



# Predator-Prey Models in Heterogeneous Environment: Emergence of Functional Response

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**Abstract**—In this work, we are interested in prey-predator models. More precisely, we study the spatial heterogeneity effects on the amount of prey eaten per predator per unit time, when different time scales occur. This amount and its relation with the amount of predators produced via the predation are interesting from an ecological point of view. Indeed, the knowledge of these quantities permits us to quantify the transfer of the biomass in the food chain. Our aim is to show how the spatial heterogeneity acts on these amounts. We consider prey-predator systems in a multi-patch environment. We show that density dependent migrations make emerge new models on the total population level and we exhibit some examples. Furthermore, we show that the aggregation method is a good tool for describing the mechanisms hidden behind complex models.

**Keywords**—Predator-prey models, Functional response, Emergence, Aggregation method.

## INTRODUCTION

In the years 1925–1926, Lotka and Volterra have proposed the first mathematical predator-prey model

$$\begin{aligned}\frac{dN}{dt} &= rN - aNP, \\ \frac{dP}{dt} &= -\mu P + cNP.\end{aligned}\tag{1}$$

This model assumes that the prey density growth exponentially in the absence of the predator and that the predator density decays exponentially (Malthus Law). The second main assumption is that the amount of prey disappearing per unit time and the amount of predator produced per unit time are proportional to the number of the encounters (Mass Action Law). If these laws could be acceptable in an homogeneous environment, as it is the case in some chemistry examples, their applications are limited in ecological environments, which are generally heterogeneous ones. More complex models have been proposed in order to avoid the problems of the Lotka-Volterra model (see [1,2] for example). Some authors proposed mechanistic arguments to explain their model: their mechanisms use assumptions on the individual behavior. In this paper, we show why the aggregation method provides a tool for the construction of predator-prey models via a mechanistic approach.

In the next section, we present a detailed model with two time scales: one is associated to the individuals level, the other one is associated to the population level. We use the aggregation method in order to obtain simpler models governing the population densities and in which emerge some complex functional responses. In the following section, we give some examples where the

emerging functional responses are known (Holling Type II and Beddington-de Angelis functional responses). In the fourth section, we give an example in which a new model emerges.

## THE MODEL

Many predator-prey models have been proposed. Among these models, a large part consist of models which has the following form:

$$\begin{aligned}\frac{dN}{dt} &= f(N)N - g(N, P)P, \\ \frac{dP}{dt} &= eg(N, P)P - \mu P.\end{aligned}\tag{2}$$

where  $f(N)$  is the per capita prey growth rate in the absence of the predator,  $\mu$  is the predator per capita death rate in the absence of the prey,  $g(N, P)$  is the amount of prey eaten per predator and per unit time and  $eg(N, P)$  is the per capita production of predator due to predation. Note that in this case, the predator growth rate is proportional to the amount of eaten prey. The function  $g(N, P)$  is generally called the functional response and the per capita production of predator due to predation,  $eg(N, P)$ , is called the numerical response. The functional response plays a main role in models (2): the knowledge of this function determines the dynamics of the whole system and it determines the transfer of the biomass in the food chain because it is proportional to the numerical response.

Many authors proposed different functional responses (one can refer to [3–5] for comparative tables). These functions are build on the basis of phenomenological arguments. In this paper, we are interested in the construction of functional responses with mechanistic arguments. By using the aggregation methods, we can understand the link between the functional response and the individuals dynamics.

Now, we propose a predator-prey model in a multi-patch environment. It permits us to take into account the spatial heterogeneity. Furthermore, we shall consider some aspects of the individuals behavior: the individuals migrations depend on their behavior. Consequently, we assume that the migrations process takes place at the individuals time scale which is shorter than the population time scale. The interaction between the populations are assumed to be as simple as possible: for example, by considering that each patch is quasi-homogeneous, we apply the Mass Action Law on each patch. For the sake of simplicity, the model presented here is a two patches model. The general case can easily be deduced from our model but the calculations should be more complicated and should not present any interest. The global model has the following form:

