



# Cooperation and stability for complex systems in resource-limited environments

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## Abstract

Resource-limited complex systems are ubiquitous in the natural world, as is the potential for instability in such systems. Classic models of interacting species have provided a basis for our understanding of stability in these systems, and suggest that stable coexistence requires weak, rare, and asymmetric interactions. But missing from these models is an explicit understanding of how resource exchange and resource limitation can drive or prevent instability. Here, we show that systems based on general rules for the consumption and exchange of resources are guaranteed to be stable when exchange of resources is reciprocated by each pair of partners. These cooperative, mutualistic interactions can be arbitrarily strong and yet not disrupt stability. More general modes of exchange will lead to instability when supply rates are low, but when resource supply from outside the system is sufficiently high, arbitrary exchange is consistent with a stable equilibrium.

**Keywords** Consumer–resource dynamics · Mutualism · Stability

## Introduction

The general properties of large, interacting ecological systems have often been modeled using pairwise interactions between species, where changes in the population size of one species directly affect the growth rate of another (Lotka 1926; Volterra 1926). While the strength of any given interaction is challenging to infer from empirical community data (Schoener 1983; Tilman 1987; Marino et al. 2013), simple null models have been used to gain general insights into equilibria and stability in these systems (Gardner and Ashby 1970; May 1972). These results have shown that equilibria will tend to become unstable to small perturbations once either the number or strength of interactions passes a certain threshold (Allesina and Tang 2012), and that

asymmetric mutualistic interactions enhance stability (Bascompte et al. 2006). Beyond strictly ecological applications, these insights have been leveraged in other complex biological and social networks comprising multiple, heterogeneous component parts (Farmer 2002; Haldane and May 2011; Suweis and D'Odorico 2014; Bardoscia et al. 2017). For example, while nodes in an ecological network are species and links typically represent interactions, in economic systems nodes have been interpreted as financial entities and links in terms of transactions between them (May et al. 2008). It is therefore fair to say that these stability results have deeply informed our understanding of interacting complex systems in general.

However, missing from this approach are the explicit mechanisms underlying interactions between individuals. Consumer–resource models meet this need by explicitly considering the consumption and preferences of individuals for resources (MacArthur 1970; Tilman 1977; 1980; 1982; Schaffer 1981; Chesson 1990; 2000; Abrams 2009), and can lead to dynamics that differ from models based on direct species interactions (Tilman 1987; O'Dwyer 2018). Recent work has extended these analyses to large, open systems with extensive exchange of resources (Friedman and Gore 2017; Friedman et al. 2017; Goldford et al. 2018; Butler and O'Dwyer 2018; Goyal et al. 2018; Marsland et al. 2018), and incorporating resource exchange as the mechanism underlying mutualistic interactions already

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leads to contradictions with the classical analyses using pairwise interactions. For example, if each species in a community specializes on a single resource, then local stability is guaranteed when each pair of species exchanges resources symmetrically (Butler and O'Dwyer 2018), independent of how strong those interactions are. This counters both the idea that there is a limit on the strength and prevalence of interactions, and the result that asymmetry enhances stability in the case of mutualistic interactions, leveraged in both biological (Bascompte et al. 2006) and social systems (May et al. 2008).

These earlier results establish the importance of incorporating explicit resource exchange even when tackling basic questions related to equilibria and stability, but were limited in their scope to specific modes of consumption. For example, Butler and O'Dwyer (2018) focused on consumers exchanging resources, while each specialized on consuming one particular resource. But in moving from models of direct species interactions to more mechanistic models of competition and mutualism, there is a tradeoff. Instead of describing an interaction with a single number, we now have a realm of different mechanisms to choose from, and any potentially general conclusions must be robust to different modes of consumption and exchange. Here, we begin to address the question of how robust are these earlier results, by allowing for relatively general forms for consumption and organism growth rates as a function of available resources. We use these models to address two open questions related to resource exchange in complex ecological communities. First, we show that the connection between reciprocity and stability is general, extending to more realistic models of consumption where each species' growth is colimited by multiple, essential resources. We find that exact reciprocity is again sufficient for ecological stability, regardless of the strength or prevalence of exchange, and independent of the precise form of consumption. This generalization over previous results provides significant and essential support for the wider relevance of the reciprocity–stability connection.

Second, we consider the effects of environmental context on stability in terms of resource supply rates. This question has been raised in systems with resource subsidies from outside (Rosenzweig 1971; Polis et al. 1997; Leroux and Loreau 2008), but has not been addressed for large, complex communities exchanging resources arbitrarily. It has been unclear how to model the effect of a changing environment on interaction strengths in models of direct interactions (Cadotte and Tucker 2017; Xiao et al. 2017), and so here, we consider the impact of the resource inflow rates on stability for communities that consume and exchange resources. We focus initially on the case of communities where consumers specialize on a single resource, and prove that in the limit of scarce resources any

departure from a strict set of criteria for exchange will tend to destabilize the system. These criteria include reciprocity, alongside other limited modes of exchange. Conversely, for sufficiently large resource inflows, any mode of exchange can have a stable positive equilibrium. We subsequently generalize this proof to arbitrary modes of consumption, and show numerical examples for specific cases. These illustrate that when generic modes of consumption are combined with generic modes of exchange, the result can be compatible with a stable equilibrium, as long as resource inflows are sufficiently large, and suggest that in real ecological systems there will be important interplays between resource exchange, ecological stability, and environmental context.

## Model of consumption and exchange

Our model of consumption and exchange is based on a set of  $m$  abiotic resources with densities  $R_\alpha$ , and  $m$  species with population sizes  $N_i$ . We first give three classic models of consumption processes, in order to build up the intuition for what a reasonable consumption process look like. We will then prove a set of results that apply to each of these three examples, and also extend this to more general consumption processes that incorporate these three as special cases.

### Specialism

In our first example, each species specializes on a single resource, and cannot grow without the resource being available. Exchange of resources is incorporated by allowing each species  $i$  to recycle a given proportion of its biomass back into the common pool, at a rate  $P_{\alpha i}$  for resource  $\alpha$ , while resource  $\alpha$  is supplied to the system from outside at a specific rate  $\rho_\alpha$  and removed (due to degradation or outflow) at rate  $\eta_\alpha$ . Species undergo mortality (with biomass not recycled into usable resources) at rates  $\mu_i$ .

$$\begin{cases} \dot{R}_\alpha = \rho_\alpha - R_\alpha \sum_i c_i \delta_{\alpha i} N_i + \sum_i P_{\alpha i} N_i - \eta_\alpha R_\alpha \\ \dot{N}_i = N_i (c_i \sum_\alpha R_\alpha \delta_{\alpha i} - \mu_i - \sum_\alpha P_{i\alpha}^T) \end{cases} \quad (1)$$

Here,  $c_i$  is the specific rate of consumption of species  $i$ , and the Kronecker delta symbol  $\delta_{i\alpha}$  indicates that consumption only occurs when  $\alpha$  is equal to  $i$ . Note that the rates,  $\{P_{\alpha i}\}$  form a matrix,  $P$ , and so  $P_{i\alpha}^T$  represents the row  $i$ , column  $\alpha$  entry in the transpose of  $P$ .

