

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

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April 15, 2015

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Running Head: Time scales in resource-based mutualisms

Type of article: Regular paper

Highlights:

- Simple resource-based mechanisms of mutualism are proposed
- Resource ephemerality allows the derivation of numerical responses based on production and utilization rates
- Receivers of mutualistic services experience diminishing returns due to limitations in resource delivery
- The dynamics of consumers of mutualistic resources can be described by Schoener's competition equations

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2 Many mutualisms involve inter-specific resource exchanges, making consumer-
resource approaches ideal for studying their dynamics. Also in many cases
4 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
6 response of one species with respect to the abundance of another. For
resource consumers, the numerical responses can account for intra-specific
8 competition for mutualistic resources (e.g. nectar), thus connecting competition
theory and mutualism mechanistically. For species that depend on
10 services (e.g. pollination, seed dispersal), the numerical responses display saturation
of benefits, with service handling times related with rates of resource
12 production (e.g. flower turnover time). In both scenarios, competition and
saturation have the same underlying cause, which is that resource production
14 occurs at a finite velocity per individual, but their consumption tracks
the much faster rates of population growth characterizing mutualisms. The
16 resulting models display all the basic features seen in many models of facultative
and obligate mutualisms, and they can be generalized from species
18 pairs to larger communities.

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

Introduction

22 - *Nous ne notons pas les fleurs, dit le géographe*

 - *Pourquoi ça! c'est le plus joli!*

24 - *Parce que les fleurs sont éphémères*

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

26 Early attempts to model the dynamics of mutualisms were based on phenomenologi-
28 cal 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,
30 yet insightful approach, predicts several outcomes depending on whether mutualism is
facultative or obligatory. One example is the existence of population thresholds, where
32 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 mutu-
34 alists 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
36 to assume that mutualistic benefits have diminishing returns (Vandermeer and Boucher,
1978; May, 1981), such that negative density dependence (e.g. competition) would catch
38 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
40 membrane area, minimum handling times, etc), causing saturation by excessive amounts
of benefits. Other approaches consider cost-benefit balances that change the sign of
42 inter-specific interactions from positive at low densities (facilitation) to negative at high
densities (antagonism) (Hernandez, 1998).

44 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
46 resources which are consumed by species 2 and 1, according to Holling’s type II func-
tional response, and which are converted into numerical responses by means of conver-
48 sion 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
50 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
52 assumption enables the prediction of a rich variety of outcomes, such as Allee effects,
alternative states, and transitions between mutualisms and parasitisms.

54 The work of Holland and DeAngelis (2010) uses concepts of consumer-resource theory
to study the interplay between mutualism and antagonism at population and commu-
56 nity 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
58 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-
 60 resource theory makes predictions using phenomenological relationships, like the Monod
 and Droop equations (Grover, 1997). For example, the *half-saturation* constant for mu-
 62 tualism 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 con-
 64 ceptually 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
 66 *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
 68 the dynamics of the resources associated with the interaction in a more explicit manner,
 70 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
 72 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
 74 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 comparisson with pollinators
 76 like hummingbirds, but certainly not to mayflies¹. Processes like diffusion and chemical
 reactions, can remove nutrients faster than the life cycles of their intended consumers.
 78 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
 80 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
 82 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
 84 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
 86 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
 88 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.

90 Exchanges of resources for resources

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

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

¹Mayflies 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.

where F_i is the amount of resources or food provided by species i , β_i is the per-capita
 94 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*
 96 *species j by means of the mutualism*. The resource dynamics is accounted by a second
 set of differential equations:

$$\begin{aligned}\frac{dF_1}{dt} &= \alpha_1 N_1 - \omega_1 F_1 - \beta_2 F_1 N_2 \\ \frac{dF_2}{dt} &= \alpha_2 N_2 - \omega_2 F_2 - \beta_1 F_2 N_1\end{aligned}\tag{2}$$

98 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
 100 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 don't constitute
 102 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
 104 potential consequences of different kinds of costs are briefly discussed at the end of this
 work.

106 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
 108 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
 110 or quasi-equilibrium dynamics well before the populations display significant changes.
 Thus, assuming that $dF_j/dt \approx 0$ in equations (2), the steady-state amount of resources:

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

112 can be substituted in the dynamical equations of the populations (1) using the appropri-
 ate indices:

$$\begin{aligned}\frac{dN_1}{dt} &= \left\{ G_1(\cdot) + \frac{\sigma_1 \beta_1 \alpha_2 N_2}{\omega_2 + \beta_1 N_1} \right\} N_1 \\ \frac{dN_2}{dt} &= \left\{ G_2(\cdot) + \frac{\sigma_2 \beta_2 \alpha_1 N_1}{\omega_1 + \beta_2 N_2} \right\} N_2\end{aligned}\tag{4}$$

114 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
 116 happens because the resource produced by the provider ($\alpha_j N_j$), must be shared among
 an increasing numbers of individuals, each taking a fraction $\beta_i/(\omega_j + \beta_i N_i)$. This in effect
 118 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
 120 supply rates are constant. The interaction mechanism can be generalized to multiple
 species, by adding additional consumption terms in equations (1,2). After the steady-
 122 state assumption, the multispecies version of equations (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 mutualistic partners. Similar equations apply for the other species, with changes in the appropriate indices. Equation (5) is a multi-resource extension of [Schoener \(1978\)](#) competition models.