$$\begin{aligned}\frac{dN_1}{d\tau} &= k_{12}^N N_2 - k_{21}^N N_1 + \varepsilon N_1 (r_1 - A_1 P_1), \\ \frac{dN_2}{d\tau} &= k_{21}^N N_1 - k_{12}^N N_2 + \varepsilon N_2 (r_2 - A_2 P_2), \\ \frac{dP_1}{d\tau} &= k_{12}^P P_2 - k_{21}^P P_1 + \varepsilon P_1 (\mu_1 - e_1 A_1 P_1), \\ \frac{dP_2}{d\tau} &= k_{21}^P P_1 - k_{12}^P P_2 + \varepsilon P_2 (\mu_2 - e_2 A_2 P_2),\end{aligned}\tag{3}$$

where  $N_i$  and  $P_i$  are the prey and predator densities on patch  $i$ ,  $k_{ij}^N$ , and  $k_{ij}^P$  are the prey and predator migration rates from patch  $j$  to patch  $i$  and these rates can be functions depending on the prey or predator densities,  $r_i$  is the prey growth rate in the absence of predator on patch  $i$ ,  $\mu_i$  is the predator death rate in the absence of prey on patch  $i$ ,  $A_i$  is the predator attack rate on patch  $i$  and  $e_i$  is the conversion efficiency of the predator on patch  $i$ . The small parameter  $\varepsilon \ll 1$  is used because the migration process is faster than the other ones.

Now, we construct the aggregated model: we assume that the fast part of the model (3), obtained by putting  $\varepsilon = 0$ , has an equilibrium. This equilibrium is calculated by solving the system

$$\begin{aligned} k_{12}^N(N_1, N_2, P_1, P_2)N_2 - k_{21}^N(N_1, N_2, P_1, P_2)N_1 &= 0, \\ k_{21}^N(N_1, N_2, P_1, P_2)N_1 - k_{12}^N(N_1, N_2, P_1, P_2)N_2 &= 0, \\ k_{12}^P(N_1, N_2, P_1, P_2)P_2 - k_{21}^P(N_1, N_2, P_1, P_2)P_1 &= 0, \\ k_{21}^P(N_1, N_2, P_1, P_2)P_1 - k_{12}^P(N_1, N_2, P_1, P_2)P_2 &= 0, \end{aligned} \tag{4}$$

with respect to  $N_1, N_2, P_1$ , and  $P_2$ . We denote with a star  $*$  the solutions of the system (4):  $N_1^*, N_2^*, P_1^*$ , and  $P_2^*$ . Let the total population densities be:  $N = N_1 + N_2$  and  $P = P_1 + P_2$ . These total densities are constant at the short time scale: their derivatives vanish when  $\varepsilon = 0$ . Let the equilibrium frequencies of subpopulations be:  $u_i^* = N_i^*/N$  and  $v_i^* = P_i^*/P$ . The aggregation method allows us to formulate the aggregated model in the form:

$$\begin{aligned} \frac{dN}{dt} &= (r_1 u_1^* + r_2 u_2^*) N - (A_1 u_1^* v_1^* + A_2 u_2^* v_2^*) NP + O(\varepsilon), \\ \frac{dP}{dt} &= -(\mu_1^* v_1^* + \mu_2^* v_2^*) P + (e_1 A_1 u_1^* v_1^* + e_2 A_2 u_2^* v_2^*) NP + O(\varepsilon), \end{aligned} \tag{5}$$

where  $t = \varepsilon\tau$  is the long time (population time scale). If the model (5) with  $\varepsilon = 0$  is structurally stable, then we can neglect the terms of order of  $\varepsilon$  from a qualitative point of view. Note, that in the two populations case, the set of structurally stable population models is an open and dense set in the space of the two populations models (see for example [6]). In other words, the model which are not structurally stable are rare. Hence, in this case, the functional response at the population level is:

$$g(N, P) = (A_1 u_1^* v_1^* + A_2 u_2^* v_2^*) N, \tag{6}$$

where the equilibrium frequencies can be functions on  $N$  and  $P$ , thus the functional response (6) is not necessarily a Lotka-Volterra's one. The formula (6) shows the link between the functional response at the population level and the equilibrium frequencies which are the result of the individuals dynamics. In the next section, we present two examples of known functional responses and we propose migrations behaviours which lead to these functional responses. Furthermore, in each case, we calculate the whole aggregated model.

