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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 century. Since empirical studies cannot universally demonstrate exclusion, this principle has mainly relied on mathematical proofs. Here we investigate the predictions of a new approach to derive functional responses in consumer/resource systems. Models usually describe the temporal dynamics of consumer/resource systems at a macroscopic level – i.e. at the population level. Each model may be pictured as one time-dependent macroscopic trajectory. Each macroscopic trajectory is, however, the product of many individual fates and from combinatorial considerations can be realized in many different ways at the microscopic – or individual – level. Recently it has been shown that, in systems with large enough numbers of consumer individuals and resource items, one macroscopic trajectory can be realized in many more ways than any other at the individual – or microscopic – level. Therefore, if the temporal dynamics of an ecosystem are assumed to be the outcome of only statistical mechanics – that is, chance – a single trajectory is near-certain and can be described by deterministic equations. We argue that these equations can serve as a null to model consumer-resource dynamics, and show that any number of species can coexist on a single resource in a constant, isolated environment. Competition may result in relative rarity, which may entail exclusion in finite samples of discrete individuals, but exclusion is not systematic. Beyond the coexistence/exclusion outcome, our model also predicts that the relative abundance of any two species depends simply on the ratio of their competitive abilities as computed from – and only from – their intrinsic kinetic and stoichiometric parameters.

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 century. This principle has been substantiated by some influential empirical (Gause 1934, Park 1962, Lack 1971) and theoretical studies (Volterra 1931, Levin 1970, Armstrong and McGehee 1980). However, experimental results cannot prove and hardly falsify the principle (Hardin 1960). Thus theoretical studies were presumably the main reason – perhaps in timely conjunction with the above substantiating experiments – why exclusion became the a priori expectation for any competitive interaction. This had two profound consequences for subsequent ecological research. First, competitive outcomes were often categorized as 'exclusion' even though exclusion was not actually observed (Tilman 1981, Smith and Kalff 1983, Sommer 1983, 1985, 1986). Second, much subsequent theoretical and empirical effort was devoted to finding mechanisms explaining coexistence of competing species (Connell 1978, Levins 1979, Sommer 1985, Huisman and Weissing 1999, Chesson 2000, Kelly and Bowler 2002). Indeed, when viewed as deviations from this a priori expectation, observations of diversity in natural communities (Hutchinson 1961, Connell 1978), coexistence of cryptic species (McPeek and Gomulkiewicz 2005, Leibold and McPeek 2006) and coexistence in some simple microscosms are in want of an explanation. Had the competitive exclusion principle not existed, many of these observations and experiments would likely have been interpreted differently, or done differently.

If one accepts that the principle of competitive exclusion has shaped ecologists' a priori expectations, it is worth briefly revisiting its theoretical roots. The foundations all relied on formalisms of consumer/resource interactions where consumer per capita growth rate depends only on the abundances of limiting resources (or factors), but neither on its own abundance, nor the abundance of other consumers (Levin 1970, Armstrong and McGehee 1980). However, more complex interactions, such as intra- or interspecific density-dependence – what Connell et al. (1984) called community compensatory trends – are frequently observed (Abrams and Ginzburg 2000, Wright 2002). Intraspecific density-dependence can be described mathematically. Although the most plausible formalism is currently under debate (Abrams and Ginzburg 2000), Lobry et al. (2006) recently showed that whatever the functional form of this density dependence, if it is negative, then competitors coexist. So depending on critical differences with regard to

density-dependence, models can preclude or permit coexistence of competing species. Does this challenge the validity of the principle of competitive exclusion? It depends on which formalism – density-dependent or not – is viewed as the most appropriate 'null' model for consumer/resource interactions. This paper seeks to contribute to this theoretical issue.

Most traditional approaches to modelling consumer/resource dynamics are phenomenological. Although a number of thermodynamic principles – or goal functions – have been proposed as alternatives for explaining and predicting the temporal dynamics of ecosystems (maximum entropy production, Dewar 2003, 2005, Martyushev and Seleznev 2006, maximum power principle Odum 1988, Fath et al. 2001) they remain controversial and not generally accepted. Another candidate first principle which has been overlooked is Jaynes' (1985) statistical mechanical principle (although attempts have been made to relate it to maximum entropy production, Dewar 2003, 2005). Jaynes proposed that the dynamics of non-equilibrium systems could be an outcome of 'statistical mechanics'; literally, what is observed at a given, macroscopic, scale is what can be realized in the greatest number of ways at a finer, microscopic, scale. Recently, Neill and Gignoux (2008) developed this idea to show that statistical mechanics may suffice to generate deterministic dynamics for ecosystems with large numbers of 'particles' – that is, items of living and non-living entities. Given its parsimony and simplicity as an underlying principle, such a model arguably has a part to play in our search for null models of ecosystem dynamics and consumer/resource interactions in particular. Here we investigate the predictions of a statistical mechanics model with regard to species coexistence. We first explain the statistical mechanical principle underpinning the model and the way the equations are derived. Then we apply the model to two classical case studies, namely N species consuming a single resource, and two species consuming two resources. We end by discussing the differences and similarities of the model and its predictions with previous modelling approaches.

## Methods

### Model description

We show by an example how it is possible to apply Jaynes' statistical mechanical principle to predict the dynamics of consumer/resource systems.

Consider a simple ecosystem comprising two consumer species sharing one resource. Assume that the resource has r identical items, and that each consumer species has $c_1$ and $c_2$ individuals respectively. Further assume that each consumer species needs one resource item to grow and reproduce. For simplicity's sake, we consider only a lumped growth/reproduction process for the moment; mortality processes will be introduced later. A macroscopic time course of this 'ecosystem' – its trajectory – can be described by two variables: the number $x_1$ of individuals of species 1 reproducing per unit time $\delta t$ and its counterpart $x_2$ for species 2. Any macroscopic trajectory as given by $(x_1, x_2)$ can be realized in many ways at the individual, microscopic level. Figure 1 shows two different microscopic realizations of the same macroscopic time course ($x_1 = 2$, $x_2 = 3$) with $r = 8$, $c_1 = 10$ and $c_2 = 12$. Specifically, if we consider a short enough time step, there is little chance that the same individual will reproduce twice during $\delta t$. In this framework, the number of microscopic ways the macroscopic trajectory $(x_1, x_2)$ can be realized is equal to:

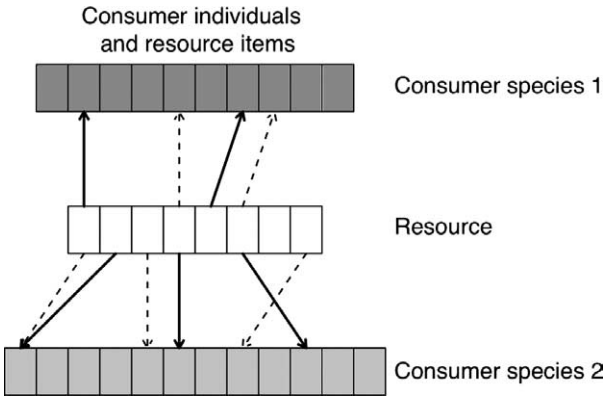


Figure 1. Microscopic multiplicity of macroscopic outcomes in a one resource/two consumer case: examples of two of very many ways (black and dashed arrows respectively) to realize at the individual level the population-level outcome where species 1 consumes 2 resource items and species 2 consumes 3 resource items during a given time interval. Squares are consumer individuals or resource items.

$$W(x_1, x_2) = \frac{r!}{x_1!x_2!(r - x_1 - x_2)!} \frac{c_1!}{x_1!(c_1 - x_1)!} \times \frac{c_2!}{x_2!(c_2 - x_2)!}$$

The first term of the product on the right hand side corresponds to the number of ways the r resource items can be dispatched between the $x_1$ reproducing individuals of species 1, the $x_2$ reproducing individuals of species 2 and the $r - x_1 - x_2$ resource items that will not be consumed during $\delta t$. The second term represents the number of ways to dispatch the $c_1$ individuals of species 1 between those that will grow and those that will not during $\delta t$; likewise the third term is the number of ways to dispatch the $c_2$ individuals of species 2. $W(x_1, x_2)$ is called the microscopic multiplicity of the trajectory $(x_1, x_2)$. From its expression, we can see that not all macroscopic trajectories have the same multiplicity (since W varies as a function of $x_1$ and $x_2$). Jaynes's statistical mechanical principle simply says that the observed macroscopic trajectory of this system is the one with maximum multiplicity, while being compatible with other known macroscopic constraints (we return to those constraints below).

