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## "Eco-Evolutionary Models of Competition for Nutritionally Complementary Resources"


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## Abstract

That natural processes in biology can be described mathematically, was already known to Gregor Mendel. Since then, new models and theories have been developed on a regular basis to represent reality as accurately as possible. In the following work we are dealing with two eco-evolutionary models, which describe the coexistence of two consumers whose nutrition is based on two complementary resources. While the ecological dynamics in both models are the same, we are exploring two different approaches to evolutionary dynamics.

In the first model an adaptive-dynamics approach is used to analyse how a trait changes due to environmental conditions. This model is extracted from the paper "Adaptive Dynamics of Competition for Nutritionally Complementary Resources: Character Convergence, Displacement, and Parallelism" by David A. Vasseur and Jeremy W. Fox and will be discussed in more detail in Chapter Two.

In Chapter Three, we develop an alternative approach to the evolutionary dynamics by using population genetics theory. Instead of adaptive dynamics, we study allele frequencies and how they evolve based on the prevailing conditions. Since analytical results were hard to achieve, our findings are largely based on numerical calculations. These were done using Mathematica, version 11.2, which we also used to provide a graphical representation of our results.

Finally, in the last chapter we will compare the two models and work out the main differences.

## Abstract

Dass natürliche Vorgänge in der Biologie mathematisch beschrieben werden können, war schon Gregor Mendel bekannt. Seitdem werden regelmäßig neue Modelle und Theorien entwickelt, um die Realität möglichst exakt abbilden zu können. In der folgenden Arbeit beschäftigen wir uns mit zwei öko-evolutionären Modellen, die das Zusammenleben zweier Konsumenten beschreibt, deren Ernährung auf zwei komplementären Ressourcen basiert. Während die ökologische Dynamik in beiden Modellen gleich ist, untersuchen wir zwei unterschiedliche Ansätze für die evolutionäre Dynamik.

Im ersten Modell wird ein adaptiv-dynamischer Ansatz verwendet, um zu analysieren, wie sich ein Merkmal aufgrund von Umweltbedingungen verändert. Dieses Modell ist der Arbeit "Adaptive Dynamics of Competition for Nutritionally Complementary Resources: Character Convergence, Displacement, and Parallelism" von David A. Vasseur und Jeremy W. Fox entnommen und wird in Kapitel zwei genauer behandelt.

In Kapitel drei entwickeln wir einen alternativen Ansatz für die evolutionäre Dynamik und verwenden die Theorie der Populationsgenetik. Anstelle der adaptiven Dynamik untersuchen wir Allelhäufigkeiten und wie sich diese aufgrund der vorherrschenden Bedingungen entwickeln. Da analytische Resultate kaum zu erzielen waren, basieren unsere Erkenntnisse zum Großteil auf nummerischen Berechnungen. Diese wurden mit Hilfe von Mathematica, Version 11.2, durchgeführt, das wir auch für die grafische Darstellung unserer Resultate verwendeten.

Abschließend widmen wir uns im letzten Kapitel einem Vergleich der beiden Modelle und arbeiten die Hauptunterschiede heraus.

# Contents

## Preface

The ability to describe natural phenomena by mathematical equations has always fascinated me. The possibility to gain interesting insights into biological processes by using mathematical analysis provides an important tool for predicting outcomes in an actual environmental situation.

In my master's thesis, I had the chance to gain first experiences in developing an eco-evolutionary model, in analysing it and in drawing conclusions of its analysis. This was a great opportunity to strengthen my mathematical skills and finding solutions to emerging problems.

At this point, I want to thank my advisor, Univ.-Prof. Dr. Reinhard Bürger who provided constant support and generously offered his time. His continuous advise helped me to tackle difficult problems and I am particularly grateful for the patience he showed me throughout the period.

Finally, I want to thank my parents for supporting me throughout my studies and always being there for me. Especially, in times of frustration and exhaustion, they offered me a home and comfort. They always encouraged me to pursue my goals and go my own way.

# 1 Introduction

The following work is based on the paper "Adaptive Dynamics of Competition for Nutritionally Complementary Resources: Character Convergence, Displacement, and Parallelism" by David A. Vasseur and Jeremy W. Fox [4].

It deals with a model for consumers feeding on resources, where the resources are nutritionally complementary to each other. Fox and Vasseur analyse the interplay between the abundances of consumer densities and resource densities, allowing the uptake for the resources to change. This reveals interesting dynamics and different eco-evolutionary outcomes. But before we are able to understand the eco-evolutionary model, we first have to understand some basic ideas underlying the approach of Fox and Vasseur.

To talk about nutrients in a resource species we consider the tissue of the resources which is composed of chemical substances. These chemical substances provide nutrients which are essential for the consumers and are ingested through the uptake of the resource species. Resource species usually contain the considered nutrients in a precise ratio, which typically does not entirely match the required ratio of the consumers. To ingest the nutrients in the exact demand ratio, the consumers need to mix their diet and divide their efforts to more than one resource. However a mixed diet is not essential for the consumer to survive if the resources are nutritionally complementary to each other. Complementary resources allow consumers to survive by ingesting only one of the resources and excreting the excess nutrients. Nevertheless, consumers may increase their fitness by adapting the uptake rates better to their needs and switching to a mixture of the resources. In order that resources are complementary it is therefore necessary that the ratios of the different resources bracket the demand ratio of the consumer.

If the resources are provided ad libitum, the best choice of the consumers is to adjust their diet in such a way that they ingest the resources and consequently the nutrients in the required ratio, which is referred to as a balanced diet. Usually one resource's composition better reflects the demand ratio of the consumer and is ingested at a high amount. The other resources serve to complete the diet of the consumer to its demand ratio. When one

resource type decreases due to preferential eating and becomes scarce, the consumer may benefit from altering its ingestion and switch its effort to a more abundant resource. The disadvantage, that the composition of this resource matches the consumer's needs less, is compensated by the higher amount of uptake and by excreting the excess nutrients.

In the work of Fox and Vasseur the model is restricted to the case of two consumers and two complementary resources, which still allows rich dynamics to happen. It is assumed that the growth of each consumer is determined by two essential nutrients. The ratio of the two essential nutrients differs in the two resources, otherwise they would be considered to be substitutable. The chemical composition of the two consumers is assumed to reflect the requirements for the two essential nutrients. These requirements are also given in a ratio of the two essential nutrients and define the demand ratio of one consumer.

Complementary resources are, in a sense, intermediate between substitutable and essential resources. For substitutable resources one consumer can shift its diet in favour of alternative resources for which there is less competition. In the case of essential resources the consumers cannot alter their ingestion of one or the other resource, because for essential resources there are no alternatives for the consumers.

In the case of complementary resources the abundances of the resources play an important role for optimal uptake rates, which again have an effect on the population densities of both resources and consumers. This creates complex feedback between the consumer-resource population dynamics and the diets of the consumers.

The model of Fox and Vasseur concentrates on describing this interesting interplay and neglects other features occurring in nature.

The derivation of their model and its eco-evolutionary dynamics are explained in the second chapter of this work. We first start to introduce the assumptions made by Fox and Vasseur and how they are implemented in their model. To gain a better understanding of the interplay between ecological dynamics and the adaptive uptake rates, we first look at them separately before we discuss the full eco-evolutionary model.

Afterwards, in Chapter Three, we develop an alternative model, where

we use a population-genetic approach instead of an adaptive-dynamics approach. The appearance of allele frequencies requires some adaptations to the eco-evolutionary model of Fox and Vasseur. Instead of continuously changing uptake rates they are now chosen to be fixed and the evolutionary dynamics occurs by a change of allele frequencies. Naturally, this has an effect on the eco-evolutionary outcome which is analysed in the last subsections of Chapter Three.

We conclude this work by comparing these two eco-evolutionary models and pointing out the main differences in Chapter Four.

# 2 The Model of Fox and Vasseur: Adaptive Dynamics of Competition for Nutritionally Complementary Resources

## 2.1 Model Assumptions

The assumptions made by Fox and Vasseur are captured in the following overview.

- **Cost-free excretion:** The authors assumed cost-free excretion of the excess nutrient. It is therefore possible, that for a consumer eating an unbalanced diet and excreting the excess nutrient is preferable to a balanced diet. They may gain a greater amount of both nutrients by eating the more abundant resource to a greater extent and just get rid of the excess of one nutrient.

  We can see that this advantage will decrease if there are additional costs for excretion due to handling time, energy requiring processes or investment and maintenance of excretory structure processing, etc. These expenses are definitely common in nature and are discussed in the electronic supplement of the paper by Fox and Vasseur, but are not pursued any further here.

  Additionally, the excreted nutrients are considered to be non-usable for resource species, even though in nature this can happen due to decomposition of excreted nutrients.

- **Competition only due to ingesting the same resources:** The consumer species are competing only for the two resources and are no immediate threats to each other. So one consumer has no direct influence on the death rate of the other consumer. The connection exists rather due to the reduction of the availability of resources for the opponent.

- **Fixed stoichiometry:** Fox and Vasseur assumed fixed stoichiometry in both resources and consumers. For resources this means for instance that the composition of the two essential nutrients does not change in the course of the seasons. Likewise the demand ratio is fixed for the

consumers and cannot be changed to reduce the requirement for the limiting nutrient. Additionally, differences owing to sex, life stage, season of the year, and other variables are neglected. Fox and Vasseur argued that it has been demonstrated that fixed-demand ratios are a good approximation in long-term evolution experiments.

