Numerical responses in resource-based mutualisms: a time scale approach

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December 17, 2013

Abstract

In mutualisms where there is exchange of resources for resources, or resources for services, the resources are typically short lived compared with the lives of the organisms that produce and make use of them. This fact allows a separation of time scales, by which the numerical response of one species with respect to the abundance of another can be derived mechanistically. These responses can account for intra-specific competition, due to the partition of the resources provided by mutualists, in this way connecting competition theory and mutualism at a microscopic level. It is also possible to derive saturating responses in the case of species that provide resources but expect a service in return (e.g. pollination, seed dispersal) instead of food or nutrients. In both situations, competition and saturation have the same underlying cause, which is that the generation of resources occur at a finite velocity per individual of the providing species, but their depletion happens much faster due to the acceleration in growth rates that characterizes mutualism. The resulting models can display all the basic features seen in many models of facultative and obligate mutualisms, and they can be generalized from species pairs to larger communities. The parameters of the numerical responses can be related with quantities that can be in principle measured, and that can be related by trade-offs, which can be useful for studying the evolution of mutualisms.

Keywords: mutualism, resources, services, steady-state, functional and numerical response

Introduction

Nous ne notons pas les fleurs, dit le géographe
Pourquoi ça! c’est le plus joli!
Parce que les fleurs sont éphémères

Le Petit Prince, Chapitre XV – Antoine de Saint-Exupéry (1943)

Early attempts to model the dynamics of mutualisms were based on phenomenological descriptions of interactions. The best known example involves changing the signs of the competition coefficients of the Lotka-Volterra model, to reflect the positive contribution of mutualism (Vandermeer and Boucher, 1978; May, 1981). This simple, yet insightful approach, predicts several outcomes depending on whether mutualism is facultative or obligatory. One example is the existence of population thresholds, where populations above thresholds will be viable in the long term, but populations below will go extinct. The same approach however, reveals an important limitation, that the mutualists can help each other to grow without limits, in an “orgy of mutual benefaction” (sic. May, 1981), yet this is never observed in nature. One way to counter this paradox is to assume that mutualistic benefits have diminishing returns (Vandermeer and Boucher, 1978; May, 1981), such that negative density dependence (e.g. competition) would catch up and overcome positive density dependence (mutualism) at higher densities. This makes intuitive sense because organisms have a finite nature (e.g. a single mouth, finite membrane area, minimum handling times, etc), causing saturation by excessive amounts of benefits. Other approaches consider cost-benefit balances that change the sign of inter-specific interactions from positive at low densities (facilitation) to negative at high densities (antagonism) (Hernandez, 1998).

Holland and DeAngelis (2010) introduced a general framework to study the dynamics of mutualisms. In their scheme two species, 1 and 2, produce respectively two stocks of resources which are consumed by species 2 and 1, according to Holling’s type II functional response, and which are converted into numerical responses by means of conversion constants. In addition, they consider costs for the interaction in one or both of the
Problematic if one attempts to explain other parameters. For example, what is the $2$ that reports one half of the maximum benefit that species $1$ can receive. But things can be conceptually half-saturation for example, the predictions using phenomenological relationships, like the Monod and Droop equations (Grover, 1997). For example, the half-saturation for mutualism in species $1$ is a trivial concept, it is just the abundance of species $2$ that reports one half of the maximum benefit that species $1$ can receive. But things can be conceptually problematic if one attempts to explain other parameters. For example, what is the handling time of a plant that uses a pollinator or seed disperser? or at which rate does a plant attack a service?