While it seems reasonable to assume that, in the absence of any other forces governing the dynamics of this system, the macro-trajectory with maximum multiplicity has the largest probability of being observed, what about the other macro-trajectories? For large enough systems, they have negligible multiplicities (Neill and Gignoux 2008). Specifically, if p is the order of magnitude of abundances in the system then 'large enough systems' means $\log(p) \ll p$. Thus

if the dynamics of a system are only driven by statistical mechanics, we can predict that it will follow a single, deterministic trajectory, the one with maximum microscopic multiplicity.

We are therefore interested in determining the macrotrajectory with maximum microscopic multiplicity that is compatible with other known macroscopic constraints. Not all macroscopic time courses are feasible during any given time step. In our example, we must have $x_1 \leq c_1$, $x_2 \leq c_2$ and $x_1 + x_2 \leq r$. These are matter conservation constraints. Another known constraint is energy conservation. Suppose we know the heat budget of our system $\delta H$ during $\delta t$ (this assumption will be relaxed thereafter); then, as all biological processes either consume or produce energy, we can write an energy conservation constraint of the form $h_1x_1 + h_2x_2 = \delta H$ where $h_1$ and $h_2$ would be the specific heats of growth/reproduction processes for species 1 and 2 respectively. Matter and energy conservation are the sole constraints we will consider here, in order to devise a minimalist model.

Let us now maximise the multiplicity subject to the above constraints. Here, $W(x_1, x_2)$ is only defined when $x_1$, $(c_1 - x_1)$, $x_2$, $(c_2 - x_2)$ and $(r - x_1 - x_2)$ are positive, so the matter conservation constraints are automatically satisfied. We can then introduce a Lagrange multiplier $\lambda$ for the energy constraint and maximise the function:

$$S(x_1,\ x_2) = \log(W) - \lambda(h_1x_1 + h_2x_2)$$

To do so we use the Stirling approximation $n! = n\log(n) - n + o(n)$. Omitting the constant terms, we get:

$$\begin{aligned} S(x_1,\ x_2) \approx & -2x_1\log(x_1) - (c_1 - x_1)\log(c_1 - x_1) \\ & - 2x_2\log(x_2) - (c_2 - x_2)\log(c_2 - x_2) \\ & - (r - x_1 - x_2)\log(r - x_1 - x_2) \\ & - \lambda(h_1x_1 + h_2x_2) \end{aligned}$$

Deriving with respect to $x_1$ and setting the derivative $\frac{\partial S}{\partial x_1} = 0$, we get:

$$-2\log(x_1) + \log(c_1 - x_1) + \log(r - x_1 - x_2) - \lambda h_1 = 0$$

Introducing $k_1 = \exp(-\lambda h_1/2)$, this yields:

$$x_1 = k_1(c_1 - x_1)^{1/2}(r - x_1 - x_2)^{1/2} \quad (1)$$

Similarly we have:

$$x_2 = k_2(c_2 - x_2)^{1/2}(r - x_1 - x_2)^{1/2} \quad (2)$$

with $k_2 = \exp(-\lambda h_2/2)$. The completion of the calculus would normally require determining $\lambda$ as a function of the heat budget $\delta H$. However, in classical statistical physics, temperature is defined as being inversely proportional to $\lambda$, which is the Lagrange multiplier associated with the energy conservation constraint. Assuming this definition holds here as well, we do not need to know the heat budget if we know the temperature, and, furthermore, if we work at constant temperature, then $k_1$ and $k_2$ can be viewed as constant kinetic parameters.

Our model is thus a system of two coupled non-linear equations whose unknowns are $x_1$ and $x_2$.This allows us to calculate the dynamics of the system, when constrained by mass and energy conservation and otherwise driven by statistical mechanics. In this example $x_1$ depends on r, $c_1$ and $c_2$. To get a sense of what the functional response $x_1/c_1$ of this model looks like in two-dimensional space, assume $c_2 = 0$. Then dividing each side of Eq. 1 by $c_1$ we have:

$$\frac{x_1}{c_1} = k_1\left(1 - \frac{x_1}{c_1}\right)^{1/2}\left(\frac{r}{c_1} - \frac{x_1}{c_1}\right)^{1/2}$$

This is a ratio-dependent functional response sensu Arditi and Ginzburg (1989). It is shown on Fig. 2 along with the

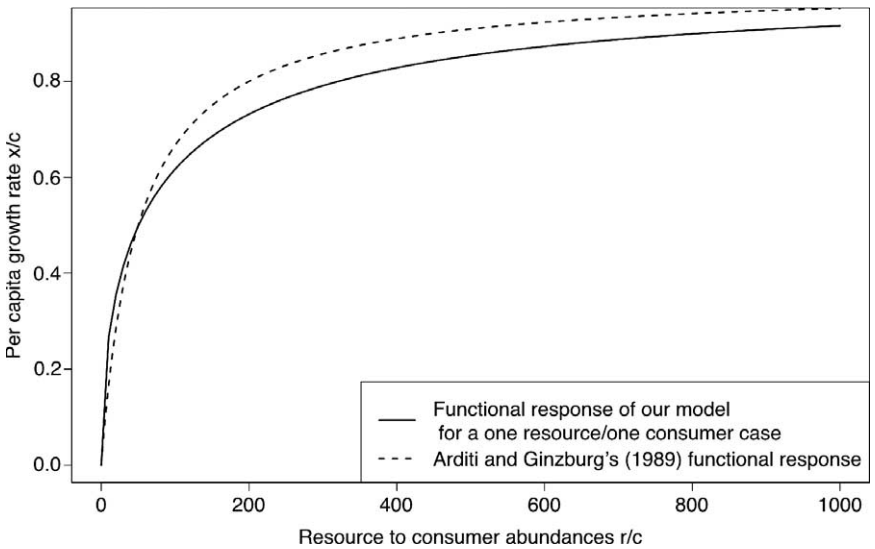


Figure 2. Model functional response $x/c = f(r/c)$ in the one resource/one consumer case (solid line) compared with the ratio-dependent functional form originally proposed by Arditi and Ginzburg (1989) $x/c = \mu\frac{r/c}{K + r/c}$. Parameter values are: $k = 0.1$ for our model; $\mu = 1$ and $K = 50$ for Arditi and Ginzburg's model. Note: both functions saturate at 1.

phenomenological functional form originally proposed by Arditi and Ginzburg (1989).

We made three core assumptions to derive this model: 1) the time step must be short enough so that any 'particle' will undergo at most one event during $\delta t$ 2) The order of magnitude p of the system should be such that $p \gg \log(p)$. 3) Fluxes $x_1$, $x_2$, $r - x_1 - x_2$, etc. . ., should be large enough for the Stirling approximation to hold. Although finding the right time step might require some fine tuning in practice, these requirements are not incompatible. Assumption 3) should follow from assumption 2). Furthermore, if we examine Eq. 1 and 2 they show some properties that might allow for a relaxation of some of the above assumptions. First, the system of Eq. (1–2) is scale-invariant: that is, if we multiply all the abundances by a factor p, the solutions will be multiplied by p as well. Therefore, from a mathematical point of view we can replace abundances by densities without changing the results. Second, provided the time step is short enough, simulations suggest that the model is insensitive to the choice of the exact duration of the time step, provided that the kinetic parameters are adjusted proportionally to it. While this remains to be formally demonstrated, it makes intuitive sense when we recall how the equations were derived: the macro-trajectory predicted by the model between times, say, $t_0$ and $t_1$ is compatible with the vast majority of micro-trajectories feasible during this time step. It therefore seems likely that its truncation over a smaller time interval is compatible with the majority of micro-trajectories over this smaller interval and therefore corresponds to the model prediction over this smaller time interval. The analytical derivation of the dependency of the kinetic parameters upon the time step is, however, not straightforward. Finally, it seems reasonable to say that the most stringent assumption for the model to hold is that the order of magnitude of the system be large (i.e. $p \gg \log(p)$).

The rationale we have followed for this simple example can be generalized for more complex ecosystems. We can consider an arbitrary number of resources ($r_j$); an arbitrary number of consumer species ($c_i$); and can add as many processes as is necessary. The most general formalism for ecosystems is given in the Supplementary material Appendix 1 and derived in Neill and Gignoux (2008). In the following we add a mortality process for each consumer species in addition to growth/reproduction (but we do not include waste recycling). Mortality could result from predation, old age and starvation. We will not consider an explicit consumption process equivalent to 'basal metabolism' at the individual level, although it would not qualitatively change the results presented here. To keep things simple and comparable with classical models, we will consider that at birth, individuals have built-in reserves for a prescribed mean life span, and that basal metabolism is the amount of resource consumed by a steady-state population as the result of concurrent reproduction events and individual deaths from starvation. Under these conditions, we choose a time step short enough that an individual either reproduces or dies – i.e. if it has died, it means in retrospect that the probability it has reproduced within the same time interval is negligible.