These equations have equilibrium solutions as follows:

$$\begin{cases} R_\alpha^* = \delta_{\alpha i} \frac{1}{c_i} (\sum_\beta P_{i\beta}^T + \mu_i) \\ N_i^* = \sum_\alpha M_{i\alpha}^{-1} (\rho_\alpha - R_\alpha^* \eta_\alpha) \end{cases} \quad (2)$$

where  $M_{\alpha i} = \delta_{\alpha i} (\sum_\beta P_{i\beta}^T + \mu_i) - P_{\alpha i}$ . Not all combinations of  $\rho_\alpha$  and  $\mu_i$  will lead to positive (so-called feasible) equilibria. While the equilibrium solutions for  $R_\alpha^*$  are always positive in this model,  $N_i^*$  is not guaranteed to be

positive. However, for a given set of  $N_i^*$ , we may find  $\{\rho_\alpha\}$  and  $\{\eta_\alpha\}$  such that  $N_i^*$  is a solution.

### Substitutable resources

In our second example, each species can consume multiple distinct resources, with uptake rates determined by  $C_{\alpha i}$ , which could also be thought of as the preference of species  $i$  for resource  $\alpha$ . A given consumer still cannot grow without availability of the right resources, but can now have a wider range of options. Exchange of resources is again incorporated by allowing each species  $i$  to recycle a given proportion of its biomass back into the common pool, at a rate  $P_{\alpha i}$  for resource  $\alpha$ , with rates  $\rho_\alpha$ ,  $\eta_\alpha$ , and  $\mu_i$  defined as before.

$$\begin{cases} \dot{R}_\alpha = \rho_\alpha - R_\alpha \sum_i C_{\alpha i} N_i + \sum_i P_{\alpha i} N_i - \eta_\alpha R_\alpha \\ \dot{N}_i = N_i (\sum_\alpha C_{\alpha i} R_\alpha - \mu_i - \sum_\alpha P_{i\alpha}^T) \end{cases} \quad (3)$$

These equations have equilibrium solutions as follows:

$$\begin{cases} R_\alpha^* = \sum_i (C_{\alpha i}^T)^{-1} (\sum_\beta P_{i\beta}^T + \mu_i) \\ N_i^* = \sum_\alpha M_{i\alpha}^{-1} (\rho_\alpha - R_\alpha^* \eta_\alpha) \end{cases} \quad (4)$$

where  $M_{\alpha i} = R_\alpha^* C_{\alpha i} - P_{\alpha i}$ .

Although in the model, feasibility is not guaranteed, for any given set of positive  $R_\alpha^*$ , there exists a set of  $\mu_i$  such that  $R_\alpha^*$  is a solution and for a given set of  $N_i^*$ , we may find  $\{\rho_\alpha\}$  and  $\{\eta_\alpha\}$  such that  $N_i^*$  is a solution.

### Colimitation by multiple resources

In this system, each species is colimited by a distinct set of resources, so that species  $i$  requires precisely  $K_{\alpha i}$  units of resource  $\alpha$  to grow new biomass. We model this consumption process using multiplicative colimitation (Droop 1974; Saito et al. 2008; Harpole et al. 2011; O'Dwyer 2018), though we also note that it would also be reasonable to consider other models of colimitation, for example, Liebig's law (von Liebig 1855; Tilman 1977; Gleeson and Tilman 1992; De Baar 1994), where each species has a single limiting resource at any given time. Each species  $i$  has a resource conversion rate of  $r_i$ . Exchange of resources is as usual incorporated by allowing each species  $i$  to recycle a given proportion of its biomass back into the common pool, at a rate  $P_{\alpha i}$  for resource  $\alpha$ , with  $\rho_\alpha$ ,  $\eta_\alpha$ , and  $\mu_i$  retaining their previous definitions.

The resulting dynamics are described by the following ordinary differential equations:

$$\begin{cases} \dot{R}_\alpha = \rho_\alpha - \sum_i K_{\alpha i} r_i N_i \prod_\beta R_\beta^{K_{\beta i}} + \sum_i P_{\alpha i} N_i - \eta_\alpha R_\alpha \\ \dot{N}_i = N_i (r_i \prod_\alpha R_\alpha^{K_{\alpha i}} - \mu_i - \sum_\alpha P_{i\alpha}^T) \end{cases} \quad (5)$$

These equations have equilibrium solutions where consumption and production balance supply and mortality:

$$\begin{cases} R_\alpha^* = \exp(\sum_i K_{i\alpha}^{-1} \log(\mu_i/r_i + \sum_\beta P_{\beta i}/r_i)) \\ N_i^* = \sum_\alpha M_{i\alpha}^{-1} (\rho_\alpha - R_\alpha^* \eta_\alpha) \end{cases} \quad (6)$$

where the matrix  $M$  is given by  $M_{\alpha i} = K_{\alpha i}(\mu_i + \sum_\beta P_{\beta i}) - P_{\alpha i}$ . Clearly, not all combinations of  $\rho$ ,  $\mu$ ,  $r_i$ ,  $K$ , and  $P$  will lead to positive (so-called feasible) solutions. On the other hand, all positive values  $N_i^*$  are possible for some choice of resource inflow  $\rho_\alpha$ . Conversely, not all resource concentrations are possible—the recycling of resources into the common pool typically places lower bounds on equilibrium resource concentrations for a given  $K$  and  $P$ , as discussed in our [Supplementary Information](#).

### General model of consumption and exchange

This variety in consumption processes simply reflects that when competition is modeled mechanistically, via the uptake and conversion of resources into biomass, there are then many distinct ways for this mechanism to occur. This contrasts with modeling competition implicitly, via direct species interactions (e.g., the competitive Lotka–Volterra equations), and means that while we may gain new insights by incorporating more explicit mechanism, we also have to deal with a potentially broader array of models. This in turn means that if we want to derive general results, for example, about the stability of equilibria, we may need to make sure that these results hold for this broad range of models, and not just one special case.

