The implicit assumptions of classic functional responses and their multi-species extensions

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Abstract

Functional responses are central to describe consumer-resource interactions. Defined as the per capita average feeding rate of consumers, since Holling's seminal papers, they have been widely used in ecology. Holling's central observation was that they often saturate as resource density increases. If the interference between consumers is strong, they also decrease with consumer density. Here we emphasize the link between individual feeding processes and emergent population-averaged feeding rates and the associated probability distributions of the different behavioral types. We do so by revisiting a classic approach based on the formulation of feeding interactions in terms of chemical reaction schemes. We highlight the common assumptions leading to the different functional forms. Our work has clear implications, on the one hand, for both model selection and parameter inference from feeding experiments, and, on the other, for the use of multi-species extensions of these functional responses in population-level food web dynamic models.

Keywords: Holling type II, Beddington-DeAngelis, Multi-species Holling type II and III, Stochastic feeding processes, Consumer-resource dynamics, Higher order interactions

Introduction

Functional responses can be regarded as a very early example in ecology of a general research agenda in science: how can processes at a lower level of aggregation —for instance, the individual level— be used to approximate the macroscopic dynamics of a system at a higher level of aggregation —for instance, the population or the community level? Holling's seminal papers show how the behavior of individual consumers gives rise to an average feeding rate over the whole consumer population, which then can be used in population-level models. Methods to derive macroscopic equations from the elementary processes affecting individuals are continuously developed in statistical physics, ecology and beyond. One well-established research line considers individuals as interacting particles and describes their interactions in terms of chemical kinetics [39]. The use of this approach in population, community ecology, and the dynamics of infectious diseases has become widespread [35, 25, 1, 3, 12, 14, 5, 2]. Here we extensively apply these methods to functional responses.

Functional responses measure how per capita average feeding rates of consumers respond to density of both resources and consumers. They have been widely applied in ecological research from more than 60 years. From an empirical perspective, feeding rate models are used to explain feeding experiments [13, 42, 31, 27, 37]. From a theoretical perspective, functional responses are also introduced in food web models to explore central questions in ecology that range from ecosystem stability [16, 32] to the role of biodiversity in maintaining ecosystem functions in response to global change [18, 4]. Both applications would benefit a great deal from a careful examination of the underlying assumptions involved in the derivation of these functional forms.

Consumers undergo different processes while feeding on resources, which can be represented by chemical-like reaction schemes. To our knowledge, this approach was first used by Real [30], who re-examined the derivation of the Holling type II functional response, and derived, for the first time, the Holling type III functional response in a clear analogy to allosteric enzymatic reactions. This functional response would arise as a consequence of an increasing attacking efficiency of predators as they become exposed to higher and higher resource densities. The predator-dependent Beddington-DeAngelis [10, 17] functional response has been also framed in terms of chemical-like reaction schemes [33], although we suggest here a more consistent derivation based on a reaction scheme that includes both direct interference and fight for resources.

In this note, we revisit then the derivation of these two classic functional responses: Holling type II [21, 22], and Beddington-DeAngelis [10, 17]. Surprisingly, we discover that the latter does not result from the underlying individual feeding processes in the same exact and consistent way as the former does, and, as a consequence, it should be interpreted rather phenomenologically, or, at most, as an approximation. By critically re-examining the derivation of these classic functional responses, our main focus is to emphasize, on the one hand, the sometimes overlooked underlying assumptions all these derivations rely on, and, on the other, the inherent stochastic nature of the feeding process [28]. Our approach can be extended to more general functional responses, as long as the hypotheses underlying the individual feeding process can be represented by discrete events conveniently described by chemical-like reactions. As an example, we derive different multi-species functional responses depending on the underlying assumptions about the individual feeding processes, leading to different alternative extensions of the classic Holling type II functional response. These multi-species derivations show clearly which individual mechanisms could be behind higher order interactions in species-rich consumer-resource communities [27, 37].

Holling Type II

Throughout this note, let us remark from the outset that we use predator-prey and consumer-resource as fully interchangeable terms, respectively.

A consumer on a single resource

In the most simple case, consumers can attack resource items, and then spend some time handling and/or digesting them, until they get ready to attack and capture new resources again. Therefore, feeding dynamics can be simply described by the following two processes:

$$X_A + X_R \xrightarrow{\alpha} \emptyset + X_{AR}\,, \tag{1}$$

$$X_{AR} \xrightarrow{\nu} X_A\,, \tag{2}$$

where individual consumers X_A encounter resource items X_R at a rate α creating a pair or "compound" X_{AR}, i.e. a handling predator, which "relaxes back" into a free consumer at rate ν. Although here space is not explicitly considered, the empty set in Eq (1) emphasizes that the actual interaction involves the jump of the predator onto the prey, which would leave empty space behind. In addition, in this derivation, we consider that resource density is kept constant, at the same resource level, n_R^0. Since no reaction leading to consumer depletion is assumed, the total number of consumers, $n_A^0 = n_A + n_{AR}$, is also kept constant. In analogy to chemical kinetics, we call these conditions of constant population for both prey and predators *chemostatic consitions* [39]. Consumers can be then in two behavioral stages, either searching new resources or handling them, X_A and X_{AR}, respectively. At any given time, since the total number of consumers is constant, we can characterize the configuration of the system only by the number of searching consumers, n_A, free and ready to attack new resources. If we assume that we can pack at most N resources in an given area where consumers *move randomly around*, their effective attack rate will be damped by the actual density of resources (n_R/N) in that area. This common assumption is usually called true *mass action* [24, 39].

In this context, we can dynamically model the feeding process by using one-step stochastic process in continuous time. This formalism allows to express the temporal evolution of the probability of finding n_A free consumers at time t, $P(n_A, t)$ through a master equation, which can be solved for stationarity. In this case, at steady-state, n_A will be binomially distributed with parameters $p = \left(1 + \frac{\alpha}{\nu} x_R^0\right)^{-1}$ and n_A^0 (see Box I and SM for details), where we have defined x_R^0 as the resource density ($\frac{n_R^0}{N}$). In particular, the average number of free consumers at stationarity will be given by $\langle n_A \rangle = p\, n_A^0$. The average rate of resource depletion caused by the total population of n_A^0 predators at stationarity will be given by $\theta \langle n_A \rangle$, where $\theta \equiv \alpha\, x_R^0$, which, when expressed on a per capita basis, gives rise to a per capita feeding rate, the Holling Type II functional response:

$$\langle f(x_R) \rangle = \frac{\alpha x_R}{1 + \frac{\alpha}{\nu} x_R}. \tag{3}$$

where we have finally dropped the superscript 0 on the densities. This emphasizes that, while x_R^0 was a parameter throughout our derivation, in Eq (3), it is no longer a parameter but a true variable. We will take this prescription also to write the final expressions of the functional responses throughout all the derivations that follow.

Notice that the classic expression by Holling includes the handling time, τ, which is the average time it takes for an individual consumer to handle and digest a resource item. In our framework, this is $1/\nu$, the average relaxation time associated to the first order kinetics represented by reaction (2).

A consumer on multiple resources

Let us consider now that a consumer individual X_A can feed on a range of S alternative resources, X_{R_i} with $i = 1, \ldots, S$. In this situation, the dynamics can be summarized by $2\,S$ individual feeding reactions:

$$X_A + X_{R_i} \xrightarrow{\alpha_i} \emptyset + X_{AR_i}, \tag{4}$$

$$X_{AR_i} \xrightarrow{\nu_i} X_A. \tag{5}$$

The first one takes into account resource preferences as involves distinct attack rates (α_i) for the different resources, and the formation of handling consumers for each of the resources. Handling times ($1/\nu_i$) are also characteristic for individual consumers feeding on each of the resource types. The total consumer population, n_A^0, is divided in $S+1$ classes, $n_A^0 = n_A + \sum_{i=1}^{S} n_{AR_i}$. As before, we could also translate the reaction scheme (4)-(5) into transition probability rates between discrete states, and solve the master equation for the temporal evolution of the probability of finding a given discrete configuration of consumer types, $(n_A, n_{RA_1}, \ldots, n_{RA_S})$, at a given time t, for stationarity. However, here we simply present instead the deterministic rate equations emerging from this reaction scheme and calculate the average number of free consumers at stationarity, which we show leads to the average feeding rate per individual consumer when feeding on a given resource type.

For convenience, we first define $n_X \equiv \langle n_X \rangle$, as continuous variable representing the different subpopulations of consumers: free consumers, n_A, and handling consumers for each resource type, n_{AR_i}. The rate of temporal change of these variables associated to the reaction scheme (4)-(5) can be written as:

$$\frac{dn_A}{dt} = \sum_{i=1}^{S} \nu_i n_{AR_i} - \sum_{i=1}^{S} \theta_i\, n_A \tag{6}$$

$$\frac{dn_{AR_i}}{dt} = -\nu_i n_{AR_i} + \theta_i\, n_A \tag{7}$$

where the effective per capita attack rate of a free consumer at a given density level of the $i-th$ resource type is a resource-specific constant parameter defined by:

$$\theta_i \equiv \alpha_i\, x_{R_i}^0 \tag{8}$$

where $x^0_{R_i}$ is the densit of the i-th resource. The system represented by Eqs (6)-(7) is a coupled system of $S+1$ ODEs. Solving it for stationarity makes use that both consumers, n^0_A, and all resource levels, $n^0_{R_i}$, are kept constant, so all θ_i are constant parameters. Under these assumptions, we obtain the following linear system of equations:

$$\mathcal{M}\begin{pmatrix} n_A \\ n_{AR_1} \\ \dots \\ \dots \\ n_{AR_S} \end{pmatrix} = \begin{pmatrix} \theta_1 & -\nu_1 & \dots & \dots & 0 \\ \theta_2 & 0 & -\nu_2 & \dots & 0 \\ \dots & \dots & \dots & \dots & 0 \\ \theta_S & 0 & 0 & \dots & -\nu_S \\ 1 & 1 & 1 & 1 & 1 \end{pmatrix}\begin{pmatrix} n_A \\ n_{AR_1} \\ \dots \\ \dots \\ n_{AR_S} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \\ n^0_A \end{pmatrix}. \tag{9}$$

By inverting the matrix $\mathcal{M}$, we can find the distribution of the different consumer subpopulations at stationarity. Notice that $n^\star_A = (\mathcal{M}^{-1})_{1\,(S+1)}\, n^0_A$, which immediately leads to:

$$n^\star_A = \frac{1}{1+\sum_{i=1}^{S}\frac{\theta_i}{\nu_i}}\, n^0_A \tag{10}$$

The subpopulation of free consumers $n^\star_A$ is responsible for the total rate of resource loss at stationarity. In particular, resource i is consumed by ready-to-attack, free individuals at a per capita rate θ_i. Therefore, total resource depletion of resource i per unit time is $n^\star_A\,\theta_i$ at stationarity, which, on a per capita basis, becomes the multi-resource Holling type II functional response of an average consumer feeding on a focal resource of the i-th type in the presence of alternative resource types:

$$\langle f_i(x_{R_1},\dots,x_{R_S})\rangle = \frac{\alpha_i\, x_{R_i}}{1+\sum_{j=1}^{S}\frac{\alpha_j}{\nu_j}x_{R_j}} \tag{11}$$

So far reaction schemes (1)-(2) and (4)-(5) assumed that the individual feeding mechanism is not affected by the presence of either conspecifics (through interference), variable levels of resource density, nor different types of resources. The feeding process is only controlled by the relative presence of the different resources, and the specific rates at which an individual consumer attacks and handles each resource type. In other words, individual attack rates (α_i) and handling times ($1/\nu_i$) for resource type i are the same regardless whether the individual feeds in total isolation or not, reacts differently to different levels of resource density, or when exposed to more than one resource type. If these parameter rates are not independent of all these factors, more complicated functional responses should be expected [37]. We also emphasize, although not always explicitly expressed, that both the single- and this multi-resource Holling type II functional responses (in either Eq. (3) or Eq. (11), respectively) are derived as per capita asymptotic average feeding rates after reaching stationarity under chemostatic conditions and mass action dynamics.

Higher order density-dependent effects

Consumer efficiency on a focal resource can be intrinsically affected not only by the level of the focal resource, as in Holling type III functional response, but also by the presence of alternative resources. In order to take this observation into account, the chemical scheme in reactions (4)-(5) should be extended, and this can be done in different ways. Consider, for instance, that a non-linear increase (or decrease) of feeding efficiency in response to both the same and alternative resource types. This would correspond to the multispecies version of Holling type III, where order $n=2$ has been assumed:

$$X_A + 2\,X_{R_i} \xrightarrow{\alpha_{ii}} X_{AR_i} + X_{R_i} \tag{12}$$

$$X_A + X_{R_i} + X_{R_j} \xrightarrow{\alpha_{ij}} X_{AR_i} + X_{R_j}, \tag{13}$$

where α_{ij} are reaction rates taking into account the effect of the density of the same ($i = j$) or alternative resources $i\ /j$ on the formation of handling consumers of the focal resource i. When comparing rates α_{ii} and α_{ij} we can see whether the feeding rate on R_i is enhanced (or damped) by the presence of an alternative resource R_j more than it is by

the presence of the same type of resource R_i. Notice that, in this case, the full reaction scheme of the individual feeding processes will be reactions (4)-(5) in addition to reactions (12)-(13). The per capita consumption rate of a free/searching individual A feeding on a focal resource i has now two terms:

$$\theta_i := \alpha_i x^0_{R_i} + \sum_{j=1}^{S} \alpha_{ij}\, x^0_{R_i}\, x^0_{R_j} \tag{14}$$

Interestingly, the same rate equations as the ones used for the previous derivation of the multi-resource Holling Type II funcional response —see Eqs. (6)-(7)— apply here but now using this new definition of θ_i, which is still a constant parameter that depends on resource type. Therefore, the same reasoning that led to Eq. (11), now leads to the following general multi-resource functional response:

$$\langle f_i(x_{R_1}, \ldots, x_{R_S})\rangle = \frac{\alpha_i\, x_{R_i} + \sum_{j=1}^{S} \alpha_{ij}\, x_{R_i}\, x_{R_j}}{1 + \sum_{j=1}^{S} \frac{\alpha_j}{\nu_j} x_{R_j} + \sum_{j=1}^{S} \frac{\alpha_{ij}}{\nu_i} x_{R_i}\, x_{R_j}} \tag{15}$$

This per capita average rate of consumers feeding on a focal resource i is not as general as we may think. It results from specific assumption that consider the type of higher order interactions (HOI) clearly specified by the full reaction scheme (4)-(5) and (12)-(13). However, other types of HOI can be considered, for instance, "prey switching" as considered in a different reaction scheme (see Supplement), which leads to a different expression for the functional response of consumers feeding on multiple resources. These two examples of average feeding rates in a multiresource context —Eqs. (15) and Eq. (108) in the Supplementary Information— are meant to emphasize that specific expressions of the functional response are contingent to the particular hypotheses assumed by a given reaction scheme. Although it is true that two different hypotheses on the individual feeding mechanism may lead the the same population-averaged per capita feeding rate of consumers [37], parameter interpretation will be completely different, and this coincidence should not be expected in general.