In the following, we applied this formalism to two case studies, namely N species consuming a single resource, and two species consuming two resources. We derive analytical results for species coexistence on one or two resources (equilibrium existence and stability analysis) but also present numerical simulations as illustrations. Calculations and methods for the numerical simulations are presented in the Supplementary material Appendix 1.

## Results

### Species coexistence on a single resource

Consider a situation where a resource is continuously supplied with input rate I to a community of N consumer species with abundances $c_i$, and let $x_i$ and $z_i$ denote the number of individuals of species i, respectively reproducing and dying per unit time step $\delta t$. Variations in consumer and resource abundances per unit time step follow the difference equations:

$$\delta c_i = x_i - z_i \tag{3}$$

$$\delta r = I - \sum\nolimits_i \nu_i x_i \tag{4}$$

Equation 4 states that the amount of resource taken up by a consumer species i is proportional to its growth rate $x_i$, the coefficient of proportionality being equal by definition to $\nu_i$, the number of resource items required to build a new individual of that species – we will call it the stoichiometric coefficient of that consumer species for this resource (see Table 1 for a summary of parameters). As explained in the methods section, the $x_i$'s and $z_i$'s can be calculated from a set of 2N coupled equations:

$$x_i = k_i (c_i - x_i - z_i)^{\frac{1}{(1+\nu_i)}} \left( \frac{r - \sum_k \nu_k x_k}{\nu_i} \right)^{\frac{\nu_i}{(1+\nu_i)}} \tag{5}$$

$$\text{and} \quad z_i = m_i (c_i - x_i - z_i) \tag{6}$$

$$\text{for } 1 \leq i \leq N$$

We show (Supplementary material Appendix 1) that there exists a unique non-trivial equilibrium where all species coexist. We further show that this equilibrium is always feasible and stable (Supplementary material Appendix 1). Consumer abundances at equilibrium are proportional to the resource level, so that consumer relative abundances do not depend on the resource level (or ultimately on the resource input rate I). In fact, consumer relative abundances as given by Eq. 7 below are character-

Table 1. Summary of model parameters and variables.

| | |
|---|---|
| $c_i$ | Number of individuals of consumer species i |
| $r_j$ | Number of items of resource j (index omitted if only one resource) |
| $\nu_{ij}$ | Stoichiometric coefficient: number of items of resource j needed to build a new individual of species i |
| $k_i$ | Growth kinetic constant of species i (adimensional) |
| $m_i$ | Mortality kinetic constant of species i (adimensional) |
| $x_i$ | Growth rate of species i: number of individuals reproducing per unit time step |
| $z_i$ | Mortality rate of species i: number of individuals dying per unit time step |
| D | Dilution rate |
| $h_j$ | Heat requirement of a process per unit event |
| I | Resource input rate per unit time step |

istic of a steady-state for consumers that can be achieved at any resource level and maintained in spite of resource abundance variations if the changes in resources are slow enough. The relative abundance of species i with respect to species j is determined by their stoichiometric requirements, and their kinetic constants for growth and mortality:

$$\frac{c_i}{c_j} = \frac{(1 + 2m_i)}{(1 + 2m_j)} \frac{\nu_j}{\nu_i} \left(\frac{k_i}{m_i}\right)^{(1+\nu_i)/\nu_i} \left(\frac{m_j}{k_j}\right)^{(1+\nu_j)/\nu_j} \quad (7)$$

Equation 7 shows that a consumer will be more abundant relative to its competitors if it has a lower mortality kinetic constant, a higher growth kinetic constant, and a lower stoichiometric requirement for its resource (Fig. 3). In the situation where two species have similar stoichiometric requirements and kinetic constants, they will tend to even proportions. Adding a constant dilution rate D in the model does not affect the existence 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 Eq. 7. Thus high dilution rates reduce the abundance of species with low mortality rates $m_i$ to a greater degree than that of other species.

## Two species coexistence on two resources in a chemostat

The model can also be expanded to address more complex cases such as a chemostat with two resources and two consumer species. Consider two competitors feeding on two essential resources. In a chemostat with dilution rate D, the dynamics of the system will be:

$$\delta r_j = D(r_{j0} - r_j) - \nu_{1j}x_1 - \nu_{2j}x_2$$

$$\delta c_i = x_i - z_i - Dc_i$$

with

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

$$z_i = m_i(c_i - x_i - z_i)$$

where here $r_{j0}$ is the concentration of the jth resource in the reservoir, $\nu_{ij}$ is the stoichiometric coefficient of species i for resource j, and $\nu_i = 1 + \nu_{i1} + \nu_{i2}$.

Although these equations are not readily tractable analytically, it is possible to show that for all resource ratios, there exists a unique, non-trivial equilibrium where the two consumers coexist and it is always feasible (Supplementary material Appendix 1). Numerical simulations suggest it can often be stable (Fig. 4). The consumer relative abundances at equilibrium will, in general, vary with the resource ratio (Fig. 4). However, species having similar stoichiometric requirements – irrespective of their kinetic constants – will exhibit buffered variations in their relative abundances (Fig. 4, Supplementary material Appendix 1). Again, species having both similar stoichiometric and kinetic constants will tend to even proportions.

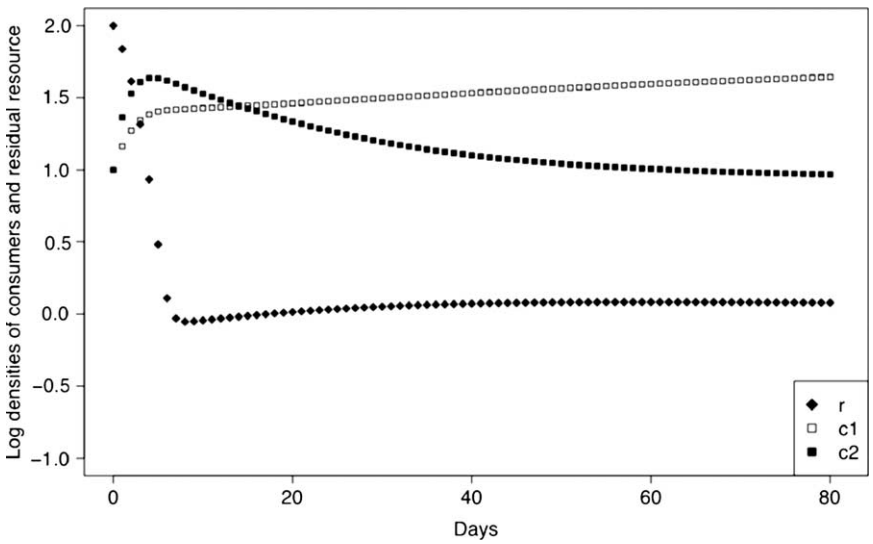


Figure 3. Model illustration for a one resource/two consumer case. Featured densities are log scaled. Species 2 can grow faster than species 1 but also has a higher mortality kinetic constant and a lower resource use efficiency. As a result, we see a classical succession pattern where species 2 ($c_2$, closed squares) dominates first, but is eventually dominated by species 1 ($c_1$, open squares). Although dynamics until day 40 might suggest slow exclusion, the two species actually tend to a coexistence equilibrium (Supplementary material Appendix 1). Resource density: r, closed diamonds. Parameter values used: growth kinetic constants (log scaled) $k_1 = -2.2$, $k_2 = -1.7$, mortality kinetic constants (log scaled) $m_1 = -3.1$, $m_2 = -2.5$, stoichiometric coefficients $\nu_1 = 1$, $\nu_2 = 2$, resource input rate $I = 0.01$.