- **No consumer is intrinsically better at resource consumption:** The consumers are to have the same total per capita uptake rate, so that none of them could have an advantage of resource utilisation. In the case of Fox and Vasseur the total per capita uptake rate is fixed at unity.

- **Linear trade-off:** It is assumed, that for each consumer the trade-off between the uptake rates for the resources is linear. This means that in reducing the uptake rate of one resource this reduction is equally added to the uptake rate of the other resource.

- **Adaptive diet choice:** Fox and Vasseur allowed the consumers to change their uptake rates so that they can increase their fitness by adapting to the abundance of the resources. This change of the uptake rates in response to resource abundance is referred to as the evolutionary dynamics. The interplay between optimal diet choice and consumer-resource population dynamics creates rich and complex dynamics, also in the relatively simple model of Fox and Vasseur.

Fox and Vasseur built a model based on the work of Hsu et al. [3] and Abrams [1] which aims to capture all these assumptions and still is a relatively simple model that allows rich dynamics to happen.

## 2.2 Ecological Dynamics

As described above, Fox and Vasseur considered the case of two consumers ($C_j$ where $j = 1, 2$) competing for two resources ($R_i$ where $i = 1, 2$). Let us recall that the requirements and composition of consumers and resources are determined by two chemical nutrients, say $a$ and $b$. We are therefore interested in the ratio of the two nutrients in the consumers as well as in the resources.

For resource $i$ the amount of nutrient $b$ relative to nutrient $a$ in each unit is given by the fixed composition ratio

$$\alpha_i = \frac{1 - k_i}{k_i}. \tag{1}$$

The variable $k_i$ gives the proportion of nutrient $a$ to the overall nutrients in the composition of each unit of resource $i$. The word "fixed" corresponds to the assumption of fixed stoichiometry in the resources.

To get complementary resources the composition ratios are not allowed to coincide and therefore $\alpha_1 \neq \alpha_2$ is required, otherwise they would be substitutable.

Similarly, the ratio $\beta_j$ for consumer $j$ stands for the composition of nutrient $b$ relative to nutrient $a$ and constitutes the demand ratio of its consumer. Again, this ratio should be fixed according to the fixed stoichiometry of the consumers. Furthermore, we have $\beta_1 \neq \beta_2$ because, firstly, it is empirically implausible for species to have identical stoichiometry and secondly, it would be impossible for them to coexist.

Without loss of generality it is assumed that resource $R_1$ is relatively rich in nutrient $a$, whereas resource $R_2$ is relatively rich in nutrient $b$ leading to $\alpha_1 < \alpha_2$. Likewise for the consumers, where it follows that $\beta_1 < \beta_2$ by assuming without loss of generality that consumer $C_1$ demands relatively more of nutrient $a$ and consumer $C_2$ relatively more of nutrient $b$.

Additionally, it is necessary that the composition ratios of the resources bracket the consumers demand ratios $\alpha_1 < \beta_j < \alpha_2$, $j = 1, 2$ to have complementary resources.

For consumer $j$, the uptake rates are denoted by $u_j$ for the uptake rate of resource $R_1$ and, because the total per capita uptake rate is fixed at unity and considering a linear trade-off, we get $1-u_j$ for the uptake rate of resource $R_2$.

Fox and Vasseur displayed their model by the following schematic representation.

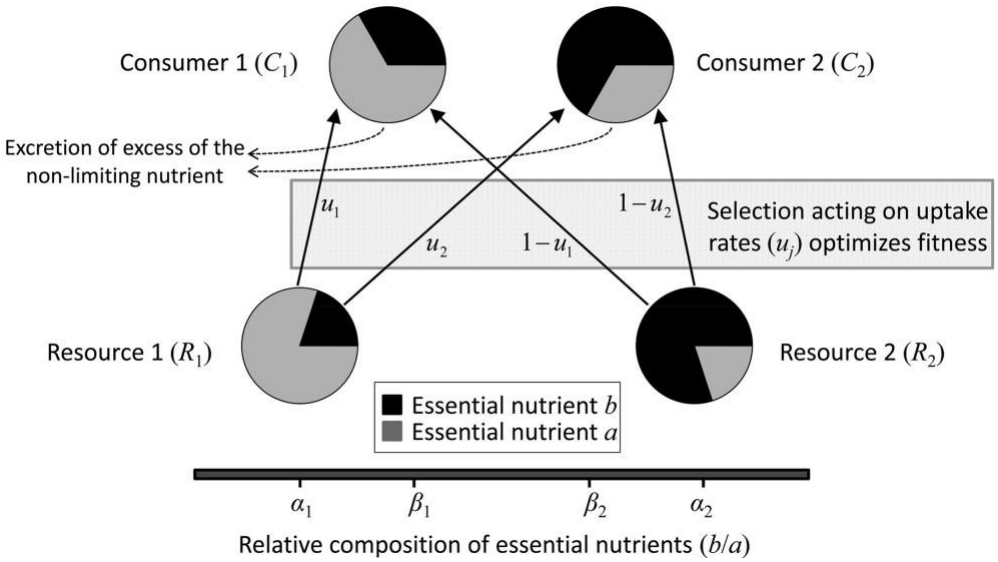


**Figure 1:** Schematic representation of the eco-evolutionary model of competition for complementary resources. Two nutrients ($a$ and $b$) are essential for two consumers ($C_1$ and $C_2$), but they are available only through the uptake of resources ($R_1$ and $R_2$) that differ in their relative compositions of the two nutrients. When the ratio in which a consumer demands nutrients ($\beta_j$) is bracketed by the ratios in which they are supplied by the two resources ($\alpha_i$), resources are complementary. Using an adaptive dynamics model, Fox and Vasseur investigated how uptake rates ($u_j$) evolve when two consumers compete for complementary resources. [From Fox and Vasseur [4]]

As mentioned before, the ingestion of the two nutrients $a$ and $b$ determine the growth of the consumers. The amount of ingested nutrients depends on the abundance of the two resources $R_1$ and $R_2$, the nutrient composition of those and on the uptake rates. Nutrient $a$, for example, is obtained from resource $R_1$ at an amount of $u_j$ and of course only by considering the proportion ($k_1$) of $a$ in resource $R_1$ and likewise obtained from resource $R_2$ at a rate $(1-u_j)k_2$. The uptake of nutrients $a$ and $b$ of consumer $j$ ($g_{aj}$ and $g_{bj}$, respectively) is therefore described by the two equations:

$$g_{aj} = u_j k_1 R_1 + (1-u_j)k_2 R_2, \tag{2a}$$

$$g_{bj} = u_j(1-k_1)R_1 + (1-u_j)(1-k_2)R_2. \tag{2b}$$

The sum $g_{aj}+g_{bj}$ gives the total amount of ingested nutrients of consumer $j$. However, the ratio $g_{bj}/g_{aj}$ may not match the demand ratio and the ingested nutrients cannot be utilised entirely by the consumer. To implement this condition into the model, Fox and Vasseur introduced the assimilation fraction $(1-\delta_j)$. The assimilation fraction should be equal to 1 if the consumer $j$ ingests the nutrients in the required ratio to balance its diet and should be smaller than 1 if there is an excess of one nutrient.

The approach is based on the following observations. When taking up too much of nutrient $b$, the ratio $g_{bj}/g_{aj}$ is greater than the one required, i.e., $g_{bj}/g_{aj} > \beta_j$. This leads to the excess $g_{bj} - g_{aj}\beta_j > 0$ of nutrient $b$, which is excreted at no cost and not usable for the other species. Likewise, we get for the excess of nutrient $a$ that $g_{bj}/g_{aj} < \beta_j$, and again $g_{aj} - g_{bj}\beta_j^{-1} > 0$ is excreted cost-free and in a non-usable form. Putting the excess in relation to the total amount of ingested nutrients, the assimilation fraction

$$1-\delta_j = 1 - \max\left(\frac{g_{bj}-g_{aj}\beta_j}{g_{aj}+g_{bj}}, \frac{g_{aj}-g_{bj}\beta_j^{-1}}{g_{aj}+g_{bj}}\right) \tag{3}$$

fulfils the requirements. In (3), the maximum of the two expressions is always non-negative because we either have excess of one nutrient leading to an expression greater than zero or the consumer ingests a nutritionally balanced diet and both expressions evaluate to zero. It is always smaller or equal 1 because the excess of one nutrient can never exceed the total amount of ingested nutrients and the expressions represent the excess in relation to the total amount of uptake. Thus $1-\delta_j$ gives the fraction of the ingested nutrients that can be utilised by consumer $j$.

After these preparations and by assuming chemostat dynamics and linear functional responses, the dynamics of consumer and resource abundances can

be described in the following way:

$$\frac{dR_1}{dt} = D(S_1 - R_1) - R_1 \sum_j u_j C_j, \tag{4a}$$

$$\frac{dR_2}{dt} = D(S_2 - R_2) - R_2 \sum_j (1 - u_j) C_j, \tag{4b}$$

$$\frac{dC_j}{dt} = C_j[(1 - \delta_j)(g_{aj} + g_{bj}) - d_j]. \tag{4c}$$

The chemostat makes sure that the ratio of the two nutrients remains the same in the composition of the resources. The supply concentration $S_j$ flows as fresh medium into the culture system, providing the resources with nutrients at a constant rate. These nutrients support the growth of the resources when the density is low, but as the resources reach a certain size these nutrients become depleted leading to a decrease in resource density. This interaction between the supplemented nutrients and the growth of resources is self-regulating and protects the resources from extinction. A certain amount is washed out of the system which is captured by the dilution rate $D$. Additional to this self-regulating process, the resource densities are reduced by the uptake of the consumers.

