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A competitive coexistence principle

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Competitive exclusion – n species cannot coexist on fewer than n limiting resources in a constant and isolated environment – has been a central ecological principle for the past century¹⁻³. Coexistence in natural communities^{4,5} and even in simple microcosms^{6,7} would seem to belie such a principle. Nevertheless, because competitive exclusion has been substantiated by some influential empirical^{2,8,9} and theoretical studies^{1,10-12}, most ecologists have accepted it as a principle and devoted substantial effort to find mechanisms explaining coexistence of competing species^{7,13-15}. As with empirical studies, mathematical proofs do not universally demonstrate exclusion. Many biologically sensible models with density-dependent per capita growth rates allow competitive coexistence¹⁶. Here we show that, when consumer-resource dynamics are solely governed by statistical mechanics, arguably the most parsimonious, fundamental driving force for the dynamics of a system, coexistence emerges as the norm rather than the exception. Any number of species can coexist on a single resource in a constant, isolated environment. Moreover species tend to coexist at constant relative abundances irrespective of variation in the abundance of the total community or the resource. Depending on species characteristics, competition can cause rarity, which may subsequently lead to extinction in small populations due to stochastic mortality events. However, our model shows that ecological similarity does not lead to rarity; on the contrary, the

more similar species are, the more even their proportions will be. Thus limiting similarity in the niches of species is not required to explain coexistence.

All mathematical formalisms of consumer/resource interactions convey critical assumptions about the way consumer *per capita* growth rate varies with its own abundance, the abundance of resources and the abundance of other consumers¹⁷. Depending on these assumptions, models can preclude or permit coexistence of competing species^{11,16}. Here we introduce a very different kind of model, using a mathematical formalism deduced entirely from first principles, of energy and mass conservation, and statistical mechanics. The sole assumptions are that a consumer can only process a given amount of resources at a given time (discrete events), that essential resources are required in fixed proportions (stoichiometry), and that process events require some activation energy in order to occur, as with chemical reactions. Energy and mass conservation constraints then restrict the range of possible trajectories for the dynamics of a consumer/resource system - the phase space. In general, this is not sufficient to determine the system trajectory. However, statistical mechanics makes some trajectories in phase space more probable than others. Statistical mechanics is literally¹⁸ the basic combinatorial principle by which a given macroscopic system trajectory is more probable than others if it can be realized in more ways at the microscopic, individual level (box 1). It has previously been shown¹⁹ that, in a phase space defined by energy and mass conservation constraints, statistical mechanics can drive an ecosystem along a *deterministic* trajectory that can be fully characterized by a system of difference equations (box 1). The mathematical formalism obtained was argued to be more realistic in many respects than Lotka-Volterra or Monod formulations¹⁹. Above all, since it predicts the expected behaviour of a consumer/resource system when there is no driving force other

than statistical mechanics affecting its trajectory, predictions can be viewed as the most parsimonious, or null, expectations for competitive outcomes.

Here we consider ecosystems with N consumers and one or two resources. First consider the case of a system with an arbitrary number of consumer species $(C_i)_{i \leq N}$ feeding on a single resource R (Fig. 1 depicts the two consumer species case). To apply the formalism of statistical mechanics, the possible processes must first be specified. Here resource uptake and consumer growth are treated as a single process. We assume the i^{th} consumer C_i can take up and process an amount ν_i of resource R at a given time, and that this yields one new consumer item (changing the resource to consumer yield would not affect the results presented here) and some waste by-products of growth, W . This can be written as a mass-balance equation: $C_i + \nu_i R \rightarrow 2C_i + W$. We call ν_i a stoichiometric coefficient or requirement (here it is also the inverse of a yield). We further assume that the i^{th} consumer turns over, $C_i \rightarrow W$, where turnover can be losses due to predation, maintenance and mortality *sensu stricto*. The magnitudes of consumption and turnover processes in a given time interval depend on their activation energy and on temperature via a kinetic constant (see box 1). We use the term “affinity” for kinetic constants associated with resource consumption, and “mortality rate” for kinetic constants corresponding to mortality. The greater the activation energy required for a consumer to take up a resource and grow the lower its affinity for that resource.