In this note I will show that in some scenarios of mutualism, it is very convenient to consider the dynamics of the resources associated with the interaction in a more explicit manner, before casting them in terms of the abundances of the mutualists. As it turns out in many situations, these resources have life times that are on average much shorter than the lives of the individuals producing and profiting from them. For example, the life of a tree can be measured in years and that of a small frugivore in months, but many fruits do not last more than a few weeks. This also apply for flowers in relation to pollinators like hummingbirds, but certainly not to mayflies (so called Ephemeroptera because of their very short lives as adults). Taking advantage of this fact, the resources can be assumed to attain a steady-state, and thus be quantified in terms of the present abundances of the providers and the consumers in a mechanistic manner. This approach has been used extensively to derive some of the most important relationships in biology from enzyme kinetics (Briggs and Haldane, 1925), to the Lotka-Volterra model of competition itself (MacArthur, 1970), functional responses (Real, 1977), and the dynamics of infectious diseases (May and Anderson, 1979). Using this approach, it is possible to derive not just the numerical responses in terms of populations abundances, but also to do it in terms of parameters that could be measured, such as the rates of resource production, their decay, and consumption. Intra-specific competition for mutualistic benefits can be related to consumption rates, and concepts such as the handling time of a plant can be given a meaning. This in turn opens the possibility of framing the costs of mutualism by means of trade-offs relating vital parameters. The examples in this note are meant to promote more thinking in this direction, that of considering separation of times scales, in order to tie together mutualism, competition, and exploitation, in more mechanistic ways.

### Exchanges of resources for resources

Consider two species $i, j = 1, 2$ that provide food to each other. Their populations ($N_i$) change in time ($t$) according to the differential equations:

$$
\frac{dN_i}{dt} = G_i(N_i)N_i + \sigma_i \beta_i F_j N_i
\tag{1}
$$

where $F_j$ is the amount of resources provided by species $j$, $\beta_i$ is the per-capita consumption rate per unit resource by species $i$, and $\sigma_i$ is the conversion ratio of eaten resources into biomass by species $i$. The function $G_i$ is the per-capita rate of change of species $i$ when it does not interact with species $j$ by means of the mutualism. The food dynamics is accounted by a second set of differential equations:

$$
\frac{dF_j}{dt} = \alpha_j N_j - \omega_j F_j - \beta_i F_j N_i
\tag{2}
$$

Here I assume that the resource is produced in proportion to the biomass of the provider with per-capita rate $\alpha_j$, and it is lost or decays with a rate $\omega_j$ if it is not consumed. I also assume that the physical act of eating by the receiver does not have an negative impact such as damage or death, on the provider, e.g. the food is secreted in the external environment. As stated in the introduction, the lifetime of the food items are much shorter than the dynamics of the populations, i.e. $\alpha_j, \omega_j$, and $\beta_i$ are large compared to $G_i$. This scenario allows the food to achieve a steady-state or quasi-equilibrium dynamics before the populations attain their long-term dynamics. Thus, assuming that $dF_j/dt \approx 0$ in equations (2), the steady-state amount of food:

$$
F_j \approx \frac{\alpha_j N_j}{\omega_j + \beta_i N_i}
\tag{3}
$$

can be substituted in the dynamical equations of the populations (1):
\[
\frac{dN_i}{dt} = \left\{ G_i(N_i) + \frac{\sigma_i\beta_i\alpha_i N_i}{\omega_j + \beta_i N_i} \right\} N_i \tag{4}
\]

In this model, the larger the receiver population, the lower the per-capita rates of acquisition of mutualistic benefits. The decrease in returns experienced by receiver \( i \) happens because the resource produced by the provider \( (\sigma_j N_j) \), must be shared among an increasing numbers of individuals, each taking a fraction \( \beta_i/(\omega_j + \beta_i N_i) \). This in effect describes intra-specific competition for a finite source of energy or resources, as originally modeled by \textit{Schoener (1978)}, with the only difference that in \textit{Schoener’s} model the supply of resources is at a constant rate.

Characterizing the system dynamics requires explicit formulations of the growth rates in the absence of the mutualism, \( G_i \). These functions can range from very simple to very complicated depending on the particular assumptions about the biology of species, the existence of alternative food sources, whether mutualism is obligate or facultative, the mechanisms of self-regulation, and the interactions (positive or negative) with other species (even perhaps between species 1 and 2 by means other than mutualism). For illustration, I will consider that \( G_i \) is a linear decreasing function of species \( i \) abundance following \textit{Holland and DeAngelis (2010)}:

\[
G_i(N_i) = r_i - c_i N_i \tag{5}
\]