If we look at the equations of the consumers, we can see that the amount of utilisable nutrients is directly transformed into the growth rate of the consumer. This growth rate however is regulated by a constant death rate $d_j$, at which consumer $j$ is washed out of the system. These rates are assumed to be independent of the chemostat dilution rate $D$.

One can see from the differential equations of the consumers, that one consumer has no direct impact on the growth of the other consumer. The influence is visible in the population dynamics of the resource species, where the abundance of the consumers defines the amount of loss of one's resource species. The resource's impact on consumer growth is hidden in the rates $g_{aj}$, $g_{bj}$ at which nutrients $a$ and $b$ are ingested by consumer $j$.

Another important quantity is the ratio of available nutrients, referred to as the "nutrient supply ratio". This ratio is given by the current resource densities $R_1$ and $R_2$ and by taking the composition of both resources into

account. This leads to the nutrient supply ratio

$$\alpha_S = \frac{(1-k_1)R_1 + (1-k_2)R_2}{k_1 R_1 + k_2 R_2}, \tag{5}$$

again, giving the proportion of nutrient $b$ relative to nutrient $a$ but now in the total amount of resource densities. Obviously, this ratio is bounded by the two composition ratios of both resources, $\alpha_1 \leq \alpha_S \leq \alpha_2$.

## 2.3 Results for the Ecological Dynamics

Before we start to introduce the evolutionary dynamics, that allows adaptive changes of uptake rates, we analyse the pure ecological dynamics first by taking the uptake rates as fixed.

As is usual with ecological models we are especially interested in equilibria and their stability.

The resource species are always existent due to the constant supply concentrations. Even though the abundances change over time, they can never become extinct. This is in contrast to the consumers who can die out. If an equilibrium is reached, the per capita growth rate of consumer $j$ is 0. Taking the uptake rate $u_j$ as fixed, this zero-net-growth isocline (ZNGI) of each consumer $j$ is defined by combinations of the two resource species $R_1$ and $R_2$. Because of the maximum function in the consumer's growth rate, the ZNGIs of one consumer are convex combinations of two segments of straight lines in the $R_1$-$R_2$-phase plane. Since the excess of one nutrient leads to growth limitation by the other, each line segment denotes limitation by a different nutrient. At the intersection of the two line segments the consumers are therefore colimited by both nutrients, which exactly happens when the rate of the ingested nutrients matches the demand ratio of the consumer. So by setting $dC_j/dt = 0$ in (4$c$) and expressing the ZNGIs as functions of $R_1$ in

the $R_1$-$R_2$-phase plane we get

$$R_2(j) = \max\left[\frac{d_j(1+\beta_j)^{-1} - k_1 u_j R_1}{k_2(1-u_j)}, \frac{d_j\beta_j(1+\beta_j)^{-1} - (1-k_1)u_j R_1}{(1-k_2)(1-u_j)}\right], \quad j \in \{1,2\}. \tag{6}$$

The following image shows two representative ZNGIs of one consumer for fixed uptake rates $u_j$.

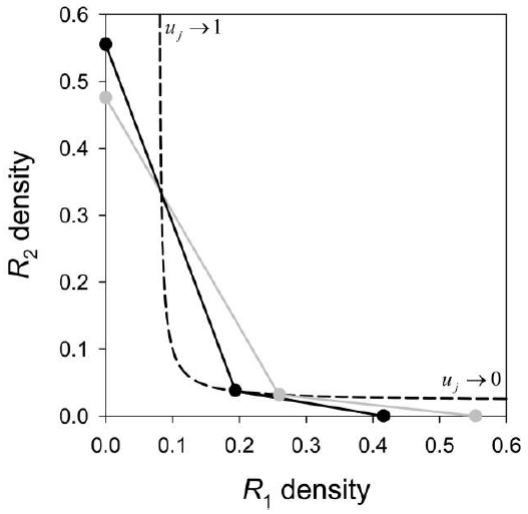


**Figure 2:** Consumer's zero-net-growth isocline is formed by a convex intersection of two line segments in the $R_1$-$R_2$-phase plane given by equation (6). For comparison, the isocline is shown for two values of $u_j$ ($u_j = 0.4$, solid black line; $u_j = 0.3$, grey line). The intersection of the segments denotes the point where consumers are colimited. As a function of $u_j$ this point follows a path through the $R_1$-$R_2$-phase space, which can be found analytically by equating the two cases in equation (6) (dashed line). Here $\alpha_1 = 0.25, \alpha_2 = 4.0, \beta_j = 0.5$, and $d_j = 0.1$. [From Fox and Vasseur [4]]

The dashed line tracks the intersection point of the two line segments if we alter the uptake rate $u_j$, but still taking it as fixed. For the chosen parameters there is an excess of nutrient $b$ for small $R_1$ and therefore limitation by nutrient $a$. For higher values than the $R_1$ level, where the intersection takes place, we get a $b$-limited growth rate.

In this (ecological) model we are of course interested in the ZNGIs of both

consumers. If the per capita growth rates are 0 for the two consumers at the same time, the model is in equilibrium, since the resource densities change with respect to the consumer abundances. Under the condition that both per capita growth rates are 0, either the two ZNGIs of the two consumers have to cross or one of the consumers is absent and the equilibria are given by the other consumer's ZNGIs as we explored in Fig.2. Four cases are illustrated in Fig.3 for different choices of the $u_j$s.

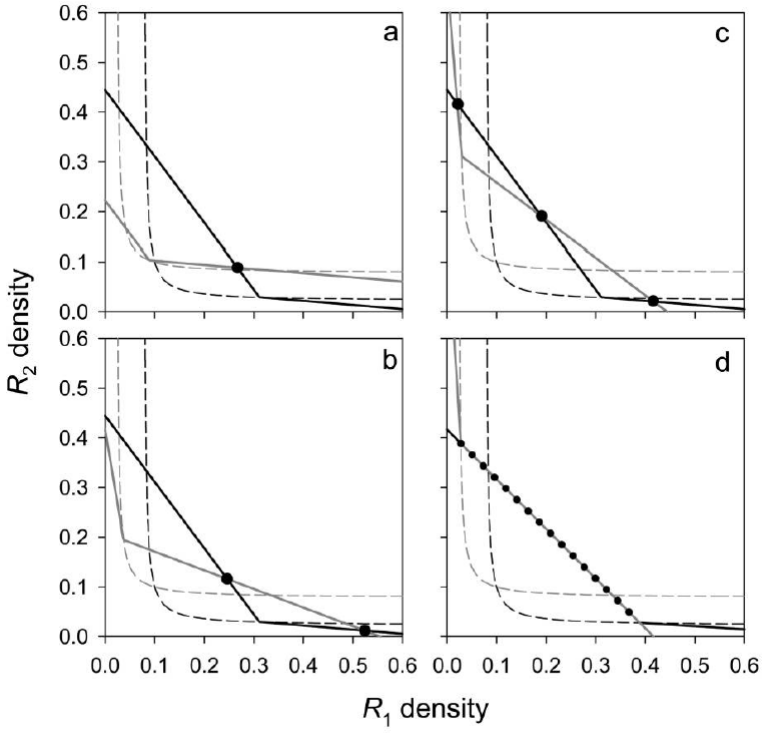


**Figure 3:** Equilibrium resource densities occur at the intersection between the zero-net-growth isoclines of consumer 1 (black lines) and consumer 2 (grey lines). In *a*, there is only a single intersection (circle); however, varying uptake rates ($u_j$) can generate two (*b*), three (*c*), or a linear set of equilibria (*d*; diagonal line) in the positive-valued resource phase space. Dashed lines trace the set of colimitation points for each consumer. Here $\alpha_1 = 0.25, \alpha_2 = 4.0, \beta_1 = 0.5, \beta_2 = 2.0$, and $d_1 = d_2 = 0.1$, and ($u_1$, $u_2$)=(0.25, 0.25), (0.25, 0.6), (0.25, 0.75), and (0.2, 0.8) in *a*-*d*, respectively. [From Fox and Vasseur [4]]

There can exist as many as 6 equilibria: one trivial equilibrium where both consumers are absent, two equilibria where one of the consumers is absent, but the other is present, and one to three equilibria where both con-

sumers coexist, depending on the number of intersections of the ZNGIs. For a unique set of parameters, it is possible for segments of the ZNGIs of the consumers to be overlaid causing neutrally stable dynamics, as is the case in Fig.3d. Fox and Vasseur do not examine cases of neutral stability any further, arguing that these appear only in connection with strongly maladapted consumers.

Assuming positive initial consumer densities, one consumer will always survive. This is due to the fact, that with a positive supply concentration, the resources are always existing. Therefore, if one consumer dies out this increases the amount of available resources for the other consumer. Hence the only possible scenarios in this case are equilibria where either both consumers survive, or one of the two consumers goes extinct. Whether coexistence or extinction of one consumer occurs, depends on the combination of the uptake rates and sometimes even on initial conditions.