Characterizing the system dynamics requires explicit formulations of the growth rates in the absence of mutualistic benefits, i.e. the G_i functions. These functions can range from very simple to very complicated depending on the biology of the species, alternative food sources, whether mutualism is obligate or facultative, self-regulation mechanisms, interactions with other species, and even the interactions between species 1 and 2 by means other than mutualism ([Holland and DeAngelis, 2010](#)). For illustration, I will consider the widespread assumption ([Holland and DeAngelis, 2010](#); [Johnson and Amarasekare, 2013](#)) that G_i is linearly decreasing on species i abundance:

$$G_i(N_i) = r_i - c_i N_i \quad (6)$$

where $c_i > 0$ is a coefficient of self-limitation and r_i is the intrinsic growth rate of i , which is positive for facultatives and zero or negative for obligate mutualists. By substituting (6) in (4), it turns out that species 1 increases ($dN_1/dt > 0$) if:

$$N_2 > \frac{(c_1 N_1 - r_1)(\omega_2 + \beta_1 N_1)}{\sigma_1 \beta_1 \alpha_2} \quad (7)$$

and decreases otherwise. With an equal sign (7) is the nullcline of species 1. The nullcline is an increasing parabola in the positive part of the $N_1 N_2$ plane. This nullcline has two roots in the N_1 axis, one at $-\omega_2/\beta_1$ which is always negative, and one at r_1/c_1 which is negative or zero if species 1 is an obligate mutualist, or positive if it is a facultative mutualist. For a facultative mutualist r_1/c_1 is also its carrying capacity, while for an obligate mutualist a negative r_1 can be its intrinsic mortality. Species 2 nullcline is similar with the indices swapped. 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. The dynamics under the steady approximation (4) is quantitatively different that in the original mechanism (1, 2), but this discrepancy can be very low if the resource dynamics is fast enough, as shown numerically in the Appendix.

Note that in this resource-for-resource model, the resources are assumed to be released in an external pool, which is accessible, in principle, for all members of each population. A good example are non-symbiotic bacteria that raise soil nitrogen, which is absorbed by the plants, which in turn release organic exudates in the soil, which is taken by the bacteria ([Vadakattu and Paterson, 2006](#)). Another good example is provided by lichens, where algae provide photosynthetic products to fungi, which in turn provide nutrients to

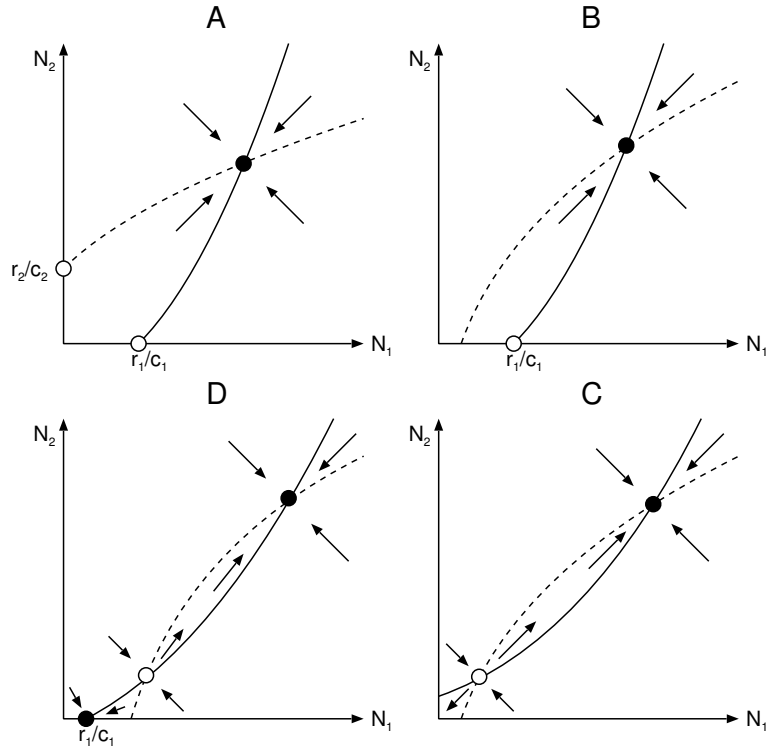


Figure 1: Nullclines in mutualisms with exchange of resources for resources (4), assuming linear self-limitation for each species. Species 1 (2) has the solid (dashed) nullcline. Black and white circles represent stable (nodes) and unstable (saddle) equilibria respectively (also indicated by arrows nearby). 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).