where \( c_i > 0 \) is a coefficient of self-limitation and \( r_i \) is the intrinsic growth rate of \( i \), which will be positive for a facultative mutualist and negative for an obligate mutualist. By substituting \( G_i \) in \( 4 \), turns out that species \( i \) increases \( (dN_i/dt > 0) \) only if:

\[
N_j > \frac{(c_i N_i - r_i)(\omega_i + \beta_i N_i)}{\alpha_i \beta_i \omega_j} \tag{6}
\]

and decreases otherwise. With an equal sign, \( dN_i/dt \) is the nullcline of species \( i \) \( ( \text{zero-net-growth-isocline, formally}) \). The nullcline is an increasing parabola in the positive part of the \( N_1 N_2 \) plane. Species \( i \) nullcline has two roots in the \( N_i \) axis, one at \( -\omega_j/\beta_j \), which is always negative, and one at \( r_i/c_i \), which is negative if \( i \) is an obligate mutualist, or positive if \( i \) is a facultative mutualist. For a facultative mutualist \( r_i/c_i \) is also its carrying capacity, while for an obligate mutualist \( r_i \) could be its intrinsic mortality. Figure 1 shows the possible outcomes of the interaction, which ranges from having a globally stable mutualistic equilibrium when both species are facultative mutualists, to a locally stable equilibrium and dependence on the initial conditions when one or both species are obligate mutualists.

Figure 2 show simulations of the original model \( 1 \), in which the resource dynamics is explicitly accounted by \( 2 \). The growth rates \( r_i \) and self-limitation coefficients \( c_i \) were set at very low values compared with flower production \( \alpha_i \), decay \( \omega_i \) and consumption \( \beta_j \) rates, in some cases the differences are more than two orders of magnitude. This makes resource dynamics much faster than population dynamics. We can see that in the majority of the cases, the amount of resources change very after a very short time, compared with the time that it takes the populations to reach an equilibrium. There a few instances of course, in which the resources vary as much as the population densities during the same time frame.

Next to the simulation of the original model, the dynamics of the model with resources under steady-state \( 3 \) is simulated using the same parameters and initial conditions. For this model, the resources follow equation \( 3 \) instead of a differential equation. This leads to the same equilibria as the original model, since the derivation of equation \( 3 \) is part of the procedure to find the equilibrium in system \( 1 \). We also see that the transient dynamics is very similar to the dynamics in the original model. In fact, the differences between both models can be chosen to be as little as desired, by widening the time scales between population and resource dynamics.

Interestingly, using model \( 1 \), we can approximate the dynamics of the resources. The derivation of \( 3 \) with respect to time results in:

\[
\frac{dF_i}{dt} = \alpha_i \left( \frac{\omega_i + \beta_j N_j}{\omega_i + \beta_i N_i} N_i \right) \frac{dN_i}{dt} - \beta_i N_i \frac{dN_i}{dt} \tag{7}
\]

Rather than substituting \( 1 \) above and complicating it even more, it is more enlightening to consider the following two scenarios. When both species have very low densities \( 7 \) becomes \( dF_i/dt \approx (\alpha_i/\omega_i) dN_i/dt \), i.e. the resources track the dynamics of the providers only. From Figure 2 we can see that this is a bad approximation, because in many simulations the resources decrease despite the fact that the populations are increasing. Now, if the populations are instead large enough \( (N_j \gg \omega_i/\beta_j) \), equation \( 7 \) is better approximated by:

\[
\frac{dF_i}{dt} \approx \left( \frac{\alpha_i}{\beta_j} \right) N_i \frac{dN_i}{dt} - \frac{N_i \frac{dN_i}{dt}}{N_j^2} \tag{8}
\]