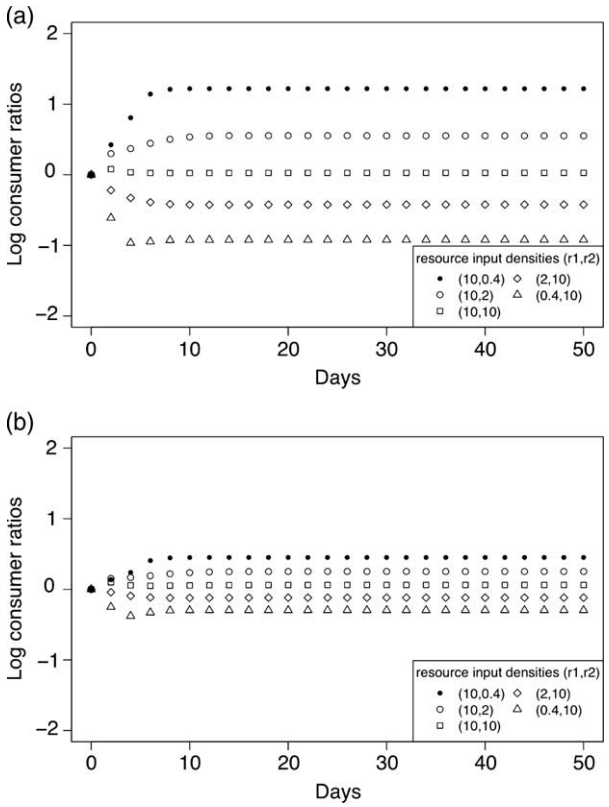


Figure 4. Two examples for the time course of the consumer abundance ratio (log scaled) in a chemostat with two essential resources and two consumers at different resource input ratios. In both examples (a and b), dilution rate $D = 0.005$, resource input densities $r_1 = (10,10,10,2,04.)$, $r_2 = (0.4,2,10,10,10)$, consumer initial densities $c_1 = c_2 = 0.1$, growth kinetic constants (log scaled) $k_1 = -2.3$, $k_2 = -2$, mortality kinetic constants (log scaled) $m_1 = -1.3$, $m_2 = -1$, and stoichiometric coefficients $\nu_{11} = \nu_{22} = 1$. (a) $\nu_{12} = \nu_{21} = 2$ (dissimilar species), and (b) $\nu_{12} = \nu_{21} = 1.3$ (similar species).

## Discussion

### The modelling approach

The modelling approach we have used here is very different from classical approaches. It rests on a statistical mechanical principle, that Jaynes (1985) qualified as 'so simple that one almost hesitates to utter it'. This principle says: what you observe at a macroscopic level is what can happen in the greatest number of ways at a microscopic level. Although probabilistic in essence, statistical mechanics does yield deterministic equations for large enough systems, and these can be readily compared with other existing models, particularly as regard to coexistence predictions. We return to that issue below.

The implementation of the principle entails finding the feasible macroscopic trajectory of a system that has maximum microscopic multiplicity. This might sound very much like a principle of entropy maximisation if we define entropy as the log multiplicity, as some may be inclined to do. But this definition of entropy would not fit with other applications of entropy maximisation. There is actually no consensus over what entropy is and what the principle of entropy maximisation applies to (Haegeman and Loreau 2008). Therefore, we point out that the approach described here does not rely on any entropy function, and that the multiplicity of a trajectory is straightforward to understand and calculate given the correct framework.

Others might construe the model presented here as a neutral model. We do not think so. There are many differences between this model and neutral models in the sense of Hubbell (2001). First and foremost, in our model, species, let alone individuals, are not equivalent; parameters (stoichiometric and kinetic) are species-specific. Second, there is no ecological drift in the equations presented here since they are deterministic. Finally, in our model there is no immigration, emigration or speciation. In sum, in our model, coexistence is neither explained by species equivalence, ecological drift nor speciation/immigration processes, all of which are essential to coexistence in neutral models.

Nevertheless, in the same way that neutral models are seen as generating null predictions with regard to diversity-abundance relationships on large spatio-temporal scales, we think our statistical mechanical model could be viewed as generating null expectations for consumer/resource dynamics. Real consumer/resource dynamics can obviously be more complex than what this model predicts. However, there is no doubt that mass and energy conservation, and statistical mechanics are at work in Nature: given that they are sufficient to generate determinism out of chance, it is hard to imagine that they are unnecessary for understanding consumer/resource dynamics. We thus argue that in some ways this model is a minimalist basis for making a prediction and, as such, is a null model.

Statistical mechanics do not always generate determinism, though: it requires systems with a large enough number of 'particles'. We saw that for small systems, several macro-trajectories could be equally probable, such that the determinism collapses and the system might display a stochastic behaviour. One may also question the validity of the model for systems with sparse densities. Although one could imagine a system so big that in spite of sparse densities, it would contain large numbers of 'particles', as a rule sparse densities are synonymous with small abundances – especially in experimental systems. Therefore the same restrictions should apply to sparse systems and small systems. What do we mean by 'large', 'sparse' or 'small'? We saw that from a statistical mechanical view point, less probable macro-trajectories could be neglected when the order of magnitude of the system satisfied $p \gg \log(p)$. This might not be easy to assess for real systems. A good proxy condition for the model to apply could be reproducibility (Jaynes 1985). Indeed, if a system is large enough and its dynamics are driven by statistical mechanics, then it should behave in a deterministic, and thus reproducible way. Conversely, any system whose behaviour is not reproducible to a reasonable degree – intrinsically stochastic systems – cannot be modelled with the statistical approach presented here.

Bearing in mind these restrictions, we can now discuss the predictions of the model with respect to coexistence.

## Species coexistence

In our model, any number of species can stably coexist on a single resource in a constant and isolated environment (i.e. no immigration). This obviously contrasts sharply with the principle of competitive exclusion.

Mathematically, this finding follows from density-dependencies in our model. We show in Supplementary material Appendix 1, as a corollary from the stability analysis, that consumer per capita growth rates $\frac{x_i}{c_i}$ are decreasing functions of their own abundances $c_i$ as well as the abundances of other consumers $c_j$, while per capita mortality rates $\frac{z_i}{c_i}$ are inversely related to per capita growth rates. As a result, and as noted earlier by Connell et al. (1984), over-abundant species are constrained and rarer species favoured (Wright 2002). Our results parallel that of Lobry et al. (2006). They showed within a more classical framework, in continuous time, that negative density-dependent functional responses allowed for stable coexistence in consumer/resource systems.

However, in contrast with phenomenological models, these mathematical properties are emergent properties in our model. Therefore they are only a proximate explanation for coexistence. Ultimately, the only 'mechanisms' at work in our model are statistical mechanics, i.e. chance, mass and energy conservation. Density-dependencies could result mainly from mass conservation. Indeed, mass conservation implies that a given resource unit cannot be consumed twice within the same time interval, whether by individuals of the same or of a different species. Therefore, it seems natural that, at fixed resource abundance r, the proportion of individuals from species i that will reproduce during $\delta t$, $\frac{x_i}{c_i}$ decreases with $c_i$ or $c_j$. Similarly, the inverse relation between per capita growth and mortality rates stems from the fact that if an individual has died during a given time interval, then we assumed it did not have time to reproduce during the same time interval.

It seems logical as well that, as a result of chance, these density-dependencies take the form of a ratio-dependence sensu Arditi and Ginzburg (1989). Indeed, $\frac{r}{c_i}$ reflects the mean number of resource items available per individual of species i, and $\frac{c_j}{c_i}$ the mean number of competitors of species j per individual of species i. While simple ratio-dependent models have been subject to substantive criticism (Abrams 1994, 1997), those criticisms are not relevant to our model. Reviewing them in depth is beyond the scope of this paper, but in summary: first ratio-dependence is not programmed into the model, it emerges from its theoretical foundations; second, the model is mathematically well defined for any consumer and resource values; last, it is not appropriate to use the model at infinitely sparse densities, as we pointed out earlier.

Despite appearances, our model does not preclude competitive exclusion to occur in some circumstances. Indeed, as the model has limits, so do its predictions. Thus for small systems with stochastic dynamics, we should not expect systematic coexistence. Such intrinsic stochasticity might explain some of Park's (1962) experiments with beetles where, among replicates, one of the two species involved – but not always the same species – would dominate and exclude the other. Even when the system is large enough to display deterministic behaviour, the model does not preclude competition from systematically leading to local extinction in some circumstances. A simple example illustrates this point. Suppose the competitive ratio of two species i and j is such that we expect $\frac{c_i}{c_j} = 10^3$, as given by Eq. 7. The total abundance of the two competitors is set by the resource input rate I. If I is low enough, this might be less than $10^3$. Consequently, $c_j < 1$, which, in a real world with discrete individuals means that species j will go extinct. Again, we stress that if one species has low abundance, stochastic extinction can also occur, all the more so in a variable environment. Consequently our findings do not invalidate the existence of other mechanisms that can promote coexistence if competition drives one species to very low abundances (Connell 1978, Levins 1979, Sommer 1985, Huisman and Weissing 1999, Chesson 2000, Kelly and Bowler 2002). In particular, poor competitors may certainly benefit from niche partitioning.

Our model therefore does not rule out competitive exclusion but it certainly does not preclude coexistence. Rather, the model enables us to go beyond the coexistence/exclusion dichotomy to predict the relative abundance of two species as a function of their intrinsic characteristics.