For consumers with reciprocal demand ratios about the nutrient supply ratio, $\beta_1 \leq \alpha_S \leq \beta_2 = 1/\beta_1$, the different combinations of uptake rates display the following ecological outcome:

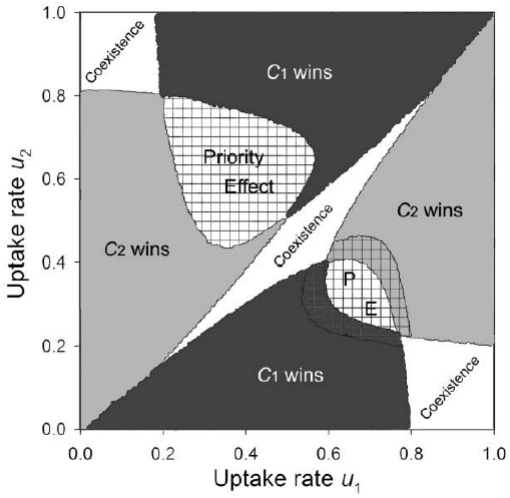


**Figure 4:** Ecological outcome of competition in trait space. In the white regions, coexistence is stable. In the black (grey) regions, consumer 1 (consumer 2) excludes the other consumer. In the hatched regions, exclusion of one competitor occurs via a priority effect. In the shaded hatched region, a priority effect selects between exclusion of one consumer and coexistence. Ecological outcomes were determined numerically by simulating the model for 5,000 time steps, using two different initial conditions, $(C_1, C_2) = (0.1, 1.0)$ and $(1.0, 0.1)$, and numerically discovering transitions between the regions. Precisely at $u_1, u_2 = 0.2, 0.8$, the dynamics are neutrally stable (as in Fig.3*d*). Other parameters are as follows: $\alpha_1 = 0.25, \alpha_2 = 4.0, \beta_1 = 1/1.2, \beta_2 = 1.2, d_1 = d_2 = 0.1$, $S_1 = S_2 = 1, D = 0.1, R_1(0) = R_2(0) = 0.2$. [From Fox and Vasseur [4]]

The three white regions present the area of stable coexistence, where both consumers survive in the long run. Nevertheless, over most of the state space extinction of one consumer happens, marked by regions in black ($C_1$ wins) and grey ($C_2$ wins). There also exist areas where the outcome depends on initial conditions designated by hatching. These so-called "priority effects" appear where the ZNGIs cross multiple times and the outcome depends on the initial values of $R_1$, $R_2$, $C_1$ and $C_2$. One can see, that there are three distinct hatched areas, the white one where always one consumer will exclude the other and two shaded regions by grey or black where either one consumer will die out (which one is highlighted by the aforesaid colouring) or the ecological system is resulting in stable coexistence.

Let us take a closer look at the different combinations of the uptake rates

and the resulting outcomes. For the coexistence regions in the upper-left and lower-right area in the $u_1$-$u_2$-phase plane we have very different uptake rates for the both consumers. In the first case, each consumer concentrates on the resource that least reflects their needs which leads to strong nutrient limitation and an equilibrium with low consumer densities. Consumer 1 requires a higher amount of nutrient $a$, but has a comparatively low uptake rate $u_1$ for resource 1 which would resemble the demand ratio of consumer 1 to a higher degree. The ratio $g_{b1}/g_{a1}$ of the two ingested nutrients lies above the demand ratio, since the small value of $u_1$ leads to an excess of nutrient $b$. The growth of consumer 1 is therefore limited by nutrient $a$ and analogously consumer 2 is limited by nutrient $b$.

This nutrient limitation is resembled by the ZNGIs of the two consumers, which intersect at the line segments indicating the limitation by the corresponding nutrient. In the case above, the intersection takes place where the line segment of consumer 1, displaying limitation by nutrient $a$, crosses the line segment of the ZNGI of consumer 2, where consumer 2 is $b$-limited. In the second case, in the lower-right region, the consumers have uptake rates, such that they specialize on the resources that most reflects their demand ratio. Therefore, they ingest enough of the more required nutrient and are limited by the other one leading to a high consumer density in equilibrium. Hence we get that consumer 1 is $b$-limited and consumer 2 is $a$-limited.

In the central area of the $u_1$-$u_2$-phase plane, the coexistence results from similar values for $u_1$ and $u_2$ and from omitting extreme uptake rates close to zero or one, preventing consumers to specialize on one resource. Fox and Vasseur detected that in this coexistence region, consumers are usually limited by different nutrients. Nevertheless, there exist combinations of $u_1$ and $u_2$ where, although limitation by the same nutrient is the case, this still leads to coexistence. The reason or explicit values are not mentioned any further.

Usually, limitation by the same nutrient leads to extinction of one of the consumers. This is due to the fact, that the consumer which can utilise the limiting nutrient to a greater extent will have a higher density than its opponent. Over time, its increasing density will occupy more and more of the resources, leaving less for the other consumer, which on the other hand

is causing a decline in this consumer's density. Typically, this interaction between the densities of the two consumers results in the extinction of one consumer, where the better competitor for the limiting nutrient will prevail in the long run. This outcome is outlined by the regions coloured in grey and black in the $u_1$-$u_2$-phase plane.

The remaining regions are the hatched ones, referred to as priority effects, and where the ecological outcome depends on initial conditions. As already mentioned, in the shaded hatched regions coexistence is possible in the long run, but likewise extinction of one consumer can occur. In the white hatched regions the decision is only whether consumer 1 or consumer 2 will die out, because although the ZNGIs cross three times none of the equilibria (leading to coexistence) are stable.

The illustrative ZNGIs for the different regions with the corresponding intersections are displayed in Fig.5.

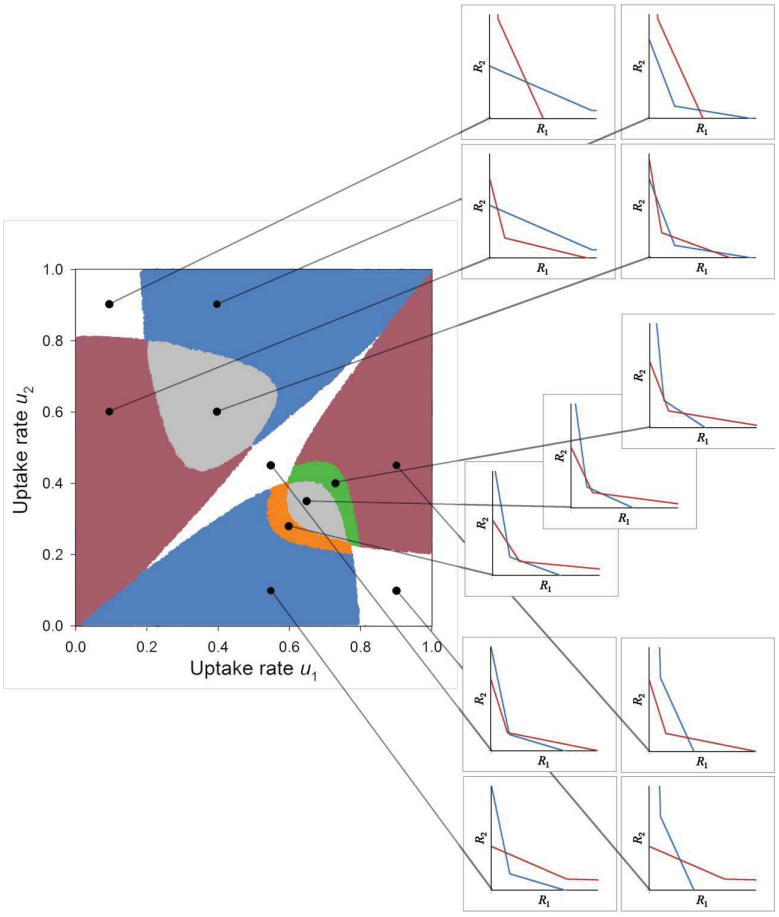


**Figure 5:** Ecological outcome of competition in trait space and zero-net-growth isoclines (ZNGIs) for the 11 regions. In the white regions, coexistence is stable. In the blue (red) regions, consumer 1 (2) excludes the other consumer. In the grey regions, exclusion of one competitor occurs via priority effect. In the orange (green) region, a priority effect selects between exclusion of consumer 2 (1) and coexistence. The inset panels show the orientation of consumer ZNGIs for each of the 11 regions, where the ZNGIs of consumer 1 (2) are blue (red) [. . . – author's note]. Ecological outcomes were determined numerically by simulating the model for 5,000 time steps, using two different initial conditions, $(C_1, C_2) = (0.1, 1.0)$ and $(1.0, 0.1)$. Precisely at $u_1, u_2 = 0.2, 0.8$, the dynamics are neutrally stable (as in Fig.3*d*). Other parameters were $\alpha_1 = 0.25, \alpha_2 = 4.0, \beta_1 = 1/1.2, \beta_2 = 1.2, d_1 = d_2 = 0.1, S_1 = S_2 = 1, D = 0.1, R_1(0) = R_2(0) = 0.2$. [From Fox and Vasseur [4]]

The previous analysis was based on reciprocal values for the demand ratios around the nutrient supply ratio of the two consumers, as well as the composition of the two resources also being reciprocal to each other. The outcome can be transferred to altered ratios, where the regions change

and relocate depending on the new values, but letting the mathematical explanations remain true. An important quantity is the nutrient supply ratio and Fox and Vasseur examined the impact of the demand ratios $\beta_j$ of the consumers, when they increasingly deviate from the nutrient supply ratio. These increasingly different demand ratios allow more combinations of uptake rates for the ZNGIs to cross on different branches of the line segments leading to limitation by different nutrients. This in turn implies a larger range of uptake rates where consumers can coexist in the long run. The effect is illustrated by the graphic of ecological outcome in Fig.6, where the regions of extinction of one of the consumer and those depending on initial conditions recede, giving the coexistence regions in the central area and the lower-right corner space to join in a larger coexistence region.