At very large densities, population growth is forced to slow down because of self-limitation. Indeed, before attaining an equilibrium, populations ought to be growing at rates that are sub-exponential (for an explanation
Figure 1: Nullclines (dashed curves) and equilibrium points in mutualisms with exchange of resources for resources, assuming linear self-limitation for each species. Black and white circles represent stable (nodes) and unstable (saddle) equilibria respectively (also indicated by arrows nearby). A: When both species are facultative mutualists, their nullclines always cross once giving rise to a single globally stable mutualistic equilibrium. When species 1 is facultative and species 2 is an obligate mutualist their nullclines may cross as in B: once, giving rise to a single globally stable mutualistic equilibrium; or as in C: twice, giving rise to an unstable and a locally stable mutualistic equilibrium. When both species are obligate mutualists, their nullclines may cross at two points (never a single one), an unstable and a locally stable mutualistic equilibrium. The existence of an unstable mutualism means that the obligate species (species 2 in C, both species in D) may go extinct depending on the initial conditions or external perturbations. With the exception of case A, the nullclines may also never cross, leading to the extinction of one or both species (not shown).
Figure 2: Dynamics of the original mutualistic model \(1, 2\) in the left column, and of the steady-state model \(4\) in the right column. \(G_i\) is defined by \(5\) in both models. For each simulation in the original model a simulation in the steady-state model is done using the same initial conditions. Blue color is for species \(i = 1\) and green for \(i = 2\); \(r_i = \{0.007, 0.01\}, c_i = \{0.002, 0.001\}, \sigma_i = \{0.5, 0.3\}, \alpha_i = \{0.02, 0.03\}, \omega_i = \{0.2, 0.1\}, \beta_i = \{0.1, 0.15\}.

We can see from the simulations (Figure 2), that somewhere before the decelerating phase, population growth rates can be approximated as linear in time, i.e. \(dN_i/dt \approx k_i\). We know that \(dN_i/dt \approx 0\) eventually, but let see what happens if we substitute linear growth in the resource dynamics described in approximation above:

\[
\frac{dF_i}{dt} \approx \left(\frac{\alpha_i}{\beta_i}\right) \frac{k_i N_j - k_j N_i}{N_j^2}
\]

The numerator of this rate is linear and the denominator is quadratic. It is easy to see that when the populations are large enough and growing \(dF_i/dt \to 0\). In addition, since the populations will eventually attain an equilibrium, \(k_i\) and \(k_j\) must also decrease in time. Thus, the stabilization of the resources will happen even sooner than the stabilization of the populations, and for this reason the steady-state assumption is reasonably correct.

Exchanges of resources for services

This time consider that only species 1 is the food provider, and species 2 gives a service to species 1 as a consequence of food consumption. This situation occurs under pollination or in seed dispersal for example. Thus, let us assume that species 1 is a plant and species 2 an animal. The dynamical equations for plants and animals are:

\[
\begin{align*}
\frac{dN_1}{dt} &= G_1(\cdot)N_1 + \sigma_1 \beta_o F N_o + \sigma_1 \beta F N_2 \\
\frac{dN_2}{dt} &= G_2(\cdot)N_2 + \sigma_2 \beta F N_2
\end{align*}
\]

In this scheme \(F\) is the number of flowers or fruits produced by the plant, and \(\beta\) is the rate of pollination or frugivory by the animal. The animal’s equation is not different than before. The plant’s equation must be changed to reflect that plants do not eat anything from the animals, they instead grow in proportion to the number of flowers pollinated or fruits eaten (after all, they contain ovules or seeds). As pollination or frugivory takes place at the rate of \(\beta F N_2\), the plants increase their chances of fertilization or seed dispersal, with a yield \(\sigma_1\) that depends on the balance of the many benefits and risks involved in their interaction with the animals (e.g. seed mastication), as well as the number of ovules per flower or seeds per fruit. The purpose of an additional term \(\sigma_1 \beta_o F N_o\) is to account for the fact that pollination and seed dispersal can happen in the
the absence of the animal species explicitly considered, for example by the actions of another animal (species “o”) or thanks to abiotic factors like wind (then \( \beta_o, N_o \) would be proxies of e.g. wind velocity, and \( \sigma_o \) the corresponding yield).

