

On predator prey

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1 Non evolutionary scenario

In this setting the model is as in the draft but without the evolution of costs functions. The parameters are common to all the species and I report them here for reference: resources consumption rate η , predators (on both levels) resource gain γ , reproduction threshold d , primary resource regeneration rate λ and a catch rate q which represent the probability that, when they meet, a predator catches a prey (it is the same for predators on both levels). The linear dimension of the grid is denoted by L .

1.1 Mean-field theory

In order to understand the dynamics I formulated a mean-field theory for the problem based on the observation that the relevant dynamical quantities are the internal resources of the agents. I denote the internal resources of the n -th prey as k_p^n and do the same for first and second level predators, respectively $k_{\pi_1}^n$ and $k_{\pi_2}^n$ as in the draft. The first step is to assume a well mixed population which allows to neglect spatial structure and build the theory. In the following I derive the dynamical equations for the total resources held by each species to leverage then on their conservation at stationarity in order to obtain expression for the densities of agents.

Let me start with the second level predators π_2 , and consider the evolution of the internal resources of a single agent (valid $\forall n$)

$$\Delta_t k_{\pi_2}^n = -\eta + \gamma q P_{\pi_1}, \quad (1)$$

where $\Delta_t f \equiv f(t + \Delta t) - f(t)$, being Δt a time step, and P_{π_1} stands for the probability of the agent to encounter, in the grid cell where it moved, *at least one* predator π_1 . To obtain P_{π_1} one can notice that the probability of each of the N_{π_1} first level predator to be found in a given cell is $1/L^2$ (in force of the well mixing assumption). This implies that, denoting the density of predators π_1 with $\rho_{\pi_1} = N_{\pi_1}/L^2$, the number random number ξ of π_1 in a grid point is Poisson distributed

$$\mathcal{P}_{\rho_{\pi_1}}(\xi) = \frac{\rho_{\pi_1}^\xi}{\xi!} e^{-\rho_{\pi_1}}, \quad (2)$$

therefore $\mathcal{P}_{\rho_{\pi_1}}(0) = e^{-\rho_{\pi_1}}$ and $P_{\pi_1} = 1 - e^{-\rho_{\pi_1}}$. If I now sum over all the π_2 and divide by the grid size L^2 , denoting $k_{\pi_2} = \sum_{n=1}^{N_{\pi_2}} k_{\pi_2}^n$, I obtain

$$\frac{\Delta_t k_{\pi_2}}{L^2} = -\eta \rho_{\pi_2} + \gamma q (1 - e^{-\rho_{\pi_1}}) \rho_{\pi_2}. \quad (3)$$

Before deriving the other two equations let me stress that it is possible to absorb a parameter, η , in the definition of time (a sort of metabolic timescale) and redefining all the other parameters as $\lambda/\eta \leftarrow \lambda$, $\gamma/\eta \leftarrow \gamma$, $d/\eta \leftarrow d$ and $q/\eta \leftarrow q$ we can get rid of it (perfectly confirmed numerically).

The single agent equation for π_1 predators is *mutatis mutandis* the same as Eq. (1)

$$\Delta_t k_{\pi_2}^n = -1 + \gamma q(1 - e^{-\rho_p}), \quad (4)$$

where $(1 - e^{-\rho_p})$ is the probability that at least one preys is present on the grid point visited by the agent. A predator π_1 , though, can be killed by predators π_2 and when this happen the internal resources $k_{\pi_1}^n$ are lost; this has to be taken into account when looking at the total resources k_{π_1} . I have

$$\frac{\Delta_t k_{\pi_1}}{L^2} = -\rho_{\pi_1} + \gamma q(1 - e^{-\rho_p})\rho_{\pi_1} - q(1 - e^{-\rho_{\pi_2}})\frac{k_{\pi_1}}{L^2}\rho_{\pi_1}, \quad (5)$$

where $q(1 - e^{-\rho_{\pi_2}})$ is the rate at which predators π_1 are killed. One can write $k_{\pi_1}/L^2 = \rho_{\pi_1} k_{\pi_1}/N_{\pi_1} = \rho_{\pi_1} d\alpha_{\pi_1}$ assuming that at stationarity the average amount of resources held by a single π_1 is a fraction α_{π_1} of the reproduction threshold d and arrive at

$$\frac{\Delta_t k_{\pi_1}}{L^2} = -\rho_{\pi_1} + \gamma q(1 - e^{-\rho_p})\rho_{\pi_1} - qd\alpha_{\pi_1}(1 - e^{-\rho_{\pi_2}})\rho_{\pi_1}. \quad (6)$$

