



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

mutualistic partners. Similar equations apply for the other species, with changes in the appropriate indices. Eq. (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. Fig. 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 than that in the original mechanism (1) and (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 is 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 the algae (Holland and DeAngelis, 2010), yet neither algal cells nor fungal hyphae live inside each other bodies. A very common scenario, however, involves one species hosting an endosymbiont (Holland and DeAngelis, 2010), like, e.g. legumes (hosts) and 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 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 micorrhizal populations (a detail seldom considered by generalized models of mutualism).

3. Exchanges of resources for services

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 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 are

$$\begin{aligned} \frac{dN_1}{dt} &= G_1(\cdot)N_1 + \sigma_o \beta_o F N_o + \sigma_1 \beta F N_2 \\ \frac{dN_2}{dt} &= G_2(\cdot)N_2 + \sigma_2 \beta F N_2 \end{aligned} \quad (8)$$

In this scheme F is the number of flowers or fruits produced by the plant, and β is 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 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 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 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 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 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. water and nutrients). Of course, risks associated with the interactions with the animal (e.g. pollen eating and seed mastication), means that the yield can end up being smaller than 1.

The additional plant term $\sigma_o \beta_o F N_o$ acknowledges that pollination or seed dispersal could be performed by a different animal than species 2 (species "o"), or by abiotic factors 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 withering, rotting, pollination or consumption:

$$\frac{dF}{dt} = \alpha N_1 - \omega F - \beta_o F N_o - \beta F N_2 \quad (9)$$

The case of flowers deserves particular attention. Whereas a single act of frugivory 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, 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 quantity due to pollination ($\beta F N_2$) involves a certain amount of decrease in quality, rendering them useless for plants and animals, a little bit each time. Thus, the pollination rate in (9) shall rather be 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 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 time. Thus, Eqs. (8) and (9) are only valid after some pollinators have already visited some flowers.

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 $F \approx \alpha N_1 / (\omega + \beta_o N_o + \beta N_2)$,

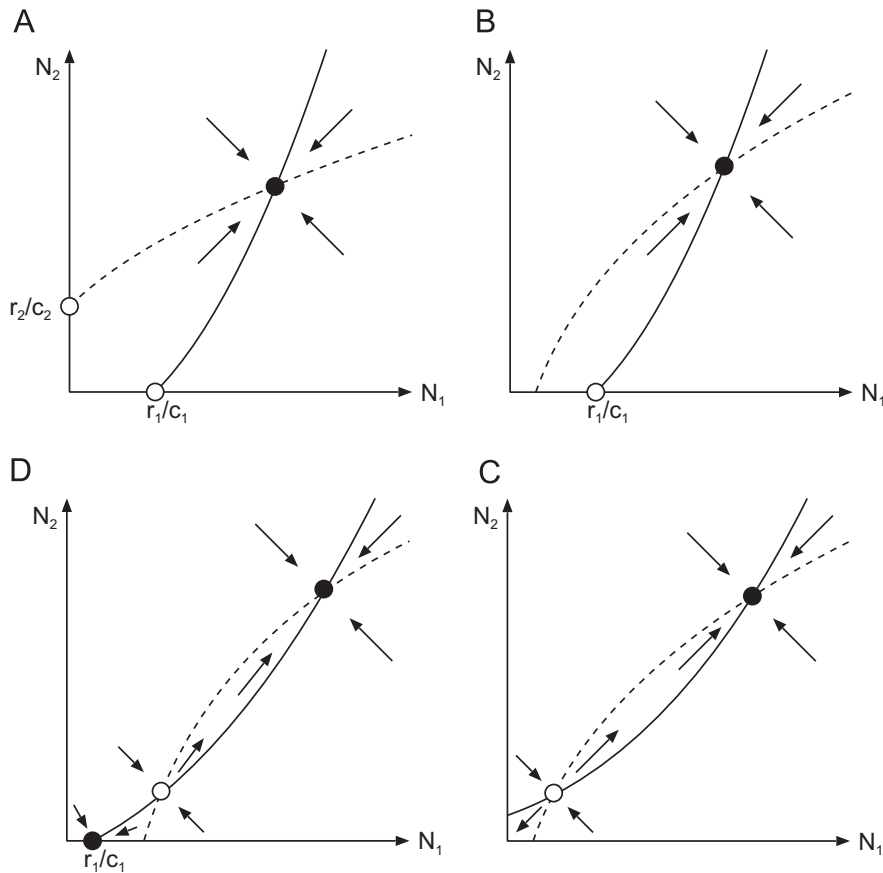


Fig. 1. Nullclines in mutualisms with exchange of resources for resources (4), assuming linear self-limitation for each species. Species 1 (2) has the solid (dashed) nullcline. Black and white circles represent stable (nodes) and unstable (saddle) equilibria respectively (also indicated by arrows nearby).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