First consider a “batch” situation where a resource is initially provided to a community of consumers but is not renewed. We show (see Supplementary Information for equations) that when governed by statistical mechanics, such a system tends toward a quasi-steady state; all consumers adjust to the resource level and they coexist with constant relative abundances as long as there is some resource remaining. The community therefore reaches dynamic homeostasy, i.e., total abundance may vary but species relative proportions do not. The relative abundance of C_i with respect to C_j is

determined by their stoichiometric requirements, their affinities for the resource, and their mortality rates:

$$\frac{c_i}{c_j} = \frac{(1+2m_i)}{(1+2m_j)} \left(\frac{m_j}{k_j}\right)^{(1+v_j)/v_j} \left(\frac{k_i}{m_i}\right)^{(1+v_i)/v_i} \frac{v_j}{v_i} \quad (1)$$

where k_i is the affinity of resource uptake by consumer C_i and m_i its mortality rate.

Equation (1) shows that a consumer will be more abundant relative to its competitors if it has a low mortality rate, a high affinity, and a low stoichiometric requirement for its resource, all intuitive predictions. One important feature of equation (1) is that the relative abundances of two species depend only on their own characteristics, irrespective of which other competitors might be present in the community. Such a prediction is testable and might prove useful for predicting community change following biodiversity loss or species introductions. Another noteworthy property of the model is that, despite the intricacy of its mathematical formalism, very simple kinetics emerges for consumer and resource dynamics; they follow first order kinetics with respect to either consumer or resource abundances (Fig. 1 and supplementary equations).

A straightforward consequence of the emergence of first order kinetics for resource uptake is that the system will reach an equilibrium if the resource is continually supplied at a constant input rate. Landmark empirical as well as theoretical studies^{6,7,12} on coexistence have often examined the equilibrium behaviour of flow-through cultures (or chemostats), as opposed to batch cultures. Adding a constant dilution rate D in the model does not affect the occurrence of an equilibrium where all consumer species coexist, however it does shift their competitive balance, and simple calculations show that $\frac{D}{(1-D)} + m_i$ has to be substituted for m_i in eqn (1). Thus high dilution rates will primarily affect species with comparatively low mortality rates m_i .

Next, consider a situation where two consumers share two resources, a situation relevant to resource-ratio theory¹². Although the equations are not readily analytically tractable, random simulations (>100) show that after a short transient period, consumers adjust to their resource levels and their relative abundances remain constant thereafter (Fig. 2 depicts examples with essential resources). The community is again homeostatic, even though resources are continually depleted and are not taken up at equal rates. The same pattern holds for substitutable resources (not shown). Whether resources are essential or substitutable only changes the fate of the community after one resource has become exhausted. When both resources are essential, the community collapses. In contrast, when resources are substitutable, a progressive “phase” transition occurs during which the community pattern shifts towards one that reflects the relative abilities of the consumers to obtain the one remaining resource (although we do not have an analytical equation akin to (1) for the two resource case, the community pattern depends on the amount and identity of all available resources). In chemostats with two essential resources, an equilibrium will be reached with the two species coexisting whatever the resource input ratios (see Supplementary equations). This is in contrast to resource-ratio theory although the equilibrium consumer ratios will depend on the resource input ratio, as in resource-ratio theory (Fig. 3).

We briefly address the issue of variable stoichiometry, such as observed with plants²⁰. The most straightforward way to account for it is to distinguish between various components of a consumer or resource biomass (such as storage vs structural biomass). From a consumer's perspective, this adds a new resource, and will likely promote coexistence²¹. From the resource's perspective, this adds a new “consumer”. However, since our model allows consumers to coexist irrespective of their number, this will not affect coexistence but may shift competitive balances between consumers.

Our results show that when community dynamics are constrained by energy and mass balance equations, and otherwise driven by statistical mechanics, species should be expected to coexist, even on a single limiting resource, in a constant homogeneous and isolated environment (i.e., no immigration). These results stand in sharp contrast to previous theoretical work. In our view, they illuminate the incongruity of impossible coexistence between competitors and our everyday observations; species share resources and scarce resources are likely to be limiting for whole communities, yet species coexist.