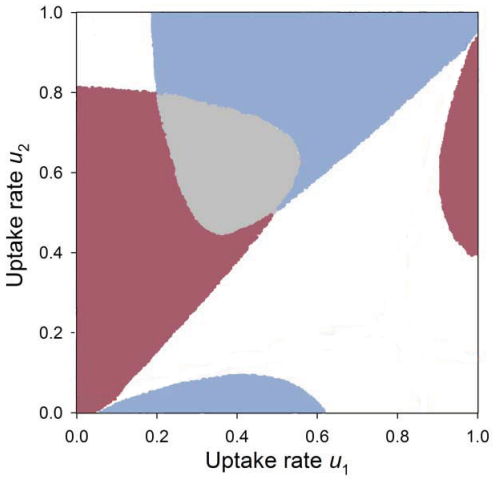


**Figure 6:** Ecological outcome for demand ratios that deviate relatively more from the nutrient supply ratio (colour coding is described in Fig.5). Initial densities were $R_1(0) = R_2(0) = 0.2; C_1(0) = 1.0; C_2(0) = 0.99$. Other parameters are $\alpha_1 = 0.25, \alpha_2 = 4.0, \beta_1 = 1/2, \beta_2 = 2, d_1 = d_2 = 0.1, S_1 = S_2 = 1, D = 0.1$. [From Fox and Vasseur [4]]

Fox and Vasseur interpret the growing area of stable coexistence as a resemblance to essential resources, where the stable coexistence conditions are similar to those found for highly different demand ratios. In both cases the consumers must ingest more of the resource that limits its growth rate. For increasingly different demand ratios the variety of uptake rates that allows for limitation by different nutrients grows and provides more combinations

for coexistence.

After analysing the pure ecological dynamics of the model of Fox and Vasseur, we now come to the implementation of the evolutionary dynamics.

## 2.4 Evolutionary Dynamics

As we mentioned in the overview on the assumptions of the Fox-Vasseur model, the evolutionary dynamics are based on adaptive uptake rates. Fox and Vasseur allowed the consumers to adapt to the abundances of the two resources and react to changing conditions. It is assumed that change of the uptake rates is the only possible adaptation of the consumers. Dispersion to other habitats for a greater occurrence of the favoured resource is not allowed nor are alterations of their nutrient requirements. The approach is based on "adaptive dynamics", used by several authors before. Since the adaptation of the uptake rate should relate to the growth of the consumer, we are interested in the partial derivative of the fitness of one consumer with respect to the uptake rate $u_j$. This selection differential is scaled by a rate parameter $\nu_j$, with various possible biological interpretations and allowing adjustments on different timescales. The change of the trait $u_j$ with respect to time is denoted as follows

$$\frac{du_j}{dt} = \nu_j \frac{\partial[1/C_j)(dC_j/dt)]}{\partial u_j}. \tag{7}$$

The variety of biological interpretations results from multiple possible ways to derive equation (7) and leads to a widely applicable description of the rate parameter $\nu_j$. Since Fox and Vasseur are mainly interested in equilibrium states, the derivation of $\nu_j$ is not outlined any further, since it has no impact on these solutions. In the appendix of their paper, they present a continuous approximation to $1-\delta_j$ in equation (7), which has a discontinuous partial derivative due to the maximum function in the consumer's fitness gradient. The continuous approximation makes the integration of the full eco-evolutionary model possible.

## 2.5 Evolutionary Dynamics of a Consumer Living in Allopatry

We first start to analyse the adaptive dynamics of an allopatric consumer. In allopatry, one consumer lives in an isolated habitat and is not affected by a competitor. This is in contrast to sympatric consumers, which share a habitat and may compete for the same resources and which is explored afterwards. Adaptation of uptake rates prevents the consumer from specialization on a resource until this resource gets drawn to a very low density and enables the consumer to change its uptake according to abundances of the resources. As we mentioned in the introduction of the model of Fox and Vasseur, it may be advantageous for a consumer to switch its effort to a more abundant, but less matching, resource in favour of a higher amount of uptake. Since the excess is excreted at no cost, and in an unusable form for other species, this still incorporates a higher growth rate in many cases. Whether a balanced diet or limitation by one nutrient is favourable, is now explored below.

The optimal uptake rates depend on which nutrient limits the growth of the consumer, so either on one of the nutrients or on both in the case of colimitation. We will show the calculation in one case explicitly, the others are obtained in a similar way and will not be explained in detail. If nutrient $a$ is limiting the growth, we have a relative uptake of the two nutrients above the demand ratio, $g_{bj}/g_{aj} > \beta_j$. To maximize the amount of nutrients in the diet, we are interested in the maximum of $g_{aj}$ with respect to the uptake rate $u_j$. This is obtained by setting the derivative with respect to $u_j$ equal to zero

$$0 = \frac{\partial g_{aj}}{\partial u_j} = k_1 R_1 - k_2 R_2. \tag{8}$$

For an optimal uptake rate $u_j$ this leads to the same distribution of nutrient $a$ in the two resources. Substituting $k_1 R_1 = k_2 R_2$ into the ZNGI of consumer $j$ for the branch where $a$-limitation occurs leads to the following expressions

for the resource densities at equilibrium

$$R_{1(a)}(j) = \frac{d_j}{k_1(1+\beta_j)},\ j \in \{1,2\}, \tag{9a}$$

$$R_{2(a)}(j) = \frac{d_j}{k_2(1+\beta_j)},\ j \in \{1,2\}. \tag{9b}$$

The subscript $(a)$ indicates the limitation by nutrient $a$.

In equilibrium, the equations $(4a)$ and $(4b)$ yield an additional expression for the resource densities, $R_1(j) = DS_1/(u_jC_j + D)$ and $R_2(j) = DS_2/[(1 - u_j)C_j + D]$. These two expressions for the equilibrium resource densities provide a representation for the optimal uptake rate $u_j$ in case of limitation by nutrient $a$:

$$u_{j(a)} = \frac{S_1k_1(1+\beta_j) - d_j}{S_1k_1(1+\beta_j) + S_2k_2(1+\beta_j) - 2d_j}. \tag{10}$$

The optimal uptake rates for limitation by nutrient $b$ are obtained analogously. For colimitation, the fact that a balanced diet is ingested implies $g_{aj}/g_{bj} = \beta_j$ and together with $(4c)$ the optimal uptake rate $u_j$ under nutrient colimitation can be derived.

The model of Fox and Vasseur does not consider only the evolutionary dynamics, but the resource densities' impact on the choice of optimal uptake rates. The ecological dynamics influence the uptake rates to a great extent and the analytical results are presented below. In Fig.7, the evolutionary stable strategy (ESS) is given as a solid black line and presented in dependence of the consumer's demand ratio. For a colimited diet the equation for the optimal uptake rate $u_j$ is a reversed S-shaped curve, as we can see in Fig.7. The equation (10) for the optimal uptake rate $u_j$ under $a$-limitation decreases almost linearly with respect to the variable $\beta_j$ and is the upper one compared to the similar curve for the optimal uptake rate under $b$-limitation. One can see, that colimitation only maximizes fitness where the demand ratio of the consumer is sufficiently near to the nutrient supply ratio.