and the dynamical system (8) as

$$\begin{aligned} \frac{dN_1}{dt} &= \left\{ G_1(\cdot) + \frac{\sigma_0 \beta_0 \alpha N_0 + \sigma_1 \beta \alpha N_2}{\omega + \beta_0 N_0 + \beta N_2} \right\} N_1 \\ \frac{dN_2}{dt} &= \left\{ G_2(\cdot) + \frac{\sigma_2 \beta \alpha N_1}{\omega + \beta_0 N_0 + \beta N_2} \right\} N_2 \end{aligned} \quad (10)$$

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 equation for the plant is, however, very different, because its numerical response saturates with respect to the abundance of its mutualistic partner, species 2. If N_0 is taken as the population abundance of another animal species, we can see that model (10) can be generalized to account for many species, i.e. the equation for plant 1 (and other plants) will be of the form:

$$\frac{dN_1}{dt} = \left\{ G_1(\cdot) + \frac{\alpha_1 \sum_j \sigma_{j1} \beta_{1j} N_j}{\omega_1 + \sum_j \beta_{1j} N_j} \right\} N_1 \quad (11)$$

where multiple benefits are to be pooled together as a saturating multi-species numerical response using appropriate indices. The equations for the animals will be like in model (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 animal diets (e.g. β_{ij} , where $i \in \text{plants}, j \in \text{animals}$), but this would require more elaborate mechanisms (see Discussion).

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

$$N_1 < \frac{r_1}{c_1} + \frac{\sigma_0 \beta_0 \alpha N_0 + \sigma_1 \beta \alpha N_2}{c_1 (\omega + \beta_0 N_0 + \beta N_2)} \quad (12)$$

$$N_1 > \frac{(c_2 N_2 - r_2) (\omega + \beta_0 N_0 + \beta N_2)}{\sigma_2 \beta \alpha} \quad (13)$$

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 model (4) only that ω becomes $\omega + \beta_0 N_0$. The plant’s nullcline differs from the previous model, it is a rectangular hyperbola, with a single root on the plant axis:

$$\frac{r_1}{c_1} + \frac{\sigma_0 \beta_0 \alpha N_0}{c_1 (\omega + \beta_0 N_0)}$$

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. $\beta_0 N_0 > 0$) 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 or zero, 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 (α) times the returns (σ_1) from the mutualism, must