With this in mind, we now define a more general model of consumption, incorporating as special cases the three examples above, but allowing for combinations of processes (e.g., the possibility that a consumer may generate biomass through more than one combination of essential resources—i.e., by one of multiple metabolic pathways). This model takes the form as follows:

$$\begin{cases} \dot{R}_\alpha = \rho_\alpha - \sum_i R_\alpha N_i \frac{\partial g_i}{\partial R_\alpha} + \sum_i P_{\alpha i} N_i - \eta_\alpha R_\alpha \\ \dot{N}_i = N_i (g_i(\{R_\alpha\}) - \sum_\alpha P_{\alpha i} - \mu_i) \end{cases} \quad (7)$$

The freedom in choosing the consumption function,  $g_i(\{R_\alpha\})$ , as a function of resource concentrations allows us to straightforwardly recover any of the three earlier examples, in addition to a broad range of generalizations. Third, the form of the depletion of resources as a result of consumption generically takes the form  $\sum_i R_\alpha N_i \frac{\partial g_i}{\partial R_\alpha}$  because we assume that the dependence of  $g_i$  on  $R_\alpha$  captures the effective number of units of resource  $\alpha$  required to build one new consumer, as in the case of multiplicative colimitation. We note that while covering a large set of plausible forms of consumption, and hence we describe it as general, this model is far from completely general. For

example, a Michaelis–Menten form for resource uptake and depletion would not fall into this category; neither would the functional forms found in the models studied in Tilman (1982) and Huisman and Weissing (2001), where a species may consume more than one resource, but their growth rate is determined by one limiting resource (i.e., Liebig’s law). In essence, what we generalize to here are cases where uptake is limited by the rate of *finding* all necessary resources moving diffusively in a given environment, so that it is not species’ intrinsic ability to metabolize nutrients that limits their growth rates. In real systems where resources are low, perhaps in oligotrophic environments, then we expect our approximation to work well. Finally, we put a restriction on the functional form of the consumption process, by requiring that the matrix with components

$$\frac{1}{R_\alpha} \frac{\partial}{\partial R_\alpha} (-\dot{R}_\alpha) = \frac{1}{R_\alpha} \frac{\partial}{\partial R_\alpha} \left( \sum_i N_i R_\alpha \frac{\partial g_i}{\partial R_\alpha} + \eta_\alpha R_\alpha \right) \quad (8)$$

is a positive semi-definite matrix. More explicitly, this condition imposes that if we inflate or deflate resource concentrations by allowing  $R_\alpha \rightarrow R_\alpha(1 + \epsilon_\alpha)$  for an arbitrary vector of small quantities  $\epsilon_\alpha$ , then

$$\sum_\alpha \epsilon_\alpha \Delta \dot{R}_\alpha \leq 0 \quad (9)$$

where  $\Delta \dot{R}_\alpha$  is the small change in growth rates  $\dot{R}_\alpha$  caused by the small change in resource concentrations  $\epsilon_\alpha R_\alpha$ . As an example, if all resources are inflated by a the same factor, so that  $\epsilon_\alpha = \epsilon$ , then this condition tells us that the sum of all depletion rates must increase. In essence, this condition imposes that resource depletion cannot decrease if resource concentrations increase.

## Quantifying species interaction strengths

In models where interactions are not mediated by explicit resources, the rate or strength of a species interaction is a part of the definition of the model. That is not the case here, and so if we want to state or discuss the properties of these models and how they depend on species interactions, we first need the right definition of interaction strength. In earlier work on exchange among specialist consumers, it was natural to define the elements of the exchange matrix  $P$  as the strength of mutualism between each pair of species, because there was a one-to-one relationship between resource use and consumer identity, i.e., the entries of the exchange matrix  $P$  already gave us a natural definition of mutualism. However, in all of our more general cases, from substitutable resources through to the general consumption process encoded by Eq. 7, the “strength” of mutualism is more subtle.

Therefore, to make progress, we now derive a metric to measure the strength of mutualism due to exchange between

each pair of species. To simplify notation, we will in places use matrix-vector notation. Specifically, we define  $\mathbf{R}$ ,  $\mathbf{N}$ ,  $\mathbf{g}$ ,  $\rho$ ,  $\mu$ , and  $\eta$  to represent vectors of the values of  $R_\alpha$ ,  $N_i$ ,  $g_i$ ,  $\rho_\alpha$ ,  $\mu_i$ , and  $\eta_\alpha$  respectively. We define  $R_d$ ,  $N_d$ , and  $G_d$  to be matrices formed by placing  $\mathbf{R}$ ,  $\mathbf{N}$ , or  $\mathbf{g}$  along the diagonal with zeros on the off-diagonal. We also define  $Dg$  by  $Dg_{\alpha i} = \frac{\partial g_i}{\partial R_\alpha}$ , and we let  $W = R_d Dg G_d^{-1}$ . First, we interpret the matrix,  $W$ . Its components look like as follows:

$$W_{\alpha i} = R_\alpha \frac{\frac{\partial g_i}{\partial R_\alpha}}{g_i} \quad (10)$$

so that  $W_{\alpha i}$  represents the current relative effect of resource  $\alpha$  on species  $i$ ’s growth rate multiplied by the current resource density. We assume that  $W^* = R_d^* Dg^* [G_d^*]^{-1}$ , the matrix  $W$  evaluated at equilibrium, is of full rank, and hence invertible. In essence, this is an assumption that each species is distinct in terms of its phenotype. We can therefore define a matrix as follows:

$$\Theta^* = [W^*]^{-1} P \quad (11)$$

where  $P$  is the matrix describing the production of resources by each species. We note that this definition of interaction strength is reminiscent of earlier work characterizing empirical interactions in terms of resource flows (Gross et al. 2009).

We can interpret the components of  $\Theta^*$  by considering their relationship to the components of  $W^*$  and  $P$ :

$$P_{\alpha j} = \sum_i \Theta_{ij}^* W_{\alpha i}^*$$

so that

$$\begin{pmatrix} P_{1j} \\ P_{2j} \\ \vdots \\ P_{mj} \end{pmatrix} = \Theta_{1j}^* \begin{pmatrix} W_{11}^* \\ W_{21}^* \\ \vdots \\ W_{m1}^* \end{pmatrix} + \Theta_{2j}^* \begin{pmatrix} W_{12}^* \\ W_{22}^* \\ \vdots \\ W_{m2}^* \end{pmatrix} + \dots + \Theta_{mj}^* \begin{pmatrix} W_{1m}^* \\ W_{2m}^* \\ \vdots \\ W_{mm}^* \end{pmatrix}$$

which can be written concisely as follows:

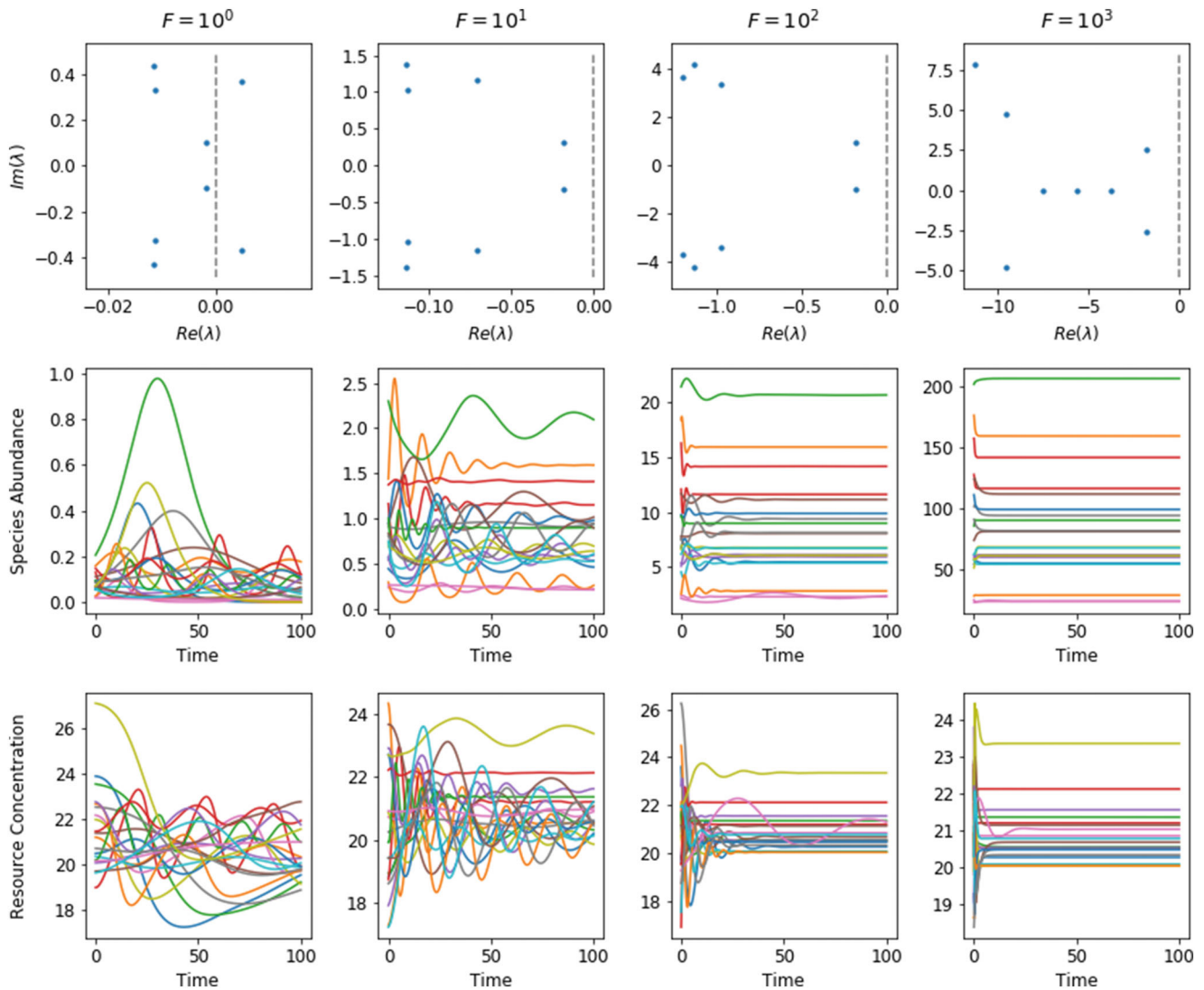
$$\mathbf{P}^{(j)} = \sum_i \Theta_{ij}^* \mathbf{W}^{*(i)}$$

where  $\mathbf{W}^{*(i)}$  is a vector describing the resource requirements of species  $i$  (i.e., the  $i$ th column of the matrix  $W^*$ ) and  $\mathbf{P}^{(j)}$  describes the production of resources by species  $j$ . It can be seen that the production of resources by  $j$  is a sum of components, each proportional to the resource requirements of another species,  $i$ , with the constant of proportionality equal to  $\Theta_{ij}^*$ . Hence, for all  $\Theta_{ij}^*$  positive, we interpret  $\Theta_{ij}^*$  biologically as the strength of exchange from species  $j$  to species  $i$ . We note though that our sufficient condition for stability will require that all  $\Theta_{ij}^*$  are non-negative, and so we restrict our analysis to systems with non-negative  $\Theta^*$ .

### Non-negative mutualistic interaction strengths

We have shown that the production of resources by species  $j$  is a sum of components, each proportional to the resource requirements of another species,  $i$ , with the constant of proportionality equal to  $\Theta_{ij}^*$ . Hence, for all  $\Theta_{ij}^*$  positive, we interpret  $\Theta_{ij}^*$  biologically as the strength of exchange from

species  $j$  to species  $i$ . Our sufficient condition for stability will also require that all  $\Theta_{ij}^*$  are non-negative (although we note that this is technically not a necessary condition), and so we consider it reasonable in this context to restrict our analyses to systems with non-negative  $\Theta^*$ . We also note that several of our examples also ensure that  $\Theta$  is positive even away from equilibria.



**Fig. 1** Resource supply and the onset of instability for specialist consumers. This example shows four communities of 20 consumer species, each specializing on one of 20 distinct resources, with consumption rates drawn from the absolute values of a normal distribution with mean zero and standard deviation one. Inflow and mortality rates are chosen so that equilibrium concentrations and abundances are also randomly drawn from the absolute values of a normal distribution, and the exchange matrix  $\Theta$  has a connectance = 0.2, with non-zero entries drawn from the absolute values of a Gaussian (also with mean zero and sd one). From left to right, we show the effect of changing resource supply on the dynamics of this community near equilibrium. Resource

supply rates,  $F\rho$ , are increased by a factor of ten from each panel to the next, reflected in the increase of consumer abundances by the same factor. This shift demonstrates that reducing resource supplies alone can change a stable community equilibrium into an unstable equilibrium, mediated by the corresponding change in consumer abundances. The top panels illustrate the same phenomenon by focusing on the eigenvalue spectrum of the Jacobian near the equilibrium in each case. Note that the plots are zoomed-in to show detail near the imaginary axis and so not all eigenvalues appear. As resource supply is increased, the spectrum loses eigenvalues with positive real part