Beddington-DeAngelis: predator density-dependence

Two predators may eventually interfere by engaging in contests due to different reasons (fights for a territory, competition for resources, etc.). This interference behavior prevents them from resource search and consumption and, therefore, may potentially decrease population-averaged consumption rates. While the interference process lasts, the two consumers involved are entangled together. When the interference ends, at the point the actual fight finishes, the two consumers return simultaneously back again to the searching stage. This corresponds to the formation of a two-individual complex or a "triplet", which breaks down into the two separate individuals, on average, after a finite amount of time. The interference process can thus be modelled through a *relaxation* rate. This point is important because it has been overlooked in previous derivations of predator-dependent functional responses based on reaction schemes [33, 38]. These authors implicitly assume in their reaction schemes that two predators enter an interfering stage, simultaneously, at the moment they encounter each other, but relax back to the searching stage independently from each other, which is not consistent nor realistic.

Here, we assume two types of interference processes. First, consumers can directly interfere while searching. Second, a searching consumer can encounter a consumer individual that is handling a resource item, and engage in a fight, in the hope of obtaining perhaps a share of the resource. More complicated interference processes can be considered by adding other behavioral stages (consumers recovering from a fight, consumer watching out for or hiding from top predators, etc). The processes we considered here are minimal.

They can be represented by the following reaction scheme:

$$X_A + X_R \xrightarrow{\alpha} \emptyset + X_{AR}\,, \tag{16}$$
$$X_{AR} \xrightarrow{\nu} X_A \tag{17}$$
$$X_{AR} + X_A \xrightarrow{\chi_{ARA}} X_{ARA} + \emptyset\,, \tag{18}$$
$$X_{ARA} + \emptyset \xrightarrow{\eta_{ARA}} X_{AR} + X_A\,, \tag{19}$$
$$X_A + X_A \xrightarrow{\chi_{AA}} X_{AA} + \emptyset\,, \tag{20}$$
$$X_{AA} + \emptyset \xrightarrow{\eta_{AA}} X_A + X_A\,, \tag{21}$$

where we added the dynamics of pairs, AA, and what we call triplets, ARA. These are interference complexes formed by two searching individuals, A, and a searching, A, and a handling consumer, AR, respectively. Resource level, n_R^0, is assumed constant. As a consequence, the actual consumption rate of a free individual, A, is still given by $\theta \equiv \alpha\, x_R^0$. Since no process depleting the consumer population is considered, the total number of consumers, n_A^0 is also kept constant, and will be distributed among four different types. This adds a constraint to the dynamics: $n_A^0 = n_A + n_{AR} + 2n_{ARA} + 2n_{AA}$. These types correspond to different behavioral stages: free consumers, A, handling/feeding consumers, AR, and interfering consumers engaged in either pairs, AA, or triplets, ARA. Once this distribution reaches steady state, there will be a steady number of free consumers, $n_A^\star$, ready to search and attack new resources. This subpopulation will be directly responsible for total resource depletion at a constant steady-state rate, which will determine a population-averaged per capita feeding rate, the functional response.

We consider continuous variables representing the different subpopulations of consumers, n_A, n_{AR}, n_{ARA}, and n_{AA}. Again, a stationary distribution of behavioral types can be calculated for the reaction scheme (16)-(21) (see Box I and appendix for details). Although this is an abuse of notation, for simplicity, we use the same notation for both continuous deterministic and discrete stochastic variables. The context will make it clear. The value of $n_A^\star$ is defined by the steady-state that emerges from the deterministic rate equations associated to the reaction scheme (16)-(21), which reads:

$$\begin{aligned}\frac{dn_A}{dt} &= -\theta\, n_A + \nu\, n_{AR} + \eta_{AA}\, n_{AA} + \eta_{ARA}\, n_{ARA} \\ &\quad - \chi_{ARA}\frac{n_{AR}}{N}\, n_A - \chi_{AA}\frac{n_{AR}}{N},\end{aligned} \tag{22}$$
$$\frac{dn_{AR}}{dt} = \eta_{ARA} n_{ARA} - \nu n_{AR} + \theta\, n_A - \chi_{ARA}\frac{n_{AR}}{N}\, n_A, \tag{23}$$
$$\frac{dn_{ARA}}{dt} = \chi_{ARA}\frac{n_{AR}}{N}\, n_A - \eta_{ARA} n_{ARA}. \tag{24}$$
$$\frac{dn_{AA}}{dt} = \chi_{AA}\frac{n_A}{N}\, n_A - \eta_{AA}\, n_{AA}. \tag{25}$$

By making the rate equations equal to zero, and using the constraint given by $n_A^0 = n_A + n_{AR} + 2n_{ARA} + 2n_{AA}$, we obtain a value for n_A at steady-state:

$$n_A^\star = \frac{2\, n_A^0}{1 + \frac{\theta}{\nu} + \sqrt{\left(1 + \frac{\theta}{\nu}\right)^2 + 8\left(\frac{\chi_{ARA}}{\eta_{ARA}}\frac{\theta}{\nu} + \frac{\chi_{AA}}{\eta_{AA}}\right) x_A^0}} \tag{26}$$

which leads to the expression of the population-averaged per capita feeding rate:

$$\langle f(x_R, x_A)\rangle = \frac{2\alpha\, x_R}{1 + \frac{\alpha}{\nu}\, x_R + \sqrt{\left(1 + \frac{\alpha}{\nu}\, x_R\right)^2 + 8\,\frac{\chi_{ARA}}{\eta_{ARA}}\frac{\alpha}{\nu}\, x_R\, x_A \;+\; 8\,\frac{\chi_{AA}}{\eta_{AA}}\, x_A}}. \tag{27}$$

where we recall that we have dropped the 0 superscripts for short and simplicity.

Notice that this is the predator-dependent functional response that generalizes Holling Type II. If there is no interference ($\chi_{AA} = \chi_{ARA} = 0$), we recover Eq. (3). If there is

only a fight for resources ($\chi_{AA} = 0$), we recover the functional response presented by [28]. This nested property is very useful for model selection and parameter inference. Previous derivations of the predator-dependent functional response [33, 38] clearly do not pass this check.

Discussion

Here we have shown that reaction schemes represent a common framework to derive both single-resource functional responses and their multi-resource extensions [34, 29, 37, 27]. This approach has several advantages. First, the underlying hypotheses and particular assumptions leading to the different functional forms become evident. Second, through the use of stochastic processes in continuous time, not only expected average feeding rates but also their whole distribution across replicates can be calculated. This provides a natural link between individual stochastic descriptions of the feeding processes, and their population-averaged deterministic analogs [12]. And, third, the resulting functional responses are fully nested, which is a useful property in model selection contexts. However, it is important to emphasize also the limitations of the functional responses emerging from reaction schemes. First, they are population-level, per capita averages only asymptotically valid at stationarity. Second, they are based on the mass action assumption (individuals encounter resources and each other at random), and third, these derivations also rely on chemostatic conditions (resource and consumer population levels are kept constant while the steady state is reached). Stationarity (1), mass action (2), and chemostatic conditions (3) are three implicit assumptions underlying classic functional responses that have been sometimes overlooked.

Conditions (1) and (2) are related. Stationarity should be reached fast enough before any extra processes affecting resource and consumer population levels become important. In particular, common use of functional responses of this type in population dynamic models requires in general a strong time scale separation between a fast (behavioral) time scale controlling feeding dynamics, and a slow (demographic) time scale characterizing processes such as death, migration and reproduction. This strong time scale separation allows for feeding dynamics to reach a steady-state characterized by average consumption rates, which can be then introduced in the population-level model. This separation of time scales is emphasized in recent derivations of classic consumer-resource models from individual processes, such as the Rosenzweig-MacArthur and Beddington-DeAngelis consumer-resource models, which consider a consumer species feeding on a logistically growing resource [15, 36, 28]. The use of these population models relies implicitly on this strong time-scale separation assumption. They are effective models in the sense that they encapsulate the whole complexity of a low-level behavioral process occurring at a rapid time scale in a single per capita average macroscopic feeding rate, which in turn depends on effective parameters. For instance, a time-scale separation argument allows to recover the classic Rosenzweig-MacArthur consumer-resource model from slightly different feeding and population processes. However, the precise interpretation of functional-response effective parameters differs in each case [15, 36, 28].

Interactions rates are governed by the rate at which individuals encounter, and this, in turn, results from the way individuals move, when, for instance, they search for food. A rich research area focuses on both measuring and theoretically deriving optimal movement distributions of foraging animals depending on total food density and its distribution over an area [7, 9, 8]. In the search for functional responses, a recent study shows that different functional forms emerge when individuals do not mover randomly but following more realistic trajectories, such as Levy walks [20].

Advances in technology (optics, data compression, computation capacity, robotics) have made it increasingly feasible to automate behavioral assays in the laboratory and thereby collect more animal data with minimal human intervention [19]. Feeding experiments can potentially benefit a lot from these novel methods in conjunction with the ideas presented in this note. We have shown, for instance, that the distribution of free

consumers allows for accurate estimates of attack rates and handling times even if the number of consumers is very low (Fig 1). This approach requires the ability to identify distinct predator behavioral stages. Predators in different behavioral feeding stages may move in identifiable, distinct ways. In fact, the segmentation of moving trajectories into distinct behavioural stages is becoming more and more accessible due to novel machine learning and artificial intelligence methods[40, 26].

In recent years, functional responses have been addressed by using different stochastic approaches. Van der Meer and Smallegange [38] use a stochastic analysis that differs from ours because it focus only on the stationary distribution of a discrete-time model. Billiard et al [11] make use of general renewal processes to estimate the average and the variance of feeding rates as an approximation when the number of consumers is large. Here, we emphasize that chemical-like reactions schemes already provide a natural link between deterministic and stochastic dynamics because they can lead to both deterministic rate equations for average densities, and one-step stochastic master equations in continuous time for the whole exact probability distribution of the different behavioral types. We highlight that this property has a huge potential for parameter inference and model selection in the context of feeding experiments, particularly, when the number of prey and predators is low.

Finally, several derivations of the Beddington-DeAngelis functional response abound in the literature [33, 23, 41, 38], which describe predator's interference at both the individual and the population level. However, the derivation we present in this note, resulting in Eq (27), is the only one that considers the same three common assumptions as the classic Holling Type II functional response, and should be then regarded as its natural generalization, under both direct interference and fight for resources. It is only under very restricted conditions that this expression collapses into the classic Beddington-DeAngelis functional response [28], and, only within these strict conditions, we can safely say that the classic expression approximates the true per capita average feeding rate of interfering consumers. According to Eq (27), when consumer interference for resources (formation of triplets) is strong, this is, dominates over the rest of the feeding processes, then total resource depletion, i.e., $\langle f(n_R^0, n_A^0)\rangle\, n_A^0$, scales as the square root of the product of prey and predator densities. Interestingly, this square root scaling prediction has been found in recent empirical estimates of total predation rates from macroecological food web data across many species and orders of magnitude in biomass [6].

Box I: stationary distribution of searching predators

Holling Type II feeding dynamics can be simply described by two discrete events: (1) the attack of resources, this is, an event that decreases the number of searching predators by one, and (2) the handling process, an event by which a handling predator relax back into the searching stage, and, as a consequence, the number of searching predators increases by one. This type of stochastic processes are known as birth-death or one-step stochastic processes. The master equation for one-step one-dimensional stochastic processes can be written as [39]:

$$\frac{dP_n(t)}{dt} = r_{n+1}\, P_{n+1}(t) + g_{n-1}\, P_{n-1}(t) - (r_n + g_n)\, P_n(t),$$

where n is a non-negative integer number in population contexts, and $P_n(t)$ is the probability for the system to have n individuals at time t. Notice that $r_0 = 0$, since the population cannot decrease from zero. In this situation, the last equation is valid only as long as $n > 0$, and a particular equation determines $P_0(t)$:

$$\frac{dP_0(t)}{dt} = r_1\, P_1(t) - g_0\, P_0(t).$$

The feeding process described by Eqs. (1)-(2) is governed by the conditional prob-

ability rates:

$$r_{n_A} := T[n_A - 1|n_A] = \theta\, n_A,$$
$$g_{n_A} := T[n_A + 1|n_A] = \nu(n_A^0 - n_A),$$

where θ is the effective per capita attack rate of a free consumer at a given level of resource density, i.e., here a constant parameter defined by $\theta := \alpha \frac{n_R^0}{N}$, and n_A^0 is the overall number of predators (constant as well). These rates control the temporal evolution of the probability of finding n_A free consumers at time t, $P(n_A, t)$.

As $t \to \infty$, the distribution $P(n_A, t)$ may tend to a stationarity. Let $P(n_A)$ be this stationary distribution. We show in the Supplement that

$$P(n_A) = \binom{n_A^0}{n_A} p^{n_A}(1-p)^{n_A^0 - n_A} \quad \text{with} \quad p = \frac{1}{1 + \frac{\alpha}{\nu}\frac{n_R^0}{N}}. \tag{B1}$$

Therefore, we obtain that the stochastic variable n_A follows the binomial distribution at stationarity for Holling Type II feeding dynamics.

Feeding dynamics with interference. In the main text we consider feeding dynamics including two types of interference processes: predator interference while searching for resources (pairs), and while a predator encounters another individual handling a resource (triplets). Ignoring pair processes, i.e., for $\chi_{AA} = 0$ and $\eta_{AA} = 0$ in the reaction scheme (16)–(21), we can compute the distribution for the number of searching predators, n_A, at stationarity.