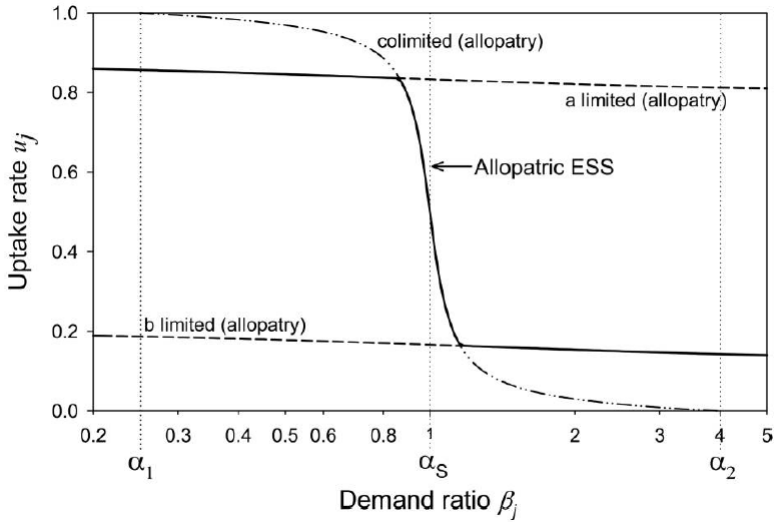


**Figure 7:** Trait values leading to the evolutionary stable strategy (ESS) for a single consumer (allopatry) are given as a function of the demand ratio ($\beta_j$) by the solid black line. The allopatric ESS follows the curve defining nutrient colimitation only when the demand ratio is sufficiently near to the supply ratio ($\alpha_S$). When colimitation requires a more extreme uptake rate than an $a$-limited or $b$-limited state adaptation selects a nutrient-limited ESS. Nutrient-limited states are favoured over colimitation because of the dynamic renewal of resources; colimitation by extreme specialization on a single resource leads to reduced density of that resource and release of the other resource from consumption pressure. Parameter values are as follows: $\alpha_1 = 0.25, \alpha_2 = 4.0, d_1 = d_2 = 0.1, S_1 = S_2 = 1, D = 0.1$. [From Fox and Vasseur [4]]

If the demand ratio becomes increasingly different to the nutrient supply ratio, colimitation becomes suboptimal. This is due to the fact that the consumer eats a high amount of the more matching resource and drives it to a low density, implying a smaller growth rate for the consumer. In those cases it is beneficial for a consumer to alter it's uptake rates and put more effort into the uptake of the more abundant but less matching resource. Then the optimal uptake rates are calculated under $a$- and $b$-limitation respectively. This constant interplay between the resource densities and the adapting uptake rates define the eco-evolutionary dynamics. For uptake rates above (below) the optimal uptake rate for $a$-limitation ($b$-limitation), this optimal uptake rate simultaneously is the ESS. For intermediate cases of uptake rates, the colimited uptake rate is the convergent stable strategy for a single consumer

in allopatry.

Fox and Vasseur argue that this adaptation in allopatry seems to "preadapt" the consumer for a habitat shared with a second consumer and is resulting from the relatively loose conditions for coexistence on complementary resources.

## 2.6 Evolutionary Dynamics of a Consumer Living in Sympatry

After discussing the eco-evolutionary outcome of a consumer in allopatry, we are now interested in a habitat with two consumers relying on the same two resources and have, therefore, consumers living in sympatry.

Again, we will see that the nutrient supply ratio plays an important role in the eco-evolutionary dynamics for consumers living in sympatry. If the demand ratios of the consumers fall on the same side of the nutrient supply ratio $\alpha_S$, there will always be exclusion of one consumer. Which one is going to survive depends on the closeness to $\alpha_S$: The consumer with a demand ratio between the nutrient supply ratio and the demand ratio of the second consumer will prevail in the long run. This is due to the fact that both uptake rates adapt to the same single nutrient limitation, but the consumer with the closer demand ratio to $\alpha_S$ can utilise the non-limiting nutrient to a greater extent while still ingesting the limiting nutrient as much as possible. This shrinks the availability of the limiting nutrient such that the other consumer becomes extinct.

Therefore, we require for coexistence in sympatry that the demand ratios fall on opposite sides of the nutrient supply ratio and since we already assumed demand ratios bracketed by the composition ratios of the two resources, we assume without loss of generality $\alpha_1 < \beta_1 < \alpha_S < \beta_2 < \alpha_2$.

Because of this assumption, the only possibilities would be limitation by different nutrients or colimitation. In allopatry the advantage of single-nutrient limitation is the greater amount of uptake of the more abundant but less matching resource. This advantage is lost for consumers living in sympatry, because in a shared habitat and with demand ratios where one demand ratio is smaller and one greater than the nutrient supply ratio, each

consumer favours a different resource. It is therefore not beneficial to switch to the less matching resource, regardless of the demand ratios, since the abundance is decreased by the opposed consumer such that it cannot make up for the relative loss of the preferred nutrient. As a result, colimitation in equilibrium is the only possible outcome for sympatric consumers and their adapting uptake rates.

The optimal uptake rates of consumers living in sympatry can be derived in a similar way as in the allopatric case. By setting the growth in consumer densities $dC_j/dt$ equal zero, we get two equations for the resource densities at equilibrium. The demand ratios and the consumer densities do not appear in the equations of the equilibrium densities. This is because the demand ratios and the equilibrium consumer densities are compensatory, implying a higher equilibrium density for a demand ratio closer to the nutrient supply ratio and the other way around. Under these constraints and by substituting the equilibrium resource densities into the conditions for colimitation $g_{bj}/g_{aj} = \beta_j$, $j = 1, 2$, we derive the optimal uptake rates for both consumers analytically. We will not express them explicitly, since they give no additional evolutionary insight, but we will discuss the eco-evolutionary dynamics with a representative illustration in Fig.8.

That this sympatric ESS will always lead to a stable coexistence of the two consumers for the previously discussed parameter range, cannot be shown analytically. However, Fox and Vasseur used numerical analysis to claim that the stable coexistence is robust for all parameterizations where both consumers can persist in allopatry. Their results put the relative abundances of the consumers in relation to the closeness of the demand ratios to the nutrient supply ratio. The consumer with a demand ratio that better reflects the nutrient supply ratio will gain a higher equilibrium density than the consumer with a more deviating demand ratio.

Hereafter, convergence, divergence and parallel shifts in uptake rates are discussed and outlined in Fig.8, followed by eco-evolutionary explanations.

Fox and Vasseur assume adaptation of consumers to allopatric conditions, before they are forced into sympatry. The evolutionary outcome shows three different patterns, character convergence, divergence, and parallel shifts, depending on the demand ratios of the two consumers and their relative prox-

imity to the nutrient supply ratio.

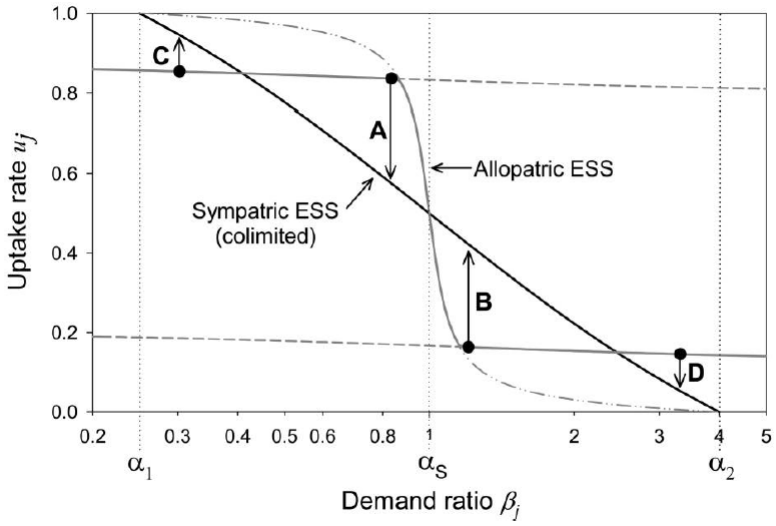


**Figure 8:** Trait values at the sympatric and allopatric evolutionarily stable strategies (ESSs), as a function of the demand ratio ($\beta_j$), are given by the solid black line and the grey line, respectively. Preadaptation to allopatric conditions leads to three possible relative directions of trait adaptation in sympatry: consumers with demand ratios corresponding to A and B demonstrate trait convergence, C and D represent trait divergence, and A and D (and C and B) represent parallel trait shifts. Pairings A and C and B and D are ecologically unstable at their evolutionary optimum because both consumers have demand ratios on the same side of the supply ratio ($\alpha_S$); the more proximate consumer to the supply ratio will exclude the other as adaptation occurs. Exemplary transient dynamics are shown in appendix B in the online edition of the *American Naturalist*. Parameter values are as follows: $\alpha_1 = 0.25, \alpha_2 = 4.0, d_1 = d_2 = 0.1, S_1 = S_2 = 1, D = 0.1$. [From Fox and Vasseur [4]]

For demand ratios that are close to the nutrient supply ratio for both consumers (but still on opposite sides, corresponding to the coexistence conditions discussed above), the uptake rates will become more similar to each other describing convergence in trait change, see **A** and **B** in Fig.8. The reason for uptake rates changing to take up more of the less matching resource is the reduction of this resource by the second consumer. The second consumer prefers this resource and will take up a high amount leading to a decrease of its density. The first consumer must still maintain enough of the unfavoured resource and therefore, has to increase its effort accordingly

compared to the allopatric case. Since this holds for both consumers, the uptake rates experience character convergence. This trait change does not happen in a strict and straight way, but undergoes several trait states and different ecological territories (which describe the pure ecological outcome with assuming uptake rates as fixed). One example of character convergence is displayed in Fig.9, where the parameters are again chosen to be symmetric with reciprocal demand ratios.