the algae (Holland and DeAngelis, 2010), yet neither algal cells nor fungal hyphae live
 158 inside each other bodies. A very common scenario however, involves one species hosting
 an endosymbiont (Holland and DeAngelis, 2010), like for example legumes (hosts) and
 160 micorrhizal fungi (symbionts). In this case, each plant assimilates the nutrients (e.g.
 nitrogen) provided by its private population of fungi, which in turn can only take the
 162 organic compounds provided by its plant. For this scenario, equations like (1) account for
 the biomass dynamics of an individual plant, instead of all plants, and for their private
 164 micorrhizal populations (a detail seldom considered by generalized models of mutualism).

Exchanges of resources for services

166 This time I will 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
 168 pollination or in frugivorous 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
 170 are:

$$\begin{aligned}\frac{dN_1}{dt} &= G_1(\cdot)N_1 + \sigma_o\beta_oFN_o + \sigma_1\beta FN_2 \\ \frac{dN_2}{dt} &= G_2(\cdot)N_2 + \sigma_2\beta FN_2\end{aligned}\tag{8}$$

In this scheme F is the number of flowers or fruits produced by the plant, and β is
 172 the rate of pollination or frugivory by the animal. The animal's equation is not different
 than before (1). The plant's equation must be changed to reflect that plants do not eat
 174 anything provided by the animals. This is an important detail that makes the conversion
 ratios or yields (σ_i) very different between plants and animals. For animals it is generally
 176 assumed, in particular when populations are accounted by biomass rather than numbers,
 that conversion ratios are smaller than 1 ($\sigma_2 < 1$). For plants however, the overall yield
 178 can be smaller or larger than one. This is because each flower or fruit can give rise to a
 potentially large number of new adult plants (a so called "amplification factor" by Fagan
 180 et al., 2014), with upper limits imposed by the number of ovules or seeds, per flower or
 fruit respectively. This is not just valid if populations are accounted by numbers, but
 182 also if we consider biomass: a new generation of plants does not grow out of resources
 taken from the animals, but from resources that are not accounted by the model (e.g.
 184 water, nutrients). Of course, risks associated with the interactions with the animal (e.g.
 pollen eating, seed mastication), means that the yield can end up being smaller than 1.

186 The additional plant term $\sigma_o\beta_oFN_o$ acknowledges that pollination or seed dispersal
 could be performed by a different animal than species 2 (species "o"), or by abiotic factors
 188 like wind (then β_o , N_o would be proxies of e.g. wind flux, and σ_o the corresponding yield).
 Flower or fruit production is proportional to plant's abundance, and losses occur due to
 190 withering, rotting, pollination or consumption:

$$\frac{dF}{dt} = \alpha N_1 - \omega F - \beta_o FN_o - \beta FN_2\tag{9}$$

192 The case of flowers deserves particular attention. Whereas a single act of frugivory
 194 denies a fruit to other individuals *ipso facto*, a single act of pollination will hardly destroy
 a flower. Certainly, each pollination event brings a flower closer to fulfilling its purpose,
 196 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
 198 damaged. This means that the decrease in flower *quantity* due to pollination (βFN_2)
 involves a certain amount of decrease in *quality*, rendering them useless for plants and
 200 animals, a little bit each time. Thus, the pollination rate in (9) shall rather be cast as
 $\kappa\beta FN_2$ where $0 < \kappa \leq 1$ is the probability that a flower stops working as a consequence
 202 of pollination. This complication can be relevant in specific scenarios, but it does not
 affect the generality of the results derived, which is why it is not considered (so $\kappa = 1$).
 A second important detail concerning flowers is that the visit by an individual pollinator
 may not cause pollination, because that individual has not yet visited a flower for the first
 204 time. Thus, equations (8, 9) are only valid after some pollinators have already visited
 some flowers.

206 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
 208 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
 210 ($dF/dt \approx 0$) compared with the much slower demographies. The number of flowers or
 fruits can be cast a function of plant and animal abundances $F \approx \alpha N_1 / (\omega + \beta_o N_o + \beta N_2)$,
 212 and the dynamical system (8) as:

$$\begin{aligned}
 \frac{dN_1}{dt} &= \left\{ G_1(\cdot) + \frac{\sigma_o \beta_o \alpha N_o + \sigma_1 \beta \alpha N_2}{\omega + \beta_o N_o + \beta N_2} \right\} N_1 \\
 \frac{dN_2}{dt} &= \left\{ G_2(\cdot) + \frac{\sigma_2 \beta \alpha N_1}{\omega + \beta_o N_o + \beta N_2} \right\} N_2
 \end{aligned} \tag{10}$$