Transition probabilities for reactions (16)–(19) are given by

$$T_{-+}(n_A, n_{AR}) := T[n_A - 1, n_{AR} + 1|n_A, n_{AR}] = \theta n_A,$$
$$T_{+-}(n_A, n_{AR}) := T[n_A + 1, n_{AR} - 1|n_A, n_{AR}] = \nu n_{AR},$$
$$T_{--}(n_A, n_{AR}) := T[n_A - 1, n_{AR} - 1|n_A, n_{AR}] = \frac{\chi}{N} n_A n_{AR},$$
$$T_{++}(n_A, n_{AR}) := T[n_A + 1, n_{AR} + 1|n_A, n_{AR}] = \frac{\eta}{2}(n_A^0 - n_A - n_{AR}),$$

where we have omitted the subscript ARA in rates in rates χ and η. The master equation for the joint probability distribution $P_{n_A, n_{AR}}(t)$ is more complicated in this case (see Supplement), but the stationary joint distribution can be calculated analytically, as well as the marginal distributions of the number of searching predators, pair compounds and triplets. For n_A^0 an even number, the distribution of the number of searching predators is given by

$$P(n_A) = \left(\frac{\theta}{\nu}\right)^{\sigma_{n_A}} \frac{{}_1F_1\left(-\left\lfloor \frac{n_A^0 - n_A}{2}\right\rfloor, \frac{1}{2} + \sigma_{n_A}; -\frac{\mu}{4}\right) \rho^{\left\lceil \frac{n_A}{2}\right\rceil}}{{}_1F_1\left(-\frac{n_A^0}{2}, \frac{1}{2}; -\frac{\rho}{4}\left(1 + \frac{\theta}{\nu}\right)^2\right) n_A!} \left(\frac{n_A^0}{2}\right)_{\left\lceil \frac{n_A}{2}\right\rceil}, \tag{B2}$$

and the distribution of the number of pair compounds is

$$P(n_{AR}) = \left(\frac{\nu}{\theta}\right)^{\sigma_{n_{AR}}} \frac{{}_1F_1\left(-\left\lfloor \frac{n_A^0 - n_{AR}}{2}\right\rfloor, \frac{1}{2} + \sigma_{n_{AR}}; -\frac{\rho}{4}\right) \mu^{\left\lceil \frac{n_{AR}}{2}\right\rceil}}{{}_1F_1\left(-\frac{n_A^0}{2}, \frac{1}{2}; -\frac{\rho}{4}\left(1 + \frac{\theta}{\nu}\right)^2\right) n_{AR}!} \left(\frac{n_A^0}{2}\right)_{\left\lceil \frac{n_{AR}}{2}\right\rceil}. \tag{B3}$$

Both discrete distributions have a finite support ($n_A \in \{0, 1, \ldots, n_A^0\}$). The distribution of the number of triplets, for n_A^0 even, is

$$P(n_{ARA}) = \frac{\left[\sqrt{\rho}\left(1 + \frac{\theta}{\nu}\right)\right]^{n_A^0 - 2n_{ARA}}}{{}_1F_1\left(-\frac{n_A^0}{2}, \frac{1}{2}; -\frac{\rho}{4}\left(1 + \frac{\theta}{\nu}\right)^2\right)(n_A^0 - 2n_{ARA})!} \left(\frac{n_A^0}{2}\right)_{\frac{n_A^0}{2} - n_{ARA}}, \tag{B4}$$

where now $n_{ARA} \in \left\{0, 1, \ldots, \frac{n_A^0}{2}\right\}$. Similar formulae for n_A^0 odd are given in the Supplement.

In the expressions above we used the following notation: (i) $\lfloor x \rfloor$ ($\lceil x \rceil$) stands for the greatest (smallest) integer less (greater) than or equal to x; (ii) $\sigma_n = 0$ if n is integer and even and $\sigma_n = 1$ if n is odd; (iii) the falling factorial is defined by $(x)_n = \prod_{k=1}^{n}(x-k+1)$; (iv) ${}_1F_1(a,b;z)$ stands for the Kummer's confluent hypergeometric function with parameters a and b; and (v) we used the combinations $\rho := \frac{N\nu\eta}{\theta\chi}$ and $\mu := \frac{N\theta\eta}{\nu\chi}$ in terms of chemical reaction rates. Similar expressions for n_A^0 an odd number are provided in the Supplement.

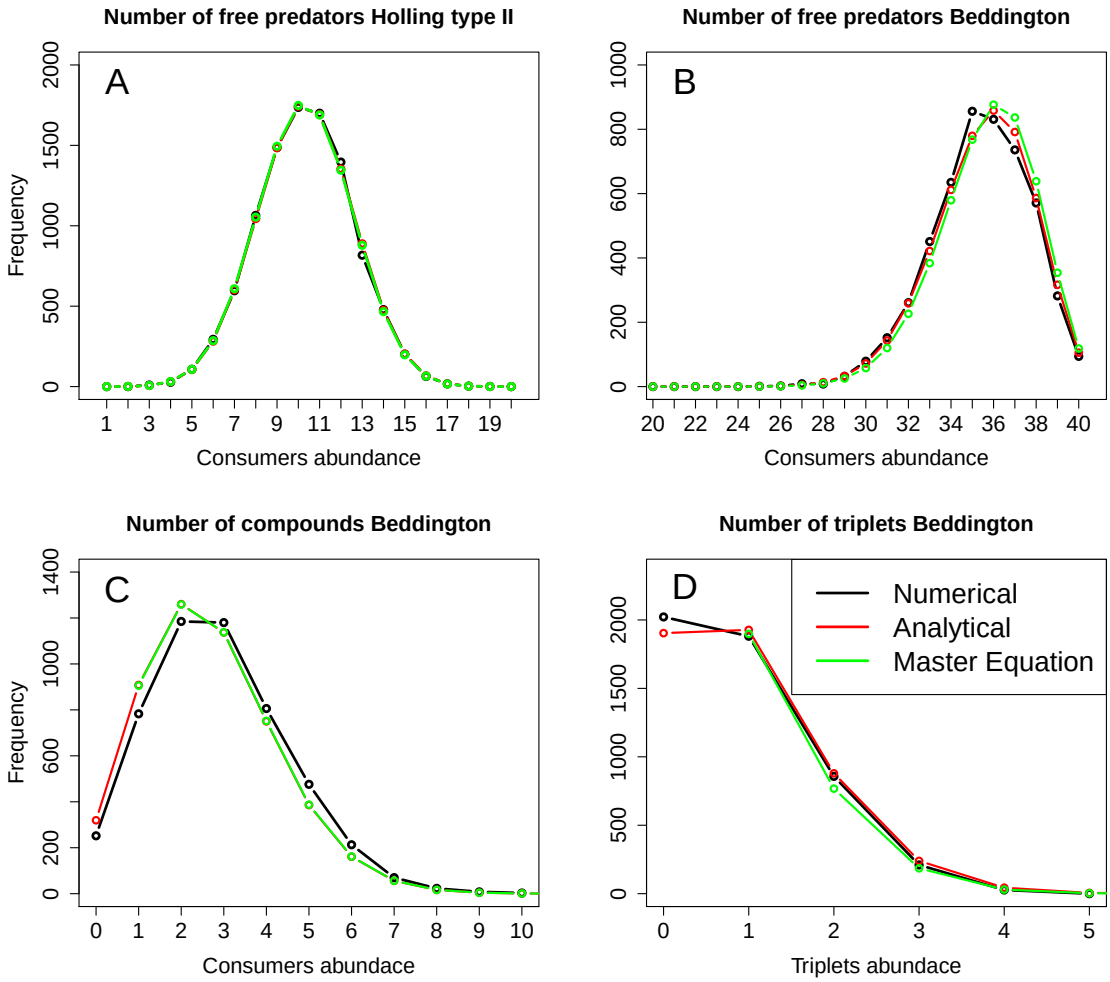

Figure 1: Panel A: Empirical (black curve), numerical solution of the master equation (green curve) and analytical expression (red curve, expression B1) for the distribution of free consumers. Simulations (using the Gillespie algorithm) consisted of 10000 replicates with $n_A^0 = 20$ individual consumers, with attack rate $\alpha = 2.5$, handling rate $\nu = 1$ feeding on a (fixed) total number of resource items given by $n_R^0 = 3750$ individuals, when the total volume of the system is $N = 10000$. Panels B-D: Empirical (black curve), numerical solution of the master equation (green curve) and analytical expression (red curve, expression B2, B3, B4) of the distributions of free consumers (panel B), pairs or compounds (panel C) and triplets (panel D), calculated after a transient of 11000 events. Simulations (using the Gillespie algorithm) consisted of 5000 replicates with $n_A^0 = 40$ individual consumers, with attack rate $\alpha = 2.5$, handling rate $\nu = 10$, interference rates of $\chi = 100$ and $\eta = 1$ feeding on a (fixed) total number of resource items given by $n_R^0 = 3000$ individuals, when the total volume of the system is $N = 10000$.

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The implicit assumptions of classic functional responses and their multi-species extensions
Supplementary Information

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1 Stationary distribution of predator behavioral types

1.1 Holling Type II feeding dynamics

As mentioned in the main text, Holling Type II feeding dynamics is described as a birth-death stochastic process (also known as one-step process), because elemental changes either increase or decrease population numbers by one. These two events are: (i) predators attack resources, so the number of searching (free) predators decreases by one while attacking the prey, and (ii) handling predators abandon the resource and come back to the searching stage, so the number of searching predators increases by one.

For a general one-step one-dimensional stochastic process (i.e., a process that focuses on a single stochastic variable, in this case, the population number of free predators in the system), the general expression of the master equation is [1]

$$\frac{dP_n(t)}{dt} = r_{n+1}\, P_{n+1}(t) + g_{n-1}\, P_{n-1}(t) - (r_n + g_n)\, P_n(t), \tag{1}$$

where, in general, n is an integer number, and $P_n(t)$ denotes the probability of observing the value n at (continuous) time t. The temporal dynamics $n(t)$ is described by the fraction of times a particular value of n is observed at time t over a large number of stochastic realizations of the process, i.e., by the probability $P_n(t)$. The dynamics is mathematically defined once the transition probability death and growth rates (r_n and g_n, respectively) are specified as functions of n.

For convenience, we re-write the master equation as:

$$\frac{dP_n(t)}{dt} = (r_{n+1}\, P_{n+1}(t) - g_n\, P_n(t)) - (r_n\, P_n(t) - g_{n-1}\, P_{n-1}(t))\,. \tag{2}$$

In population contexts, n should be a positive integer representing the number of individuals in the population, and then $P_n(t)$ is the probability for the system to have n individuals at time t. The death rate must satisfy $r_0 = 0$, because the population number cannot decrease from zero. In this situation, Eq. (2) is valid only for all probabilities as long as $n > 0$, and $P_0(t)$ is determines by

$$\frac{dP_0(t)}{dt} = r_1\, P_1(t) - g_0\, P_0(t). \tag{3}$$

As $t \to \infty$, the distribution $P_n(t)$ may reach a steady-state distribution which is independent of t. Let $P(n) = P_n$ be this stationary distribution. By definition, this probability distribution should make all right-hand sides of Eqs. (2)–(3) for all n vanish, so the (infinite) set of coupled differential equations reaches an equilibrium point. A sufficient condition for stationarity is the so-called detailed balance condition,

$$r_{n+1}\, P(n+1) - g_n\, P(n) = 0, \tag{4}$$

which has to be satisfied for all $n \geq 0$. Due to the telescopic form of (4), the two terms in the right hand side of (2) vanish independently. If we find a solution for the detailed balance condition, then we will have found the stationary distribution.

For $n = 0$, Eq. (4) is basically the condition that equals to zero the right-hand side of Eq. (3). Then it follows that the first two values of the steady-state probability distribution, $P(0)$ and $P(1)$, should be in the right proportion:

$$P(1) = \frac{g_0}{r_1}\, P(0). \tag{5}$$

Eq. (5) for $n = 1$ yields

$$P(2) = \frac{g_1}{r_2}\, P(1). \tag{6}$$

If we repeat this process, recurrently, for $n = 2$ and so on, we obtain the general expression for $P(n)$:

$$P(n) = \frac{g_{n-1}\, \cdots\, g_0}{r_n\, \ldots\, r_1}\, P(0). \tag{7}$$

This simple relation gives the stationary distribution up to a normalization constant $P(0)$.

Now we particularize the distribution for the Holling type II feeding dynamics defined by the transition probability rates

$$\begin{aligned} r_{n_A} &:= T[n_A - 1|n_A] = \theta\, n_A, \\ g_{n_A} &:= T[n_A + 1|n_A] = \nu(n_A^0 - n_A), \end{aligned} \tag{8}$$

where ν is the per-capita probability rate of AR pair compounds disintegration, and $\theta := \alpha\, \frac{n_R^0}{N}$ is the product of the rate α of AR pair formation times the number of resources n_R^0 relative to the total number of sites N. Therefore, θ is a constant because the resource level n_R^0 is assumed to be constant.

If we use then the probability rates (8) in Eq. (7) —where n is now the number of searching predators, n_A— to determine the stationary distribution $P(n_A)$ of the number of free predators, we obtain

$$P(n_A) = \left(\frac{\nu}{\theta}\right)^{n_A} \frac{n_A^0 \ldots (n_A^0 - n_A + 1)}{\theta^{n_A}\, n_A!}\, P(0), \tag{9}$$

which can be written as

$$P(n_A) = \binom{n_A^0}{n_A} \left(\frac{\nu}{\theta}\right)^{n_A} P(0). \tag{10}$$

This computes the distribution up to a normalization constant $P(0)$, which can be obtained by the normalization condition, $\sum_{n_A=0}^{n_A^0} P(n_A) = 1$. This condition, together with (7) determines $P(0)$ as

$$P(0) = \left[\sum_{n_A=0}^{n_A^0} \binom{n_A^0}{n_A} \left(\frac{\nu}{\theta}\right)^{n_A}\right]^{-1}. \tag{11}$$

Using the binomial expansion we can write

$$P(0)^{-1} = \sum_{n_A=0}^{n_A^0} \binom{n_A^0}{n_A} \left(\frac{\nu}{\theta}\right)^{n_A} = \left(1 + \frac{\nu}{\theta}\right)^{n_A^0}. \tag{12}$$

Therefore,

$$P(n_A) = \binom{n_A^0}{n_A} \frac{(\nu/\theta)^{n_A}}{(1+\nu/\theta)^{n_A^0}} = \binom{n_A^0}{n_A} \frac{(\theta/\nu)^{n_A^0 - n_A}}{(1+\theta/\nu)^{n_A^0}} = \binom{n_A^0}{n_A} \frac{1}{(1+\theta/\nu)^{n_A}} \left(\frac{\theta/\nu}{1+\theta/\nu}\right)^{n_A^0 - n_A}. \tag{13}$$

Finally, we obtain that the stochastic variable n_A follows the binomial distribution $B(n_A^0, p)$ at stationarity, with probability distribution function given by

$$P(n_A) = \binom{n_A^0}{n_A} p^{n_A} (1-p)^{n_A^0 - n_A}, \tag{14}$$

with parameters n_A^0 and

$$p = \frac{1}{1 + \frac{\theta}{\nu}} = \frac{1}{1 + \frac{\alpha}{\nu}\frac{n_R^0}{N}}. \tag{15}$$

1.2 Interfering predator feeding dynamics

In the chemical reaction formulation we have considered a feeding dynamics including two types of interference processes: predator interference while searching for resources, and while a predator encounters another individual handling a resource. For the case $\chi_{AA} = 0$ (which also implies $\eta_{AA} = 0$), in which there is no interference between pairs of predators, the reaction scheme introduced in the main text reduces to

$$X_A + X_R \xrightarrow{\alpha} X_{AR} + \emptyset, \tag{16}$$

$$X_{AR} \xrightarrow{\nu} X_A \tag{17}$$

$$X_A + X_{AR} \xrightarrow{\chi_{ARA}} X_{ARA} + \emptyset, \tag{18}$$

$$X_{ARA} + \emptyset \xrightarrow{\eta_{ARA}} X_{AR} + X_A. \tag{19}$$

Here we will compute the steady-state distribution for predator behavioral types. As for the Holling type II derivation, we assume that the resource level n_R^0, and the overall number of predators, remain constant along the process. Accordingly, we use the notation $\theta = \alpha \frac{n_R^0}{N}$, for N the number of sites. Then the overall number of predators is $n_A^0 = n_A + n_{AR} + 2n_{ARA}$, because there are n_A free predators, n_{AR} handling predators, and n_{ARA} compounds of two predators interfering for a resource. We describe the process in terms of variables n_A and n_{AR}, and then compute the number of triplets in terms of the other two, $n_{ARA} = \frac{1}{2}(n_A^0 - n_A - n_{AR})$. In what follows we will omit the subscript ARA in rates χ and η.