## Results

### Reciprocity implies stability

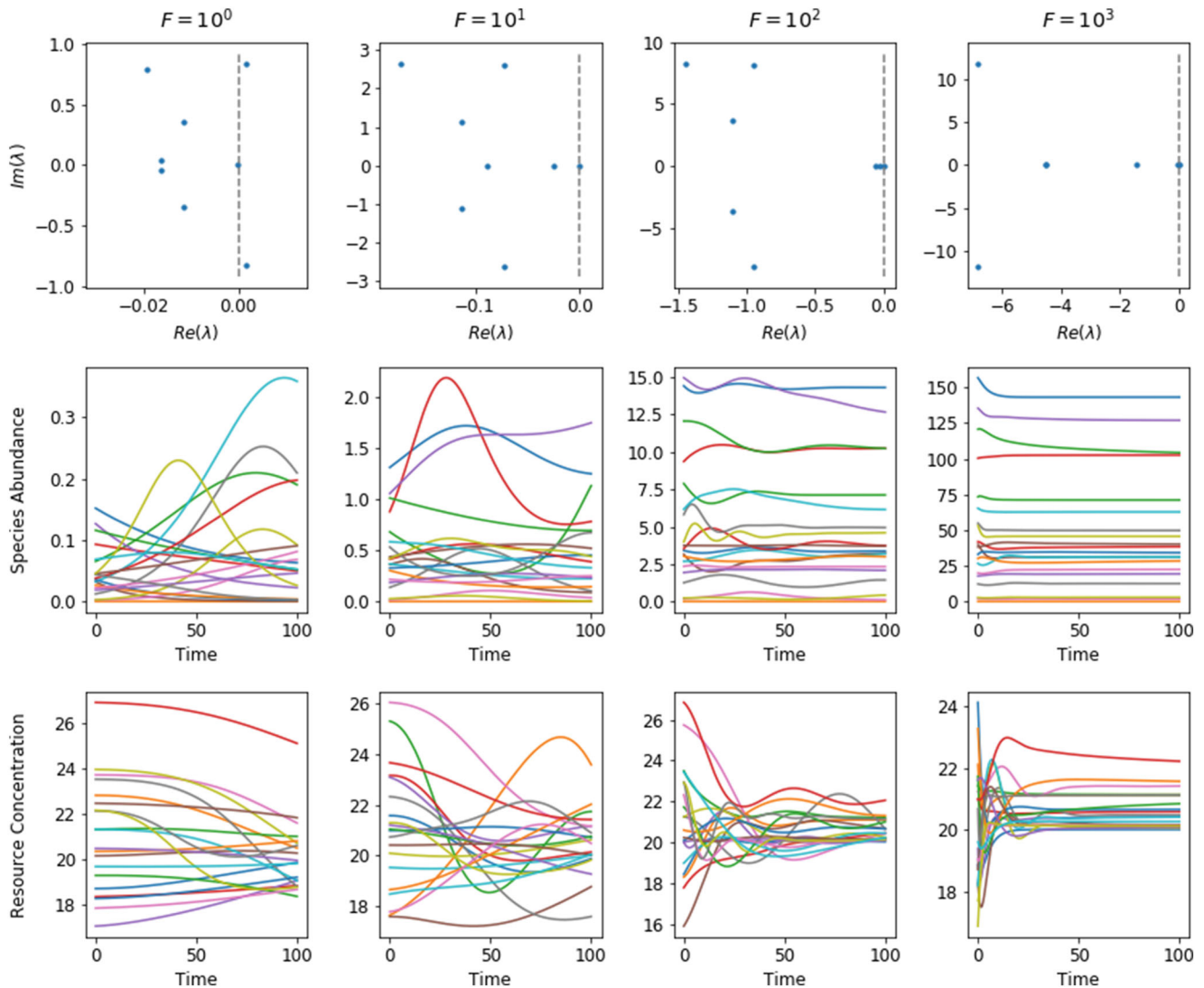
Our model with generalized consumption, restated using the matrix-vector notation as follows:

$$\begin{cases} \dot{\mathbf{R}} = \rho - W(G_d - \Theta)\mathbf{N} - R_d\eta \\ \dot{\mathbf{N}} = N_d(\mathbf{g} - (W\Theta)^T\mathbf{1} - \mu) \end{cases} \quad (12)$$

In our [Supplementary Information](#), we prove that the equilibrium solution to Eq. 12 will be stable to small perturbations when the following conditions are met:

1.  $Dg^*$  is nonsingular
2.  $\mu > |[\Theta^*]^T\mathbf{1} - [\Theta^*]^T[W^*]^T\mathbf{1}|$
3.  $\frac{\Theta_{ij}^* N_j^*}{G_i^*} = \frac{\Theta_{ji}^* N_i^*}{G_j^*}$  for all  $i$  and  $j$

The first two conditions set bounds on species consumption and production. The first condition states that



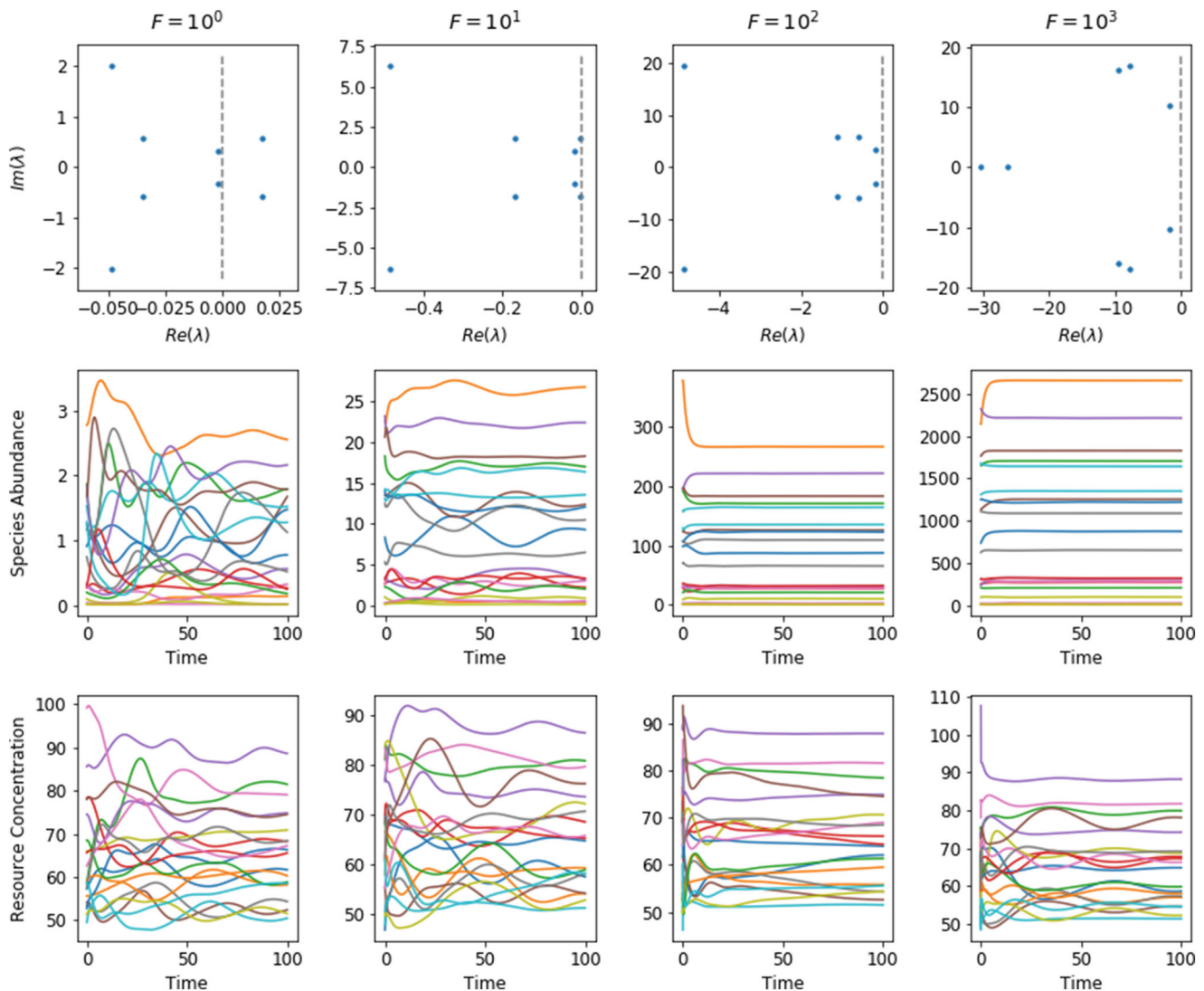
**Fig. 2** Resource supply and the onset of instability for substitutable resources. This example shows four communities of 20 consumer species, each able to use two of 20 distinct resources. Consumption rates are such that the matrix  $C$  has diagonal entries non-zero, and also one other entry non-zero for each row and column. Entries are again drawn from absolute values of normal distributions. Inflow and mortality rates are chosen so that equilibrium concentrations and abundances are also randomly drawn from the absolute values of a normal distribution, and the exchange matrix  $\Theta$  has a connectance = 0.2, with

non-zero entries drawn from the absolute values of a Gaussian with mean zero and sd one. Resource supply rates,  $F\rho$ , are increased by a factor of ten from each panel to the next, reflected in the increase of consumer abundances by the same factor. The top panels illustrate the same phenomenon by focusing on the eigenvalue spectrum of the Jacobian near the equilibrium in each case. Note that the plots are zoomed-in to show detail near the imaginary axis and so not all eigenvalues appear. As resource supply is increased, the spectrum loses eigenvalues with positive real part

species' responses to changes in resource densities should be sufficiently different. The second condition ensures that the eigenvalues of  $G_d^* - \Theta^*$  will be positive. This can be interpreted as the total strength of a species' production/exchange being bounded by its consumption.