We showed that species should coexist at constant relative abundances in constant environments. Ecological assemblages could therefore persist with a constant, recognizable pattern under constant environmental conditions, but possibly varying resource levels. Such a holistic behaviour need not depend on the assemblage of particular species with complementary niches, but arises as the most probable behaviour of any community of competing species. The temporal component of species relative abundance distributions on ecological timescales has received little attention^{22,23}. However, in fossil records, where coarse time resolution presumably averages out community variability due to changing environmental conditions, there is intriguing evidence that homeostatic communities can persist over millions of years²⁴.

Our results do not preclude competition from incidentally leading to local extinction in some circumstances. According to eqn (1), if, in a given environment, a species has a high mortality rate and a low affinity for the one most limiting resource, and/or a large stoichiometric requirement for that resource, then it may only achieve an extremely low relative abundance compared to its competitors. In finite, real-world populations (and particularly experimental ones), the competitive balance may be so unfavourable to that species that only very few, if any, of its individuals can survive. Under such circumstances, Darwin's insight that “rarity is the precursor of [stochastic] extinction” (quoted from ref 3) still holds. Consequently our findings can explain

“apparent competitive exclusion” and they do not, of course, invalidate other mechanisms that promote coexistence^{7,13-15} if competition drives one species to very low densities.

Finally, limiting similarity in species' niche may not be needed to explain species coexistence. On the contrary, in our model, ecologically similar species, such as cryptic species^{25,26}, are expected to tend towards similar abundances, with identical species (i.e., conspecifics) having identical abundances, as intuitively expected. This may have ramifications for sympatric speciation and adaptive dynamics (but see also ref 27).

Box 1

How statistical mechanics determines system dynamics can be best understood with the dog-flea model of the Erhenfest's^{28,29}. Two dogs A and B infested by fleas are lying side by side. Fleas can jump from one dog to the other. Suppose we know each dog has 5 fleas at time zero. We want to predict the number n of fleas jumping from A to B and conversely the number p of fleas going from B to A during a time interval τ . Assume that energy constraints let us know that 4 fleas will change dogs during τ . Then any combination (n,p) satisfying $n+p=4$ is a possible macroscopic event in this system. In turn, any possible macroscopic event (n,p) can be realized in many ways at the microscopic, flea-level; specifically, the macro-event (n,p) can be realized in $W(n, p) = C(5, n) C(5, p)$ micro-events, where $C(i, j)$ is the binomial coefficient and $W(n,p)$ is the multiplicity of the macro-event (n,p) . Because not all macro-events have equal multiplicities, some will be more probable than others. In fact, for sufficiently large numbers of fleas, one macro-event will be overwhelmingly more probable than any other. We can thus make a deterministic prediction (n,p) describing the dynamics of this system.

Previously, Neill & Gignoux¹⁹ showed that it is possible to extend this rationale to ecosystems. Specifically, consider an ecosystem consisting of an arbitrary set (S_i) of N

living or non-living species (the dogs), consisting of identical items (the fleas) interacting through a number R of processes (the jumps). We assume that each process can be described by an energy and mass-balance equation, $\sum_i \nu_{ir} S_i \rightarrow \sum_i \eta_{ir} S_i$, where ν_{ir} and η_{ir} are stoichiometric coefficients. When constrained by mass and energy conservation and driven by statistical mechanics, the trajectory of this system proved quasi-deterministic under very general conditions (small enough time interval τ , and large enough number of items of each species). Moreover, this trajectory can be fully specified by the magnitude $(x_r)_{r \leq R}$ of each process during τ , which must satisfy the following system of non-linear equations :

$$x_r = k_r \prod_r \left(\frac{s_i - \sum_t \nu_{it} x_t}{\nu_{ir}} \right)^{\frac{\nu_{ir}}{\nu_r}}$$

where s_i is the abundance of S_i , $\nu_r = \sum_i \nu_{ir}$, and k_r is a kinetic adimensional constant depending on temperature and on the amount of activation energy required for one process event to occur.