Transition probabilities for each reaction are given by

$$\begin{aligned}
T_{-+}(n_A, n_{AR}) &:= T[n_A - 1, n_{AR} + 1 | n_A, n_{AR}] = \theta n_A, \\
T_{+-}(n_A, n_{AR}) &:= T[n_A + 1, n_{AR} - 1 | n_A, n_{AR}] = \nu n_{AR}, \\
T_{--}(n_A, n_{AR}) &:= T[n_A - 1, n_{AR} - 1 | n_A, n_{AR}] = \frac{\chi}{N} n_A n_{AR}, \\
T_{++}(n_A, n_{AR}) &:= T[n_A + 1, n_{AR} + 1 | n_A, n_{AR}] = \frac{\eta}{2}(n_A^0 - n_A - n_{AR}).
\end{aligned} \tag{20}$$

The master equation for the probability distribution $P_{n_A,n_{AR}}(t)$ can be written in a compact form as

$$\begin{aligned}
\frac{d}{dt} P_{n_A,n_{AR}} = &(E_A E_{AR}^{-1} - \mathbb{I})(T_{-+} P_{n_A,n_{AR}}) + (E_A^{-1} E_{AR} - \mathbb{I})(T_{-+} P_{n_A,n_{AR}}) \\
&+ (E_A E_{AR} - \mathbb{I})(T_{--} P_{n_A,n_{AR}}) + (E_A^{-1} E_{AR}^{-1} - \mathbb{I})(T_{++} P_{n_A,n_{AR}}),
\end{aligned} \tag{21}$$

in terms of the one-step operators, defined as

$$\begin{aligned}
E_A f(n_A, n_{AR}) &= f(n_A + 1, n_{AR}), \\
E_{AR} f(n_A, n_{AR}) &= f(n_A, n_{AR} + 1), \\
E_A^{-1} f(n_A, n_{AR}) &= f(n_A - 1, n_{AR}), \\
E_{AR}^{-1} f(n_A, n_{AR}) &= f(n_A, n_{AR} - 1),
\end{aligned} \tag{22}$$

for an arbitrary function $f(n_A, n_{AR})$. In the master equation, $\mathbb{I}$ stands for the identity operator, which does not changes the arguments of $f(n_A, n_{AR})$.

We focus on the steady-state distribution, that satisfies $\frac{d}{dt} P_{n_A,n_{AR}} = 0$. From (20)–(21), the steady-state condition for the joint distribution $P(n_A, n_{AR}) = P_{n_A,n_{AR}}$ reduces to

$$\begin{aligned}
0 = &\theta(n_A + 1) P(n_A + 1, n_{AR} - 1) - \theta n_A P(n_A, n_{AR}) \\
&+ \nu(n_{AR} + 1) P(n_A - 1, n_{AR} + 1) - \nu n_{AR} P(n_A, n_{AR}) \\
&+ \frac{\chi}{N}(n_A + 1)(n_{AR} + 1) P(n_A + 1, n_{AR} + 1) - \frac{\chi}{N} n_A n_{AR} P(n_A, n_{AR}) \\
&+ \frac{\eta}{2}(n_A^0 - n_A - n_{AR} + 2) P(n_A - 1, n_{AR} - 1) - \frac{\eta}{2}(n_A^0 - n_A - n_{AR}) P(n_A, n_{AR}).
\end{aligned} \tag{23}$$

In this case it is easy to solve the system of equations above because two detailed balance conditions are satisfied: first,

$$\theta(n_A + 1) P(n_A + 1, n_{AR} - 1) = \nu n_{AR} P(n_A, n_{AR}), \tag{24}$$

which, upon changing $n_A \to n_A - 1$ and $n_{AR} \to n_{AR} + 1$, implies that $\theta n_A P(n_A, n_{AR}) = \nu(n_{AR}+1) P(n_A - 1, n_{AR}+1)$ and the two first terms in (23) cancel if (24) holds. Similarly, if

$$\frac{\chi}{N}(n_A + 1)(n_{AR} + 1) P(n_A + 1, n_{AR} + 1) = \frac{\eta}{2}(n_A^0 - n_A - n_{AR}) P(n_A, n_{AR}) \tag{25}$$

holds, then the two last terms in (23) cancel out. Then, if both (24) and (25) hold, then (23) is automatically satisfied. Above we will use these two detailed balance conditions to find either the joint equilibrium distribution $P(n_A, n_{AR})$, together with the marginal distribution of free predators $P(n_A) = \sum_{n_{AR}} P(n_A, n_{AR})$ at stationarity.

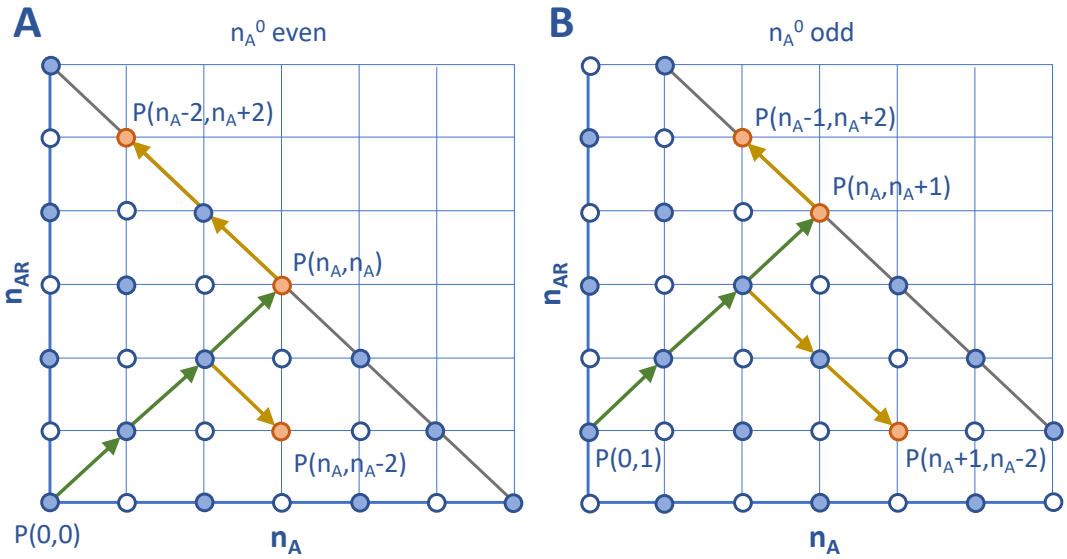

Figure 1: Scheme of the calculation of $P(n_A, n_{AR})$. **A**, n_A^0 even. Recursive application of Eq. (26) (green arrows) allows to compute $P(n_A, n_A)$ in terms of $P(0,0)$ until the (grey) line $n_A + n_{AR} = n_A^0$. The remaining probabilities $P(n_A, n_{AR})$ can be computed recursively using (28) (orange arrows). Target points are marked in orange. **B**, same as **A** for n_A^0 odd.

1.2.1 Joint probability distribution

Closed-form expressions for the steady-state joint distribution $P(n_A, n_{AR})$ can be found. First, notice that (25) implies that

$$P(n_A + 1, n_{AR} + 1) = \frac{\eta N(n_A^0 - n_A - n_{AR})}{2\chi(n_A + 1)(n_{AR} + 1)} P(n_A, n_{AR}). \tag{26}$$

An important remark is on purpose here: observe that, if $n_A + n_{AR} > n_A^0$, then (26) would immediately yield negative probabilities. To preclude the recursive formulae to yield these non-meaningful values, it must hold that $P(n_A, n_{AR}) = 0$ for $n_A + n_{AR} > n_A^0$. Therefore, probabilities $P(n_A, n_{AR})$ are non-zero up to the line in the (n_A, n_{AR}) plane defined by $n_A + n_{AR} = n_A^0$ (see Figure 1). This implies that the probability distribution has a bounded support determined by the restrictions $n_A + n_{AR} \leq n_A^0$, $n_A \geq 0$, and $n_{AR} \geq 0$. Moreover, Eq. (26) also implies that $P(n_A, n_{AR}) = 0$ within this domain ($n_A + n_{AR} \leq n_A^0$, $n_A \geq 0$, and $n_{AR} \geq 0$) if the sum $n_A + n_{AR}$ has different parity than n_A^0. Because, otherwise, the iteration of (26) would allow to cross the line $n_A + n_{AR} = n_A^0$, yielding negative probabilities as well, which are precluded. An equivalent way of thinking about it is that the number of triplets, n_{ARA},

$$n_{ARA} = \frac{1}{2}\left(n_A^0 - n_A - n_{AR}\right) \tag{27}$$

should be an integer number, which requires this *parity* restriction. Notice the different supports for the probability distribution, $P(n_A, n_{AR})$, this restriction generates (see Fig 1).

Observe also that (24) implies

$$P(n_A + 1, n_A - 1) = \frac{\nu n_A}{\theta(n_A + 1)} P(n_A, n_A). \tag{28}$$

Using Eqs. (26) and (28) we can reconstruct all the non-zero values of the joint distribution up to a normalization constant, $P(0,0)$ or $P(0,1)$, depending on the parity of n_A^0.

At this point, we separate the calculation in two different cases: (i) n_A^0 is an even number, and (ii) n_A^0 is odd. If n_A^0 is even, then start with the point $(0,0)$, for which the joint probability is non-zero. Then, using (26), we can iterate recursively from this point up to $(n_A^0/2, n_A^0/2)$ along the line $n_{AR} = n_A$ to obtain $P(n_A, n_A)$ for $0 < n_A \leq n_A^0/2$. The calculation goes as follows: Eq. (26) reduces to

$$P(n_A+1, n_A+1) = \frac{\eta N(n_A^0/2 - n_A)}{\chi(n_A+1)^2} P(n_A, n_A), \tag{29}$$

which is a one-term recursion that can be easily solved iteratively, yielding

$$P(n_A, n_A) = \left(\frac{\eta N}{\chi}\right)^{n_A} \frac{\left(\frac{n_A^0}{2}\right)_{n_A}}{(n_A!)^2} P(0,0) \tag{30}$$

for $0 < n_A \leq n_A^0/2$. Here we have introduced the falling factorial notation, defined as $(x)_n = \prod_{k=1}^{n}(x-k+1)$ for $n \geq 1$ and $(x)_0 = 1$. In the above expression, $P(0,0)$ appears as a free constant that can be determined later by normalization of the distribution. In the case of even n_A^0, every probability can be expressed in terms of $P(0,0)$.

Second, observe that (24) keeps constant the sum of the arguments of $P(n_A, n_{AR})$ in the left and right hand sides of the equation. Therefore, we can use this symmetry to move from (n_A, n_A) along the lines of constant $n_A + n_{AR}$ (see Figure 1). For example, from (28) we can compute $P(n_A+1, n_A-1)$ in terms of $P(n_A, n_A)$, which is explicitly given by (30). Similarly,

$$P(n_A{+}2, n_A{-}2) = \frac{\nu(n_A-1)}{\theta(n_A+2)} P(n_A{+}1, n_A{-}1) = \left(\frac{\nu}{\theta}\right)^2 \frac{n_A(n_A-1)}{(n_A+2)(n_A+1)} P(n_A, n_A). \tag{31}$$

Therefore, it is easy to generalize, for $0 < k \leq n_A$,

$$P(n_A+k, n_A-k) = \left(\frac{\nu}{\theta}\right)^k \frac{(n_A)_k}{(n_A+1)^{(k)}} P(n_A, n_A), \tag{32}$$

for $0 < k \leq n_A$. In the expression above we have used the rising factorial of x, defined as $(x)^{(n)} = \prod_{k=1}^{n}(x+k-1)$ for $n > 1$ integer, with $(x)^{(0)} = 1$.

We can move in the opposite direction along lines of constant $n_A + n_{AR}$. Indeed, if one particularizes (24) making the changes $n_A \to n_A - 1$ and $n_{AR} \to n_{AR} + 1$, one gets

$$\theta n_A P(n_A, n_{AR}) = \nu(n_{AR}+1) P(n_A - 1, n_{AR} + 1), \tag{33}$$

from which one can compute $P(n_A - 1, n_A + 1)$ in terms of $P(n_A, n_A)$,

$$P(n_A - 1, n_A + 1) = \frac{\theta n_A}{\nu(n_A+1)} P(n_A, n_A). \tag{34}$$

Recursive iteration of the expression above gives

$$P(n_A - k, n_A + k) = \left(\frac{\theta}{\nu}\right)^k \frac{(n_A)_k}{(n_A+1)^{(k)}} P(n_A, n_A), \tag{35}$$

for $0 < k \leq n_A$. Thus, Eqs. (30), (32) and (35) allow to compute the bivariate probability distribution $P(n_A, n_{AR})$ up to the normalization constant $P(0,0)$, which can be evaluated numerically by summing over the (finite) support of the distribution and imposing the normalization condition $\sum_{n_A, n_{AR}} P(n_A, n_{AR}) = 1$ —see, however, section 1.2.5 for an explicit expression of the normalization constant in terms of hypergeometric functions. This completes the calculation of the bivariate distribution for n_A^0 even.