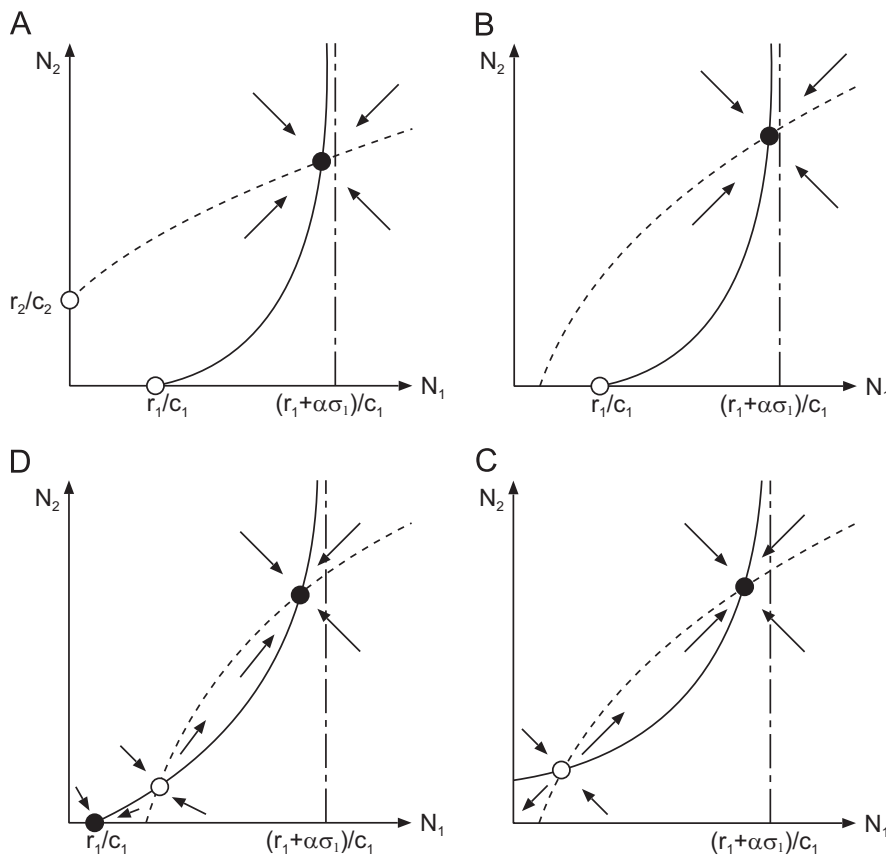


Fig. 2. Nullclines (species 1: continuous line, species 2: dashed line) and equilibrium points in mutualisms with exchange of resources for services (10), with linear self-limitation for each species (species 1 receives services from species 2 only, i.e. $N_o = 0$). The explanations for A–D are the same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

overcome mortality ($\alpha\sigma_1 > -r_1$), otherwise the abundance of species 2 will not prevent the extinction of the plant. Fig. 2 shows the graphs of the nullclines. The outcomes are qualitatively the same as in model (4), as shown by Fig. 2. The numerical discrepancies between the dynamics in the original model (8) and (9) and its steady-state approximation (10) are shown and discussed in the Appendix.

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 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 numerator and the denominator of the numerical response by β , it can be written in the Michaelis–Menten form:

$$\frac{vN_2}{K + N_2} = \frac{\alpha N_2}{\left(\frac{\omega}{\beta}\right) + N_2} \tag{14}$$

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 $K = \omega/\beta$ 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, the half-saturation constants is inverse of the *affinity* between an enzyme and 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 ω , it can be

written like Holling's disc equation:

$$\frac{aN_2}{1 + ahN_2} = \frac{\left(\frac{\alpha\beta}{\omega}\right)N_2}{1 + \left(\frac{\alpha\beta}{\omega}\right)\left(\frac{1}{\alpha}\right)N_2} \tag{15}$$

where the rate at which the provider acquires benefits $a = \alpha\beta/\omega$ is proportional to fruit 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 $h = 1/\alpha$, i.e. the average time it takes to create new flowers or fruits.

4. Discussion

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 of one species abundance on the growth rate of another, is mechanistically grounded, rather than purely phenomenological. 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. I avoid using the term *functional 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). 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 Eq. (2) is a type I functional response), the models derived (e.g. Eq. (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 both of the scenarios considered (resource-for-resource and resource-for-service), intra-specific competition for mutualistic resources emerges because resource production occurs at a finite rate per individual provider, independently of its population size. If the 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, 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 ($\omega_i \gg \beta_j N_j$). 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 co-specifics (Schoener, 1978).

In the case where only one species provides the resource, this occurs in the form of an organ (e.g. flower and fruit) used by the provider (e.g. plant) to capture a service (e.g. pollination and seed dispersal) from the consumer (e.g. pollinator and frugivore). These organs 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. 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 (α_i/ω_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. Keep in mind, however, that diminishing returns or saturating responses are typically not enough 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 mutualistic services. One step in this direction is the optimal foraging model of Valdivinos 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.

I assumed that resource consumption follows simple mass action laws. In reality, consumption likely displays saturating functional responses (here the use of *functional* rather 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 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 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 (Beddington, 1975; DeAngelis et al., 1975) 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, diminish 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. Another complication not considered is that flowers and fruits are lost when plants die, but these processes are supposed to be very slow.

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 e.g. that the 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 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 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 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 shape of the nullclines shown in Figs. 1 and 2, they can lead to important changes in the 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.