214 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 equation for
 the plant is however very different, because its numerical response saturates with respect
 216 to the abundance of its mutualistic partner, species 2. If N_o is taken as the population
 abundance of another animal species, we can see that model (10) can be generalized to
 218 account for many species, i.e. the equation for plant 1 (and other plants) will be of the
 form:

$$\frac{dN_1}{dt} = \left\{ G_1(\cdot) + \frac{\alpha_1 \sum_j \sigma_{j1} \beta_{1j} N_j}{\omega_1 + \sum_j \beta_{1j} N_j} \right\} N_i \tag{11}$$

220 where multiple benefits are be pooled together as a saturating multi-species numerical
 response using appropriate indices. The equations for the animals will be like in model
 222 (5). Notice that the plants do not experience competition for animal benefits, like animals
 do for plant resources. In principle, plants would compete very indirectly by influencing
 224 animal diets (e.g. β_{ij} , where $i \in \text{plants}, j \in \text{animals}$), but this would require more
 elaborate mechanisms (see Discussion).

226 Using (6) for G_i , it is straightforward to conclude that species 1 and 2 will respectively
grow ($dN_i/dt > 0$) if:

$$N_1 < \frac{r_1}{c_1} + \frac{\sigma_o \beta_o \alpha N_o + \sigma_1 \beta \alpha N_2}{c_1(\omega + \beta_o N_o + \beta N_2)} \quad (12)$$

$$N_1 > \frac{(c_2 N_2 - r_2)(\omega + \beta_o N_o + \beta N_2)}{\sigma_2 \beta \alpha} \quad (13)$$

228 and decrease if the signs of the inequalities are respectively reversed. The nullclines are
the same as above with “=” signs instead. The animal’s nullcline is a parabola like in
230 model (4) only that ω becomes $\omega + \beta_o N_o$. The plant’s nullcline differs from the previous
model, it is a rectangular hyperbola, with a single root on the plant axis: $\frac{r_1}{c_1} + \frac{\sigma_o \beta_o \alpha N_o}{c_1(\omega + \beta_o N_o)}$.
232 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.
234 $\beta_o N_o > 0$) 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 or zero,
236 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
238 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 (α) times
240 the returns (σ_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 2 shows
242 the graphs of the nullclines. The outcomes are qualitatively the same as in model (4),
as shown by Figure 2. The numerical discrepancies between the dynamics in the original
244 model (8, 9) and its steady-state approximation (10) are shown and discussed in the
Appendix.

246 The numerical response of the plant in (10) enables mechanistic interpretations for the
saturation constants, rates and handling times, of species that rely on services rather
248 than material resources (e.g. food). Let us assume for the moment that the plant relies
exclusively on species 2 for pollination or dispersal services (or $N_o = 0$). Dividing the
250 numerator and the denominator of the numerical response by β , it can be written in the
Michaelis–Menten form:

$$\frac{v N_2}{K + N_2} = \frac{\alpha N_2}{(\omega/\beta) + N_2} \quad (14)$$

252 where the maximum rate at which a plant acquires benefits $v = \alpha$ is set by the rate
at which it can produce fruits or flowers, and the half-saturation constant $K = \omega/\beta$
254 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
256 enzyme kinetics where the Michaelis–Menten formula is widely used, the half-saturation
constants is inverse of the *affinity* between an enzyme and its substrate. If the analogy
258 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
260 flowers or fruits of the plant. Now, if we decide instead to divide the numerator and the