From Fig. 1B we observe that we can reconstruct probabilities for n_A^0 odd using the calculation for n_A^0 even, just by changing n_A in Eqs. (30), (32) and (35) by $n_A - 1$ in the first argument. This gives: (i)

$$P(n_A - 1, n_A) = \left(\frac{\eta N}{\chi}\right)^{n_A - 1} \frac{\left(\lfloor \frac{n_A^0}{2} \rfloor\right)_{n_A - 1}}{n_A!(n_A-1)!} P(0,1), \tag{36}$$

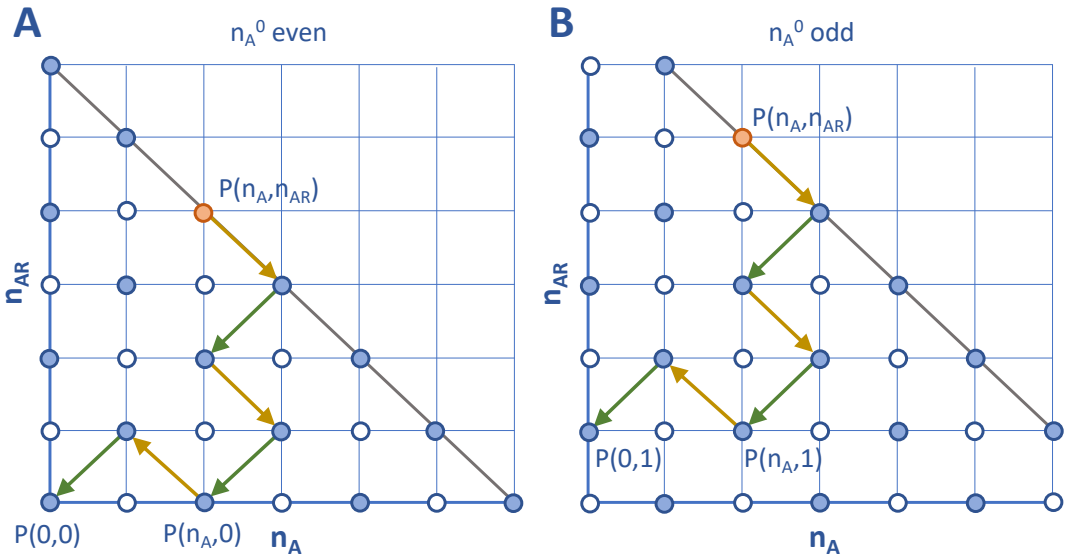

Figure 2: Scheme of the calculation of the marginal distribution $P(n_A)$ of the number of free predators, n_A. The target probability $P(n_A, n_{AR})$ is marked in orange. Then we can use Eqs. (24) (green arrows) and (26) (orange arrows) to compute $P(n_A, 0)$ if n_A^0 is even (panel **A**) or $P(n_A, 1)$ if n_A^0 is odd (panel **B**), keeping n_A fixed. This allows to sum over the values of n_{AR} and marginalize the distribution. Then we keep $n_{AR} = 0$ or $n_{AR} = 1$ to write the probabilities $P(n_A, 0)$ or $P(n_A, 1)$ in terms of $P(0, 0)$ or $P(0, 1)$, respectively, depending on the parity of n_A^0.

for $1 \leq n_A \leq \lceil \frac{n_A^0}{2} \rceil$, where $\lfloor n \rfloor$ ($\lceil n \rceil$) stands for the greatest (smallest) integer less (greater) than or equal to n; (ii)

$$P(n_A + k - 1, n_A - k) = \left(\frac{\nu}{\theta}\right)^k \frac{(n_A)_k}{(n_A)^{(k)}} P(n_A - 1, n_A), \tag{37}$$

for $0 < k \leq n_A$; and (iii)

$$P(n_A - k - 1, n_A + k) = \left(\frac{\theta}{\nu}\right)^k \frac{(n_A - 1)_k}{(n_A + 1)^{(k)}} P(n_A - 1, n_A), \tag{38}$$

for $0 < k \leq n_A - 1$. Probabilities are all computed depending on the probability $P(0, 1)$, which can be determined by normalization of the distribution.

1.2.2 Marginal distribution of free predators

The procedure we have presented to evaluate the joint probability distribution can be used to obtain explicit expressions for the marginal distribution of free predators at stationarity, $P(n_A) = \sum_{n_{AR}} P(n_A, n_{AR})$. This distribution is to be compared with the binomial distribution obtained in the Holling type II case. Figure 2 shows schematically how we proceed in this case. The idea in this case is to obtain a recursion that relates probabilities at constant n_A, so we can sum them up to marginalize. From (24) and (25) we get

$$P(n_A, n_{AR} + 2) = \frac{\theta(n_A + 1)}{\nu(n_{AR} + 2)} P(n_A + 1, n_{AR} + 1) = \frac{\mu(n_A^0 - n_A - n_{AR})}{2(n_{AR} + 2)(n_{AR} + 1)} P(n_A, n_{AR}), \tag{39}$$

where we defined $\mu := \frac{N\theta\eta}{\nu\chi}$. This equation implies that the sum $n_A + n_{AR}$ must have the same parity as n_A^0, i.e., if n_A^0 is even (or odd), then the sum $n_A + n_{AR}$ has to be even (odd) as well. Otherwise, the iteration of (39) would lead to negative probabilities. Let $\sigma_n = 0$ if n is even and $\sigma_n = 1$ if n is odd.

As for the joint probability calculation, we have to separate the two cases depending on the parity of n_A^0. First, let n_A^0 be an even number. Then necessarily both n_A and n_{AR} have the same parity. We can write $n_{AR} = 2k + \sigma_{n_A}$. With this notation, the recurrence (39) can be iterated to obtain

$$P(n_A, 2k + \sigma_{n_A}) = \frac{\mu^k}{(2k + \sigma_{n_A})!} \left(\frac{n_A^0 - n_A - \sigma_{n_A}}{2} \right)_k P(n_A, \sigma_{n_A}), \tag{40}$$

where, again, $(x)_n = \prod_{k=1}^{n}(x - k + 1)$ stands for the falling factorial. Equivalently,

$$P(n_A, n_{AR}) = \frac{\mu^{\lfloor \frac{n_{AR}}{2} \rfloor}}{n_{AR}!} \left(\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor \right)_{\lfloor \frac{n_{AR}}{2} \rfloor} P(n_A, \sigma_{n_A}), \tag{41}$$

with $\lfloor n \rfloor$ standing for the greatest integer less than or equal to n. This formula expresses the probability $P(n_A, n_{AR})$ in terms of either $P(n_A, 0)$ or $P(n_A, 1)$, depending on the parity of n_A. For n_A^0 odd, the parity of n_{AR} equals the parity of $n_A + 1$, because $n_A + n_{AR}$ has to be an odd number, so a similar expression holds:

$$P(n_A, n_{AR}) = \frac{\mu^{\lfloor \frac{n_{AR}}{2} \rfloor}}{n_{AR}!} \left(\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor \right)_{\lfloor \frac{n_{AR}}{2} \rfloor} P(n_A, \sigma_{n_A+1}). \tag{42}$$

The marginal distribution for n_A can be expressed as

$$P(n_A) = P(n_A, \sigma_{n_A}) \sum_{k=0}^{\lfloor \frac{n_A^0 - n_A}{2} \rfloor} \frac{\mu^k}{(2k + \sigma_{n_A})!} \left(\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor \right)_k, \tag{43}$$

if n_A^0 is even, and

$$P(n_A) = P(n_A, \sigma_{n_A+1}) \sum_{k=0}^{\lfloor \frac{n_A^0 - n_A}{2} \rfloor} \frac{\mu^k}{(2k + \sigma_{n_A+1})!} \left(\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor \right)_k, \tag{44}$$

if n_A^0 is odd. This reduces the calculation of $P(n_A)$ to obtaining either $P(n_A, 0)$ or $P(n_A, 1)$. These two probabilities can be written in terms of $P(0, 0)$ and $P(0, 1)$ depending of whether n_A^0 is even or odd, respectively (see Fig. 2). The calculation goes as follows.

From Eqs. (24) and (25) we also get

$$P(n_A + 2, n_{AR}) = \frac{\rho(n_A^0 - n_A - n_{AR})}{2(n_A + 2)(n_A + 1)} P(n_A, n_{AR}), \tag{45}$$

for $\rho := \frac{N\nu\eta}{\theta\chi}$. Assume first that n_A^0 is even. Then the formula can be iterated for n_A even to obtain

$$P(n_A, 0) = \frac{\rho^{\lceil \frac{n_A}{2} \rceil}}{n_A!} \left(\frac{n_A^0}{2} \right)_{\lceil \frac{n_A}{2} \rceil} P(0, 0). \tag{46}$$

If n_A is odd, Eq. (25) allows to write

$$P(n_A, 1) = \frac{N\eta}{2\chi} \frac{n_A^0 - n_A + 1}{n_A} P(n_A - 1, 0). \tag{47}$$

Using (46) to calculate $P(n_A - 1, 0)$ we get, for n_A odd,

$$P(n_A, 1) = \frac{\theta}{\nu} \frac{\rho^{\lceil \frac{n_A}{2} \rceil}}{n_A!} \left(\frac{n_A^0}{2} \right)_{\lceil \frac{n_A}{2} \rceil} P(0, 0). \tag{48}$$

In sum, for n_A^0 even we can write

$$P(n_A, \sigma_{n_A}) = \left(\frac{\theta}{\nu} \right)^{\sigma_{n_A}} \frac{\rho^{\lceil \frac{n_A}{2} \rceil}}{n_A!} \left(\frac{n_A^0}{2} \right)_{\lceil \frac{n_A}{2} \rceil} P(0, 0), \tag{49}$$

which yields the following expression for the marginal distribution up to a normalization constant $P(0,0)$,

$$P(n_A) = P(0,0)\left(\frac{\theta}{\nu}\right)^{\sigma_{n_A}} \frac{\rho^{\left\lceil \frac{n_A}{2}\right\rceil}}{n_A!}\left(\frac{n_A^0}{2}\right)_{\left\lceil \frac{n_A}{2}\right\rceil} \sum_{k=0}^{\left\lfloor \frac{n_A^0-n_A}{2}\right\rfloor} \frac{\mu^k}{(2k+\sigma_{n_A})!}\left(\left\lfloor \frac{n_A^0-n_A}{2}\right\rfloor\right)_k, \quad (50)$$

if n_A^0 is even.

If n_A^0 is odd, the same arguments leading to (46) can be applied to get

$$P(n_A,1) = \frac{\rho^{\left\lceil \frac{n_A}{2}\right\rceil}}{n_A!}\left(\frac{n_A^0-1}{2}\right)_{\left\lceil \frac{n_A}{2}\right\rceil} P(0,1) \quad (51)$$

if n_A is even, and

$$P(n_A,0) = \frac{\nu}{\theta}\frac{\rho^{\left\lfloor \frac{n_A}{2}\right\rfloor}}{n_A!}\left(\frac{n_A^0-1}{2}\right)_{\left\lfloor \frac{n_A}{2}\right\rfloor} P(0,1) \quad (52)$$

if n_A is odd. Then we can write the marginal distribution as

$$P(n_A) = P(0,1)\left(\frac{\nu}{\theta}\right)^{\sigma_{n_A}} \frac{\rho^{\left\lfloor \frac{n_A}{2}\right\rfloor}}{n_A!}\left(\left\lfloor \frac{n_A^0}{2}\right\rfloor\right)_{\left\lfloor \frac{n_A}{2}\right\rfloor} \sum_{k=0}^{\left\lfloor \frac{n_A^0-n_A}{2}\right\rfloor} \frac{\mu^k}{(2k+\sigma_{n_A+1})!}\left(\left\lfloor \frac{n_A^0-n_A}{2}\right\rfloor\right)_k \quad (53)$$

for n_A^0 odd. Again, this completes the calculation of the distribution up to a normalization constant $P(0,1)$ for fixed (and odd) overall number of predators.

We finish this section providing closed-form expressions for the explicit sums in the marginal distributions (50) and (53) in terms of confluent hypergeometric functions. Consider first the case n_A^0 even. The sum in Eq. (50) is:

$$K = \sum_{k=0}^{\left\lfloor \frac{n_A^0-n_A}{2}\right\rfloor} \frac{\mu^k}{(2k+\sigma_{n_A})!}\left(\left\lfloor \frac{n_A^0-n_A}{2}\right\rfloor\right)_k. \quad (54)$$

Then one can show that

$$K = {}_1F_1\left(-\left\lfloor \frac{n_A^0-n_A}{2}\right\rfloor, \frac{1}{2}+\sigma_{n_A}; -\frac{\mu}{4}\right), \quad (55)$$

where we have introduced Kummer's confluent hypergeometric function ${}_1F_1(a,b;z)$, defined as

$${}_1F_1(a,b;z) = \sum_{k=0}^{\infty} \frac{(a)^{(k)}}{(b)^{(k)}}\frac{z^k}{k!}. \quad (56)$$

The calculation goes as follows. Using the relation $(x)_k = (-1)^k(-x)^{(k)}$ we can write

$$K = \sum_{k=0}^{\left\lfloor \frac{n_A^0-n_A}{2}\right\rfloor} \frac{(-\mu)^k}{(2k+\sigma_{n_A})!}\left(-\left\lfloor \frac{n_A^0-n_A}{2}\right\rfloor\right)^{(k)}. \quad (57)$$

Then, if n_A is even, it holds that

$$\frac{(2k+\sigma_{n_A})!}{4^k} = \frac{2k}{2}\cdot\frac{2k-1}{2}\cdot\frac{2k-2}{2}\cdot\frac{2k-3}{2}\cdots\frac{2}{2}\cdot\frac{1}{2} = k!\left(\frac{1}{2}\right)^{(k)}. \quad (58)$$

If n_A is odd,

$$\frac{(2k+\sigma_{n_A})!}{4^k} = \frac{2k+1}{2}\cdot\frac{2k}{2}\cdot\frac{2k-1}{2}\cdot\frac{2k-2}{2}\cdots\frac{3}{2}\cdot\frac{2}{2} = k!\left(\frac{3}{2}\right)^{(k)}. \quad (59)$$

Therefore

$$K = \sum_{k=0}^{\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor} \frac{\left(-\frac{\mu}{4}\right)^k}{k!} \frac{\left(-\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor\right)^{(k)}}{\left(\frac{1}{2} + \sigma_{n_A}\right)^{(k)}}. \tag{60}$$

Finally, because it holds that $(-n)^{(n+q)} = 0$ for any n integer and $q \geq 1$ integer as well, the finite sum in k can be substituted by and infinite sum since all the terms for $k \geq \left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor + 1$ yield zero contribution. Thus,

$$K = \sum_{k=0}^{\infty} \frac{\left(-\frac{\mu}{4}\right)^k}{k!} \frac{\left(-\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor\right)^{(k)}}{\left(\frac{1}{2} + \sigma_{n_A}\right)^{(k)}}, \tag{61}$$

which yields Eq. (55) using the definition (56), and the following expression for the marginal distribution,

$$P(n_A) = P(0,0) \left(\frac{\theta}{\nu}\right)^{\sigma_{n_A}} \frac{\rho^{\left\lceil \frac{n_A}{2} \right\rceil}}{n_A!} \left(\frac{n_A^0}{2}\right)_{\left\lceil \frac{n_A}{2} \right\rceil} {}_1F_1\left(-\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor, \frac{1}{2} + \sigma_{n_A}; -\frac{\mu}{4}\right), \tag{62}$$

for n_A^0 even, up to the normalization constant $P(0,0)$. A similar calculation gives

$$P(n_A) = P(0,1) \left(\frac{\nu}{\theta}\right)^{\sigma_{n_A}} \frac{\rho^{\left\lfloor \frac{n_A}{2} \right\rfloor}}{n_A!} \left(\left\lfloor \frac{n_A^0}{2} \right\rfloor\right)_{\left\lfloor \frac{n_A}{2} \right\rfloor} {}_1F_1\left(-\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor, \frac{1}{2} + \sigma_{n_A+1}; -\frac{\mu}{4}\right) \tag{63}$$

for n_A^0 odd. These are the formulae we reproduced in the main text's box.