Flower or fruit production is proportional to the plant’s abundance, and losses occur due to withering, rotting, pollination or consumption:

\[
\frac{dF}{dt} = \alpha N_1 - \omega F - \beta_o F N_o - \beta F N_2
\]  \hspace{1cm} (9)

The case of flowers deserves particular attention. Whereas a single act of frugivory denies a fruit to other individuals \textit{ipso facto}, a single act of pollination will hardly destroy a flower. Certainly, each pollination event brings a flower closer to fulfilling its purpose, to close, and to stop giving away precious resources (nectar). Each pollination event also makes a flower less attractive to other pollinators, as it becomes less rewarding or damaged. This means that the decrease in flower \textit{quantity} due to pollination (\( \beta F N_2 \)) involves a certain amount of decrease in \textit{quality}, rendering them useless for plants and animals, a little bit each time. Thus, the pollination rate in (9) should be rather cast as \( \kappa \beta F N_2 \) where \( 0 < \kappa \leq 1 \) is the probability that a flower stops working as a consequence of pollination. This is a complication that is relevant in specific scenarios, but it does not affect the generality of the results derived, which is why it is not considered (so \( \kappa = 1 \)). Similar to the previous scenario, assume that acts of pollination or frugivory do not entail damage for individual plants, notwithstanding the fact that flowers and fruits are physically attached to them.

Like before, consider that flowers or fruits are ephemeral compared with the lives of plants and animals. Thus \( F \) will rapidly attain a steady-state (\( dF/dt \approx 0 \)) compared with the much slower demographics. The number of flowers or fruits can be cast a function of plant and animal abundances \( F \approx \alpha N_1/(\omega + \beta_o N_o + \beta N_2) \), and the dynamical system (5) as:

\[
\frac{dN_1}{dt} = \left\{ G_1(\cdot) + \frac{\sigma_o \beta_o \alpha N_o + \sigma_1 \beta \alpha N_2}{\omega + \beta_o N_o + \beta N_2} \right\} N_1
\]

\[
\frac{dN_2}{dt} = \left\{ G_2(\cdot) + \frac{\sigma_1 \beta \alpha N_1}{\omega + \beta_o N_o + \beta N_2} \right\} N_2
\]  \hspace{1cm} (10)

where not surprisingly, the equation for the animal is practically the same as in the previous model where both species provide resources to each other. The only novelty is that the animal is sharing plant resources with other processes or animals (quantified by \( \beta_o N_o \)), thus hinting at competitive effects (more about this in the discussion). The equation for the plant is however very different, because it includes a saturating numerical response with respect to the abundance of its mutualistic partner, and it is in fact a multispecific numerical discussion). The equation for the plant is however very different, because it includes a saturating numerical response if \( o = 0 \) is the probability that a flower stops working as a fruit or seed dispersal process. The only novelty is that the animal is sharing plant resources with other species (more about this in the discussion, again).

Let us assume for the moment that the plant relies exclusively on species 2 for pollination or dispersal services (or \( N_o = 0 \)). Dividing numerator and denominator by \( \beta \), the numerical response of the plant can be written in the Michaelis-Menten form:

\[
\frac{v N_2}{K + N_2} = \frac{\alpha N_2}{(\omega/\beta) + N_2}
\]  \hspace{1cm} (11)

where the maximum rate at which a plant acquires benefits \( v = \alpha \) is limited by the rate at which it can produce fruits or flowers, and the half-saturation constant \( K = \omega/\beta \) is the ratio of the rate at which flower or fruits are wasted rather than used by the animal, in other words a quantifier of inefficiency. It turns out that in the jargon of enzyme kinetics where the Michaelis-Menten formula is widely used, half-saturation constants are seen as inverse measures of the affinity of an enzyme for its substrate. If the analogy were that of flower or fruits being substrates, and pollinators or frugivores being enzymes (i.e. facilitators), then \( 1/K = \beta/\omega \) would be the relative affinity of the animal for the flowers or fruits of the plant. Now, if we decide instead to divide the numerator and the denominator of the plant’s numerical response by \( \omega \), it can be written like Holling’s disc equation:

\[
\frac{a N_2}{1 + ah N_2} = \frac{(\alpha \beta/\omega) N_2}{1 + (\beta/\omega) N_2}
\]  \hspace{1cm} (12)

where the rate at which the provider acquires benefits \( a = \alpha \beta/\omega \) is proportional to fruit or flower production \( \alpha \), and to the ratio at which they are used instead of wasted \((\beta/\omega)\), e.g. the efficiency or affinity of the pollination or seed dispersal process. The “handling time” of the plant becomes \( h = 1/\alpha \), the average time it takes to create new flowers or fruits.