## EXAMPLES OF KNOWN FUNCTIONAL RESPONSES

Among all the known functional responses, some ones are more used because they are simple and believe empirical arguments. In this section, we show how the aggregation method leads to these models. What is the interest of presenting known results with new tools, which *a priori* seem to be more complicated than the original ones? One can answer this question with two arguments. First, the method permits to build many functional responses and as we shall show, many individuals dynamics may lead to the same functional response. The known mechanisms proposed for the known functional responses are not the only ones possible. The aggregation method permits us to find other examples of mecahnisms for a fixed functional response. Also, from a theoretical viewpoint, it is interesting to investigate what are the individuals dynamics leading to a given populations dynamics model. However, the best way from a biological point of view should be to determine what are the actual scenarii of migrations for example and then to deduce the corresponding aggregated model. The second argument is that the aggregation method is a general one for constructing population models with a mechanistic approach and, in such a case, it is necessary to verify that it "contains" the known mechanisms.

A first example of known functional response is the Holling Type II one:

$$g(N, P) = \frac{AN}{1 + BN}, \tag{7}$$

where  $A$  and  $B$  are positive numbers. The mechanism that leads to this functional response can be found in [3,5]. The main idea is the saturation of the predator when the prey density is large. Now, we propose two mechanisms leading to this functional response. In the first one, we assume that the prey migrates randomly between the patches and that the patch 2 is a refuge for the prey and a rest patch for the predator: the predator attack rate on the patch 2 is null ( $A_2 = 0$  in (3)). Finally, we assume that when the prey density on patch 1 is large, the predator migration rate from the predation patch to its rest patch increases. This scenario is the translation of the Holling mechanism in our formalism. The model (3) becomes:

$$\begin{aligned}\frac{dN_1}{d\tau} &= k_{12}^N N_2 - k_{21}^N N_1 + \varepsilon N_1 (r_1 - A_1 P_1), \\ \frac{dN_2}{d\tau} &= k_{21}^N N_1 - k_{12}^N N_2 + \varepsilon r_2 N_2, \\ \frac{dP_1}{d\tau} &= k_{12}^P P_2 - k_{21}^P P_1 - \varepsilon P_1 (\mu_1 - e_1 A_1 P_1), \\ \frac{dP_2}{d\tau} &= k_{21}^P P_1 - k_{12}^P P_2 - \varepsilon \mu_2 P_2,\end{aligned}\tag{8}$$

where  $k_{ij}^N$  are constants, and  $k_{12}^P = \gamma = C^{te}$ ,  $k_{21}^P = \delta N_1$ . In this case, a straightforward calculation shows that  $u_i^* = C^{te}$ ,  $v_1^* = \gamma / (\gamma + \delta u_1^* N)$ . Consequently, by using formula (6), we deduce that

$$g(N, P) = g(N) = A_1 u_1^* \frac{\gamma}{\gamma + \delta u_1^* N} N,\tag{9}$$

which is a Holling Type II functional response. The whole aggregated model is:

$$\begin{aligned}\frac{dN}{dt} &= rN - \frac{ANP}{1 + BN}, \\ \frac{dP}{dt} &= -\mu_1 P + \varepsilon \frac{ANP}{1 + BN},\end{aligned}\tag{10}$$

where  $A = A_1 u_1^*$ ,  $B = \delta u_1^* / \gamma$  and  $e = e_1 (\mu_1 - \mu_2) \delta / A_1 \gamma$ . It follows that the mechanism proposed by Holling can easily be interpreted in the formalism of the aggregation method. Note, that in model (10) the prey and predator densities are unbounded. Consequently, the prey densities on each patch are unbounded and one can object that the small terms in model (8) become large after a long time: the aggregation method cannot be applied after this time. It is easy to avoid this problem by replacing the malthusian prey growth by a logistic one. It does not change anything in the calculations above and lead to a logistic prey growth at the population level: then all the densities are bounded and the aggregation is always valid. We have chosen a malthusian prey growth because it shall simplify the further calculations, where the previous problem will not occur.