Methods

Full model derivation is described elsewhere¹⁹. There are two equivalent mathematical formalisms derived in ref 19. The first is given by the equation in box 1. It is the most meaningful and easily tractable analytically. The second is less intuitive and uses

Lagrange multipliers :

$$x_r = k_r \exp \left(\frac{\sum_i \nu_{ir} (\log(\frac{s_i}{\nu_{ir}}) - \mu_i)}{\nu_r} \right) \quad (2)$$

where the μ_i 's are Lagrange multipliers chosen so that the mass conservation constraints $\sum_r \nu_{ir} x_r = s_i$ are satisfied for all i (in that formulation possible processes include identical transformations $S_i \rightarrow S_i$). This latter formulation is more efficient to

implement than solving a system of non-linear equations, and was therefore used for random simulations. Following the method of Agmon et al²⁸, it can be readily shown that the vectorial function $f = (f_i)_{i \leq n}$ with $f_i(\mu_0, \dots, \mu_n) = s_i - \sum_r \nu_{ir} x_r$, whose zeros we seek to find, has a positive definite Jacobian matrix. Therefore it derives from a potential F , $F(\mu_0, \dots, \mu_n) = \sum_i \mu_i s_i + \sum_r \nu_r x_r$. whose minimum can be accurately found by a non-linear minimization algorithm. This minimum is precisely the Lagrangian multipliers we sought. The procedure is repeated at each time step. All simulations were run with a one hour time step. All source code was written using R statistical software. Random simulations were performed on a subset of relevant parameters for the two resources and two consumers case. In the batch mode, resource initial abundances were held fixed. Changing them would not alter the results because (i) the model is scale invariant, and (ii) the patterns are robust to changes in the resource ratio. Consumer initial abundances also do not matter since their abundances are eventually determined by resource levels. In addition to initial abundances, one affinity and one stoichiometric coefficient were chosen to serve as references in each case. The reference affinity was set so that a significant amount of resource would be consumed within 50 days. The other affinities were left to vary by intervals within one order of magnitude centered around the reference. Mortality rates were allowed to vary within one order of magnitude greater than affinities. This ensured that consumers reached a quasi-steady state before resources were exhausted, and allowed macroscopic properties to emerge. In the case of two consumers feeding on two essential resources, stoichiometric coefficients on the first resource R_1 , ν_{11} and ν_{21} , were taken to correspond to the inverse of carbon yields and accordingly the reference stoichiometric coefficient, ν_{11} was set to 2 (corresponding to a 0.5 yield). Stoichiometric coefficients for the second resource R_2 , ν_{12} and ν_{22} , were taken to reflect the consumers elemental C to N ratios. Stoichiometric coefficients were sampled uniformly within their interval. Kinetic parameters were sampled uniformly on a \log_{10} scale.

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Supplementary Information is linked to the online version of the paper on www.nature.com/nature.

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Figure Legends

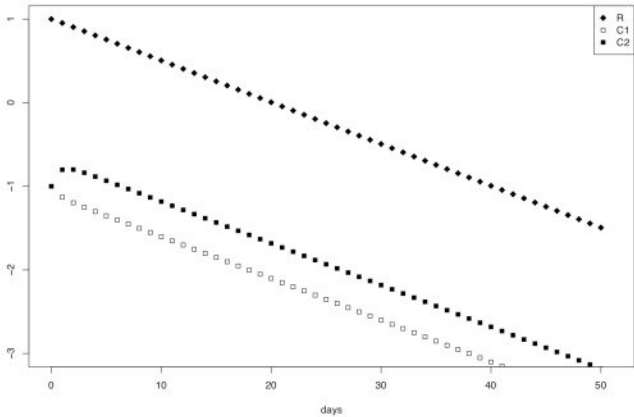
Figure 1 Model illustration for the one resource/two consumers case. All abundances are log scaled. The dynamics of the resource R (closed diamonds) follows first order kinetics. The dynamics of consumer C_1 (open squares) and C_2 (closed squares) parallel that of the resource, so that the ratios C_1/R and C_2/C_1 remain constant. Parameter values used : affinities (log scaled) $k_1 = -2.3$, $k_2 = -2$, mortality rates (log scaled) $m_1 = -1$, $m_2 = -1$, stoichiometric