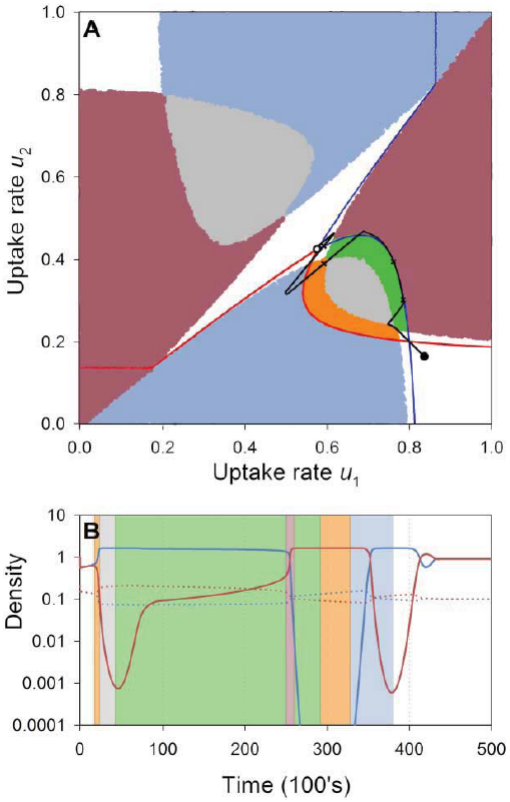


**Figure 9:** Adaptation of two consumers from their allopatric optima generates trait convergence but leads the system through trait space that is ecologically unstable. $A$, Outcome of competition in the trait space: colour coding as in Fig.5. The blue (red) lines trace the points in phase space where $C_1$ ($C_2$) is colimited. The temporal dynamics of traits (overlaid on $A$, beginning from the solid black point) and population densities ($B$) are shown, with the background colour corresponding to the region of trait space occupied at each time ($C_1$ is indicated by a solid blue line; $C_2$, a solid red line; $R_1$, a dashed blue line; $R_2$, a dashed red line). Initial densities were $R_1(0) = R_2(0) = 0.2; C_1(0) = 1.0; C_2(0) = 0.99$. Other parameters are $\alpha_1 = 0.25, \alpha_2 = 4.0, \beta_1 = 1/1.2, \beta_2 = 1.2, d_1 = d_2 = 0.1, S_1 = S_2 = 1, D = 0.1$, and $\nu = 0.0002$. [From Fox and Vasseur [4]]

The densities of consumers can be driven to a very low density close to extinction, however, preadaptation of allopatric consumers always leads to stable coexistence in the long run. In nature, these near extinctions may lead to real extinction, but in the mathematical model the consumers will recover and increase in their densities again. This transient eco-evolutionary dynamic can be detected in all evolutionary outcomes. By taking a look at

Fig.8, one can see that character convergence occurs whenever colimitation is the outcome for allopatric consumers as well as when forced into sympatry.

For allopatric uptake rates illustrated by **C** and **D** in Fig.8, the demand ratios of both consumers are extremely different from the nutrient supply ratio and both consumers' demand ratios resemble the composition ratio of one of the resources. Since the advantage of reducing ones uptake of the more matching resource is lost due to sympatric conditions, both consumers will focus their effort to their favoured resource. From one-nutrient limitation in allopatry, optimal uptake rates change to colimitation in sympatry which is achieved by character displacement.

The third and last pattern which can arise, are parallel shifts in trait changes. These occur when the demand ratios are sufficiently asymmetric about the nutrient supply ratio, as is the case for the combination **A** and **D** as well as for **B** and **C** in our representative illustration in Fig.8. Even though the uptake rates do not change in a strictly parallel way, they will both alter in the same direction either both increasing their efforts for resource 1 or both for resource 2. A biological explanation is not given by Fox and Vasseur, but may be obtained by combining the explanations for character convergence and divergence.

The pairings **A** and **C** as well as **B** and **D** lead to ecological exclusion, since both demand ratios are either both below (**A** and **C**) or above (**B** and **D**) the nutrient supply ratio.

As mentioned above, the abundance of a consumer depends on the relative proximity to the nutrient supply ratio and may be very low. Nevertheless, consumers in sympatry will always coexist under the condition of demand ratios on opposite sides of the nutrient supply ratio.

# 3 An Alternative Evolutionary Model Based on a Population-Genetic Approach

In the following sections we will discuss a different approach to the evolutionary dynamics. Instead of adaptive dynamics, in each consumer we distinguish two alleles which form haploid individuals with different uptake rates and study their evolving allele frequencies. Its implementation and the resulting eco-evolutionary dynamics will be the subject of the remaining part of this work.

## 3.1 The Model

As in the Fox-Vasseur model, the interplay between ecological and evolutionary dynamics is investigated for two consumers feeding on two resources. The assumptions made by Fox and Vasseur remain the same, except the last bulleted point, where the adaptive dynamics is replaced by a population-genetic approach. So we are not only interested in the coexistence of the consumers, but also if they can be maintained polymorphic.

### 3.1.1 Ecological Dynamics

We now distinguish two alleles in each consumer, $Y_1$ and $Y_2$ in consumer 1 and $Z_1$ and $Z_2$ in consumer 2. The frequency of allele $Y_1$ in consumer 1 is denoted by $p$, which gives $1-p$ for the allele frequency of $Y_2$, and similarly for consumer 2 with allele frequency $q$ for $Z_1$ and $1-q$ for $Z_2$. Each of the alleles possesses its particular uptake rate and by assuming a linear trade-off, they are given as follows: $Y_1$ in consumer 1 ingests resource 1 with an uptake rate $u_{11}$ leading to an uptake rate of $1-u_{11}$ for resource 2; $Y_2$ has uptake rates $u_{12}$ for $R_1$ and $1-u_{12}$ for $R_2$. Similarly, we get $u_{21}$ and $1-u_{21}$ for $Z_1$ in Consumer 2, and $u_{22}$ and $1-u_{22}$ for $Z_2$. In contrast to the Fox-Vasseur model, the uptake rates are fixed and the evolutionary dynamics occurs by a change of allele frequencies. In order to present a better overview, these assignments are listed in Table 1.

| | Consumer 1 | | Consumer 2 | |
|---|---|---|---|---|
| allele | $Y_1$ | $Y_2$ | $Z_1$ | $Z_2$ |
| frequency | $p$ | $1-p$ | $q$ | $1-q$ |
| uptake rate for $R_1$ | $u_{11}$ | $u_{12}$ | $u_{21}$ | $u_{22}$ |
| uptake rate for $R_2$ | $1-u_{11}$ | $1-u_{12}$ | $1-u_{21}$ | $1-u_{22}$ |

**Table 1:** A listing of the alleles of consumer 1 and consumer 2, with their allele frequencies and the corresponding uptake rates for resource 1 and resource 2.

We again consider two essential nutrients $a$ and $b$ which are contained in the two resources in a different ratio. Nutrient $b$ is given relative to nutrient $a$ in the ratio $\alpha_i$ in resource $R_i$. As before, the composition ratio $\alpha_i$ of resource $R_i$ is described by a parameter $k_i$, representing the ratio of nutrient $a$ to the whole nutrients in resource $R_i$, leading to

$$\alpha_i = \frac{1-k_i}{k_i}. \tag{11}$$

Similarly, the demand ratio $\beta_j$ for consumer $C_j$ represents the demand of nutrient $b$ relative to nutrient $a$.

Since we make the same assumptions as in the Fox-Vasseur model (except the adaptive-dynamics approach for the uptake rates), the composition ratios as well as the demand ratios are fixed and distinct, and without loss of generality it is assumed that $\alpha_1 < \alpha_2$ and $\beta_1 < \beta_2$. Thus, in $R_1$ nutrient $a$ is more common relative to $b$ than in $R_2$. Likewise, consumer 1 demands relatively more of nutrient $a$ compared to $b$ than consumer 2. Recalling the requirements for complementary resources, $\alpha_1 < \beta_j < \alpha_2$ holds for $j = 1, 2$.

The following schematic representation is inspired by the one of Fox and Vasseur and adapted to the population-genetic approach.

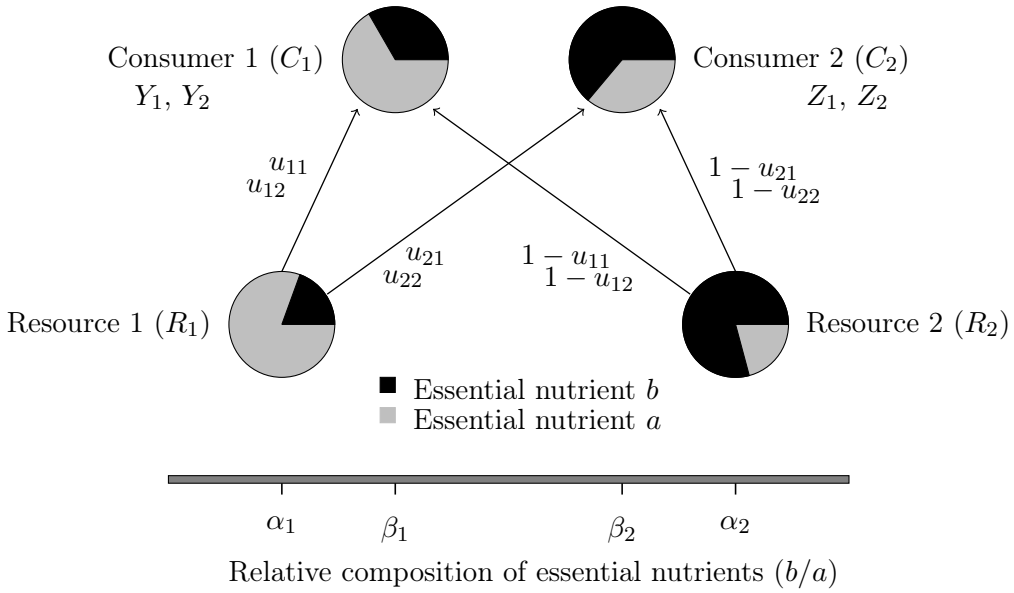


**Figure 10:** Schematic representation of the eco-evolutionary model with a population-genetic approach. The alleles $Y_1$ and $Y_2$ in consumer 1 and $Z_1$ and $Z_2$ in consumer 2 ingest two essential nutrients $a$ and $b$ by an uptake of $R_1$ and $R_2$. For allele $Y_1$ ($Y_2$) the uptake rates are denoted by $u_{11}$ ($u_{12}$) for $R_1$ and $1 - u_{11}$ ($1 - u_{12}$) for $R_2$ and similar for allele $Z_1$ ($Z_2$), $u_{21}$ ($u_{22}$) for $R_1$ and $1 - u_{21}$ ($1 - u_{22}$) for $R_2$. For complementary resources the ratios of the two nutrients in the resources ($\alpha_i$) must bracket the demand ratios of the consumers ($\beta_j$).