1.2.3 Asymptotic limit of the marginal distribution of free predators

In this subsection we consider the limit $\chi \to 0$. Given the chemical reactions (16)–(19), in this limit we should recover the binomial distribution obtained above, cf. Eq. (10), up to a normalization constant.

We show here the derivation when n_A^0 is an even number (the derivation is similar for n_A^0 odd). If $\chi \to 0$, then $\mu \to \infty$. Therefore, we can use the following asymptotic limit of the confluent hypergeometric function,

$${}_1F_1(a, b; x) \approx \frac{(-x)^{-a}\Gamma(b)}{\Gamma(b-a)}, \tag{64}$$

which is valid if a is a negative integer and $x < 0$ with $|x| \to \infty$. Here $\Gamma(x)$ is the usual gamma function. Thus, we can write

$${}_1F_1\left(-\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor, \frac{1}{2} + \sigma_{n_A}; -\frac{\mu}{4}\right) \approx \frac{\left(\frac{\mu}{4}\right)^{\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor} \Gamma\left(\frac{1}{2} + \sigma_{n_A}\right)}{\Gamma\left(\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor + \frac{1}{2} + \sigma_{n_A}\right)}. \tag{65}$$

According to (62), in the limit $\chi \to 0$ we can approximate the product

$$K = \left(\frac{\theta}{\nu}\right)^{\sigma_{n_A}} \frac{\rho^{\left\lceil \frac{n_A}{2} \right\rceil}}{n_A!} \left(\frac{n_A^0}{2}\right)_{\left\lceil \frac{n_A}{2} \right\rceil} {}_1F_1\left(-\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor, \frac{1}{2} + \sigma_{n_A}; -\frac{\mu}{4}\right) \tag{66}$$

as

$$K \approx \left(\frac{\theta}{\nu}\right)^{\sigma_{n_A}} \frac{\rho^{\left\lceil \frac{n_A}{2} \right\rceil}}{n_A!} \left(\frac{n_A^0}{2}\right)_{\left\lceil \frac{n_A}{2} \right\rceil} \frac{\left(\frac{\mu}{4}\right)^{\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor} \Gamma\left(\frac{1}{2} + \sigma_{n_A}\right)}{\Gamma\left(\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor + \frac{1}{2} + \sigma_{n_A}\right)}. \tag{67}$$

Now, using that $\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor = \frac{n_A^0}{2} - \left\lceil \frac{n_A}{2} \right\rceil$ is valid for n_A^0 even and for all n_A non-negative integer, we can write

$$\left(\frac{\theta}{\nu}\right)^{\sigma_{n_A}} \rho^{\left\lceil \frac{n_A}{2} \right\rceil} \mu^{\left\lfloor \frac{n_A^0 - n_A}{2} \right\rfloor} = \mu^{\frac{n_A^0}{2}} \left(\frac{\nu}{\theta}\right)^{2\left\lceil \frac{n_A}{2} \right\rceil - \sigma_{n_A}} = \mu^{\frac{n_A^0}{2}} \left(\frac{\nu}{\theta}\right)^{n_A}, \tag{68}$$

where we have used that $\frac{\rho}{\mu} = \left(\frac{\nu}{\theta}\right)^2$ and $2\lceil \frac{n_A}{2} \rceil - \sigma_{n_A} = n_A$ —if $n_A = 2k$ then the equality holds trivially, and if $n_A = 2k+1$ then the left hand side is equal to $2(2k+1) - 1 = 2k+1 = n_A$, so it holds for every n_A integer.

Therefore,

$$K \approx \mu^{\frac{n_A^0}{2}} \left(\frac{\nu}{\theta}\right)^{n_A} \frac{1}{n_A!} \left(\frac{n_A^0}{2}\right)_{\lceil \frac{n_A}{2} \rceil} \left(\frac{1}{4}\right)^{\frac{n_A^0}{2} - \lceil \frac{n_A}{2} \rceil} \frac{\Gamma\left(\frac{1}{2} + \sigma_{n_A}\right)}{\Gamma\left(\frac{n_A^0}{2} - \lceil \frac{n_A}{2} \rceil + \frac{1}{2} + \sigma_{n_A}\right)}. \tag{69}$$

Consider the constant

$$Q := \frac{\mu^{\frac{n_A^0}{2}}}{n_A^0!} \left(\frac{n_A^0}{2}\right)_{\frac{n_A^0}{2}} = \mu^{\frac{n_A^0}{2}} \frac{\left(\frac{n_A^0}{2}\right)!}{n_A^0!}, \tag{70}$$

and let us divide K by Q (notice that this does not alter the distribution, which is defined up to a normalization constant), so we get

$$\frac{K}{Q} \approx \left(\frac{\nu}{\theta}\right)^{n_A} \frac{n_A^0!}{n_A!} \frac{\left(\frac{n_A^0}{2}\right)_{\lceil \frac{n_A}{2} \rceil}}{\left(\frac{n_A^0}{2}\right)!} \left(\frac{1}{4}\right)^{\frac{n_A^0}{2} - \lceil \frac{n_A}{2} \rceil} \frac{\Gamma\left(\frac{1}{2} + \sigma_{n_A}\right)}{\Gamma\left(\frac{n_A^0}{2} - \lceil \frac{n_A}{2} \rceil + \frac{1}{2} + \sigma_{n_A}\right)}. \tag{71}$$

Then, comparing with Eq. (10) it only remains to show that

$$W = \frac{\left(\frac{n_A^0}{2}\right)_{\lceil \frac{n_A}{2} \rceil}}{\left(\frac{n_A^0}{2}\right)!} \left(\frac{1}{4}\right)^{\frac{n_A^0}{2} - \lceil \frac{n_A}{2} \rceil} \frac{\Gamma\left(\frac{1}{2} + \sigma_{n_A}\right)}{\Gamma\left(\frac{n_A^0}{2} - \lceil \frac{n_A}{2} \rceil + \frac{1}{2} + \sigma_{n_A}\right)} = \frac{1}{(n_A^0 - n_A)!}. \tag{72}$$

We prove it by studying separately the cases n_A even and n_A odd.

If $n_A = 2k$, then we can use the recursion $\Gamma(n+1) = n\Gamma(n)$ to get

$$\Gamma\left(\frac{n_A^0}{2} - \lceil \frac{n_A}{2} \rceil + \frac{1}{2} + \sigma_{n_A}\right) = \underbrace{\left(\frac{n_A^0}{2} - k - \frac{1}{2}\right)\left(\frac{n_A^0}{2} - k - \frac{3}{2}\right) \cdots \frac{3}{2} \cdot \frac{1}{2}}_{\frac{n_A^0}{2} - k \text{ terms}} \Gamma\left(\frac{1}{2}\right). \tag{73}$$

Thus, the $\frac{n_A^0}{2}$ terms can be combined with the factor $\left(\frac{1}{2}\right)^{\frac{n_A^0}{2} - k}$ to obtain

$$W = \frac{\left(\frac{n_A^0}{2}\right)_k}{\left(\frac{n_A^0}{2}\right)!} \frac{\left(\frac{1}{2}\right)^{\frac{n_A^0}{2} - k}}{\left(n_A^0 - 2k - 1\right)\left(n_A^0 - 2k - 3\right) \cdots 3 \cdot 1}. \tag{74}$$

Similarly, expanding the factorials, it is easy to see that

$$\left(\frac{1}{2}\right)^{\frac{n_A^0}{2} - k} \frac{\left(\frac{n_A^0}{2}\right)_k}{\left(\frac{n_A^0}{2}\right)!} = \frac{1}{\left(n_A^0 - 2k\right)\left(n_A^0 - 2k - 2\right) \cdots 4 \cdot 2}. \tag{75}$$

Putting everything together and using that $n_A = 2k$ we obtain that $W = 1/(n_A^0 - n_A)!$, as expected.

If $n_A = 2k+1$ is odd, $\lceil \frac{n_A}{2} \rceil = k+1$ and we have to simplify the product

$$W = \frac{\left(\frac{n_A^0}{2}\right)_{k+1}}{\left(\frac{n_A^0}{2}\right)!} \left(\frac{1}{4}\right)^{\frac{n_A^0}{2} - k - 1} \frac{\Gamma\left(\frac{3}{2}\right)}{\Gamma\left(\frac{n_A^0}{2} - k + \frac{1}{2}\right)}. \tag{76}$$

Again,

$$\Gamma\left(\frac{n_A^0}{2} - k + \frac{1}{2}\right) = \underbrace{\left(\frac{n_A^0}{2} - k - \frac{1}{2}\right)\left(\frac{n_A^0}{2} - k - \frac{3}{2}\right) \cdots \frac{5}{2} \cdot \frac{3}{2}}_{\frac{n_A^0}{2} - k - 1 \text{ terms}} \Gamma\left(\frac{3}{2}\right). \tag{77}$$

Substituting into (76),

$$W = \frac{\left(\frac{n_A^0}{2}\right)_{k+1}}{\left(\frac{n_A^0}{2}\right)!} \frac{\left(\frac{1}{2}\right)^{\frac{n_A^0}{2}-k-1}}{\left(n_A^0-2k-1\right)\left(n_A^0-2k-3\right)\cdots 5\cdot 3}, \tag{78}$$

and expanding the factorials we find that

$$\left(\frac{1}{2}\right)^{\frac{n_A^0}{2}-k-1} \frac{\left(\frac{n_A^0}{2}\right)_{k+1}}{\left(\frac{n_A^0}{2}\right)!} = \frac{1}{\left(n_A^0-2k-2\right)\left(n_A^0-2k-4\right)\cdots 4\cdot 2}. \tag{79}$$

Introducing this result into (78), and given that $n_A = 2k+1$ in this case, we obtain again that $W = 1/(n_A^0 - n_A)!$ if n_A is an odd integer.

Therefore, we have shown that the distribution of free predators (62), in the limit $\chi \to 0$, tends to

$$P(n_A) \approx \frac{C n_A^0!}{n_A!(n_A^0-n_A)!}\left(\frac{\nu}{\theta}\right)^{n_A} = C\binom{n_A^0}{n_A}\left(\frac{\nu}{\theta}\right)^{n_A} \tag{80}$$

up to a normalization constant C. Consistently with the chemical reactions defined above, we recover the binomial distribution (10) in this limit. A similar calculation yields the same distribution for n_A^0 an odd integer number.

A final comment is on purpose here. We have derived the binomial distribution as the limit $\chi \to 0$ of the marginal distribution (62). The key result we have used to calculate the limit is the asymptotic expansion of the confluent hypergeometric function, cf. Eq. (64). The derivation we have presented in this subsection remains valid as long as the combination $\mu = \frac{N\theta\eta}{\nu\chi} = \frac{\alpha\eta n_R^0}{\nu\chi}$ goes to infinity. If θ and ν are kept constant (because they represent the consumer-resource feeding processes without interference to be obtained in the limit $\mu \to \infty$), we observe that the binomial distribution will be recovered in the limit of large η, small χ, or in the limit of large system size, $N \to \infty$.

1.2.4 Marginal distribution of pair compounds

The calculations we have carried out can be straightforwardly extended for the marginal distribution $P(n_{AR})$ of the number of pairs n_{AR}. We take advantage on the fact that the calculation of $P(n_A)$ was based on Eq. (39) (see section 1.2.2), which allowed us to keep n_A constant as long as the variable n_{AR} was iterated, so we could effectively sum over n_{AR}. In order to calculate $P(n_{AR})$, we want to keep n_{AR} constant and iterate over n_A. This is precisely what Eq. (45) does: we reproduce that equation here for the sake of clarity,

$$P(n_A+2, n_{AR}) = \frac{\rho(n_A^0 - n_A - n_{AR})}{2(n_A+2)(n_A+1)} P(n_A, n_{AR}). \tag{81}$$

From this equation one can easily recover the key equation of the calculation of $P(n_A)$, cf. Eq. (39), by interchanging n_A by n_{AR} and ρ by μ, and by swapping the arguments of $P(n_A+2, n_{AR})$,

$$P(n_A, n_{AR}+2) = \frac{\mu(n_A^0 - n_A - n_{AR})}{2(n_{AR}+2)(n_{AR}+1)} P(n_A, n_{AR}). \tag{82}$$

Observe also that, by definition, interchanging ρ by μ is equivalent to interchanging ν and θ. Therefore, one can automatically reproduce procedure followed to derive the marginal distribution for n_A by simply performing the changes $n_A \leftrightarrow n_{AR}$, $\mu \leftrightarrow \rho$, and consequently $\nu \leftrightarrow \theta$ in all the steps leading to Eqs. (62) and (63). After these transformations, the distribution of pair compounds read as

$$P(n_{AR}) = P(0,0)\left(\frac{\nu}{\theta}\right)^{\sigma_{n_{AR}}} \frac{\mu^{\left\lceil \frac{n_{AR}}{2}\right\rceil}}{n_{AR}!}\left(\frac{n_A^0}{2}\right)_{\left\lceil \frac{n_{AR}}{2}\right\rceil} {}_1F_1\left(-\left\lfloor \frac{n_A^0 - n_{AR}}{2}\right\rfloor, \frac{1}{2}+\sigma_{n_{AR}}; -\frac{\rho}{4}\right), \tag{83}$$

for n_A^0 even,

$$P(n_{AR}) = P(1,0)\left(\frac{\theta}{\nu}\right)^{\sigma_{n_{AR}}} \frac{\mu^{\left\lfloor \frac{n_{AR}}{2} \right\rfloor}}{n_{AR}!} \left(\left\lfloor \frac{n_A^0}{2} \right\rfloor\right)_{\left\lfloor \frac{n_{AR}}{2} \right\rfloor} \times$$
$$\times\, {}_1F_1\left(-\left\lfloor \frac{n_A^0 - n_{AR}}{2} \right\rfloor, \frac{1}{2} + \sigma_{n_{AR}+1}; -\frac{\rho}{4}\right) \quad (84)$$

for n_A^0 odd, up to normalization constants.