Preys share the resources found on the ground, therefore for the n -th prey one can write

$$\Delta_t k_p^n = -1 + \frac{\lambda}{\rho_p}, \quad (7)$$

and thus, with obvious notation,

$$\frac{\Delta_t k_p}{L^2} = -\rho_p + \lambda - qd\alpha_p(1 - e^{-\rho_{\pi_1}})\rho_p. \quad (8)$$

It is interesting that the amount of resources acquired by the totality of the preys (per unit area) is exactly λ . An other way to recognise this would be to think directly in terms of total population. The average amount of resources in a grid point can be estimated as $\lambda/(1 - e^{-\rho_p})$, because for every time-step that preys don't visit the point it increases by λ . Therefore the total amount of resources (per unit area) acquired by the preys is this number multiplied by the fraction of occupied grid points, which is $(1 - e^{-\rho_p})$.

Collecting everything, at stationarity, I have

$$\begin{aligned} 0 &= -\rho_{\pi_2} + \gamma q(1 - e^{-\rho_{\pi_1}})\rho_{\pi_2}, \\ 0 &= -\rho_{\pi_1} + \gamma q(1 - e^{-\rho_p})\rho_{\pi_1} - qd\alpha_{\pi_1}(1 - e^{-\rho_{\pi_2}})\rho_{\pi_1}, \\ 0 &= -\rho_p + \lambda - qd\alpha_p(1 - e^{-\rho_{\pi_1}})\rho_p. \end{aligned} \quad (9)$$

Notice that in all three equations d and γ always appears multiplied by q , and the latter is never present alone, thus we can redefine $\gamma q \leftarrow \gamma$ and $dq \leftarrow d$ and absorb it (perfect numerical check). Finally the equations for the densities read

$$\begin{aligned} \rho_p &= \frac{\lambda}{1 + \alpha_p d/\gamma}, \\ \rho_{\pi_1} &= \ln \left(\frac{\gamma}{\gamma - 1} \right), \\ \rho_{\pi_2} &= \ln \left\{ \frac{1 + \alpha_{\pi_1} d - \gamma [1 - e^{-\lambda/(1 + \alpha_p d/\gamma)}]}{\alpha_{\pi_1} d} \right\}. \end{aligned} \quad (10)$$

An interesting observation from the simulation is that the fractions $\alpha_p \simeq 2/3 \simeq \alpha_{\pi_1}$ robustly w.r.t. the variation of the parameters. This is nice and intuitive because at stationarity one expects that p and π_1 , having both to support an upper trophic level (the first π_1 and the second π_2), indeed have an average amount of internal resources which is between the reproduction threshold d and $d/2$ (the initial amount of the progeny). The only parameters in the game remain d and γ , a part of course form the independent variable λ .