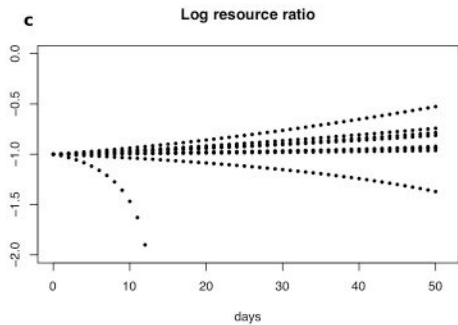
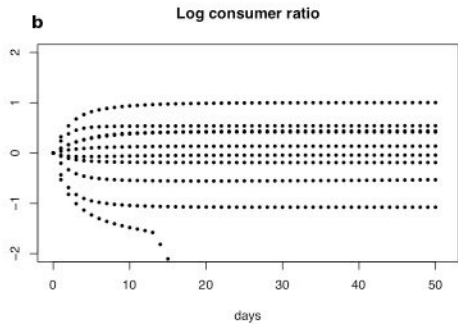
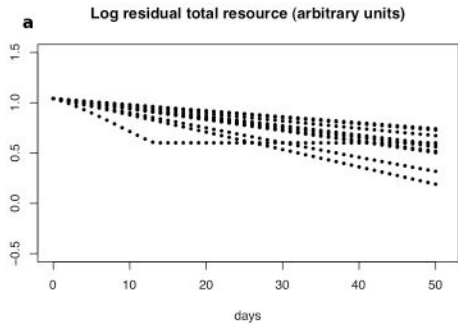
coefficients $\nu_1=2.5$, $\nu_2=2$. An analytical demonstration for any number of consumers is available in Supplementary Information.

Figure 2 Simulation results with 10 randomly drawn parameter sets in the two essential resources/two consumers case. All values are log scaled. **a**, total resource, R_1+R_2 , dynamics for each parameter set. **b**, consumer ratio dynamics for each set. **c**, resource ratio dynamics for each set. Note the transition after exhaustion of one resource for some parameter sets. The following parameters were held fixed: initial abundances: $r_1=10$, $r_2=1$, $c_1=c_2=0.1$, affinity (log scaled) $k_1=-2.8$, stoichiometric coefficient $\nu_{11}=2$. The other parameters were sampled within the following intervals: affinity (log scaled) $k_2 \in [-3.3, -2.3]$ and mortality rates (log scaled) $m_1, m_2 \in [-2, -1]$, stoichiometric coefficients $\nu_{12} \in [1.6, 3.3]$, $\nu_{12}, \nu_{22} \in [0.1, 0.4]$.

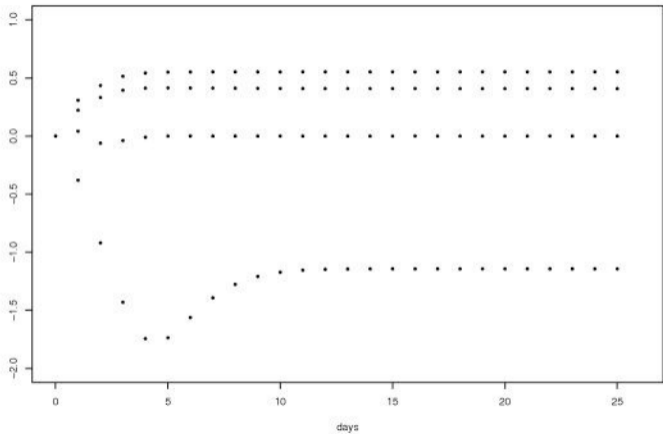
Figure 3 Examples for the time course of the consumer abundance ratio (log scaled) in a chemostat with two essential resources and two consumers at different resource input ratios. Dilution rate $D=0.01$, initial abundances $r_1=10$, $r_2=(0.2, 0.5, 1, 2)$, $c_1=c_2=0.1$, affinities (log scaled) $k_1=k_2=-1$, mortality rates (log scaled) $m_1=m_2=-1.3$, stoichiometric coefficients $\nu_{11}=1.6$, $\nu_{21}=3.3$, $\nu_{12}=0.2$, $\nu_{22}=0.07$.