Another kind of cost associated with mutualisms arises because the interaction between the species also include antagonisms. These costs are typically experienced at 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, 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 consumer's abundance, which is why they are typically subtracted as saturating functional responses in the provider's biomass dynamics (Holland and DeAngelis, 2010). An important consequence of such density-dependent costs are changes in nullcline shapes, from monotonically increasing (i.e. Figs. 1 and 2), into more complex folding curves that 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, 2009, 2010).

The use of time scale arguments is widespread in the ecological literature. The derivation 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 models derived by Schoener (1978), which consider the partition of resource inflows (e.g. Eq. (3)). Holling's (1961) disc equation assumes a predation cycle embedded into 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 considering 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 simplify the study of ant protection mutualisms.

The scenarios suggested herein are far from exhaustive and the mechanistic details can 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, 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 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 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 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.

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Appendix

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

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

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

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

In Fig. A1 we compare the dynamics of both models (A.1) and (A.2) numerically using 10 replicates. In these simulations the growth rates r_i and self-limitation coefficients c_i were 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.

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

$$\frac{dN_1}{dt} = (r_1 - c_1 N_1)N_1 + \sigma_1 \beta F N_0 + \sigma_1 \beta F N_2$$

$$\begin{aligned} \frac{dN_2}{dt} &= (r_2 - c_2 N_2)N_2 + \sigma_2 \beta F N_2 \\ \frac{dF}{dt} &= \alpha N_1 - \omega F - \beta F N_0 - \beta F N_2 \end{aligned} \tag{A.3}$$

in which $G_i = r_i - c_i N_i$ and $\sigma_0 = \sigma_1, \beta_0 = \beta$ for simplicity. Following the steady-state approximation ($dF_j/dt = 0$) this model becomes

$$\begin{aligned} \frac{dN_1}{dt} &= \left\{ r_1 - c_1 N_1 + \frac{\sigma_1 \beta \alpha N_0 + \sigma_1 \beta \alpha N_2}{\omega + \beta N_0 + \beta N_2} \right\} N_1 \\ \frac{dN_2}{dt} &= \left\{ r_2 - c_2 N_2 + \frac{\sigma_2 \beta \alpha N_1}{\omega + \beta N_0 + \beta N_2} \right\} N_2 \\ F &= \frac{\alpha N_1}{\omega + \beta N_0 + \beta N_2} \end{aligned} \tag{A.4}$$

In Fig. A2 we compare the dynamics of both models (A.3) and (A.4) numerically using 10 replicates. Most of the parameters are similar to those used in the model of exchange of resources for resources ($r_i, c_i, \alpha, \omega, \beta$), in order to make the resource dynamics much faster than population dynamics. However, whereas the conversion efficiency of the resource consumer is less than 1 as before, for the service receiver (species 1) it is larger than 1, for the reasons stated in the main text.

For both models the simulations show discrepancies at starting times because for equations like (A.1) and (A.3) the initial values of F_j can be arbitrary, whereas in models like (A.2) and (A.4) they are determined by the initial species abundances. After less than 10 time units, the transient dynamics are very similar in both models. 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.

Using again the resource for service model (A.3), one last calculation illustrates the large difference between population and resource time scales. When plants and animals do not interact, they grow logistically as in $dN_i/dt = (r_i - c_i N_i)N_i$. Thus, their doubling times at low population densities, and perturbation half-times around their carrying capacities, are $\tau_i = \log_e(2)/r_i$. Using

