$. For each combination of parameters 100 simulations were performed.

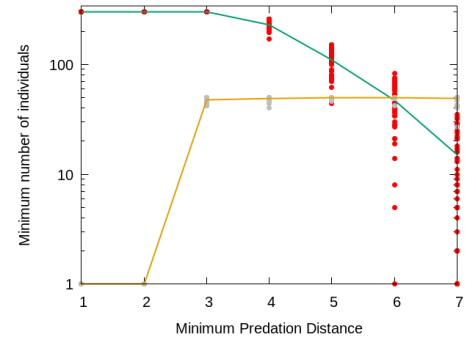


Figure 6: Same as Figure 5, but here the x axis, corresponds to the parameter Minimum Predation Distance. The parameters used for this figure are $I_R = 300$, $d_R = 8$, $I_P = 50$. For each combination of parameters 50 simulations were performed.

close results for the parameters explored. In both cases a stable solution exists where both species are maintained in the system, see Figures 3 and 8, and in both systems invasion of one of the species is possible under certain values of predation intensity, see the Invasibility section and Figure 4. A striking pattern is that in all stable solutions observed for the IBM the Predator is very abundant relatively to the Resource, as shown in Figures 5 and 8 a pattern that is expected given the form of R 's and P 's isoclines: as mentioned earlier, see Isoclines section, the possible equilibrium points are located very close to the y axis yielding a community where the Predator is very abundant and the Resource close to extinction. This similarity could be caused by the use of identical mathematical formulation of the reproduction rates which constrains the

IBM to mimic the behaviour of the ODE. This could also simply mean that in under certain conditions both models produce similar behaviour and that the spatial environment is similar in behaviour to a well-mixed system. The dispersal abilities, d_R, d_P , could be too important relative to the size of the environment $250 \cdot 250$ which would make the emergence of uncoupled local dynamics impossible: the latter has been proved to cause significant differences in the population dynamics compared to the equivalent well-mixed system [deRoos et al., 1991]. Another possibility is that the work presented here is not sufficient to have a complete understanding of the system and make valuable comparisons. The only exception to the abundance pattern described above is for certain values of the minimum predation distance, $d_{min} \in [3, 6]$, see Figure 6, where the Resource is relatively more abundant than the Predator in the community. This is not expected, since even for small value of α the equilibrium points of the ODE system remain close to the y axis. We again are left interpreting how to understand this predation term and to compare it to a combination of the IBM parameters, d_{min}, d_R, d_P, W, H . Indeed, the predation term is critical for the comparison of both systems and gathers many different aspects of the IBM model in one variable which interpretation remains obscure at the least. The strategy I have developed here is to construct the two systems in a similar way to enable comparisons, but the inherent complexity of the IBM framework compared to the ODE hinders this comparison. Here, maybe using simpler IBM and thus ODE systems [deRoos et al., 1991] might make comparisons easier and generally the analysis of the IBM less tedious. Another interesting aspect of this comparison that was not developed here, is the aggregation of individuals in the spatial environment. This phenomena has already been observed in communication models [Baalén and Jansen, 2003], with two morphs: an honest signaler and a cheater. The aggregation of honest individuals together permitted to keep this morph in simulations even though analytically the cost of being honest was too important to maintain any honest individuals in the environment. Similarly, random spatial aggregation was observed for number of simulations with high predation levels (data not shown) where Resource's individuals were *escaping* the Predator population in the spatial environment long enough to replenish their population size and maintain themselves in the environment. Further investigating how individuals perceive their local environment would help determine if spatial aggregation plays a role in enabling coexistence in this model. Understanding how spatial aggregation of individuals impacts population dynamics and community dynamics would be especially useful in the context of conservation ecology, where it has been shown that aggregation can be associated with higher population growth [Letcher et al., 1998].

VI. CONCLUSION

To summarise, our comparison found both models to exhibit very similar behaviours of stability and community composition, Predator with high relative abundance. But for small values of the minimum predation distance, d_{min} , we observe an inversion of the community composition, Resource with

high relative abundance. I found the formulation of a predation term, α , to be conceptually intricate and gathering multiple aspects of a complex spatial interaction, which is described by at least 3 and up to 5 parameters in the corresponding IBM: d_{min}, d_R, d_P, W, H . This shows the necessity to explore further the impact of the spatial environment on this interaction term and study what are the mechanisms linking the numerous parameters governing relative dispersion abilities (relative to other individuals, species and relative to the size of the environment), consumption, perception of the local environment and the individuals interactions. This work has showed the difficulty of comparing models constructed with different frameworks and the necessity of developing a general protocol for this task, as already explored by Siekmann.

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VIII. APPENDICES

A. Appendix 1

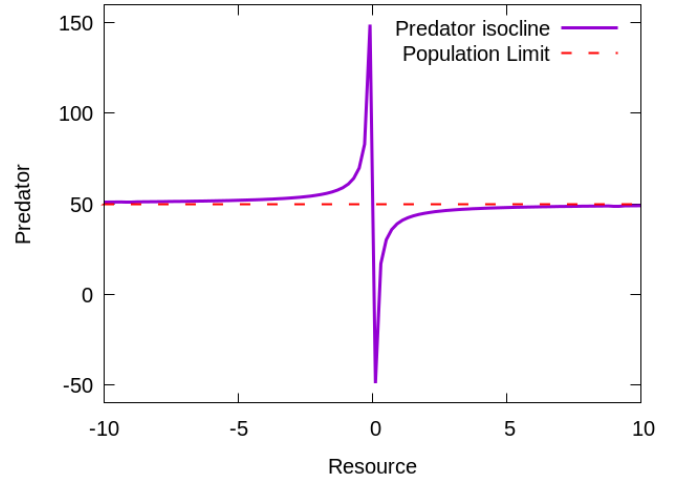


Figure 7: Isocline curve, P^* , for the Predator, P , in the R, P domain.

B. Appendix 2

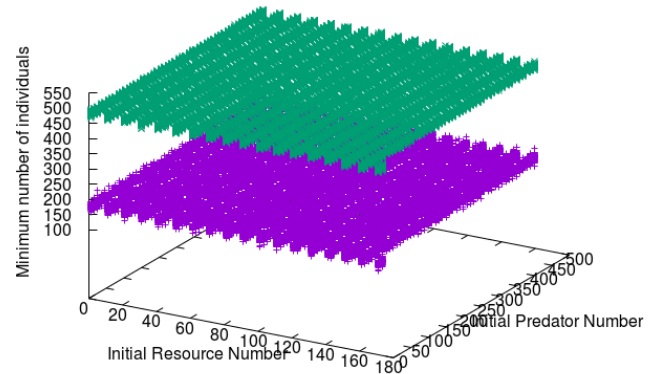


Figure 8: Each dot represents the minimum number of individuals, Resource in violet ●, Predator in green ●, as measured by the z axis. The x axis corresponds to the initial population of the Resource. The y axis corresponds to the initial population of the Predator. The parameters used for this figure are the default values in Table I. For each combination of parameters 50 simulations were performed.