The third condition defines reciprocity. This is a condition on the structure of the exchange network. An exchange between two species,  $i$  and  $j$ , is reciprocal if

species  $j$  produces as much of what species  $i$  needs relative to its growth rate, as species  $i$  does for species  $j$ . If this is true for all pairs  $i$  and  $j$ , then (when combined with the other conditions) the whole community will stably coexist. Note that although reciprocity is not a necessary condition for stability, it is not superfluous. Figures 1, 2, and 3 show that in a range of cases where reciprocity is absent, there are transitions from stability to instability as resource inflow is



**Fig. 3** Resource supply and the onset of instability for essential resources. This example shows four communities of 20 consumer species, each using an essential combination of multiple resources drawn from a set of 20 distinct resources. The matrix  $K_{ai}$  describing how many units of resource  $\alpha$  are needed by species  $i$  was chosen to have a connectance of 0.3, and each entry is randomly drawn from a list containing 1, 2, and 3 with different weightings, i.e., each species uses on average 6 resources, and requires either one, two, or three units of each, with one unit being the most likely in this example, followed by two and three. From left to right, we show the effect of changing

resource supply on the dynamics of this community near equilibrium. Resource supply rates,  $F\rho$ , are increased by a factor of ten from each panel to the next, reflected in the increase of consumer abundances by the same factor. The top panels illustrate the same phenomenon by focusing on the eigenvalue spectrum of the Jacobian near the equilibrium in each case. Note that the plots are zoomed-in to show detail near the imaginary axis and so not all eigenvalues appear. As resource supply is increased, the spectrum loses eigenvalues with positive real part

decreased. This suggests that generic positive interactions will not guarantee stability for all resource inflows, in contrast to the case of reciprocal positive interactions.

### Specialism

We now explore these criteria and their interpretation in each of our three example models. The specialist consumer model rewritten using the matrix-vector notation is as follows:

$$\begin{cases} \dot{\mathbf{R}} = \rho - (\mathbf{R}_d \mathbf{C} - P) \mathbf{N} - \mathbf{R}_d \eta \\ \dot{\mathbf{N}} = \mathbf{N}_d (C^T \mathbf{R} - P^T \mathbf{1} - \mu) \end{cases} \quad (13)$$

where  $C$  is a diagonal matrix.

The three conditions for stability become as follows:

1.  $C$  is nonsingular
2.  $\mu > |P|^T \mathbf{1} - P^T [R_d^* C [C^T \mathbf{R}^*]^{-1}]^T \mathbf{1}$
3.  $\frac{(P_{\alpha j} \delta_{\alpha i}) N_j^*}{c_i R_{\alpha}^* \delta_{\alpha i}} = \frac{(P_{\alpha i} \delta_{\alpha j}) N_i^*}{c_j R_{\alpha}^* \delta_{\alpha j}}$  for all  $i$  and  $j$

By definition, this model satisfies the first condition. The second condition holds because  $P$  is non-negative,  $\mu$  is positive, and  $[R_d^* C [C^T \mathbf{R}^*]^{-1}]^T = I$ . Only the third condition (reciprocity) may or may not hold. If we consider the special case of  $c_i = c$  and  $N_i^* = n$  for all  $i$ , and  $R_{\alpha}^* = r$  for all  $\alpha$ . Then, if  $P$  is symmetric, the third condition will hold, recapitulating the earlier result in Butler and O'Dwyer (2018).

### Substitutable resources

The model for substitutable resources rewritten using matrix-vector notation is as follows:

$$\begin{cases} \dot{\mathbf{R}} = \rho - (\mathbf{R}_d \mathbf{C} - P) \mathbf{N} - \mathbf{R}_d \eta \\ \dot{\mathbf{N}} = \mathbf{N}_d (C^T \mathbf{R} - P^T \mathbf{1} - \mu) \end{cases} \quad (14)$$

and the sufficient conditions take the form as follow:

1.  $C$  is nonsingular
2.  $\mu > |\Theta^*|^T \mathbf{1} - [\Theta^*]^T [R_d^* C [C^T \mathbf{R}^*]^{-1}]^T \mathbf{1}$
3.  $C^{-1} [R_d^*]^{-1} P N_d^*$  is symmetric

where  $\Theta^* = [C^T \mathbf{R}^*]_d C^{-1} [R_d^*]^{-1} P$ . We assume the first condition for our model. This model satisfies the second condition for positive  $\Theta^*$  because  $[R_d^* C [C^T \mathbf{R}^*]^{-1}]^T \mathbf{1} = \mathbf{1}$ . In order to ensure stability, the third condition must be verified using the equilibrium values for a given model.

### Colimitation by multiple resources

The model in matrix-vector notation is as follows:

$$\begin{cases} \dot{\mathbf{R}} = \rho - (K G_d - P) \mathbf{N} - R_d \eta \\ \dot{\mathbf{N}} = N_d (\mathbf{g} - P^T \mathbf{1} - \mu) \end{cases} \quad (15)$$

The sufficient conditions for stability become as follow:

1.  $[R_d^*]^{-1} K G_d^*$  is nonsingular
2.  $\mu > |\Theta|^T \mathbf{1} - \Theta^T K^T \mathbf{1}$
3.  $[G_d^*]^{-1} \Theta N_d^*$  is symmetric

where  $\Theta = K^{-1} P$  and  $G_d$  is the diagonal matrix with  $(G_d)_{ii} = r_i \prod_{\alpha} R_{\alpha}^{K_{\alpha i}}$ . The first condition holds for full-rank  $K$  and  $(G_d^*)_{ii} > 0$ , which we assume for our model. The second condition holds for  $\Theta$  with non-negative entries by noticing that  $K$  has integer entries is assumed nonsingular so that  $K^T \mathbf{1} \geq \mathbf{1}$ . Only reciprocity, the third condition, may fail for this model.