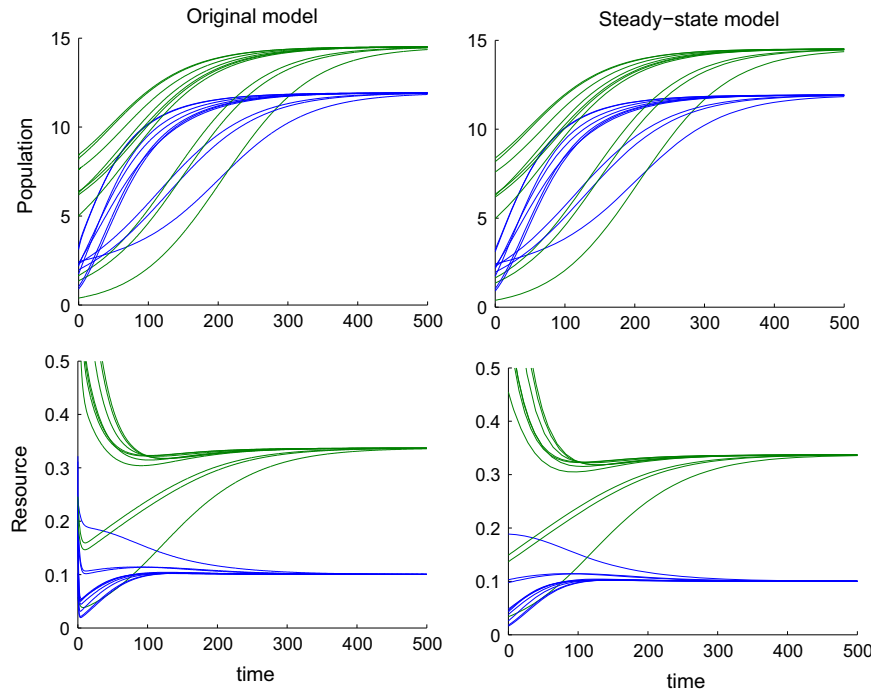


Fig. A1. Dynamics of the original mutualistic model (A.1) in the left column, and of the steady-state model (A.2) in the right column. For each simulation in the original model a simulation in the steady-state model is done using the same initial conditions for species abundances. Blue (green) lines are for species $i = 1$ ($= 2$); $r_i = \{0.007, 0.01\}$, $c_i = \{0.002, 0.001\}$, $\sigma_i = \{0.5, 0.3\}$, $\alpha_i = \{0.02, 0.03\}$, $\omega_i = \{0.2, 0.1\}$, $\beta_i = \{0.1, 0.15\}$. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

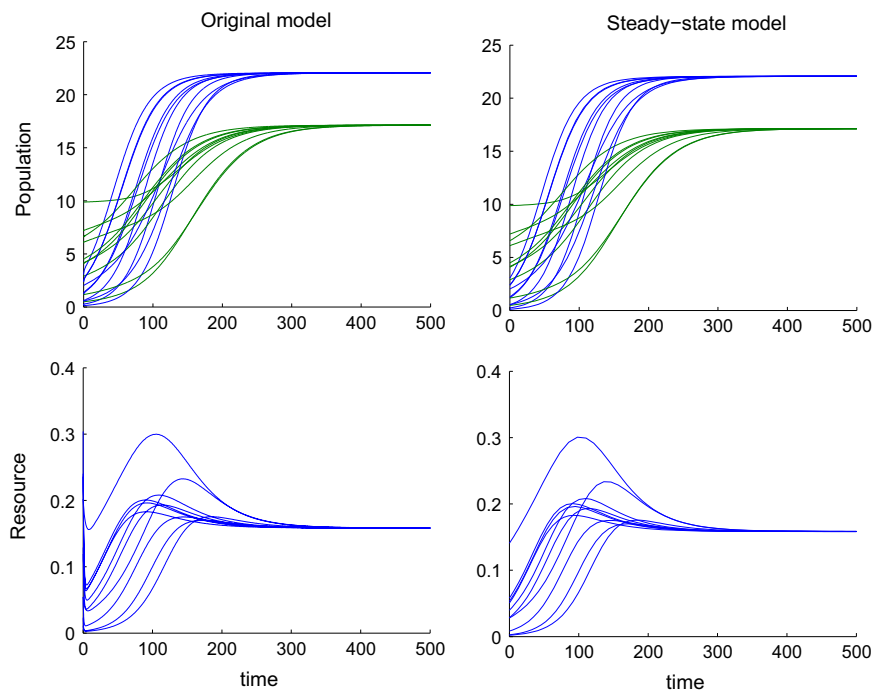


Fig. A2. Dynamics of the original mutualistic model (A.3) in the left column, and of the steady-state model (A.4) in the right column. For each simulation in the original model a simulation in the steady-state model is done using the same initial conditions for species abundances. Blue (green) lines 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 $N_0 = 0.1$. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

the parameter values of Fig. A2, 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

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

where $N_1(0) = r_1/c_1 = 1.4$, $N_2(0) = r_2/c_2 = 10$ and $F(0)$ are the initial conditions ($t=0$). 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 required to halve the difference between the steady-state and the initial condition (the square bracket), this can be calculated by setting:

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

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 are halfway from the steady-state originally set by the producer and the consumer, they would have grow or decrease less than 1%.

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