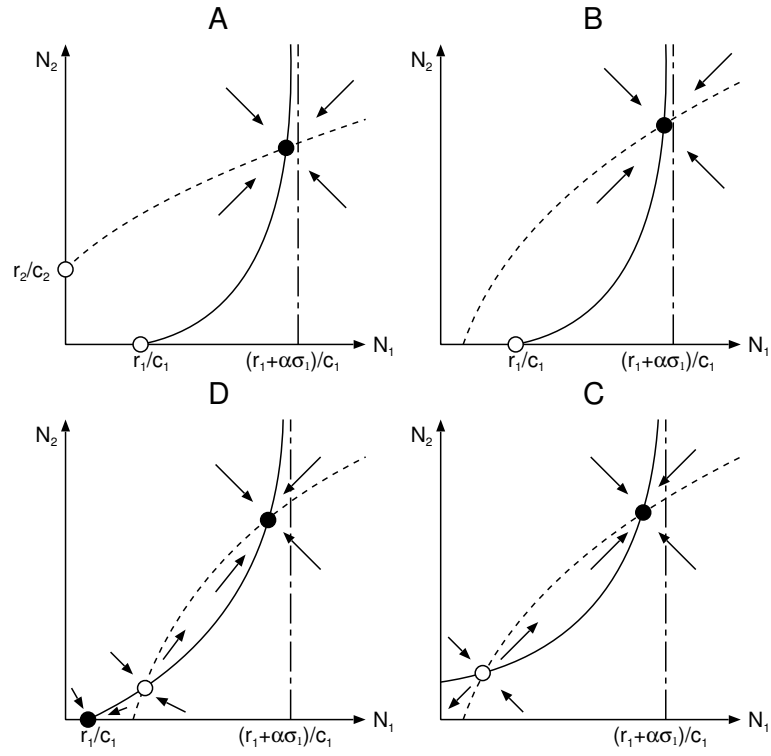


Figure 2: Nullclines (species 1: continuous line, species 2: dashed line) and equilibrium points in mutualisms with exchange of resources for services (10), with linear self-limitation for each species (species 1 receive services from species 2 only, i.e. $N_o = 0$). The explanations for A,B,C,D are the same as in Figure 1.

denominator of the plant’s numerical response by ω , it can be written like Holling’s disc
262 equation:

$$\frac{aN_2}{1 + ahN_2} = \frac{(\alpha\beta/\omega) N_2}{1 + (\alpha\beta/\omega) (1/\alpha) N_2} \quad (15)$$

where the rate at which the provider acquires benefits $a = \alpha\beta/\omega$, is proportional to fruit
264 or flower production α , and to the use to waste ratio (β/ω), e.g. the efficiency or affinity
of the pollination or seed dispersal process. The “handling time” of the plant becomes
266 $h = 1/\alpha$, i.e. the average time it takes to create new flowers or fruits.

Discussion

268 By using a separation of time scales and the assumption of fast resource dynamics, it is
possible to derive simple models for mutualistic interactions. In these models, the effect
270 of one species abundance on the growth rate of another, is mechanistically grounded,
rather than purely phenomenological. These *numerical responses* display decrease due
272 to intra-specific competition, or because of diminishing returns in the acquisition of
benefits, enhancing the stability of the interaction. I avoid using the term *functional*
274 *response* because it refers to a consumption rate, whereas a numerical response describes
the effect of resource density on consumer growth rates (Solomon, 1949; Holling, 1961).
276 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),
278 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
280 the present context.

In both of the scenarios considered (resource–for–resource, resource–for–service), intra-
282 specific competition for mutualistic resources emerges because resource production occurs
at a finite rate per individual provider, independently of its population size. If the
284 population of the provider is kept constant, this results in constant amounts of resources
provided per unit time, that will be partitioned among the members of the other species,
286 in their role as consumers. If the consumer population is low, then each individual receives
a constant share, since the resource decay rate is much larger than the consumption rate
288 ($\omega_i \gg \beta_j N_j$). 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
290 co-specifics (Schoener, 1978).

In the case where only one species provides the resource, this occurs in the form of
292 an *organ* (e.g. flower, fruit) used by the provider (e.g. plant) to *capture* a service (e.g.
pollination, seed dispersal) from the consumer (e.g. pollinator, frugivore). These organs
294 must be regularly replaced as they are used or decay, but, as in the first scenario, this
provision happens at a finite rate per individual no matter how large is its population.
296 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
298 on the production to decay ratio (α_i/ω_i), such that doubling the number of consumers

doubles the benefits for the plants. When the consumer population is large, providers
300 cannot regenerate the resource providing organs faster than the rate at which they are
302 used. For this reason, the more the provider helps the consumer to grow, the lower its
304 capacity to benefit from that increase, which explains the diminishing returns. Keep in
306 mind however, that diminishing returns or saturating responses are typically not enough
308 to ensure stability; this requires additional factors such as negative density dependence
in growth rates (6) or interference among consumers (Johnson and Amarasekare, 2013).
In contrast with the resource–for–resource model, in the resource–for–service model the
resource provider (e.g. plant) does not experience intra-specific competition for mutu-
alistic services. One step in this direction is the optimal foraging model of Valdovinos
et al. (2013), in which plants experience lottery-like competition for pollinator visits. This
model explicitly accounts for nectar production and consumption, using equations like
2, being just one step short of the kind models here proposed.

312 I assumed that resource consumption follows simple mass action laws. In reality, con-
sumption likely displays saturating functional responses (here the use of *functional* rather
314 than *numerical* is correct). In an interaction such as frugivory, saturation could follow
the disc equation mechanism (Holling, 1961), where the searching time of the consumer
316 decreases with the number of fruits, leading to an hyperbolic function of the number
of fruits. In pollination however, the fraction of time during which a flower is not vis-
318 ited, 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
320 consider simultaneous saturation in plants and animals, and the Beddington-DeAngelis
function (Beddington, 1975; DeAngelis et al., 1975) would be a reasonable choice de-
322 scribing 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.
324 The absence of these complexities in the present formulation does not however, diminish
the approach taken, which stresses the importance of considering the ephemeral nature of
326 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
328 dynamical bottlenecks in the acquisition of benefits that ought to be considered, inde-
pendently of the resource consumption patterns. Another complication not considered is
330 that flowers and fruits are lost when plants die, but these processes are supposed to be
very slow.