We propose now a second mechanism which leads again to the Holling Type II functional response. We assume again that the patch 2 is a refuge patch for the prey and a rest patch for the predator. However, we assume now that the predator migrates randomly and that the prey migration rate from the predation patch to its refuge increases when its density is large. Finally, we assume that the growth in the refuge is negative because this patch does not contain resource, for example. It follows that  $A_2 = 0$  again and that  $r_2 = -d_2 < 0$ . The migration rates are  $k_{ij}^P = C^{te}$  for the predator and  $k_{12}^N = \alpha = C^{te}$ ,  $k_{21}^N = \beta N$  for the prey. The complete model has still the form of the model (8). The equilibrium frequencies are  $u_1^* = \alpha / (\alpha + \beta N)$  and  $v_i^* = C^{te}$ . The formula (6) gives again the functional response:

$$g(N, P) = g(N) = A_1 \frac{\alpha}{\alpha + \beta N} v_1^* N.\tag{11}$$

In this case, we still obtain the Holling Type II functional response with another mechanism. It can be proved [7] that in this example, the prey growth in the absence of the predator in the population model is a logistic one. So, all the densities are bounded which means that the aggregation method is valid without time limitation. The predator equation has the same form as in model (2).

We shall study the case of another functional response which is now depending on both prey and predator densities: the Beddington-de Angelis functional response. Its expression is:

$$g(N, P) = \frac{AN}{1 + BN + CP}, \quad (12)$$

where  $A, B$  and  $C$  are positive numbers. One can refer to [4,5] for more details. The main ideas hidden behind this formula are:

- there is a saturation effect when the prey density is large,
- when the predator density is large, the individuals must fight to obtain their food and spend some time before the catching: their attack rate decreases.

Once again, we translate these ideas in our formalism by using the migration rates. Yet, the form of the model is that of model (3). We assume that the patch 1 is a refuge patch for the prey and that for the predator, the patch 2 corresponds to a state in which the individuals do not take care of the prey (they fight or they rest for example). The prey migrates randomly between its refuge and the predation patch. When the prey density on the predation patch is large, the predator finds easily its food, it stops to forage rapidly: its passage rate from the foraging state to the rest state increases. Furthermore, when the predator density increases, its passage rate from the foraging state to the fighting for food state increases too. The "migration" rates can be written as follows:  $k_{ij}^N$  are constant and  $k_{12}^P = \gamma = C^{te}$ ,  $k_{21}^P = \delta N_1 + \lambda P$ . The equilibrium frequencies corresponding to these rates are:  $u_i^* = C^{te}$ ,  $v_1^* = \gamma / (\gamma + \delta u_1^* N + \lambda P)$ . One can now deduce the functional response of the population model by using formula (6):

$$g(N, P) = \frac{AN}{1 + BN + CP}, \quad (13)$$

where  $A = A_1 u_1^*$ ,  $B = \delta u_1^* / \gamma$  and  $C = \lambda / \gamma$ . The known mechanism of the Beddington-de Angelis functional response can thus be included in the aggregation method formalism. The whole population model is:

$$\begin{aligned} \frac{dN}{dt} &= rN - g(N, P)P, \\ \frac{dP}{dt} &= -\mu(P)P + e(P)g(N, P)P, \end{aligned} \quad (14)$$

where  $g(N, P)$  is given by formula (13),  $\mu(P) = (\mu_1 \gamma + \mu_2 \lambda P) / (\gamma + \lambda P)$  and  $e(P) = e_1 + (\mu_2 - \mu_1) (\delta \lambda P) / (A_1 \gamma (\gamma + \lambda P))$ .

An important consequence of these expressions is that the numerical response is not proportional to the functional response. The mechanism proposed for the Beddington-de Angelis functional response breaks the structure of the models (2). It means that when we use a mechanistic approach in order to study a part of a model, we must consider the effects of the mechanism on the other parts. This fact seems obvious but it must be recalled as it has important consequences.

Let us consider another scenario leading to the same functional response. We still consider the model (8) where we assume that  $r_2 = -d_2 < 0$ , the predator migrates randomly. The prey migration rate from the predation patch to its refuge is assumed to increase when the prey density is large or also when the predator density on the predation patch increases (the prey tries to avoid the capture). The migration rates are  $k_{ij}^P = C^{te}$  for the predator and  $k_{12}^N = \alpha = C^{te}$ ,