## Consumer relative abundances

According to Eq. 7, the model suggests a continuum from exclusion to competitive equivalence (even abundances). Before going into the details of what determines the competitive ability of a species with respect to another, we note one important feature of Eq. 7: the relative abundance of any two species depends only on their own characteristics, irrespective of which other competitors might be present in the community. That is, the relative abundance of species i and j does not depend on the abundance or the parameters of any other species. Such a prediction is testable with, for example, community change following biodiversity loss or species introductions.

If we look more closely at Eq. 7 we can see that a competitor will be more abundant if it has a high growth kinetic constant, and/or a low mortality kinetic constant, and/or a low stoichiometric requirement for the resource (i.e. high resource use efficiency). These predictions are not that different from the R* rule of Tilman (1982), if one substitutes 'dominance' for 'exclusion'. The predictions are also consistent with various ecological strategies based on tradeoffs between growth ability, low mortality and resource use efficiency (r and K strategies for instance, Pianka 1970). Another aspect worth pointing out is the importance of low mortality in competitivity. For some reason, one often reads in the literature that competitive ability equals high growth rates (but see Strom 2008 as a counter-example). Our

model shows that the better competitors might not be the ones that can grow faster (i.e. with a higher growth kinetic constant), but the ones that die less (have a smaller mortality kinetic constant) because they will eventually accrue more biomass. Such an outcome has been observed in various communities (Kelly and Bowler 2002, Strom 2008) and generally fits with plant successional patterns. This issue is also relevant to chemostat experiments. We showed that in chemostats, dilution artificially raises mortality kinetic parameters in a way that is more detrimental to species with low mortality constants. This could explain why so few species coexist in chemostat experiments, if one accepts the premise that there is no principle of competitive exclusion. Indeed, these experiments were often carried out at very high dilution rates (Tilman 1981, Sommer 1983, 1985, 1986). High dilution rates ($>0.4\ d^{-1}$ for algae) contribute to the elimination of many species whose competitive strategy is not to grow fast, but to die less. In contrast, continuous culture experiments with lower dilution rates (for algae, $<0.1\ d^{-1}$) allowed for up to 4–5 coexisting algal species out of 10 on one limiting nutrient (Smith and Kalff 1983, Neill unpubl.).

Equation 7 further shows that ecological similarity does not lead to relative rarity. On the contrary, in our model, ecologically similar species are expected to tend towards similar abundances. This result holds for a chemostat with two resources and two consumer species as well, where, in addition, species having similar stoichiometric requirements – irrespective of their kinetic constants – will exhibit buffered variations in their relative abundances along a resource ratio gradient. This finding might seem at odds with the theory of limiting similarity or resource ratio theory. In resource ratio theory for example, exclusion is not only systematic at either ends of a resource ratio gradient but the region of coexistence becomes increasingly smaller, and the shift in consumer relative abundances along a resource ratio gradient is all the more dramatic, when species have similar stoichiometric requirements. Yet we also know that in classical models, the more similar species are, the slower the rate of exclusion. Slower exclusion can even generate clusters of coexisting look-a-likes species along some niche axis (Sheffer and van Nes 2006). Therefore over short time periods, the behaviour of our model might not differ that much from classical models with regard to the similarity limit. Over longer time periods however, envisaging the coexistence of similar species as stable rather than unstable may have ramifications for sympatric speciation and adaptive dynamics (but see also Geritz et al. 1998). It might help explain the existence of cryptic species, for example (McPeek and Gomulkiewicz 2005, Leibold and McPeek 2006).

## Conclusion

In summation, we have used a model for consumer/resource interactions where community dynamics are the outcome of statistical mechanics. We have argued that this model could play the role of null model. While our model does not preclude competitive exclusion, it predicts that any number of species could coexist on a single limiting resource in a constant homogeneous and isolated environment. The model predicts that the relative abundance of two species is a continuous function of their intrinsic parameters with respect to growth, mortality and resource use efficiency. These results seemingly stand in sharp contrast to previous theoretical work. However, if we are willing to question the competitive exclusion principle, these predictions are consistent with observations and not necessarily that different from earlier theory. Although it would be tempting to suggest a competitive coexistence principle instead, it is perhaps more reasonable to suggest that neither principle is valid and that consumer relative abundances simply depend on their relative competitive abilities.

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Supplementary material (available online as Appendix O17522 at <www.oikos.ekol.lu.se/appendix>). Appendix 1

Oikos

**O17522**

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# Appendix 1

## Model description

It is possible to extend the rationale presented in the main text to any ecosystem. Specifically, consider an ecosystem consisting of N living or non-living components (consumers or resources, or both). Each component contains a number $s_i$ of discrete items (individuals or resource items, corresponding to the abundances $c_i$ or $r_j$ in the main text) that may be involved in a number of processes (mainly trophic processes). We assume that each process is constrained at the individual scale by specific stoichiometric and heat requirements. Written as a mass-balance equation, it reads $\sum_i \nu_{ij} S_i + h_j \rightarrow products$, where $\nu_{ij}$ is the stoichiometric coefficient of an item $S_i$ viewed as a reactant in the jth process and $h_j$ is the heat requirement (or more rarely heat production) of one process event. Note that $\nu_{ij}$ can be zero (a given component may not be involved in a given process) and $h_j$ can be negative. It is meaningful to define the magnitude of a process per unit time step $\delta t$ as $x_j = \frac{\delta s_i}{\nu_{ij}}$ for any i such that $\nu_{ij} > 0$, where $\delta s_i$ is the amount of component i undergoing the jth process during $\delta t$. Then the dynamics of this ecosystem can be fully specified by the set of process magnitudes $(x_j)_{j \leq J}$. Assume for now that the heat budget during $\delta t$ is known. For any given component, and provided the time step is small enough, conservation of matter implies in addition that $\sum_i \nu_{ij} x_j \leq s_i$ (thus we assume newly formed items during $\delta t$ do not react during $\delta t$). Under these constraints, only a certain range of macroscopic behaviours $(x_j)_{j \leq J}$ are possible. But, as illustrated in the main text, any possible macro-behaviour $(x_j)_{j \leq J}$ can be realized in many ways at the individual level. Specifically its multiplicity is :

$$W(x_1, \ldots x_J) = \frac{\prod_i s_i!}{(s_i - \sum_j \nu_{ij} x_j)! \prod_j (\nu_{ij} x_j)!}$$

The key result is that for a large enough number of items of each component, there is one macro-behaviour which has an overwhelmingly larger multiplicity than any other one, and is thus near-

certain. This near-certain macro-behaviour is found by maximizing W as a function of $(x_j)_{j \leq J}$ under constraints of material conservation and heat budget. This yields a system of non-linear equations (Neill and Gignoux 2008):

$$x_j = k_j \prod_i \left( \frac{s_i - \sum_l \nu_{il} x_l}{\nu_{ij}} \right)^{\frac{\nu_{ij}}{\nu_j}} \quad (1)$$

where $\nu_j = \sum_i \nu_{ij}$, and $k_j$ is a kinetic adimensional parameter depending only on temperature and on $h_j$. Thus $k_j$ is constant at constant temperature and the system heat budget need not be known.

Note that although a macro-behaviour entailing the disappearance of a given species i during $\delta t$ (through $\sum_i \nu_{ij} x_j = s_i$) is among the feasible dynamics of our ecosystem, it is never the most probable one. Depending on its parameters, a given species abundance may nevertheless tend towards zero just as in an exponential decay; the value zero is never actually reached but this is an artefact of working with continuous variables. In the real world, a species consisting of discrete entities whose abundance tends towards zero will eventually disappear. Therefore, when applied to consumer/resource systems, the model does not preclude competitive exclusion a priori.

Equation 1 is the general equation that we have transposed to particular configurations of consumer/resource systems, with slightly different, less general notations. For instance, in the main text and below, the corresponding stoichiometric coefficients of a consumer species are always 1 and those of resources in growth processes are noted $\nu_{ij}$ where the subscript i now refers to the subscript of the consumer species and the subscript j refers to that of the resource, as indicated in Table 1 in the main text.