332 The parameters in models such as (4) and (10) are very likely related by trade-offs
(Johnson and Amarasekare, 2013). It is reasonable to assume for example, that the
334 energy or time used to deliver resources for another species, could be spent to raise the
provider’s intrinsic growth rate in (6), thus $\partial r_i / \partial \alpha_i < 0$. Trade-offs could also affect
336 the resource quality, e.g. fruits or flowers can be cheaper to produce, but at the cost of
being very fragile or short-lived ($\partial \omega_i / \partial \alpha_i > 0$) (Primack, 1985). From the perspective of
338 a consumer, assimilation ratios (σ_i) can be inversely related to consumption rates (β_i).
And for generalist consumers with population dynamics described by (5), one typically
340 assumes that increasing the consumption rate for one resource causes the decrease in
the consumption rates of others. Although these trade-offs do not change the general
342 shape of the nullclines shown in Figures (1, 2), they can lead to important changes in the

344 qualitative properties of the mutualism. For example, if the costs of providing benefits
can go as far as changing the sign of r_i from positive to negative, a species could turn
from a facultative mutualist into an obligatory one.

346 Another kind of cost associated with mutualisms arises because the interaction be-
tween the species also include antagonisms. These costs are typically experienced at
348 similar time scales as the population dynamics (e.g. herbivory), thus they were not in
the scope of this paper. An example are leafcutter ants that provide substrates to fungus,
350 but they eat them too; or butterflies that pollinate when adults, but are leaf eaters when
larva (Revilla and Encinas-Viso, 2015). The costs of these interactions increase with the
352 consumer’s abundance, which is why they are typically substracted as saturating func-
tional responses in the provider’s biomass dynamics (Holland and DeAngelis, 2010). An
354 important consequence of such density-dependent costs are changes in nulleline shapes,
from monotonically increasing (i.e. Figures 1,2), into more complex folding curves that
356 can intersect multiple times, giving rise to alternative states that favor one species over
another, depending on the initial conditions (Hernandez, 1998; Holland and DeAngelis,
358 2009, 2010).

The use of time scale arguments is widespread in the ecological literature. The deriva-
360 tion of the competitive Lotka-Volterra equations by MacArthur (1970) is a well known
example. A lesser cited example but the most relevant here, are the competitive mod-
362 els derived by Schoener (1978), which consider the partition of resource inflows (e.g.
equation 3). Holling’s (1961) disc equation assumes a predation cycle embedded into
364 a longer time scale of population dynamics. Fishman and Hadany (2010) derived a
Beddington-DeAngelis functional response in the specific case of bee pollination, by con-
366 sidering details such as flower and patch states, and flower–nest traveling times. And for
protection mutualisms Morales et al. (2008) employed time scale arguments in order to
368 simplify the study of ant protection mutualisms.

The scenarios suggested herein are far from exhaustive and the mechanistic details can
370 be higher. But on the other hand, the models developed are of a general nature, they
can encompass most plant–frugivore mutualisms in addition to plant–pollinator ones,
372 when the resources are traded for services. They may not capture all the intricacies of
plant–mycorrhizae systems, or coral–zooxanthellae, where organic compounds are traded
374 directly and privately between individuals, but they capture simple facilitation or mutual
saprophytism of the kind described by Vadakattu and Paterson (2006), or in lichens. One
376 goal of this work is to see, to what extent, simple time scale assumptions can help unify
consumer–resource, mutualism and competition theories. Another goal concerns the
378 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
380 decay, and consumption rates.

Acknowledgements

382 I thank Luis Fernando Chaves, Francisco Encinas-Viso, Vlastimil Křivan and colleagues at
the Centre for Biodiversity Theory and Modelling in Moulis (France) for comments and

384 suggestions. I also acknowledge the advice of Nathaniel Holland and several anonymous
reviewers. This work was supported by the TULIP Laboratory of Excellence (ANR-
386 10-LABX-41). Support provided by the Institute of Entomology (RVO:60077344) and
Postdok-BIOGLOBE (CZ.1.07/2.3.00/30.0032) co-financed by the European Social Fund
388 and the state budget of the Czech Republic is acknowledged.