$k_{21}^N = \beta N + \sigma P_1$  for the prey. The resulting equilibrium frequencies are  $u_i^* = \alpha / (\alpha + \beta N + \sigma v_1^* P)$  and  $v_i^* = C^{te}$ . The formula (6) again permits us to calculate the functional response:

$$g(N, P) = \frac{AN}{1 + BN + CP}, \quad (15)$$

where  $A = A_1 v_1^*$ ,  $B = \beta / \alpha$ , and  $C = \sigma v_1^* / \alpha$ . The mechanism described above provides us a second mechanism for the Beddington-de Angelis functional response. The whole population model can be expressed as follows:

$$\begin{aligned} \frac{dN}{dt} &= f(N)N - G(N, P)P, \\ \frac{dP}{dt} &= -\mu P + e_1 g(N, P)P, \end{aligned} \quad (16)$$

where  $g(N, P)$  is given by (15),  $f(N)N = (r_1 \alpha N) / (\alpha + \beta N) (1 - (d_2 \beta N) / (r_1 \alpha))$  and  $G(N, P)$  is the impact of one predator on the prey density per unit time. A calculation proves that:

$$G(N, P) = g(N, P) + (r_1 - d_2) \frac{\sigma}{A_1 \alpha} \left( 1 + \frac{\beta N}{\alpha + \beta N} \right) g(N, P). \quad (17)$$

As a consequence, the predator acts on the prey density not only by the predation, but also by forcing the prey to migrate to a patch where its growth rate is less favourable (see [8] for more details). Once again, the structure of the model (2) is broken while it occurred in each patch and a new structure emerges at the population level.

In the next section, we propose an example where the functional response and the aggregated model are new.

### EXAMPLE OF A NEW PREDATOR-PREY MODEL WITH A NEW FUNCTIONAL RESPONSE

In the previous section, our reasoning was to find the individuals dynamics leading to a given functional response. We proceed in another way in this section. Indeed, now, we choose migration rates and we investigate the population model corresponding to them. We study the obtained dynamics.

The general form of the complete detailed model is still form (3) with  $r_2 = -d_2 < 0$  and we assume again that the patch 2 is a refuge for the prey ( $A_2 = 0$ ). We assume that the predator migrates randomly. The prey avoids the predator in the predation patch and when the prey density increases, the prey migration rate from the refuge to the predation patch increases. The expressions of the migration rates are:

$$\begin{aligned} k_{12}^N &= \alpha N, \\ k_{21}^N &= \beta P_1, \\ k_{12}^P &= \gamma = C^{te}, \\ k_{21}^P &= \delta = C^{te}. \end{aligned} \quad (18)$$

The resulting equilibrium frequencies are:

$$\begin{aligned} u_1^* &= \frac{\alpha N}{\alpha N + \beta v_1^* P}, \\ u_2^* &= \frac{\beta P}{\alpha N + \beta v_1^* P}, \\ v_1^* &= \frac{\gamma}{\gamma + \delta} = C^{te}, \\ v_2^* &= \frac{\delta}{\gamma + \delta} = C^{te}. \end{aligned} \quad (19)$$

As the formula (6) always holds, the functional response is:

$$g(N, P) = \frac{A_1 \alpha v_1^* N^2}{\alpha N + \beta P}. \quad (20)$$

Note, that the aggregation can be applied only if the prey density or the predator density on patch 1 are sufficiently large else the prey migration rates should be small and the fast process should become slow.

The aggregated model reads:

$$\begin{aligned} \frac{dN}{dt} &= \left( r_1 - \frac{(r_1 + d_2)\beta v_1^* + \alpha A_1 v_1^* P}{\alpha N + \beta v_1^* P} \right) N, \\ \frac{dP}{dt} &= -\mu P + \frac{e_1 A_1 v_1^* \alpha}{\alpha N + \beta v_1^* P} P, \end{aligned} \quad (21)$$

where  $\mu = \mu_1 v_1^* + \mu_2 v_2^*$ . The mathematical analysis of this model can be found in the appendix. It shows that this model has a positive equilibrium which is a focus. A Hopf bifurcation can occur when the parameter values vary. In fact, if the prey death rate  $d_2$  in the refuge is greater than the predator death rate  $\mu$  then the focus is unstable and it is stable when  $d_2$  is lower than  $\mu$ .

The main goal of this section was to show that simple individuals dynamics models associated to the aggregation method leads to new predator-prey models (refer to [8] for other more complex examples). Furthermore, it proves again that even if the local models (in each patch) have the structure of model (2) then the aggregated model has an emergent structure in which the role of the functional response is not the most important.

