



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



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HIGHLIGHTS

- Simple resource-based mechanisms of mutualism are proposed.
- Resource ephemerality allows the derivation of mechanistic numerical responses.
- Limitations in resource delivery cause diminishing returns of mutualistic service.
- Consumers of mutualistic resources follow Schoener's competition equations.

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ABSTRACT

Many mutualisms involve inter-specific resource exchanges, making consumer–resource approaches ideal for studying their dynamics. Also in many cases these resources are short lived (e.g. flowers) compared with the population dynamics of their producers and consumers (e.g. plants and insects), which justifies a separation of time scales. As a result, we can derive the numerical response of one species with respect to the abundance of another. For resource consumers, the numerical responses can account for intra-specific competition for mutualistic resources (e.g. nectar), thus connecting competition theory and mutualism mechanistically. For species that depend on services (e.g. pollination, seed dispersal), the numerical responses display saturation of benefits, with service handling times related with rates of resource production (e.g. flower turnover time). In both scenarios, competition and saturation have the same underlying cause, which is that resource production occurs at a finite velocity per individual, but their consumption tracks the much faster rates of population growth characterizing mutualisms. The resulting models 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.

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1. 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

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 inter-specific competition coefficients of the Lotka–Volterra model, to reflect the positive effects 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,

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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 mutualists, which are functions of the resources offered to the other species, also with diminishing returns. In their analyses, the resources that mediate benefits and costs are replaced by population abundances as if the species were the resources themselves. This assumption enables the prediction of a rich variety of outcomes, such as Allee effects, alternative states, and transitions between mutualisms and parasitisms.

The work of Holland and DeAngelis (2010) uses concepts of consumer-resource theory to study the interplay between mutualism and antagonism at population and community levels, but the functional responses are not actually derived from first principles. In other words, there is no explicit mechanism that justifies why the resource provided by species 1, can be replaced by the abundance of species 1 (or some function of it). If the functional responses are considered phenomenologically that is not a problem, consumer-resource theory makes predictions using phenomenological relationships, like the Monod and Droop equations (Grover, 1997). For example, the *half-saturation* constant for mutualism in species 1 is a trivial concept, it is just the abundance of species 2 that produces half of the maximum benefit that species 1 can possibly receive. But things can be conceptually problematic when these saturating responses are rewritten and interpreted in the style of Holling's type II disc equations (Vázquez et al., 2015) because, 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?

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, or the resource providing organs, have life times that are on average much shorter than the lives of their producers and consumers. 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. Given their fragility and cost (Primack, 1985; McCall and Irwin, 2006), flowers are definitely ephemeral in comparison with pollinators like hummingbirds, but certainly not to mayflies.¹ Processes like diffusion and chemical reactions, can remove nutrients faster than the life cycles of their intended consumers. Taking advantage of this fact, the resources can be assumed to attain a steady-state against the backdrop of the population dynamics, and thus be quantified in terms of the present abundances of the providers and the consumers in a mechanistic manner. Using this approach, it is possible not just to derive 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 would make sense, not just intuitively. This in turn opens the possibility of framing the costs of mutualism by means of trade-offs relating vital parameters. The scenarios presented here are meant to promote more thinking in this direction, that of considering the separation of time scales, in order to tie together mutualism, competition, and consumer-resource theories in more mechanistic ways.

¹ Mayflies belong to the order *Ephemeroptera* a word derived from the Greek *ephemera* meaning short-lived, and *ptera* meaning wings. This is a reference to the short lifespan of most adult mayflies.

2. Exchanges of resources for resources

Consider two species $i, j = 1, 2$ providing resources to each other. Their population biomasses (N_i) change in time (t) according to the differential equations:

$$\begin{aligned}\frac{dN_1}{dt} &= G_1(\cdot)N_1 + \sigma_1\beta_1F_2N_1 \\ \frac{dN_2}{dt} &= G_2(\cdot)N_2 + \sigma_2\beta_2F_1N_2\end{aligned}\quad (1)$$

where F_i is the amount of resources or food provided by species i , β_i is the per-capita consumption rate per unit resource by species i , and σ_i its conversion ratio into biomass. 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 resource dynamics is accounted by a second set of differential equations:

$$\begin{aligned}\frac{dF_1}{dt} &= \alpha_1N_1 - \omega_1F_1 - \beta_2F_1N_2 \\ \frac{dF_2}{dt} &= \alpha_2N_2 - \omega_2F_2 - \beta_1F_2N_1\end{aligned}\quad (2)$$

Here I assume that the resource is produced in proportion to the biomass of the provider with per-capita rate α_i , and it is lost or decays with a rate ω_i if it is not consumed. I also assume that the physical act of resource consumption does not have an instantaneous negative impact such as damage or death, on the provider (e.g. they do not constitute vital body parts). There are costs associated with resource production, but they do not affect the derivations that follow here as well as in the next section. Nevertheless, the potential consequences of different kinds of costs are briefly discussed at the end of this work.

As stated in the introduction, the life time of food or resource items can be much shorter than the dynamics of the populations; in other words, we can consider a slow dynamics for the populations and a fast one for the resources (Rinaldi and Scheffer, 2000). As a consequence, the resources will asymptotically approach a steady-state or quasi-equilibrium dynamics well before the populations display significant changes. Thus, assuming that $dF_j/dt \approx 0$ in Eqs. (2), the steady-state amount of resources

$$F_j \approx \frac{\alpha_j N_j}{\omega_j + \beta_i N_i} \quad (3)$$

can be substituted in the dynamical equations of the populations (1) using the appropriate indices:

$$\begin{aligned}\frac{dN_1}{dt} &= \left\{ G_1(\cdot) + \frac{\sigma_1\beta_1\alpha_2N_2}{\omega_2 + \beta_1N_1} \right\} N_1 \\ \frac{dN_2}{dt} &= \left\{ G_2(\cdot) + \frac{\sigma_2\beta_2\alpha_1N_1}{\omega_1 + \beta_2N_2} \right\} N_2\end{aligned}\quad (4)$$

In model (4), 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 ($\alpha_j N_j$) must be shared among an increasing number 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 Schoener (1978), with the only difference that in Schoener's models resource supply rates are constant. The interaction mechanism can be generalized to multiple species, by adding additional consumption terms in Eqs. (1) and (2). After the steady-state assumption, the multispecies version of Eqs. (4) for species 1 will be

$$\frac{dN_1}{dt} = \left\{ G_1(\cdot) + \sum_j \frac{\sigma_{j1}\beta_{j1}\alpha_j N_j}{\omega_j + \sum_k \beta_{jk} N_k} \right\} N_1 \quad (5)$$

where the index k belongs to species in the same guild as species 1 (its competitors, including itself), and index j belongs to the guild of its

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