1.2.5 Marginal distribution of triplet compounds

We conclude the analysis of the distributions of feeding types with the calculation of $P(n_{ARA})$, the marginal distribution for triplets formed by two predators interfering for a single resource. Due to the chemostatic conditions, which maintain constant the overall number of predators n_A^0, the number of triplets can be calculated as

$$n_{ARA} = \frac{1}{2}(n_A^0 - n_A - n_{AR}). \quad (85)$$

We observe that this number remains unchanged along the lines that keep $n_A + n_{AR}$ constant. Let $n = n_A + n_{AR}$. Our strategy to obtain the marginal distribution $P(N_{ARA})$ relies in the calculation of the distribution $P(n)$ along these lines of constant n. Once we have calculated explicitly $P(n)$, the sought distribution $P(n_{ARA})$ follows immediately by substituting the variable n by $n_A^0 - 2n_{ARA}$.

As before, we first consider the case n_A^0 even. To begin with the derivation, let us rewrite Eq. (24) as

$$P(n_A, n_{AR}) = \frac{\theta(n_A+1)}{\nu n_{AR}} P(n_A+1, n_{AR}-1). \quad (86)$$

As we know, this recursion conserves the sum $n = n_A + n_{AR}$ Because the sum $n_A + n_{AR}$ must conserve the parity of n_A^0 (see Fig. 1), which is even, then n has to be even as well. Upon recursion, we can write

$$P(0,n) = \frac{\theta}{\nu n} P(1, n-1) = \left(\frac{\theta}{\nu}\right)^2 \frac{1\cdot 2}{n(n-1)} P(2, n-2) = \cdots = \left(\frac{\theta}{\nu}\right)^n P(n,0). \quad (87)$$

Iterating the recursion, one can write every probability along the line $n_A + n_{AR} = n$ in terms of $P(n,0)$ as

$$P(q, n-q) = \binom{n}{q}\left(\frac{\theta}{\nu}\right)^{n-q} P(n,0). \quad (88)$$

Therefore, the distribution of n is the sum of all the probabilities that lie in the line of constant $n_A + n_{AR} = n$, with n even,

$$P(n) = \sum_{q=0}^{n} \binom{n}{q}\left(\frac{\theta}{\nu}\right)^{n-q} P(n,0) = \left(1 + \frac{\theta}{\nu}\right)^n P(n,0). \quad (89)$$

Now, taking into account Eq. (46) is valid for $n = n_A$ even, the we find a closed-form formula for $P(n)$ up to normalization,

$$P(n) = P(0,0)\frac{\rho^{\left\lceil \frac{n}{2} \right\rceil}}{n!}\left(\frac{n_A^0}{2}\right)_{\left\lceil \frac{n}{2} \right\rceil}\left(1 + \frac{\theta}{\nu}\right)^n. \quad (90)$$

Using the same properties of confluent hypergeometric functions used above, the normalization constant can be evaluated as

$$P(0,0)^{-1} = \sum_{q=0}^{\frac{n_A^0}{2}} \frac{\rho^k}{(2q)!}\left(1 + \frac{\theta}{\nu}\right)^{2q}\left(\frac{n_A^0}{2}\right)_q = {}_1F_1\left(-\frac{n_A^0}{2}, \frac{1}{2}; -\frac{\rho}{4}\left(1 + \frac{\theta}{\nu}\right)^2\right) \quad (91)$$

because n can be written as $n = 2q$. This formula is very relevant, because provides explicitly the normalization constant $P(0,0)$ that appears in the marginals for n_A and n_{AR}, as well as in the joint distribution for n_A^0 even —cf. Eqs. (50) and (62).

Since n is even, $P(n)$ can be expressed as

$$P(n) = \frac{\left[\sqrt{\rho}\left(1+\frac{\theta}{\nu}\right)\right]^n}{{}_1F_1\left(-\frac{n_A^0}{2}, \frac{1}{2}; -\frac{\rho}{4}\left(1+\frac{\theta}{\nu}\right)^2\right) n!} \left(\frac{n_A^0}{2}\right)_{\frac{n}{2}} \tag{92}$$

where n is an even number. The final result for the marginal distribution of the number of triplets is simply obtained by substituting n by $n_A^0 - 2n_{ARA}$,

$$P(n_{ARA}) = \frac{\left[\sqrt{\rho}\left(1+\frac{\theta}{\nu}\right)\right]^{n_A^0 - 2n_{ARA}}}{{}_1F_1\left(-\frac{n_A^0}{2}, \frac{1}{2}; -\frac{\rho}{4}\left(1+\frac{\theta}{\nu}\right)^2\right)(n_A^0 - 2n_{ARA})!} \left(\frac{n_A^0}{2}\right)_{\frac{n_A^0}{2} - n_{ARA}}, \tag{93}$$

whose support is the set of integers $n_{ARA} \in \left\{0, 1, \ldots, \frac{n_A^0}{2}\right\}$ for n_A^0 even.

Finally, for n_A^0 odd, to conserve parity it must hold that $n = n_A + n_{AR}$ is an odd number as well, taking the values $n = 1, 3, \ldots, n_A^0$. The same arguments above lead to Eqs. (87)–(89) where n is odd. Now, using Eq. (52) in (89) we get

$$P(n) = P(0,1)\frac{\nu}{\theta}\frac{\rho^{\lfloor \frac{n}{2} \rfloor}}{n!}\left(1+\frac{\theta}{\nu}\right)^n \left(\left\lfloor \frac{n_A^0}{2} \right\rfloor\right)_{\lfloor \frac{n}{2} \rfloor}. \tag{94}$$

In order to normalize the distribution, let us write the expression above as

$$P(n) = P(0,1)\frac{\nu}{\theta}\left(1+\frac{\theta}{\nu}\right)\frac{\rho^{\lfloor \frac{n}{2} \rfloor}}{n!}\left(1+\frac{\theta}{\nu}\right)^{n-1} \left(\left\lfloor \frac{n_A^0}{2} \right\rfloor\right)_{\lfloor \frac{n}{2} \rfloor}. \tag{95}$$

We have to sum over $n = 1, 3, \ldots, n_A^0$. Given that $n = 2q + 1$ and

$$\sum_{q=0}^{\lfloor \frac{n_A^0}{2} \rfloor} \frac{\rho^q}{(2q+1)!}\left(1+\frac{\theta}{\nu}\right)^{2q}\left(\left\lfloor \frac{n_A^0}{2} \right\rfloor\right)_q = {}_1F_1\left(-\left\lfloor \frac{n_A^0}{2} \right\rfloor, \frac{3}{2}; -\frac{\rho}{4}\left(1+\frac{\theta}{\nu}\right)^2\right), \tag{96}$$

we can write the normalization constant as

$$\left[P(0,1)\left(1+\frac{\nu}{\theta}\right)\right]^{-1} = {}_1F_1\left(-\left\lfloor \frac{n_A^0}{2} \right\rfloor, \frac{3}{2}; -\frac{\rho}{4}\left(1+\frac{\theta}{\nu}\right)^2\right), \tag{97}$$

i.e.,

$$P(0,1)^{-1} = \left(1+\frac{\nu}{\theta}\right){}_1F_1\left(-\left\lfloor \frac{n_A^0}{2} \right\rfloor, \frac{3}{2}; -\frac{\rho}{4}\left(1+\frac{\theta}{\nu}\right)^2\right), \tag{98}$$

which determines the normalization factor in Eqs. (53) and (63). Our final expression for the distribution of n_{ARA} for n_A^0 odd is

$$P(n_{ARA}) = \frac{\rho^{\left\lfloor \frac{n_A^0}{2} - n_{ARA} \right\rfloor}\left(1+\frac{\theta}{\nu}\right)^{n_A^0 - 2n_{ARA} - 1}}{{}_1F_1\left(-\left\lfloor \frac{n_A^0}{2} \right\rfloor, \frac{3}{2}; -\frac{\rho}{4}\left(1+\frac{\theta}{\nu}\right)^2\right)(n_A^0 - 2n_{ARA})!} \left(\left\lfloor \frac{n_A^0}{2} \right\rfloor\right)_{\left\lfloor \frac{n_A^0}{2} - n_{ARA} \right\rfloor}, \tag{99}$$

where we have applied the change of variable $n = n_A^0 - 2n_{ARA}$. In the last expression, $n_{ARA} \in \left\{0, 1, \ldots, \left\lfloor \frac{n_A^0}{2} \right\rfloor\right\}$.

2 Multi-resource Holling Type II under prey switching

Here we consider that individuals X_A can feed on a range of S alternative resources, X_{R_i} with $i = 1, \ldots, S$. In addition, handling consumers, when they encounter another resource type, can release the one they have been handling and switch to the new one (at rate η_{ij}) —prey switching.

In this situation, the dynamics can be summarized by $4\,S$ individual feeding reactions:

$$X_A + X_{R_i} \xrightarrow{\alpha_i} \emptyset + X_{AR_i}, \tag{100}$$

$$X_{AR_i} \xrightarrow{\nu_i} X_A. \tag{101}$$

$$X_{AR_i} + X_{R_j} \xrightarrow{\eta_{ij}} X_{R_i} + X_{AR_j} \tag{102}$$

$$X_{AR_j} + X_{R_i} \xrightarrow{\eta_{ji}} X_{R_j} + X_{AR_i}, \tag{103}$$

When we consider the full feeding hypothesis given by the reaction scheme in (100)-(103), the associated rate equations read:

$$\frac{dn_A}{dt} = \sum_{i=1}^{S} \nu_i n_{AR_i} - \sum_{i=1}^{S} \theta_i\, n_A \tag{104}$$

$$\frac{dn_{AR_i}}{dt} = -\nu_i n_{AR_i} + \theta_i\, n_A - \sum_{j\neq i}^{S} \hat{\eta}_{ij} n_{AR_i} + \sum_{j\neq i}^{S} \hat{\eta}_{ji} n_{AR_j} \tag{105}$$

where we have defined:

$$\hat{\eta}_{ij} \equiv \eta_{ij}\, \frac{n^0_{R_j}}{N} \tag{106}$$

and θ_i is still given by (see Eq (8) in the main text):

$$\theta_i \equiv \alpha_i\, \frac{n^0_{R_i}}{N} \tag{107}$$

This is a coupled system of $S + 1$ ODEs. Solving it for stationarity makes use that both consumers, n^0_A, and all resource levels, $n^0_{R_i}$, are kept constant, so all $\hat{\eta}_{ij}$ and θ_i can be considered as constant parameters. Under these assumptions, we obtain a linear system of equations, analogous to Eq. (9) of the main text, for the different subtypes of consumers at stationarity, $(n_A, n_{AR_1}, \ldots, n_{AR_S})$, where now the $\mathcal{M}$ matrix reads:

$$\mathcal{M} = \begin{pmatrix} \theta_1 & -(\nu_1 + \sum_{j\neq 1}^{S} \hat{\eta}_{1j}) & \hat{\eta}_{21} & \ldots & \hat{\eta}_{S1} \\ \theta_2 & \hat{\eta}_{12} & -(\nu_2 + \sum_{j\neq 2}^{S} \hat{\eta}_{2j}) & \ldots & \hat{\eta}_{S2} \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ \theta_S & \hat{\eta}_{1S} & \ldots & \hat{\eta}_{(S-1)S} & -(\nu_S + \sum_{j\neq S}^{S} \hat{\eta}_{Sj}) \\ 1 & 1 & 1 & 1 & 1 \end{pmatrix} \tag{108}$$

Again $n^\star_A$ can be calculated in terms of a single element of the inverted matrix, $\mathcal{M}^{-1}$, this is, $n^\star_A = (\mathcal{M}^{-1})_{1\,(S+1)}\, n^0_A$, which leads the following functional response:

$$\langle f_i(n^0_{R_1}, \ldots, n^0_{R_S})\rangle = \theta_i\, (\mathcal{M}^{-1})_{1\,(S+1)} \tag{109}$$

3 Maximum likelihood estimates and likelihood profiles

3.1 Holling Type II

We conducted a *silicon* feeding experiment with 20 individual consumers ($n^0_A = 20$), a controlled resource density ($x_R = 0.3750$) under Holling Type II stochastic dynamics with attack rate ($\alpha = 2.5$), unit handling time ($\nu = 1.0$), and a fixed system volum ($N = 10000$), up the system reached stationarity ($t = 1.5$). At that point, we recorded the number of free consumers, this is, those in attack mode (n_A). We repeated the experiment 100