## CONCLUSION

As we showed in this work, the aggregation method provides an efficient tool for the construction of models with a mechanistic approach. A formula as (6) proves that it is possible to relate analytically the individuals dynamics and the population dynamics. In the predator-prey models case, we have noted that the known reasoning used to build models can easily be included in the aggregation method formalism. Furthermore, we have proved that some simple other individuals behaviors could lead to the known functional responses. An important point to notice is that with the mechanistic approach, the structure of the models (2), which is generally used, can be broken. When one explains a part of a model with a mechanism, one must study the effects of this mechanism on the other parts.

From a biological viewpoint, the method should be used in an other way. An interesting way to proceed is to determine how the individuals migrate for example, to modelize the fast part and finally, to apply the method in order to obtain the populations dynamics models.

## APPENDIX

### MATHEMATICAL ANALYSIS OF MODEL (21)

Let us consider the system:

$$\begin{aligned} \frac{dN}{dt} &= \left( r_1 - \frac{(r_1 + d_2)\beta v_1^* + \alpha A_1 v_1^* P}{\alpha N + \beta v_1^* P} \right) N, \\ \frac{dP}{dt} &= -\mu P + \frac{e_1 A_1 v_1^* \alpha}{\alpha N + \beta v_1^* P} P. \end{aligned} \quad (A.1)$$

We begin by performing a change of coordinates in order to simplify the system. We consider the following variables:

$$x = \alpha N, \quad y = \beta v_1^* P, \quad \text{and} \quad \theta = r_1 t. \quad (A.2)$$

In this system of coordinates, the system (A.1) reads:

$$\begin{aligned}\frac{dx}{d\theta} &= x \left( 1 - \frac{(r_1 + d_2)\beta v_1^* + \frac{A_1 v_1^*}{\alpha}}{x + y} \frac{y}{r_1 v_1^* \beta} \right), \\ \frac{dy}{d\theta} &= -\frac{\mu}{r_1} y \left( 1 - \frac{e_1 A_1 v_1^*}{\mu \alpha} \frac{x^2}{x + y} \right).\end{aligned}\tag{A.3}$$

We can again simplify the expression of the system by considering the new parameters:

$$\begin{aligned}A &= \frac{r_1 + d_2}{r_1} > 1, \\ B &= \frac{A_1 v_1^*}{\alpha \beta v_1^* r_1} > 0, \\ \rho &= \frac{\mu}{r_1} > 0, \\ \nu &= \frac{e_1 A_1 v_1^*}{\alpha \mu}.\end{aligned}\tag{A.4}$$

We multiply the system by the positive function  $(x, y) \mapsto x + y$ , hence the resulting system has the same trajectories. It is the following:

$$\begin{aligned}\frac{dx}{d\theta} &= x(x - (A - 1)y - Bxy), \\ \frac{dy}{d\theta} &= -\rho y (x + y - \nu x^2).\end{aligned}\tag{A.5}$$

There are equilibria out the axis, they are given by the formulas:

$$\begin{aligned}x^* &= \frac{-((A - 1)\nu - B) \pm \sqrt{(((A - 1)\nu - B)^2 + 4AB\nu)}}{2B\nu}, \\ y^* &= x^*(\nu x^* - 1).\end{aligned}\tag{A.6}$$

There is at most one positive equilibrium, obtained in putting the sign  $+$  in the first formula in (A.6). In fact, one can easily check that this equilibrium exists for all values of the positive parameters. Now, we look at its stability and we show that a Hopf bifurcation occurs when the parameters vary. The linear part of (A.5) is given by the matrix:

$$\begin{pmatrix} x^*(1 - By^*) & x^*(1 - A - Bx^*) \\ -\rho y^*(1 - 2\nu x^*) & -\rho y^* \end{pmatrix}.\tag{A.7}$$

Let  $T$  be the trace of this matrix and  $D$  be its determinant. One can check that

$$T = y^*(A - 1 - \rho),$$

and that

$$D = \rho x^* y^* (B\nu(x^*)^2 + A).$$

This equilibrium is then a focus or a node. The sign of  $T$  determines its stability. Clearly, it is possible to choose the parameter  $\rho$  more or less large, in a such way that the sign of  $T$  changes. This change leads to a Hopf bifurcation.



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