Log abundances of residual resource and consumers (arbitrary units)





Log consumer ratio



A competitive coexistence principle

Supplementary equations

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Coexistence of an arbitrary number of consumers on a single resource

Consider a system with n consumers C_1, \dots, C_n and one resource R . Each consumer may feed on the resource according to the following mass-balance equation :

$\nu_i R + C_i \rightarrow 2C_i + W$, where W stand for waste and ν_i is the stoichiometric requirement for R of C_i . Each consumer also turns over according to $C_i \rightarrow W$. Let x_i and z_i denote the magnitudes of consumption and mortality processes during one time step. Note that the model is scale-invariant so that the units used for abundances and process magnitudes do not matter as long as the relative stoichiometry does not change (ref 19 of the main text).

According to the model (box 1 in the main text), the dynamics of this system are given by :

$$\begin{aligned} \delta r &= -\sum_i \nu_i x_i \quad (1) \\ \delta c_i &= x_i - z_i \quad (2) \end{aligned} \quad \text{with}$$

$$x_i = k_i (c_i - x_i - z_i)^{\frac{1}{(1+\nu_i)}} \left(\frac{r - \sum_j \nu_j x_j}{\nu_i} \right)^{\frac{\nu_i}{(1+\nu_i)}} \quad (3)$$

$$\text{and } z_i = m_i (c_i - x_i - z_i) \quad (4)$$

Let us first assume that we are at quasi steady-state, ie $x_i \approx z_i$ for all i . Substituting (4) into (3) and then using the steady-state assumption yields, for all i :

$$x_i = k_i \left(\frac{x_i}{m_i} \right)^{\frac{1}{(1+\nu_i)}} \left(\frac{r - \sum_j \nu_j x_j}{\nu_i} \right)^{\frac{\nu_i}{(1+\nu_i)}}$$

Rearranging gives :

$$\nu_i x_i = \left(\frac{k_i^{(1+\nu_i)}}{m_i} \right)^{1/\nu_i} \left(r - \sum_j \nu_j x_j \right) \quad (5)$$

Summing (5) over i gives the expected result that total ($\sum_i \nu_i x_i$) and individual (x_i) consumption fluxes are proportional to r. Using equation (3) again, it is easy to show that the consumer abundances c_i will be proportional to r as well. Using (4) and (5) we can also compute the quasi-steady state relative abundance of any two consumers c_i and c_j :

$$\frac{c_i}{c_j} = \frac{(1+2m_i)}{(1+2m_j)} \frac{m_j}{m_i} \frac{x_i}{x_j} = \frac{(1+2m_i)}{(1+2m_j)} \left(\frac{m_j}{k_j} \right)^{(1+\nu_j)/\nu_j} \left(\frac{k_i}{m_i} \right)^{(1+\nu_i)/\nu_i} \frac{\nu_j}{\nu_i}$$

To show that the system will reach this quasi-steady state, consider a state where all consumers are at quasi steady-state except for one, say C_1 . Suppose for instance that $c_1 < c_1^\circ$, where c_1° would be the quasi steady-state value for C_1 given the resource level. We want to show that, necessarily, $\delta c_1 = x_1 - z_1 > 0$. Equation (5) remains valid for all $i > 1$ since we assume those consumers to be at quasi steady-state. Therefore summing over all $i > 1$ yields :

$$\begin{aligned} \sum_{i>1} \nu_i x_i &= k' (r - \nu_1 x_1 - \sum_{i>1} \nu_i x_i) \\ \sum_{i>1} \nu_i x_i &= \frac{k'}{1+k'} (r - \nu_1 x_1) \quad (6) \end{aligned}$$

Now eliminating z_1 in (4), substituting in (3) for $i=1$ and using also (6) gives

$$x_1 = k_1 \left(\frac{m_1}{1+m_1} \right)^{\frac{1}{(1+\nu_1)}} (c_1 - x_1)^{\frac{1}{(1+\nu_1)}} \left(\frac{1}{(1+k')} \frac{r - \nu_1 x_1}{\nu_1} \right)^{\frac{\nu_1}{(1+\nu_1)}}$$