### Abundant resource inflow implies stability

This connection between reciprocity and stability may seem like it must be highly finely tuned—i.e., a very unlikely special case. We now think about the implications for non-reciprocal exchange, and show that (making some additional assumptions) non-reciprocal modes of exchange *can* lead to stable equilibria, but in some cases only when resource inflows are large. Viewed in this light, even being near to a condition of reciprocity may extend the range of environmental contexts in which a given system will have a stable, positive equilibria. In other words, reciprocity guarantees stability in our models for any set of resource supply rates, but a broader range of modes of exchange will be compatible with stability in a given environmental context defined by a finite set of supply rates.

To explore this, we first consider our simplest example above, where each species specializes on a single resource. We choose  $\eta_{\alpha} = 0$  and choose  $\rho_{\alpha}$  and  $\mu_i$  such that each resource has the same equilibrium concentration,  $\mathbf{R}^* = r \mathbf{1}$ , and each species has the same equilibrium abundance  $\mathbf{N}^* = n \mathbf{1}$ . Hence, also all consumers have the same growth rate at this equilibrium  $\mathbf{G}^* = g \mathbf{1}$ , balanced by mortality.

For this model, the condition defining the equilibrium solution is as follows:

$$\begin{cases} \mu = g \mathbf{1} - \Theta^T \mathbf{1} \\ \rho = (g I - \Theta) n \mathbf{1} \end{cases} \quad (16)$$

and the Jacobian matrix for small perturbations around this feasible equilibrium solution is as follows:

$$L = \begin{bmatrix} -\frac{gn}{r} I & -(g I - \Theta) \\ \frac{gn}{r} I & 0 \end{bmatrix}. \quad (17)$$

From the block form of this matrix, if  $\lambda$  is an eigenvalue of  $L$ , and  $\gamma$  is an eigenvalue of  $\Theta$ , then these eigenvalues are related by the following:

$$\lambda = \frac{1}{2} \left( -\frac{gn}{r} \pm \sqrt{\left( \frac{gn}{r} \right)^2 - 4 \frac{gn}{r} (g - \gamma)} \right) \quad (18)$$

The condition for the equilibrium to be stable to local perturbations ( $Re(\lambda) < 0$ ) leads to the following necessary



and sufficient condition for all  $\gamma$  (Butler and O'Dwyer 2018):

$$(\text{Im}(\gamma))^2 < \frac{gn}{r}(g - \text{Re}(\gamma)). \quad (19)$$

Note that these systems with two species and two resources are always stable. This is because the entries of  $\Theta$  are all positive, and thus  $\gamma$  is real. This fact underlines the importance of considering systems with more than just a few interacting species (Johnson and Bronstein 2019; Holland and DeAngelis 2010).

We now consider what happens when environmental conditions cause the resource influx rate to be reduced. We assume the resource influx is rescaled to  $F\rho$ , where  $F$  is a positive real number, and  $F$  may vary. Then, the conditions defining the equilibrium solution become as follows:

$$\begin{cases} \mu = g\mathbf{1} - \Theta^T \mathbf{1} \\ F\rho = (g\mathbf{I} - \Theta)F\mathbf{n}\mathbf{1}. \end{cases} \quad (20)$$

So now, the equilibrium abundances of all consumers are  $F\mathbf{n}$ , and the necessary and sufficient criterion for stability becomes as follows:

$$(\text{Im}(\gamma))^2 < F \frac{gn}{r}(g - \text{Re}(\gamma)). \quad (21)$$

In the limit of scarce resources, i.e., as  $F \rightarrow 0$ , the only  $\Theta$  that will satisfy this inequality are such that  $\text{Im}(\gamma) = 0$  for all  $\gamma$ , thus restricting the form of  $\Theta$  to a relatively specific set of matrices, including reciprocal exchange, alongside (for example) exchange networks without feedback loops. On the other hand, when resources are plentiful, i.e., when  $F > \sup \left( \frac{\text{Im}(\gamma)^2}{\frac{gn}{r}(g - \text{Re}(\gamma))} \right)$ , where the supremum is taken over all eigenvalues of  $\Theta$ , then this system will be stable.

In Supplementary Information Section C, we extend this result, and show that for our more general consumption process, positive equilibria will be stable for sufficiently high resource inflow rates, even if they are unstable for lower resource rates. To prove this, we state some specific conditions on growth and exchange, but importantly we do not assume reciprocity or any specific structure for the matrix of mutualistic interactions,  $\Theta$ . To illustrate the implications of this result, we also picked out some explicit examples and solved for their dynamics numerically, shown in Figs. 1, 2, and 3. In these examples, because there is no resource outflow, the feasibility of the equilibrium does not change. Also, we prove in the Supplementary Information that zero cannot be an eigenvalue of the Jacobian for our models, and so as resource inflow increases, we see a Hopf bifurcation where a stable limit cycle collapses to form a stable equilibrium point. We note that our result contrasts with the well-known paradox of enrichment (Rosenzweig 1971), and related results on the effect of spatial subsidies on stability (Polis et al. 1997; Leroux and Loreau 2008). We also note that there is no guarantee in our models that

the magnitude of the largest eigenvalue of the appropriate Jacobian decreases monotonically with increasing resource inflow, and so it is possible that in some cases there may be phenomena of “oscillating” stability and instability as a function of resource inflow, although always (eventually) resulting in stable equilibria beyond some threshold level.

### Transition from stability to instability in a slowly changing environment

The effect of a variable environment on individual species extinction has previously been quantified via the raw, direct effect of environmental parameters on species growth rates (Leigh 1981; Lande 1993; Fung et al. 2017), but there is a more limited understanding of how environmental variability might impact collective properties like community stability, in particular when species can exchange resources as well as consume them. We have been agnostic in this paper with respect to how exchange has evolved over time (Axelrod and Hamilton 1981; Taylor and Day 2004). But it is clear that generic modes of exchange could evolve (if adaptive) in the context of high resource supply rates, only to lead to community instability when supplies dry up. We provide an explicit example of this phenomenon for a three-species community with specialized consumers. For a sufficiently high set of resource inflow rates, this system has a stable equilibrium—i.e., this is just a specific example of the general case above. We now consider resource inflows to change, but now in the other direction, so that resource inflow is slowly reduced over time. If inflow rates are rescaled by a factor  $F$ , as above, and this factor varies slowly enough that the system reaches a new equilibrium for each value of  $F$ , then this system will become unstable for a sufficiently small  $F$ . We derive the threshold explicitly for this specific system, though the phenomenon is quite general for specialist consumers and matrices  $\Theta$  with any complex eigenvalues. This suggests that the condition of stability under a range of environmental contexts may be an important filter during the evolution of cooperation.

We begin with no exchange, i.e.,  $\Theta = 0$ . This system always has feasible equilibria for any positive  $\rho$  and  $\mu$ , and these equilibria are locally stable. Set  $\mu = (2, 2, 1)$ ,  $\rho = (2, 4, 4)$ . Then,  $\mathbf{G}^* = (2, 2, 1)$ ,  $\mathbf{N}^* = (1, 2, 4)$  and with  $r_i = \frac{4}{3}$  for all  $i$ , then  $\mathbf{R}^* = (\frac{3}{2}, \frac{3}{2}, \frac{3}{4})$ .