Using equation (10) to model the growth rates in the absence of the mutualism in model (10), it is straightforward to conclude that species 1 and 2 will respectively grow \( (dN_i/dt > 0) \) only if:
Figure 3: Nullclines and equilibrium points in mutualisms with exchange of resources for services, assuming linear self-limitation for each species. The explanation is the same as in Figure 1, only this time the nullcline of the resource provider (species 1) has an asymptote on its axis.

\[ N_1 < \frac{r_1 + \sigma \beta \alpha N_0 + \sigma_1 \beta \alpha N_2}{c_1(\omega + \beta \alpha N_0 + \beta N_2)} \]  
\[ N_1 > \frac{(c_2 N_2 - r_2)(\omega + \beta \alpha N_0 + \beta N_2)}{\sigma_2 \beta \alpha} \]  

and decrease if the signs of the inequalities are respectively reversed. The nullcline of the animal (ineq. 14 with “=” instead of “>”) is a parabola with the same properties of the nullclines in the previous model, only that \( \omega \) becomes \( \omega + \beta \alpha N_0 \). The plant’s nullcline (ineq. 13 with “=” instead of “<”) differs from the previous model as its graph is a rectangular hyperbola instead of a parabola. The plant’s nullcline has a single root on the plant axis, \( \frac{c_1}{c_1(\omega + \beta \alpha N_0)} \). If this root is negative, the plant is an obligate mutualist of species 2 because its intrinsic growth rate is negative \( (r_1 < 0) \), and other means of pollination/seed dispersal (i.e. \( \beta \alpha N_0 > 0 \)) are insufficient to compensate the losses. On the other hand if this root is positive, it may still be that the plant’s intrinsic growth rate is negative, yet pollination/seed dispersal not involving species 2 is enough to sustain the plant’s population. The maximum abundance that the plant could attain thanks to species 2 is limited by the plant’s nullcline asymptote at \( N_1 = (r_1 + \sigma_1 \alpha)/c_1 \). This means that if the plant’s intrinsic growth rate is negative, the rate of flower/fruit production \( \alpha \) times the returns \( \sigma_1 \) from the mutualism, must overcome mortality \( (\alpha \sigma_1 > -r_1) \), otherwise the abundance of species 2 will not prevent the extinction of the plant. Figure 3 shows the graphs of the nullclines.

Bearing in mind these details about the shapes of the nullclines, the dynamics of the mutualism between the plant providing the food and the animal providing the service are qualitatively the same as in the case of both species providing material aid (e.g. food or nutrients), as seen by comparing Figure 3 with Figure 1. The outcomes range from globally stable coexistence when both species are facultative mutualists, to locally stable coexistence or no coexistence when one or both are obligate mutualists.

**Discussion**

Using a separation of time scales and the assumption of fast resource dynamics, it was possible to derive simple models for mutualistic interactions. In these models, the effect of one species abundance on the growth rather of another, is grounded on microscopic principles, rather than phenomenology. These numerical responses display
decrease due to intra-specific competition, or because of diminishing returns in the acquisition of benefits, enhancing the stability of the interaction. My insistence of avoiding the term functional response and is entirely intentional. In the context of predation, functional response is meant to refer to the per-capita predation rate, whereas the numerical response describes the effect of prey density on predator growth rates (??). While it is still correct to refer to functional responses with regard to the consumption of resources provided by a mutualist (e.g. $\beta_i F_j$ in equation 2) is a type I functional response), the models derived (e.g. equation 4) describe the effect of population densities on growth rates, not consumption rates. Thus, the term numerical response is more appropriate in the present context.