Finally, dividing by c_1 we get the following equation :

$$\frac{x_1}{c_1} = k_1 \left(\frac{m_1}{1+m_1} \right)^{\frac{1}{(1+\nu_1)}} \left(1 - \frac{x_1}{c_1} \right)^{\frac{1}{(1+\nu_1)}} \left(\frac{1}{(1+k')} \left(\frac{r}{\nu_1 c_1} - \frac{x_1}{c_1} \right) \right)^{\frac{\nu_1}{(1+\nu_1)}} \quad (7)$$

Equation (7) shows that $\frac{x_1}{c_1}$ is a decreasing function of c_1 . Indeed, omitting the

multiplicative constants for clarity, and rearranging, we have :

$$\frac{(x_1/c_1)^{(1+\nu_1)}}{(1-x_1/c_1)} \propto \left(\frac{r}{\nu_1 c_1} - \frac{x_1}{c_1} \right)^{\nu_1} \quad (8)$$

The left hand side is an increasing function of $\frac{x_1}{c_1}$, whereas the right hand side is a

decreasing function of $\frac{x_1}{c_1}$. Thus, when c_1 decreases, $\frac{r}{c_1}$ increases and as a result,

$\frac{x_1}{c_1}$ must increase.

Therefore if $c_1 < c_1^\circ$ we have, necessarily, $\frac{x_1}{c_1} > \left(\frac{x_1}{c_1} \right)^\circ$. Next rearranging equation (4)

with $i=1$ yields

$$(1+m_1) \frac{z_1}{c_1} = m_1 \left(1 - \frac{x_1}{c_1} \right)$$

Therefore, $\frac{z_1}{c_1}$ is an increasing function of c_1 and we must have : $\frac{z_1}{c_1} < \left(\frac{z_1}{c_1} \right)^\circ$

Because at quasi steady-state, by definition $\left(\frac{x_1}{c_1} \right)^\circ = \left(\frac{z_1}{c_1} \right)^\circ$, this proves that $x_1 < z_1$ and

so c_1 will increase, as expected. See also the proof for the existence of a locally stable equilibrium (in chemostats) of a larger class of models, including ours, in ref 16 of the main text.

Chemostat equilibrium of two competitors on two essential resources

Consider two competitors feeding on two essential resources. With obvious notations, the dynamics of the system will be, in a chemostat with dilution rate D :

$$\delta r_j = D(r_{j0} - r_j) - v_{1j}x_1 - v_{2j}x_2 \quad (9) \quad \text{with}$$

$$\delta c_i = x_i - z_i - Dc_i \quad (10)$$

$$x_i = k_i (c_i - x_i - z_i)^{\frac{1}{v_i}} \left(\frac{r_1 - v_{11}x_1 - v_{21}x_2}{v_{i1}} \right)^{\frac{v_{i1}}{v_i}} \left(\frac{r_2 - v_{12}x_1 - v_{22}x_2}{v_{i2}} \right)^{\frac{v_{i2}}{v_i}} \quad (11)$$

$$xt_i = m_i (c_i - x_i - z_i) \quad (12)$$

where $v_i = 1 + v_{i1} + v_{i2}$.

Setting (9),(10) to zero at equilibrium, using (12) and substituting into (11) gives, for $i=1,2$:

$$x_i = k_i \left(\frac{(1-D)x_i}{D + m_i(1-D)} \right)^{\frac{1}{v_i}} \left(\frac{r_{10} - \frac{(1+D)}{D}(v_{11}x_1 + v_{21}x_2)}{v_{i1}} \right)^{\frac{v_{i1}}{v_i}} \left(\frac{r_{20} - \frac{(1+D)}{D}(v_{12}x_1 + v_{22}x_2)}{v_{i2}} \right)^{\frac{v_{i2}}{v_i}}$$

so the same procedure can be used to compute the magnitudes x_i at and out of equilibrium (although with slightly different parameters). At equilibrium, this procedure is guaranteed to converge to positive solutions satisfying

$$r_{10} - \frac{(1+D)}{D}(v_{11}x_1 + v_{21}x_2) > 0, \quad r_{20} - \frac{(1+D)}{D}(v_{12}x_1 + v_{22}x_2) > 0 \quad . \text{ So the system will}$$

have an equilibrium solution for any positive values of r_{10}, r_{20} .