We next suppose that over time, production is introduced as follows:

$$\Theta = \begin{pmatrix} 1 & 0 & 2 \\ 1 & 1 & 0 \\ 0 & 1 & 1 \end{pmatrix}$$

which has eigenvalues,  $\gamma_j = 1 - \sqrt[3]{2}e^{i\frac{(2j+1)\pi}{3}}$  for  $j = 0, 1, 2$ . The equilibrium values of this system with production,  $\Theta$ ,

are  $\mathbf{G}^* = g\mathbf{1}$  with  $g = 4$ ,  $\mathbf{R}^* = r\mathbf{1}$  with  $r = 3$ , and  $\mathbf{N}^* = n\mathbf{1}$  with  $n = 2$ . This system is stable. The eigenvalues of the Jacobian for this equilibrium are approximately  $\{-0.82 \pm 2.86i, -1.84 \pm 2.86i, -1.33 \pm 1.69i\}$  (i.e., the equilibrium is stable to local perturbations).

So we have a system with asymmetric exchange, which nevertheless in this environmental context has a stable equilibrium. We now rescale  $\rho$  to  $F\rho$ , as above so that consumer abundances are rescaled to  $n = 2F$ . The criterion above then tells us that:

$$(\text{Im}(\gamma_j))^2 < F \frac{8}{3} (4 - \text{Re}(\gamma_j)). \quad (22)$$

for all  $\gamma_i$ . In other words, there is a threshold value of  $F$  at which this equilibrium will become unstable.

We now define  $F_0$  as this threshold value of  $F$ , below which Eq. 22 fails for some eigenvalue,  $\gamma_j$ , of  $\Theta$ . The largest  $F_0$  comes from the stability criterion applied to  $\gamma_2$

$$F_0 = \frac{3}{8} \frac{(\text{Im}(\gamma_2))^2}{(4 - \text{Re}(\gamma_2))} \approx 0.12 \quad (23)$$

Therefore, for resource inflow levels below  $\rho = F_0 \times (2, 4, 4)$ , the system with production defined by  $\Theta$  is unstable. However, the original system with no resource exchange, where  $\Theta = 0$ , would still have had a positive, stable equilibrium under these reduced resource inflow conditions, implying that (with the benefit of hindsight) the addition of exchange was detrimental to stability.

## Discussion

Our study has identified two important connections between resource exchange and community stability, in the context of consumption of a set of essential resources. Our approach builds on classic consumer–resource dynamics (Tilman 1977; 1980; 1982; Chesson 1990; Abrams 2009), but incorporates the possibility of arbitrary exchanges of resources between consumers, which could be thought of in terms of the recycling of biomass into usable matter following mortality. Using this framework, we first generalized an earlier connection between pairwise reciprocity in the exchange of resources and community stability for a complex ecological system (Butler and O’Dwyer 2018). Specifically, reciprocity of resource exchange is a sufficient condition for the local stability of a positive equilibrium, even when consumption requirements of species are a complicated combination of distinct resource types. When reciprocity is absent in our models, the instability that may occur is not the result of differences between impact and consumption vectors (Tilman 1982; Huisman and Weissing 2001), but due to the exchange process. As long as reciprocity holds, the

strength of interactions and dependencies between species can be arbitrarily strong. The difference between this conclusion and the classic results arising from pairwise interactions reinforces the importance of considering explicit mechanisms underlying species interactions—even to gain an understanding of quite basic properties like the local stability of equilibria.

Our second result identifies a connection between the environmental context, characterized by the rates of resource supply from outside, and community stability. We proved that generic modes of exchange lead to stable equilibria if resource supply rates are sufficiently high. When resources are scarce, many modes of exchange will lead to instability, but in times of sufficient resource supply any mode of exchange can lead to a stable equilibrium, in contrast to classic work based on smaller, but trophically structured networks (Rosenzweig 1971). This well-known paradox of enrichment considers the interaction of nutrients, prey, and predators, and for a certain set of functional forms for predator–prey interactions, we know that increasing nutrient availability for the prey species will lead to instability. Our models do not have this three-level trophic interaction, but do allow for a much more complex “horizontal” network of exchange. And yet we find, for essentially any form of this horizontal structure, that a large enough increase in external resource inflow will eventually lead to stability.

We know that models using pairwise interactions are not, as no models are, flawless representations of the real world. To enhance the faithfulness of the representation of reality, it is reasonable to consider incorporating mechanism in a model. The results from our consumer–resource model that contradict those found using models of pairwise interactions, do not imply that such models are invalid, but rather, our model, with its distinct characteristics, provides an important alternative view.

Taken in combination, our two results suggest some extensions to the dictionary of how to be stable: either have a special network structure for positive interactions, or find a habitat with large resource inflows. Clearly, there is also an interplay between these results—it may be that even being close to a special network structure, like reciprocal exchange, even if not being exactly at that point, will allow for coexistence across a wider range of resource inflows than a more generic network of exchange. These results also bear comparison with the classic results for pairwise interactions. An intuitive reason for the instability in systems with direct species interactions described by May and others (May 1972; Allesina and Tang 2012) is that if there are sufficiently many randomly placed links between species, and they are strong enough, then these interactions will tend to generate destabilizing feedbacks. It should be noted that an unrealistic type

of instability resulting from unbounded growth can be seen in models representing mutualism as direct species interactions. Avoiding feedbacks, therefore, is a reasonable lesson to take from these systems. Some of the intuition behind these results is similar—for example, in the case of species that specialize on a single resource, acyclic exchange (like reciprocity) is an example of the special modes of exchange that will guarantee stability under all environmental contexts. On the other hand, the idea that reciprocity leads to stability is somewhat invisible in the direct interactions approach, where the received wisdom has been that asymmetric mutualisms are more likely to lead to stability (Bascompte et al. 2006). Yet, here we have shown that reciprocity is a general way to ensure stability across different modes of resource consumption.

Finally, we did not make reference to the evolution of cooperation, which in this context would allow for changes in production and exchange over time (Axelrod and Hamilton 1981), and has been used to shed light on mutualistic ecological interactions among multiple species (Wyatt et al. 2014). In the right circumstances, these evolutionary processes can lead to exact pairwise reciprocity (Taylor and Day 2004; André and Day 2007; Wyatt et al. 2014), though also to other network structures. For example, it is possible for evolutionary processes to result in cyclic non-extractive exchange, known as indirect reciprocity (Boyd and Richerson 1989). Our analysis demonstrates that ecological stability may be a non-trivial criterion along the way for any evolving system of cooperating species. For example, cyclic exchange in our models can lead to instability for certain ranges of resource inflow. This is not so much inconsistent with those evolutionary results, but adds a new criterion for stable coexistence at a positive equilibrium, explicitly depending on environmental context. Finally, we note that studies of the evolution of mutualistic exchange have invoked “biological markets” (Tasoff et al. 2015; Kallus et al. 2017), in analogy with economic markets. We therefore propose that the criteria for ecological stability derived here may also be important, or at least will provoke interesting exploration, in other complex systems where markets structure the form of exchange networks (Farmer 2002; Haldane and May 2011; Hidalgo and Hausmann 2009; O’Dwyer 2019).

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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