In the case where each species produces a resource for the other, intra-specific competition results from the fact that resource production occurs at a finite rate per individual provider, independently of its population size. If the production of the provider is kept constant, this results in constant amount of resources provided per unit time, that will be partitioned among the members of the other species, in their role as consumers. If the consumer population is low, then each individual receives a constant share, since the decay rate of the resources is much larger than the rate at which they are consumed ($\omega_i \gg \beta_j N_j$). This is no longer true when consumer populations are large, which is when competition causes every individual to get a share that decreases with the number of con-specifics (Schoener, 1978).

In the case where only one species provides the resource, that resource is an organ (e.g. flower, fruit) used by the provider (e.g. plant) to extract a service (e.g. pollination, seed dispersal) from the consumer (animal). These organs must be regularly replaced as they are used or decay, but like in the first scenario this happens at a finite rate per individual no matter how large is its population. If the population of the provider is kept constant, and the population of the consumer is low, the rate at which the provider acquires benefits per unit of consumer depends on the production to decay ratio ($\alpha_i/\omega_i$), such that doubling the number of consumers doubles the benefits for the plants. When the consumer population is large, providers cannot regenerate the resource providing organs faster than the rate at which they are used. For this reason, the more the provider helps the consumer to grow, the lower its capacity to benefit from that increase, which explains the diminishing returns.

Fishman and Hadany (2010) also used time scale assumptions in order to model functional responses. However, their model is very specific for pollination by bees, and they go into higher levels of detail, by considering flower and patch states, and flower–nest traveling times. Under certain assumptions, their result derives into the Beddington-DeAngelis function, thus providing a mechanistic underpinning to the functional forms used by Holland and DeAngelis (2010). While lacking in detail, the models developed herein are more general, they can encompass plant–frugivore mutualisms in addition to plant–pollinator ones, when the resources are traded for services, or they can model plant–mycorrhizae systems where organic compounds are traded for essential nutrients.

I assumed that the consumption of resources enabling the mutualism follow simple mass action laws. In reality, consumption is very likely to display saturating functions (here the use of functional rather than numerical is correct). In an interaction such as frugivory, saturation could follow the disc equation mechanism (Holling, 1959), where the searching time of the consumer decreases with the number of fruits, leading to an hyperbolic function of the number of flowers. In pollination however, the fraction of time during which a flower is not visited, i.e. the “flower waiting time”, would decrease with the number of pollinators which increase the “flower working time”. Thus in contrast with frugivory, pollination must consider simultaneous saturation in plants and animals, and the Beddington-DeAngelis function would be a reasonable choice describing flower use. Replacing mass action laws with highly non-linear responses in the resource dynamics will make it very difficult to derive simple results as those presented. The absence of these complexities in the present formulation does not however, belittles the approach taken, which stresses the importance of considering the ephemeral nature of many kinds of resources shared in mutualistic interactions. The fact that these resources must be continuously regenerated at rates that are limited at the individual level, causes dynamical bottlenecks in the acquisition of benefits that ought to be considered, independently of the resource consumption patterns.

The numerical responses are by itself not sufficient to stop population growth at higher densities, they merely slow down population growth. To see this, suppose that $G_i = -r$ i.e. first order mortality rates. Substituting this in models (H100), the population dynamics of a species can be written (in a compact form) as:

$$\frac{dN_i}{dt} = \left\{ \begin{array}{l} \frac{aN_i}{b+N_i} - r \quad \text{or} \quad \frac{c+aN_j}{b+N_j} - r \end{array} \right\} N_i$$

where $a, b, c$ is everything that is not a variable. Suppose that thanks to mutualism, the populations become very large ($N_i \gg b$ and $N_j \gg c/a$). In the first alternative populations will follow $dN_i/dt \approx aN_i - rN_i$ and in the second case $dN_i/dt \approx (a-r)N_i (a > r$, otherwise the population would go extinct, contradicting that mutualism caused it to be large). Both are linear systems characterized by long term exponential growth, thus an equilibrium is not possible. There are several ways to achieve population decrease at such high densities. One is that mortality increases at higher than linear rates, for example quadratically $-rN_i^2$, which by using
Another possibility suggested by Johnson and Amarasekare (2013) is to consider functions like above, but with population densities raised to the second power in the denominator, simulating interference among consumers. Interestingly, interference of the producer by the consumer can enhance stability too. I assumed that resource consumption does not cause any damage to the provider, but now suppose that resource provision can be inhibited by too many consumers. A simple way to frame this is that the rate at which producer makes resources in equation (2) is 
\[
\alpha_i N_j / (1 + \gamma_i N_j)
\]
where \(\gamma_i\) scales the inhibitory effect of consumers. Using the steady-state assumption, the resource levels will be:
\[
F_j \approx \frac{\alpha_i N_j}{(1 + \gamma_i N_j)(\omega_j + \beta_i N_j)}
\]
where the denominator is quadratic in the consumer population. Thus, the rate of mutualism in equation (4) can be lower than first order mortality rates when the populations are large, like in Johnson and Amarasekare (2013) model. This scheme also applies to the resources for services model \(mutatis mutandis\).