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442 Appendix

From the main text the original model of exchanges of resources for resources reads:

$$\begin{aligned}\frac{dN_i}{dt} &= (r_i - c_i N_i)N_i + \sigma_i \beta_i F_j N_i \\ \frac{dF_j}{dt} &= \alpha_j N_j - \omega_j F_j - \beta_i F_j N_i\end{aligned}\tag{A.1}$$

444 in which $G_i = r_i - c_i N_i$. Following the steady-state approximation ($dF_j/dt = 0$) this
 model becomes:

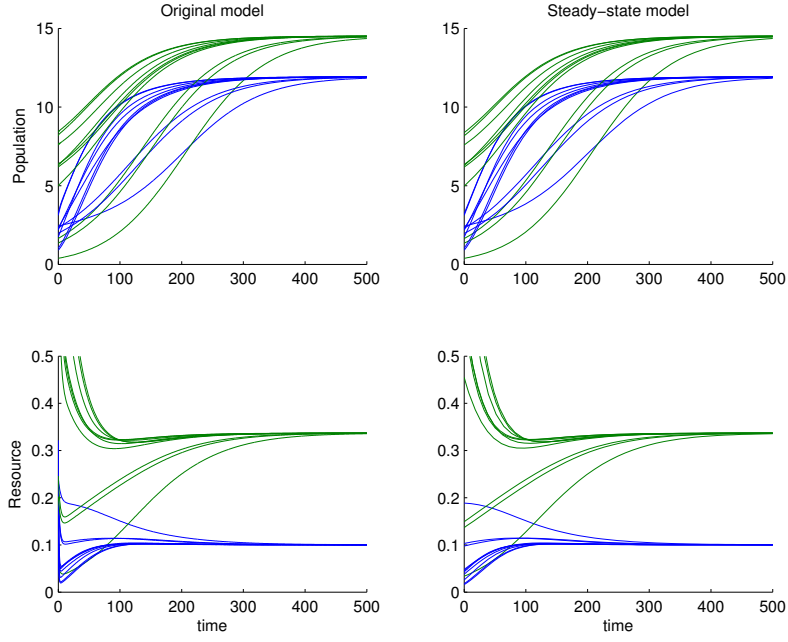


Figure A.1: Dynamics of the original mutualistic model (A.1) in the left column, and of the steady-state model (A.2) in the right column. For each simulation in the original model a simulation in the steady-state model is done using the same initial conditions for species abundances. Blue (green) lines are for species $i = 1$ ($= 2$); $r_i = \{0.007, 0.01\}$, $c_i = \{0.002, 0.001\}$, $\sigma_i = \{0.5, 0.3\}$, $\alpha_i = \{0.02, 0.03\}$, $\omega_i = \{0.2, 0.1\}$, $\beta_i = \{0.1, 0.15\}$.

$$\begin{aligned} \frac{dN_i}{dt} &= \left\{ r_i - c_i N_i + \frac{\sigma_i \beta_i \alpha_j N_j}{\omega_j + \beta_i N_i} \right\} N_i \\ F_j &= \frac{\alpha_j N_j}{\omega_j + \beta_i N_i} \end{aligned} \quad (\text{A.2})$$

446 In Figure A.1 we compare the dynamics of both models (A.1,A.2) numerically using ten
 448 replicates. In these simulations the growth rates r_i and self-limitation coefficients c_i were
 450 set at very low values compared with resource production α_i , decay ω_i , and consumption
 β_i rates; in some cases the differences are more than two orders of magnitude. This makes
 resource dynamics much faster than population dynamics. Both models start with the
 same initial values for the species population abundances.

452 From the main text the original model of exchanges of resources for services can be
 stated as:

$$\begin{aligned}
\frac{dN_1}{dt} &= (r_1 - c_1 N_1)N_1 + \sigma_1 \beta F N_o + \sigma_1 \beta F N_2 \\
\frac{dN_2}{dt} &= (r_2 - c_2 N_2)N_2 + \sigma_2 \beta F N_2 \\
\frac{dF}{dt} &= \alpha N_1 - \omega F - \beta F N_o - \beta F N_2
\end{aligned} \tag{A.3}$$

454 in which $G_i = r_i - c_i N_i$, and $\sigma_o = \sigma_1, \beta_o = \beta$ for simplicity. Following the steady-state approximation ($dF_j/dt = 0$) this model becomes:

$$\begin{aligned}
\frac{dN_1}{dt} &= \left\{ r_1 - c_1 N_1 + \frac{\sigma_1 \beta \alpha N_o + \sigma_1 \beta \alpha N_2}{\omega + \beta N_o + \beta N_2} \right\} N_1 \\
\frac{dN_2}{dt} &= \left\{ r_2 - c_2 N_2 + \frac{\sigma_2 \beta \alpha N_1}{\omega + \beta N_o + \beta N_2} \right\} N_2 \\
F &= \frac{\alpha N_1}{\omega + \beta N_o + \beta N_2}
\end{aligned} \tag{A.4}$$

456 In Figure A.2 we compare the dynamics of both models (A.3,A.4) numerically using ten
458 replicates. Most of the parameters are similar to those used in the model of exchange of
460 resources for resources ($r_i, c_i, \alpha, \omega, \beta$), in order to make the resource dynamics much faster
462 than population dynamics. However, whereas the conversion efficiency of the resource
464 consumer is less than 1 as before, for the service receiver (species 1) it is larger than 1,
466 for the reasons stated in the main text.