## Coexistence of an arbitrary number of consumers on a single resource

Consider a system with N consumer species and one resource. The dynamics of this system are given by:

$$\delta r = I - \sum_i \nu_i x_i \quad (2)$$

$$\delta c_i = x_i - z_i \quad (3)$$

where I is the resource input rate, $x_i$ the ith consumer species growth rate, $z_i$ its mortality rate and $\nu_i$ its stoichiometric requirement for the resource. According to our model, we have:

$$x_i = k_i \left( c_i - x_i - z_i \right)^{\frac{1}{1+\nu_i}} \left( \frac{r - \sum_k \nu_k x_k}{\nu_i} \right)^{\frac{\nu_i}{1+\nu_i}} \quad (4)$$

$$z_i = m_i(c_i - x_i - z_i) \quad (5)$$

(see Table 1, main text for parameter definitions). There is a unique non-trivial equilibrium in this system. First, let us examine the conditions of steady-state for consumer; we set $x_i = z$ for all i . Using Eq. 5 we have $(c_i - x_i - z_i) = \frac{x_i}{m_i}$ and substituting into Eq. 4 yields, for all i:

$$x_i = k_i \left( \frac{x_i}{m_i} \right)^{\frac{1}{(1+\nu_i)}} \left( \frac{r - \sum_k \nu_k x_k}{\nu_i} \right)^{\frac{\nu_i}{1+\nu_i}}$$

Rearranging gives:

$$\nu_i x_i = \left( \frac{k_i^{(1+\nu_i)}}{m_i} \right)^{1/\nu_i} (r - \sum_k \nu_k x_k)$$

Summing over i gives $\sum_i \nu_i x_i = a\, r$ with coefficient of proportionality a:

$$a = \frac{\sum_i \left( \frac{k_i^{(1+\nu_i)}}{m_i} \right)^{1/\nu_i}}{1 + \sum_i \left( \frac{k_i^{(1+\nu_i)}}{m_i} \right)^{1/\nu_i}}$$

Thus the total consumption flux is proportional to r (and so are the individual consumption fluxes). The steady state abundances for consumers follow from rearranging Eq. 5 into $c_i = \frac{1+2m_i}{m_i} x_i$ with $x_i$ being proportional to r. Furthermore the steady state relative abundance of any two consumers $c_i$ and $c_j$ is:

$$\frac{c_i}{c_j} = \frac{(1+2m_i) m_j x_i}{(1+2m_j) m_i x_j} = \frac{(1+2m_i)}{(1+2m_j)} \left( \frac{m_j}{k_j} \right)^{\frac{(1+\nu_j)}{\nu_j}} \left( \frac{k_i}{m_i} \right)^{\frac{(1+\nu_i)}{\nu_i}} \frac{\nu_j}{\nu_i} \quad (6)$$

None of the above results require the resource to be at equilibrium. In fact the consumers can achieve a steady state characterized by the relative abundance equation above for any resource level, and they may stay at quasi-steady state even though the resource abundance varies, and thus their own absolute abundances vary. Consumers will tend to a steady state all the more rapidly when $m_i$ is large compared to $k_i$. At steady state the resource depletion follows first order kinetics with respect either to resource or consumer abundances. The resource dynamics can thus be rewritten as $\delta r = I - ar$. Therefore the resource has an equilibrium value $r = \frac{I}{a} > 0$ , which shows that there exists a non-trivial equilibrium for the whole system, and that it is always feasible.

## Equilibrium stability

Let $h_i = x_i/c_i$ and $g_i = z_i/c_i$

From $z_i = m_i(c_i - x_i - z_i)$ we have $g_i = \frac{m_i}{1+m_i}(1-h_i)$ and thus $\frac{\partial(h_i - g_i)}{\partial y} = \frac{1+2m_i}{1+m_i}\frac{\partial h_i}{\partial y}$

where y stands for any state variable of the system. Therefore the Jacobian matrix is

$$\begin{bmatrix} -\sum_i \nu_i \frac{\partial h_i}{\partial r} c_i & \dots & -\sum_i \nu_i \frac{\partial h_i}{\partial c_j} c_i - \nu_j h_j & \dots \\ \dots & \dots & \dots & \dots \\ \frac{1+2m_i}{1+m_i}\frac{\partial h_i}{\partial r} c_i & \dots & \frac{1+2m_i}{1+m_i}\frac{\partial h_i}{\partial c_j} c_i & \dots \end{bmatrix}$$

where we have used $h_i = g_i$ at equilibrium.

The terms of that matrix can be calculated. We have

$$h_i = k_i \left(\frac{1-h_i}{1+m_i}\right)^{\frac{1}{(1+\nu_i)}} \left(\frac{r - \sum_k \nu_k c_k h_k}{\nu_i}\right)^{\frac{\nu_i}{(1+\nu_i)}} c_i^{\frac{-\nu_i}{1+\nu_i}}$$

To get the partial derivatives, we use the fact that for $y = \nu u^n$ with $\nu$ constant, we have

$$\frac{\partial y}{\partial x} = \frac{\partial}{\partial x}(\nu u^n) = n\frac{\partial u}{\partial x}\nu u^{(n-1)} = n\frac{\partial u}{\partial x}\frac{y}{u}$$

Hence $\frac{\partial h_i}{\partial c_j} = \frac{1}{1+\nu_i}\left(\frac{-\partial h_i}{\partial c_j}\right)\frac{h_i}{1-h_i} + \frac{\nu_i}{1+\nu_i}\left(-\nu_j h_j - \sum_k \nu_k c_k \frac{\partial h_k}{\partial c_j}\right)\frac{h_i}{\hat{r}} - \frac{\nu_i}{1+\nu_i}\delta_{ij}\frac{h_i}{c_i}$

where $\hat{r} = r - \sum_k \nu_k c_k h_k$ and $\delta_{ij} = 1$ if and only if i = j and 0 otherwise. Rearranging gives :

$$\frac{\partial h_i}{\partial c_j} = \frac{\frac{\nu_i}{1+\nu_i}}{\left(1 + \frac{1}{1+\nu_i}\frac{h_i}{1-h_i}\right)}\left(-\nu_j h_j \frac{h_i}{\hat{r}} - \delta_{ij}\frac{h_i}{c_i} - \frac{h_i}{\hat{r}}\sum_k \nu_k c_k \frac{\partial h_k}{\partial c_j}\right) \qquad (7)$$

Summing over i gives

$$\sum_i \nu_i c_i \frac{\partial h_i}{\partial c_j} = \sum_i \frac{\frac{\nu_i^2 c_i}{1+\nu_i}}{\left(1 + \frac{1}{1+\nu_i}\frac{h_i}{1-h_i}\right)}\left(-\nu_j h_j \frac{h_i}{\hat{r}} - \delta_{ij}\frac{h_i}{c_i} - \frac{h_i}{\hat{r}}\sum_k \nu_k c_k \frac{\partial h_k}{\partial c_j}\right) \qquad (8)$$

Let $K_i = \frac{\frac{\nu_i^2 c_i}{1+\nu_i}}{\left(1 + \frac{1}{1+\nu_i}\frac{h_i}{1-h_i}\right)}\frac{h_i}{\hat{r}}$ and $K = \sum_i K_i$ . After rearrangement, we get

$$\sum_i \nu_i c_i \frac{\partial h_i}{\partial c_i} = \frac{-\nu_j h_j K + K_j \frac{\hat{r}}{c_j}}{1+K}$$

Substituting into Eq. 7,

$$\frac{\partial h_i}{\partial c_j} = \frac{\frac{\nu_i}{1+\nu_i}}{\left(1 + \frac{1}{1+\nu_i}\frac{h_i}{1-h_i}\right)}\left(-\nu_j h_j \frac{h_i}{\hat{r}} - \delta_{ij}\frac{h_i}{c_i} + \frac{h_i}{\hat{r}}\frac{\nu_j h_j K + K_j \frac{\hat{r}}{c_j}}{1+K}\right)$$

$$...=\frac{\frac{\nu_i}{1+\nu_i}}{\left(1+\frac{1}{1+\nu_i}\frac{h_i}{1-h_i}\right)}\left(-\nu_j h_j\frac{h_i}{\hat{r}}\frac{1}{1+K}-\delta_{ij}\frac{h_i}{c_i}+\frac{h_i}{c_j}\frac{K_j}{1+K}\right)$$

Now, expanding $K_j$ and rearranging allows us to simplify the right hand side of this equation

because

$$\left(-\nu_j h_j\frac{h_i}{\hat{r}}\frac{1}{1+K}+\frac{h_i}{c_j}\frac{K_j}{1+K}\right)=\frac{h_i}{1+K}\left(-\nu_j\frac{h_j}{\hat{r}}+\frac{h_j}{\hat{r}}\frac{\nu_j^2}{1+\nu_j}\frac{1}{\left(1+\frac{1}{1+\nu_j}\frac{h_j}{1-h_j}\right)}\right)$$

$$...=\frac{1}{\hat{r}}\frac{\nu_j h_j h_i}{1+K}\left(\frac{-1}{(1+\nu_j)(1-h_j)+h_j}\right)$$