Provided that conditions of fast resource dynamics and slow population dynamics apply, models (4,10) can be generalized to larger communities. Adding as many consumption terms as consumers in equations (2,10), the steady state level of resources given by the provider will be:
\[
F_j \approx \frac{\alpha_i N_j}{\omega_j + \sum_i \beta_i N_i}
\tag{15}
\]
so, a consumer that eats several of these resources (e.g. pollinators) will follow the dynamics:
\[
dN_i/dt = \left\{ G_i(\cdot) + \sum_j \frac{\sigma_{ij} \beta_{ji} \alpha_j N_j}{\omega_j + \sum_k \beta_{jk} N_k} \right\} N_i
\]
which is a multi-resource extension of Schoener (1978) competition models. For a species that gives resources but receives services instead (e.g. flowering plants), the dynamics will follow:
\[
dN_j/dt = \left\{ G_j(\cdot) + \frac{\alpha_j \sum_i \sigma_{ji} \beta_{ji} N_i}{\omega_j + \sum_i \beta_{ji} N_i} \right\} N_j
\]
where several benefits are pooled together in a multi-specific numerical response.

The parameters of these numerical responses are rates which are very likely to be related by means of trade-offs. Consider for example, fragile flowers or fruits (high \(\omega_i\)) that are cheaper to produce (large \(\alpha_i\)); or that there is an inverse relation between the consumption rate (\(\beta_j\)) and assimilation ratio (\(\sigma_i\)), i.e. an efficiency trade-off. In multi-specific contexts, the finite nature of the individuals constrain their consumption rates (\(\beta_{ji}\)), such that the increase of one causes the decrease in others. Some of these parameters, like the provision of benefits, can be related with the intrinsic growth rates \(G_i\) (Johnson and Amarasekare, 2013); for example \(dG_i/dx_i < 0\), because the energy used to make resources for other species could have been used to improve the provider’s capacity to live on its own. Since the production of benefits by species \(i\) affects the dynamics of species \(j\) (110), the coevolution of mutualism can be investigated. Furthermore, if the costs of providing benefits can go as far as changing the sign of \(G_i\) from positive to negative, the mechanistic framework described by this paper can be used to study the evolutionary origin of obligate mutualisms.

The use of time scale arguments is widespread in the theoretical biology. In ecology, the derivation of the competitive Lotka-Volterra equations by MacArthur (1976) is a well known example. A lesser known example (but more relevant here), are the competitive models derived by Schoener (1978), which consider the partition of resource inflows. The derivation of the disc equation (Holling, 1959) requires the fractioning of a predation cycle, a period of time that is embedded into the much longer time scale of the population dynamics. The scenarios suggested herein are far from exhaustive. One goal of this note is to see, to what extent, simple time scale assumptions can help unify consumer-resource, mutualism and competition theories. Another goal concerns the mechanistic derivation of generic models, with few complexities, but based on parameters that can be potentially measured such as rates of flowering or nectar production and decay, and consumption rates.

**Acknowledgements**

I thank Luis Fernando Chaves, Bart Haegemann, Michel Loreau, Claire de Mazancourt, Jarad Mellard, Shaopeng Wang, Francisco Encinas-Viso for their helpful comments and suggestions. This work was possible thanks to the support of the TULIP Laboratory of Excellence (ANR-10-LABX-41).
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