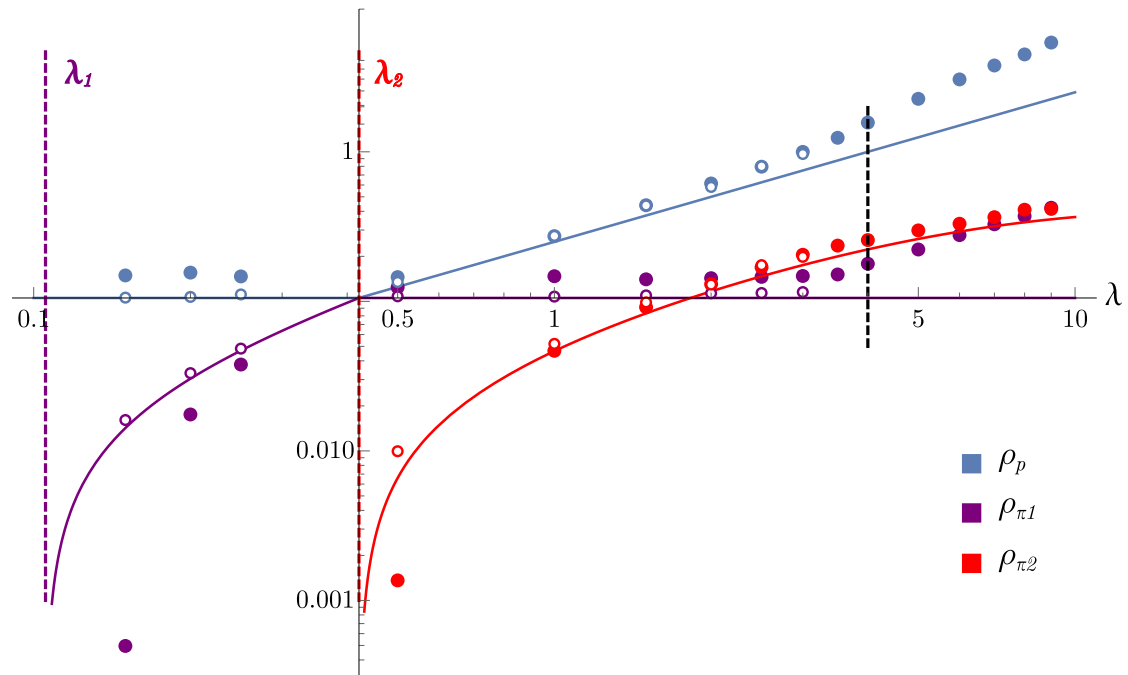


Figure 1: Prey density ρ_p (blue), first level predator density ρ_{π_1} (purple) and second level predator density ρ_{π_2} (red) are plotted against λ for fixed $d = 40$ and $\gamma = 10$. Solid lines represent mean-field theory predictions from Eqs. (10,12). Purple and red dashed vertical lines stands respectively for λ_1 (Eq. (13)) and λ_2 (Eq. (11)). Solid dots correspond to simulations with Moore connectivity while empty ones to a fully connected graph. The values are time averages from time 300 to time 3000 or from time 500 to time 5000 (where a time step consist of the movement of every agent in the grid) and L varies from 30 to 150. Both choices (time and size) are such that, at the given value of λ a stable solution is attained and the system is there for enough time to have an acceptable statistics.

In Fig. 1 are reported results of simulations (see caption for details) and compared with the mean field theory for $d = 40$ and $\gamma = 10$.

The red dashed vertical line in Fig. 1 correspond to the point

$$\lambda_2 = \left(\frac{d\alpha_p}{\gamma} + 1 \right) \ln \left(\frac{\gamma}{\gamma - 1} \right), \quad (11)$$

obtained using the last of Eqs. (10), below which no positive solution for ρ_{π_2} exists and the system reduces to a two level food web. In this regime, using the same arguments as above, the

mean-field equations for preys and predators π_1 reads

$$\begin{aligned}\rho_p &= \ln \left(\frac{\gamma}{\gamma - 1} \right), \\ \rho_{\pi_1} &= \ln \left[\frac{\ln \left(\frac{\gamma}{\gamma - 1} \right) \alpha_p d}{\ln \left(\frac{\gamma}{\gamma - 1} \right) (\alpha_p d - 1) + \lambda} \right].\end{aligned}\tag{12}$$

The value of λ below which also the population of π_1 can not be supported, i.e. when the second of Eqs. (12) becomes negative, is

$$\lambda_1 = \ln \left(\frac{\gamma}{\gamma - 1} \right),\tag{13}$$

represented by the purple dashed vertical line in Fig. 1. The phase transitions observed in the simulations (at least in the non evolutionary setting) are therefore perfectly described by the mean-field theory.

Let me discuss now the break down of the mean-field theory for high value of λ . More precisely this happens, robustly with respect to variations of d and γ , when $\rho_p > 1$, therefore, from the first of Eqs. (10), at

$$\lambda^c = 1 + \frac{\alpha_p d}{\gamma},\tag{14}$$

which is represented by the black dashed vertical line in Fig. 1. Here, numerically, happens that for a fully connected graph, the system does not have a stable stationary solution but a limit cycle (yet to be characterized) appears. Curiously enough in the case of Moore connectivity stable solutions exists (better simulations needed though to completely confirm this) but they deviate from the mean field prediction and an allometric relation between ρ_p and ρ_{π_1} sets in with roughly $\rho_{\pi_1} \sim \rho_p^{3/4}$. I have some ideas on why this happens but are too speculative for now, a discussion is in order. I want just to mention that this "strange" deviation appears for values of the parameter λ in a weird regime, meaning in a regime where the density of prey exceeds 1, and can be questioned that such regime is of interest in understanding realistic scenarios.

A part from this last point, which is though of the highest importance to clarify, the mean-field presented completely characterize the model and exclude allometric relation for reasonable (?) values of the parameters.

$$prova2\tag{15}$$