So

$$\frac{\partial h_i}{\partial c_j}=\frac{\frac{\nu_i}{1+\nu_i}}{\left(1+\frac{1}{1+\nu_i}\frac{h_i}{1-h_i}\right)}\left(\frac{-1}{\hat{r}}\frac{\nu_j h_j h_i}{1+K}\frac{1}{(1+\nu_j)(1-h_j)+h_j}-\delta_{ij}\frac{h_i}{c_i}\right)$$

$$...=\frac{K_i}{\nu_i c_i}\left(\frac{-\nu_j h_j}{1+K}\frac{1}{(1+\nu_j)(1-h_j)+h_j}-\delta_{ij}\frac{\hat{r}}{c_i}\right)$$

and

$$-\sum_i \nu_i\frac{\partial h_i}{\partial c_j}c_i-\nu_j h_j=\frac{\nu_j h_j K+K_j\frac{\hat{r}}{c_j}}{1+K}-\nu_j h_j$$

$$...=-\nu_j h_j\frac{1}{1+K}\left(\frac{1}{(1+\nu_j)(1-h_j)+h_j}\right)$$

Next

$$\frac{\partial h_i}{\partial r}=\frac{1}{1+\nu_i}\left(\frac{-\partial h_i}{\partial r}\right)\frac{h_i}{1-h_i}+\frac{\nu_i}{1+\nu_i}\left(1-\sum_k \nu_k c_k\frac{\partial h_k}{\partial r}\right)\frac{h_i}{\hat{r}}$$

$$...=\frac{\nu_i}{1+\nu_i}\frac{1}{1+\frac{1}{1+\nu_i}\frac{h_i}{1-h_i}}\frac{h_i}{\hat{r}}\left(1-\sum_k \nu_k c_k\frac{\partial h_k}{\partial r}\right)$$

Summing over i gives

$$\sum_i \nu_i c_i\frac{\partial h_i}{\partial r}=K\left(1-\sum_k \nu_k c_k\frac{\partial h_k}{\partial r}\right)=\frac{K}{1+K}$$

So that

$$\frac{\partial h_i}{\partial r}=\frac{\nu_i}{1+\nu_i}\frac{1}{1+\frac{1}{1+\nu_i}\frac{h_i}{1-h_i}}\frac{h_i}{\hat{r}}\left(\frac{1}{1+K}\right)=\frac{K_i}{\nu_i c_i}\frac{1}{1+K}$$

So now we have all the terms of the Jacobian matrix.

Let $\lambda$ be an eigenvalue of this matrix with associate eigenvector $(V_0,...,V_j,...)$. We have the following system of equations:

$$\frac{-V_0 K}{1+K} - \sum_j V_j \frac{\nu_j h_j}{1+K}\left(\frac{1}{(1+\nu_j)(1-h_j)+h_j}\right) = \lambda V_0 \qquad (9)$$

$$\frac{1+2m_i}{1+m_i}\frac{K_i}{\nu_i}\frac{V_0}{1+K} - \sum_j V_j \frac{1+2m_i}{1+m_i}\frac{K_i}{\nu_i}\left(\frac{\nu_j h_j}{1+K}\frac{1}{(1+\nu_j)(1-h_j)+h_j} + \delta_{ij}\frac{\hat{r}}{c_i}\right) = \lambda V_i \qquad (10)$$

Rearranging Eq. 10 yields

$$\frac{V_0}{1+K} - \sum_j V_j \frac{\nu_j h_j}{1+K}\frac{1}{(1+\nu_j)(1-h_j)+h_j} = \frac{\left(\lambda + \frac{1+2m_i}{1+m_i}\frac{K_i}{\nu_i}\frac{\hat{r}}{c_i}\right)}{\frac{1+2m_i}{1+m_i}\frac{K_i}{\nu_i}} V_i \qquad (11)$$

Let $a_i = \frac{1+2m_i}{1+m_i}\frac{K_i}{\nu_i}\frac{\hat{r}}{c_i} = \frac{1+2m_i}{1+m_i}\frac{\nu_i}{1+\nu_i}\frac{h_i}{1+\frac{1}{1+\nu_i}\frac{h_i}{1-h_i}}$. Subtracting Eq. 9 from Eq. 11 gives :

$$V_0 = \frac{(\lambda + a_i)}{a_i \frac{c_i}{\hat{r}}} V_i - \lambda V_0$$

$$V_i = (1+\lambda) V_0 \frac{a_i c_i}{\hat{r}(\lambda + a_i)}$$

Note that $\lambda \neq -a_i$ because otherwise $V_0 = 0$ thus $V_j = 0$ for all $j \neq i$ and thus $V_i = 0$ from Eq. 9 which is impossible. Substituting into Eq. 9 and eliminating $V_0$ yields

$$\frac{-K}{1+K} - \frac{(1+\lambda)}{(1+K)}\sum_j \frac{\nu_j h_j a_j c_j}{\hat{r}(\lambda + a_j)}\left(\frac{1}{(1+\nu_j)(1-h_j)+h_j}\right) = \lambda$$

$$\frac{-K}{1+K} - \frac{(1+\lambda)}{(1+K)}\sum_j \frac{K_j a_j}{\nu_j(1-h_j)(\lambda + a_j)} = \lambda$$

Hence $\lambda = \frac{-u}{1+u}$ with $u = K + \sum_j \frac{K_j a_j}{\nu_j(1-h_j)(\lambda + a_j)}$ (12)

In the complex plane it is easy to show that $\left|\frac{u}{1+u}\right| < 1$ if and only if $Re(u) > \frac{-1}{2}$

Now assume $|\lambda| \geq 1$

$$Re\left(K + \sum_j \frac{K_j a_j}{\nu_j(1-h_j)(\lambda + a_j)}\right) = K + \sum_j \frac{K_j}{\nu_j(1-h_j)}\frac{a_j(Re(\lambda)+a_j)}{|\lambda|^2 + a_j^2 + 2Re(\lambda)a_j}$$

We want to show that $Re\left(K + \sum_j \frac{K_j a_j}{\nu_j(1-h_j)(\lambda + a_j)}\right) > \frac{-1}{2}$

To do this we will first show that, for all j, $\frac{1}{\nu_j(1-h_j)}\frac{a_j(Re(\lambda)+a_j)}{|\lambda|^2 + a_j^2 + 2Re(\lambda)a_j} > -1$

$$a_j(Re(\lambda)+a_j) + (1-h_j)\nu_j(|\lambda|^2 + a_j^2 + 2Re(\lambda)a_j) > a_j(Re(\lambda)+a_j) + 2\nu_j(|\lambda|^2 + a_j^2 + 2Re(\lambda)a_j)$$

$$... > 2\nu_j|\lambda|^2 + (1+2\nu_j)a_j^2 + (4\nu_j+1)Re(\lambda)a_j$$

$$... > 2\nu_j|\lambda|^2 + (1+2\nu_j)a_j^2 - (4\nu_j+1)|\lambda|a_j$$

Note that at equilibrium $1-h_j=\frac{1+m_j}{1+2m_j}>\frac{1}{2}$

The polynom $2\nu_j|\lambda|^2+(1+2\nu_j)a_j^2-(4\nu_j+1)|\lambda|a_j$ , where $|\lambda|$ is the unknown, has discriminant ×

$\Delta=(4\nu_j+1)^2a_j^2-4\times2\nu_j\times(1+2\nu_j)a_j^2$

$\ldots=(16\nu_j^2+1+8\nu_j-8\nu_j-16\nu_j^2)a_j^2$

$\ldots=a_j^2$

Therefore the two roots of this polynom are $\frac{(4\nu_j+1)a_j-a_j}{4\nu_j}=a_j$ and $\frac{(4\nu_j+1)a_j+a_j}{4\nu_j}=\frac{(1+2\nu_j)}{2\nu_j}a_j$ and we can rewrite the polynom as $(|\lambda|-a_j)(|\lambda|-\frac{1+2\nu_j}{2\nu_j}a_j)$

Now both of the roots are inferior to 1. Indeed,

$a_j<\frac{1+2\nu_j}{2\nu_j}a_j=\frac{1+2m_j}{1+m_j}\frac{1+2\nu_j}{2(1+\nu_j)}\frac{h_j}{1+\frac{1}{1+\nu_j}\frac{h_j}{1-h_j}}$

$\ldots=\frac{1+2\nu_j}{2(1+\nu_j)}\frac{\frac{m_j}{1+m_j}}{1+\frac{1}{1+\nu_j}\frac{m_j}{1+m_j}}$

because at equilibrium $h_j=\frac{m_j}{1+2m_j}$ and $1-h_j=\frac{1+m_j}{1+2m_j}$ . And it is easy to verify that

$(1+2\nu_j)\frac{m_j}{1+m_j}<2(1+\nu_j)+2\frac{m_j}{1+m_j}$ ,

so $a_j<\frac{1+2\nu_j}{2\nu_j}a_j<1$

Therefore, if $|\lambda|\geq1$ , we have necessarily $2\nu_j|\lambda|^2+(1+2\nu_j)a_j^2-(4\nu_j+1)|\lambda|a_j>0$ and thus

$Re\left(K+\frac{\sum_j K_j a_j}{\nu_j(1-h_j)(\lambda+a_j)}\right)>K-\sum_j K_j>0$

but then from Eq. 12, $|\lambda|<1$ which contradicts our hypothesis. Therefore we must have $|\lambda|<1$ and the equilibrium is stable. Note this holds true whatever the value of r at equilibrium or indeed whether the resource is at equilibrium or not.