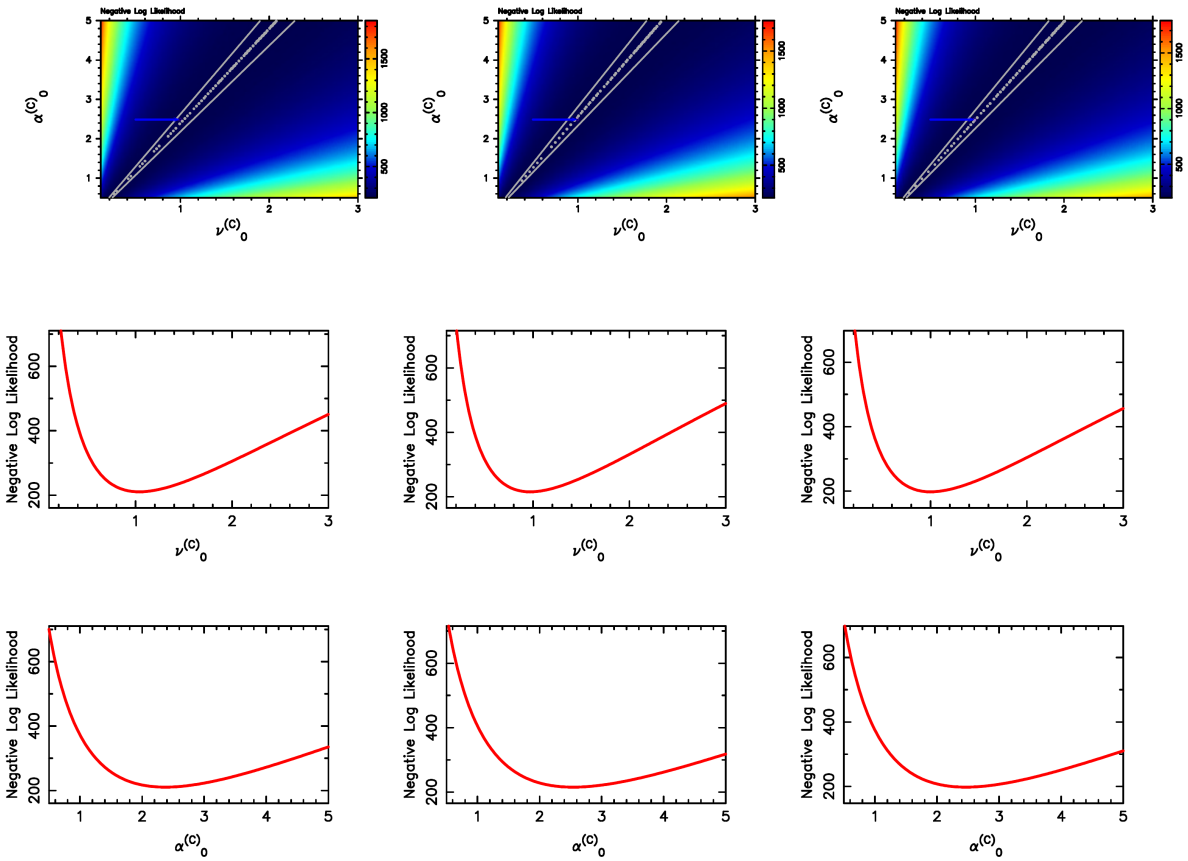

Figure 3: The whole procedure was repeated three times (in columns). Head maps represent a 2D negative log likelihood function (see Eq (110)). In the heat maps, the broken thick straight line presents the a line along which the function takes the same minimum value. The two other lines the area within 2 log likelihood unites away from this central. A blue arrow points to the true values. Likelihood profiles are extracted from the these 2D scanning plots. They are build by maintaining one parameter at its true value (either $\alpha = 2.5$ or $\nu = 1.0$) and varying the other one between the minimum and the maximum value of the corresponding ranges.

times. This furnishes an empirical data vector with 100 scalar data, $\vec{n}^{(o)} = (n_A^1, \ldots, n_A^m)$ with $m = 100$. According to the binomial probability distribution for the number of free consumers at stationarity (see Eq. (14)), since our replicates are independent realizations, we can assign a multiplicative likelihood to our empirical data vector (see Fig 3):

$$P(\vec{n}^{(o)}|\vec{\Theta}) = \prod_{i=1}^{m} P^{\star}(n_A^i|\vec{\Theta}) \tag{110}$$

where $\vec{\Theta} \equiv (\alpha, \nu, N)$, and the subscript (o) stands for observations. As you can see in Fig 3, if we know one parameter (through external information), the other parameter can be determined with enough accuracy through empirical experiments of this kind. Unfortunately, the likelihood at stationarity does not allow to identify absolute values for the parameters if both are unknown, only their their ratio.

3.2 Beddington-DeAngelis

We conducted a second *silicon* feeding experiment with 40 individual consumers ($n_A^0 = 40$), a controlled resource density ($x_R = 0.3$), under Beddington-DeAngelis stochatic dynamics (see reaction scheme in Eqs (16)-(19)), with attack rate, $\alpha = 2.5$, unit handling time ($\nu = 1.0$), consumer interaction rate ($\chi = 100$), degradation rate of interaction complexes ($\eta = 0.01$), and fixed system volume ($N = 10000$). We sampled the system at $t = 50.0$, a time large enough for the system to have reached stationarity. At this time, we recorded

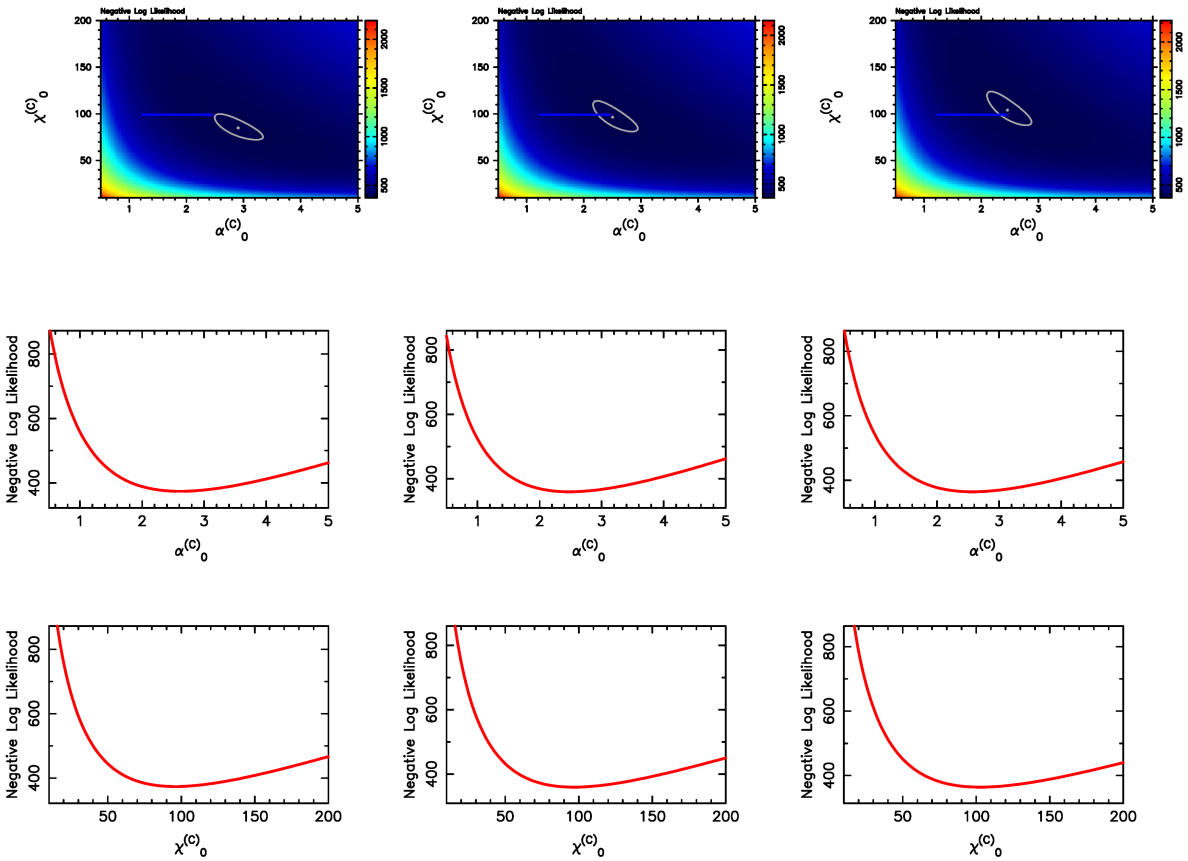

Figure 4: The whole procedure was repeated three times (in columns). Head maps represent a 2D negative log likelihood function (see Eq (111)). In the heat maps, a contour line limits the area within 2 log likelihood units away from the minimum value (white dot). A blue arrow points to the true values. Likelihood profiles are extracted from the these 2D scanning plots. They are build by maintaining one parameter at its true value (either $\alpha = 2.5$ or $\chi = 100.0$) and varying the other one between the minimum and the maximum value of the corresponding ranges.

both the number of free and handling consumers, n_A and n_{AR}, respectively. We replicated the experiment $m = 100$ times to obtain one hundred independent stochastic realizations of the system state at stationarity.

$$\mathbf{n}^{(\mathbf{o})} = \begin{bmatrix} n_A^1 & \cdots & \cdots & n_A^m \\ n_{AR}^1 & \cdots & \cdots & n_{AR}^m \end{bmatrix}$$

where $m = 100$ and subscript (o) in $\mathbf{n}^{(\mathbf{o})}$ refers to independent *observations* or stochastic realizations. As explained, before, since n_A^0 is even, Eqs (30)-(32)-(35) allow to build the full 2D probability distribution at stationary, $P^\star(n_A, n_{AR}|\vec{\Theta})$, which gives the probability of observing a pair (n_A, n_{AR}) given a model parameter vector, $\vec{\Theta} \equiv (\alpha, \nu, \chi, \eta, N)$. Again, given certain model parameter values, we can assign a multiplicative likelihood to the observed matrix, $\mathbf{n}^{(\mathbf{o})}$:

$$P(\mathbf{n}^{(\mathbf{o})}|\vec{\Theta}) = \prod_{i=1}^{m} P^\star(n_A^i, n_{AR}^i|\vec{\Theta}) \tag{111}$$

When we take logarithms of Eq (111), and change the sign, we obtain a function, which exactly corresponds to the one represented in the heat maps of Fig 4 as two free parameters vary between a mininum and a maximum value along the axes. As shown before in Eqs (30)-(32)-(35), the final expression for the 2D stationary distribution depends on two compound parameters, one controlled by the ratio α/ν and the other by the ratio χ/η. If we were able to sort out, experimentally, individuals in the different behavioral modes at stationarity (attacking *vs* handling), we could identify, as shown in Fig 111, attacking rates, χ and α, on both handling consumers and resources, respectively, provided we had

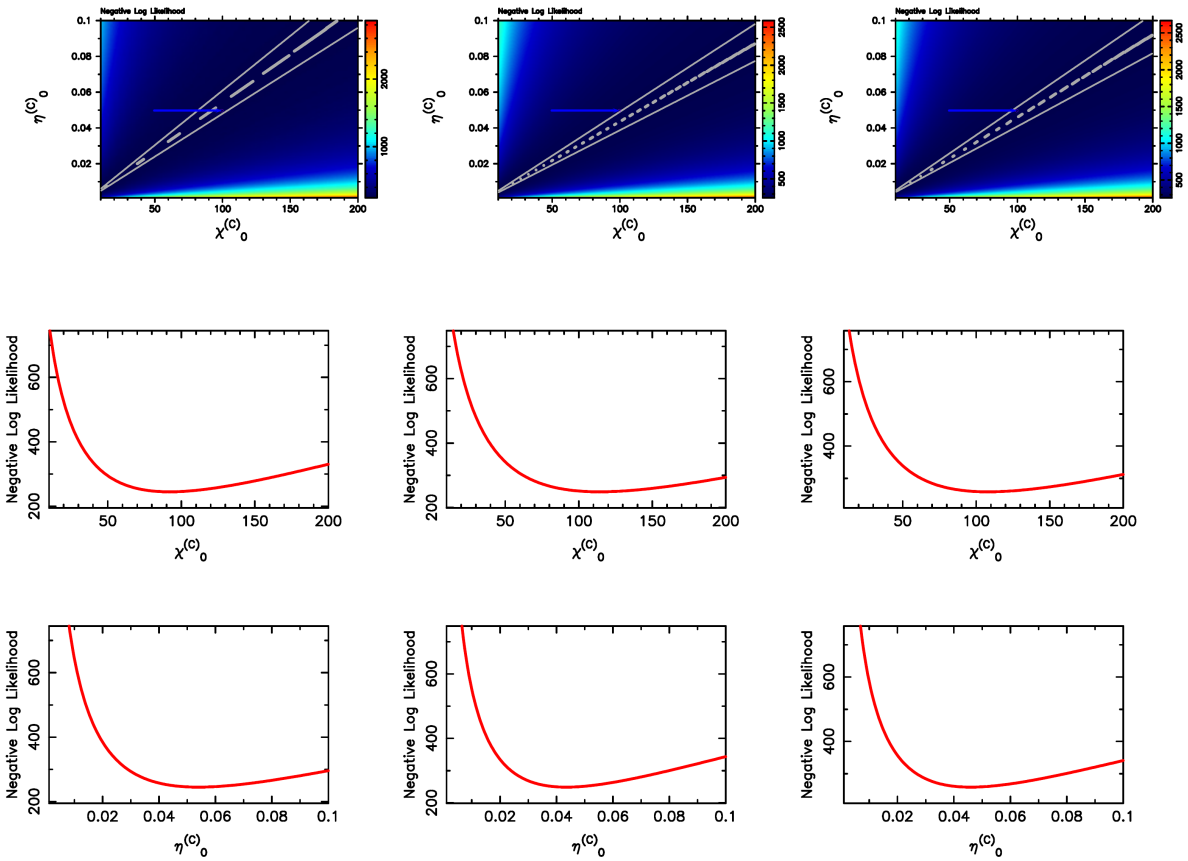

Figure 5: The whole procedure was repeated three times (in columns). Head maps represent a the 1D negative log likelihood function when we use the marginal probability distibution at stationarity. In the heat maps, the broken thick straight line presents the a line along which the function takes the same minimum value. The two other lines limit the area within 2 log likelihood unites away from the central line. A blue arrow points to the true values. Likelihood profiles are extracted from the these 2D scanning plots. They are build by maintaining one parameter at its true value (either $\chi = 100$ or $\eta = 0.05$) and varying the other one between the minimum and the maximum value of the corresponding ranges.

external information to previously determine the relaxation rates ν and η. Regarding to the rest of parameters, this is, the total number of consumers, n_A^0, resource density, and the volum, N, of the system, we believe they will be rather easy to initially fix and control in the setting of any experiment.

In case our detection device could only count the number of free consumers once the system is in a steady-state regime, then we should resort on the 1D marginal probability distribution of free consumers at stationarity to build the correct likelihood function for our estimation procedure. This is shown in a third silicon experiment in Fig 5. There, we assume that all parameters but η and χ have been previously determine through external sources. As was the case for Holling Type II dynamics (see Fig 3), since η and ν appear as the ratio of η to ν in the stationary distribution, this procedure can only be used to reliably determine there ratio, unless additional information from external sources allowed to determined one of the two parameters, as intended to exemplify with the likelihood profiles.

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