462 For both models the simulations show discrepancies at starting times because for equa-
464 tions like (A.1,A.3) the initial values of F_j can be arbitrary, whereas in models like
466 (A.2,A.4) they are determined by the initial species abundances. After less than 10 time
468 units, the transient dynamics are very similar in both models. In fact, the differences
470 between both models can be chosen to be as little as desired, by widening the time scales
472 between population and resource dynamics.

468 Using again the resource for service model (A.3), one last calculation illustrates the
470 large difference between population and resource time scales. When plants and animals
472 don't interact, they grow logistically as in $dN_i/dt = (r_i - c_i N_i)N_i$. Thus, their doubling
474 times at low population densities, and perturbation half-times around their carrying capacities,
476 are: $\tau_i = \log_e(2)/r_i$. Using the parameter values of Figure A.2, these are
 $\tau_1 \approx 99$ and $\tau_2 \approx 69$ time units for plants and animals respectively. Now consider that
they start to interact, with N_1, N_2 are nearly constant around their carrying capacities.
During the very short time this constancy holds, the fruit/flower ODE in (A.3) can be
integrated as:

$$F(t) = \frac{\alpha N_1(0)}{\omega + \beta N_2(0)} + \left[F(0) - \frac{\alpha N_1(0)}{\omega + \beta N_2(0)} \right] e^{-(\omega + \beta N_2(0))t} \tag{A.5}$$

476 were $N_1(0) = r_1/c_1 = 1.4, N_2(0) = r_2/c_2 = 10$ and $F(0)$ are the initial conditions
478 ($t = 0$). As time goes on, the resource asymptotically approaches the steady-state value
 $\alpha N_1(0)/(\omega + \beta N_2(0))$, but this could be a very long time. Instead, consider the time

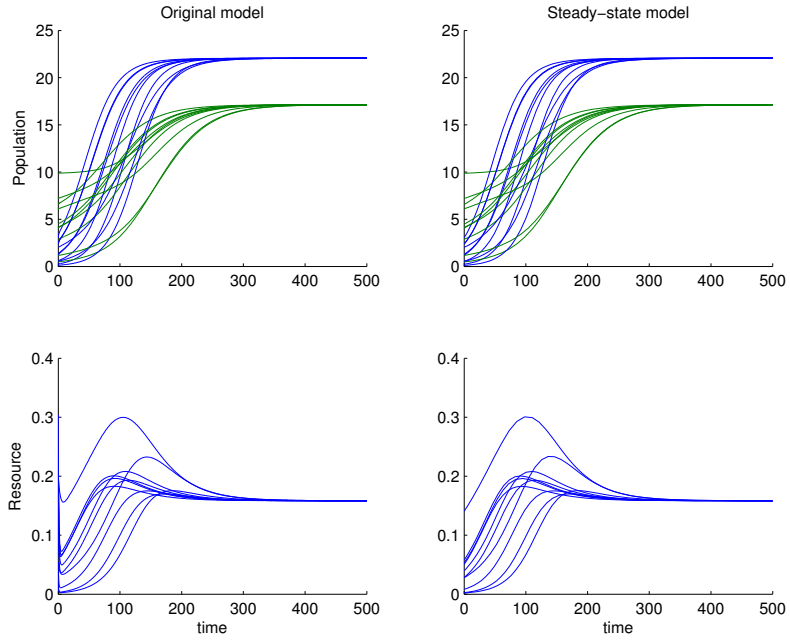


Figure A.2: Dynamics of the original mutualistic model (A.3) in the left column, and of the steady-state model (A.4) in the right column. For each simulation in the original model a simulation in the steady-state model is done using the same initial conditions for species abundances. Blue (green) lines are for species $i = 1$ ($= 2$); $r_i = \{0.007, 0.01\}$, $c_i = \{0.002, 0.001\}$, $\sigma_i = \{2, 0.3\}$, $\alpha = 0.02$, $\omega = 0.2$, $\beta = 0.15$, and $N_o = 0.1$.

480 required to halve the difference between the steady-state and the initial condition (the
square bracket), this can be calculated by setting:

$$e^{-(\omega + \beta N_2(0))t} = \frac{1}{2}$$

482 and solving for t . The result is $\tau_F = \log_e(2)/(\omega + \beta N_2(0)) \approx 0.4$ time units, which is two
orders of magnitude below τ_1 and τ_2 . To put this in perspective, by the time the resources
484 are halfway from the steady-state originally set by the producer and the consumer, they
would have grow or decrease less than 1%.