## Chemostat equilibrium of two competitors on two essential resources

Consider two competitors feeding on two essential resources. In a chemostat with dilution rate D, the dynamics of the system will be (see main text):

$$\delta r_j = D(r_{j0} - r_j) - \nu_{1j} x_1 - \nu_{2j} x_2 \quad (13)$$

$$\delta c_i = x_i - z_i - D c_i \quad (14)$$

with

$$x_i = k_i (c_i - x_i - z_i)^{\frac{1}{\nu_i}} \left( \frac{r_1 - \nu_{11} x_{11} - \nu_{21} x_2}{\nu_{i1}} \right)^{\frac{\nu_{i1}}{\nu_i}} \left( \frac{r_2 - \nu_{12} x_1 - \nu_{22} x_2}{\nu_{i2}} \right)^{\frac{\nu_{i2}}{\nu_i}} \quad (15)$$

$$z_i = m_i (c_i - x_i - z_i) \quad (16)$$

where here $\nu_i = 1 + \nu_{i1} + \nu_{i2}$ . Note that from the model construction (see below) the system given by Eq. 15 and 16 is guaranteed to have a unique solution satisfying $0 \le x_i + z_i \le c_i$ and $0 \le \nu_{1j} x_1 + \nu_{2j} x_2 \le r_j$ and this is the solution we seek whenever we apply the model. Furthermore if $c_i, r_j > 0$ for all i, j, then the solutions $x_i, z_i$ must be strictly positive. Indeed, if $x_1 = 0$ for instance, then one of the right-hand side terms in the corresponding Eq. 15 would be zero. If $c_i - x_i - z_i = 0$ then from Eq. 16 $z_i = 0$ , so $c_i - x_i - z_i = c_i = 0$ which contradicts our starting hypothesis. If $r_1 - \nu_{11} x_1 - \nu_{21} x_2 = 0$ then we must have $x_2 = 0$ as well and $r_1 = 0$ which is impossible again. Idem for the last term.

Setting Eq. 13 and 14 to zero at equilibrium, using Eq. 16 and substituting into Eq. 15 gives, for i = 1,2:

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

Rearranging, we have

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

where all constant terms have been pooled into a single constant $K_i$. This system is formally analogous to Eq. 15 and thus is guaranteed to have strictly positive solutions for $r_{10}, r_{20} > 0$ .

From Eq. 14 and 16 the equilibrium consumer ratio is proportional to the ratio $\frac{x_1}{x_2}$ , which from Eq. 17 is:

$$\frac{x_1}{x_2} = \frac{K_1}{K_2} \left( r_{10} - \frac{(1+D)}{D} (\nu_{11} x_1 + \nu_{21} x_2) \right)^{\frac{\nu_{11}}{\nu_{11} + \nu_{12}} - \frac{\nu_{21}}{\nu_{21} + \nu_{22}}} \left( r_{20} - \frac{(1+D)}{D} (\nu_{12} x_1 + \nu_{22} x_2) \right)^{\frac{\nu_{12}}{\nu_{11} + \nu_{12}} - \frac{\nu_{22}}{\nu_{21} + \nu_{22}}}$$

Therefore, the more similar the stoichiometric coefficients, the smaller the weighing of resource abundances in determining the ratio $\frac{x_1}{x_2}$ . In the limit $\nu_{11} = \nu_{21}$ and $\nu_{12} = \nu_{22}$, we have $\frac{x_1}{x_2} = \frac{K_1}{K_2}$ constant.

## Numerical methods

Full model derivation is described in Neill and Gignoux (2008). There are two equivalent mathematical formalisms derived in this paper. The first is given by Eq. 1. It is the most meaningful and readily tractable analytically. The second is less intuitive; process magnitudes can be calculated as explicit functions of Lagrange multipliers $\mu_i$ according to :

$$x_j = k_j \exp\left( \frac{\sum_i \nu_{ij} \left( \log\left(\frac{s_i}{\nu_{ij}}\right) - \mu_i \right)}{\nu_j} \right)$$

In this formulation, possible processes include identical transformations of the kind $S_i \rightarrow S_i$ with corresponding magnitude $x_{j_i} = s_i \exp(-\mu_i)$ . The unknown N Lagrange multipliers are calculated by solving for a system of N equations of matter conservation constraints $\sum_j \nu_{ij} x_j = s_i$ where the sum is over all possible processes including identical transformations. In essence, all items of component i must either undergo a 'true' process or do nothing per unit time interval. This latter formulation is more efficient to implement and was therefore used for model simulations. Following the method of Agmon et al. (1979), it can be readily shown that the vectorial function $f = (f_i)_{1 \le i \le N}$ with $f_i(\mu_1, \ldots, \mu_N) = s_i - \sum_j \nu_{ij} x_j$ , whose zeros we seek to find, has a positive definite Jacobian matrix. Therefore it derives from a convex potential $F(\mu_1, \ldots, \mu_N) = \sum_i \mu_i s_i + \sum_j \nu_j x_j$ whose minimum can be found by a non-linear minimization algorithm. This minimum is the precise 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.

## R script for the model

```
#model=list(sv,kr,numoins,nuplus,mu)

#note : the time step is not explicitly defined here, but the kinetic parameters and the number of calls to model.update will depend on it.

model.update<-function() #updates the state variables of the model when called at each time step.

{
n=length(model$kr) # kr = kinetic constants vector
p=length(model$sv) # sv = state variables of the model
sv<-t(model$sv) # sv should be a line vector
numoins<-(model$numoins) # n*p matrix with stoichiometric coefficients of the jth state variable
```

```
(ecosystem component) as a reactant in the ith process
numoins<-rbind(numoins,diag(rep(1,length(sv)))) # add the identical transformations coefficients
u<-rep(1,ncol(numoins))
nur<-numoins%*%u
nuplus<-(model$nuplus) #n*p matrix with stoichiometric coefficients of the jth state variable (ecosystem component) as a product in the ith process
zr=getzr(sv,numoins,nur,model$kr)
res<-nlm(functionF,model$mu,sv=sv,numoins=numoins,zr=zr,nur=nur)model$mu<<-res$estimate # vector of Lagrangian multipliers associated to each state variable

ksi<-getksi(model$mu,zr,sv,numoins,nur)
ksi<-as.vector(ksi)
ksi<-ksi[1:n]
numoins<-model$numoins
sil<-sv-t(ksi)%*%numoins
sil[sil<0]=0 # security, to prevent round off errors yielding negative values for state variables
sv<-sil+t(ksi)%*%nuplus
model$sv[1:p]<<-sv
}

functionF<-function(mu,sv,numoins,zr,nur)
{
ksi<-getksi(mu,zr,sv,numoins,nur)
Z<-t(nur)%*%ksi
value<-sv%*%mu+Z
grad<-as.vector(sv-t(ksi)%*%numoins)
hess<-t(diag(as.vector(ksi/nur))%*%numoins)%*%numoins
attr(value,"gradient")<-grad
attr(value,"hessian")<-hess
value
}

getksi<-function(mu,zr,sv,numoins,nur)
{
alphar<- -numoins%*%mu
ksi<-zr*exp(alphar/nur)
I<-(nur<=0)
ksi[I]<-0
ksi
}

getzr<-function(sv,numoins,nur,kr)
{
u<-rep(1,ncol(numoins))
v<-rep(1,nrow(numoins))
alphar<-numoins*log(v%*%sv/numoins)
I<-(numoins<=0)
alphar[I]<-0
alphar<-alphar%*%u
kr<-c(kr,rep(1,length(sv)))
zr<-kr*exp(alphar/nur)
I<-(nur<=0)
zr[I]<-0
zr
}
```

## References

Agmond, N. et al. 1979. An algorithm for finding the distribution of maximal entropy. – J. Comp. Phys. 30: 250–258.

Neill, C. and Gignoux, J. 2008. Prediction of non-equilibrium dynamics in ecosystems: from dogs and fleas to molecules and organisms. – J. Stat. Mech. 1: P01001.