The growth of the consumers is again determined by the uptake of the required nutrients and its reflection of the consumers' needs. What is different now to the previous model is the occurrence of two alleles in each consumer with corresponding uptake rates. We, therefore, have to adapt the equations for the uptake of nutrient $a$ and nutrient $b$ for both alleles. These two alleles both contribute to the uptake of its consumer and are implemented separately into the equation for consumer's growth. For consumer $j$ and allele 1 ($Y_1$ and $Z_1$, respectively) we derive the equations

$$g^1_{aj} = u_{j1}k_1R_1 + (1 - u_{j1})k_2R_2, \tag{12a}$$

$$g^1_{bj} = u_{j1}(1 - k_1)R_1 + (1 - u_{j1})(1 - k_2)R_2, \tag{12b}$$

and similarly for allele 2 ($Y_2$ and $Z_2$, respectively)

$$g^2_{aj} = u_{j2}k_1R_1 + (1-u_{j2})k_2R_2, \tag{13a}$$
$$g^2_{bj} = u_{j2}(1-k_1)R_1 + (1-u_{j2})(1-k_2)R_2; \tag{13b}$$

cf. eq.(2).

That consumers can only utilise the nutrients which are taken up at the required ratio still holds, hence the assimilation fractions in eq.(3) must again be implemented in our model. Since we look at the two alleles in each consumer separately, the excess and therefore the non-usable amount of nutrients can be calculated in the same way as before. This leads to the assimilation fractions

$$1-\delta^1_j = 1 - \max\left(\frac{g^1_{bj} - g^1_{aj}\beta_j}{g^1_{aj}+g^1_{bj}}, \frac{g^1_{aj} - g^1_{bj}\beta_j^{-1}}{g^1_{aj}+g^1_{bj}}\right), \tag{14a}$$
$$1-\delta^2_j = 1 - \max\left(\frac{g^2_{bj} - g^2_{aj}\beta_j}{g^2_{aj}+g^2_{bj}}, \frac{g^2_{aj} - g^2_{bj}\beta_j^{-1}}{g^2_{aj}+g^2_{bj}}\right) \tag{14b}$$

for consumer $j$ and for allele 1 and allele 2, respectively.

After these adaptations required by the population-genetic approach, we can adapt the equations (4) derived by Fox and Vasseur for the ecological dynamics by implementing our modifications:

$$\frac{dR_1}{dt} = D(S_1-R_1) - R_1[(u_{11}p + u_{12}(1-p))C_1 + (u_{21}q + u_{22}(1-q))C_2], \tag{15a}$$
$$\frac{dR_2}{dt} = D(S_2-R_2) - R_2[((1-u_{11})p + (1-u_{12})(1-p))C_1 + ((1-u_{21})q + (1-u_{22})(1-q))C_2], \tag{15b}$$
$$\frac{dC_1}{dt} = C_1[p(1-\delta^1_1)(g^1_{a1}+g^1_{b1}) + (1-p)(1-\delta^2_1)(g^2_{a1}+g^2_{b1}) - d_1], \tag{15c}$$
$$\frac{dC_2}{dt} = C_2[q(1-\delta^1_2)(g^1_{a2}+g^1_{b2}) + (1-q)(1-\delta^2_2)(g^2_{a2}+g^2_{b2}) - d_2]. \tag{15d}$$

For the chemostat dynamics, the constant supply concentration for resource $i$ is again given by $S_i$, as is the dilution rate $D$, assumed to be the same for both resources. Concerning the death rate $d_j$ of consumer $j$, we do not distinguish between the two alleles and hence we have one death rate for each consumer.

Since the nutrient supply ratio does not depend on allele frequencies or even on consumers, it is the same as in the Fox-Vasseur model:

$$\alpha_S = \frac{(1-k_1)R_1 + (1-k_2)R_2}{k_1R_1 + k_2R_2}. \tag{16}$$

As for the Fox-Vasseur model, we are interested in the zero-net-growth isocline (ZNGI) of both consumers. If we just consider the ecological dynamics, the frequencies can be taken as fixed. We now define the average uptake rate by pooling the uptake rates for both alleles with respect to their frequencies. For consumer 1 we define the average uptake rate $\bar{u}_1 := pu_{11} + (1-p)u_{12}$ and likewise for consumer 2, $\bar{u}_2 := qu_{21} + (1-q)u_{22}$. Since the allele frequencies are assumed to be fixed, the same holds for the average uptake rates. By substituting them into (15), we obtain equations analogous to the Fox-Vasseur model with $\bar{u}_j$ instead of $u_j$. Therefore, the ZNGIs for consumer $j$ are given by

$$R_2(j) = \max\left[\frac{d_j(1-\beta_j)^{-1} - k_1\bar{u}_jR_1}{k_2(1-\bar{u}_j)}, \frac{d_j\beta_j(1+\beta_j)^{-1} - (1-k_1)\bar{u}_jR_1}{(1-k_2)(1-\bar{u}_j)}\right], \quad j \in \{1,2\}. \tag{17}$$

expressed as functions of $R_1$.

Consequently, the pure ecological dynamics are the same in both models. We have nothing further to do than to replace the uptake rates $u_j$ by the uptake rates $\bar{u}_j$ for both consumers and we obtain the same ecological outcome as before. Therefore, we will not discuss the pure ecological dynamics any further.

### 3.1.2 Evolutionary Dynamics

So far our model is very similar to the Fox-Vasseur model. The main difference is in the approach to the evolutionary dynamics, where Fox and Vasseur assumed that uptake rates are a phenotypic trait that can change continuously over time following an adaptive-dynamics approach. We consider two alleles in each consumer with fixed uptake rates. Our aim is to keep track of these allele frequencies and to examine if alleles die out or if polymorphisms are possible in one or both consumers.

Recalling Table 1, we have the two allele frequencies $p$ and $q$ to keep track of. Following classical population-genetics theory (e.g. Bürger, 2000, [2]), we define the fitness of allele 1 in consumer $j$ by

$$w_j^1 := (1 - \delta_j^1)(g_{aj}^1 + g_{bj}^1) \tag{18}$$

and likewise for allele 2

$$w_j^2 := (1 - \delta_j^2)(g_{aj}^2 + g_{bj}^2). \tag{19}$$

These fitnesses express the amount of utilisable nutrients by consumer $j$ individuals carrying allele 1 or 2. Again following classical population-genetics theory, cf. (8.11) in the first chapter of [2], we derive the equations for the change in allele frequencies:

$$\frac{dp}{dt} = p(1-p)(w_1^1 - w_1^2), \tag{20a}$$

$$\frac{dq}{dt} = q(1-q)(w_2^1 - w_2^2). \tag{20b}$$

Since the frequencies $p$ and $q$ are in the interval $[0, 1]$, the signs of the derivatives depend on the terms $(w_j^1 - w_j^2)$, $j = 1, 2$. This is reasonable, as the fitness of the alleles gives us the amount of utilisable nutrients. If, for instance, $w_1^1$ is greater than $w_1^2$, hence $Y_1$ provides consumer 1 with more utilisable nutrients, the frequency $p$ of allele $Y_1$ increases. This has a positive

effect on the consumer itself, since by increasing the frequency of the fitter allele it also increases its amount of utilisable nutrients and therefore its growth rate.

An important feature of the quantities $\delta_j^1$, $\delta_j^2$, $g_{aj}^1$, $g_{aj}^2$, $g_{bj}^1$ and $g_{bj}^2$ is their dependence on the resource densities which can change over time. Therefore, the amount of utilisable nutrients is not only determined by the uptake rates, but also by the densities of the resources. This leads to an interesting interplay between ecological dynamics and evolutionary feedback.

## 3.2 Allele-Frequency Dynamics

Let us first take a brief look at the evolutionary dynamics alone, before investigating the impact of ecological dynamics.

In the case of fixed consumer and resource densities, the model reduces to one equation because the two consumers have no impact on each other. We concentrate on the change of the allele frequency $p$; results for the allele frequency $q$ can be derived analogously.

In the remaining equation $(20a)$ the fitnesses $w_1^1$ and $w_1^2$ are now constants, evaluated with fixed resource densities and, as previously assumed, fixed uptake rates. Since the deltas represent a maximum function with two possible outcomes, there are four combinations regarding $\delta_1^1$ and $\delta_1^2$. For the two cases where the uptake leads to an excess of the same nutrient for both alleles, no inner fixed point can be found. It can easily be calculated that $\beta_1$ must equal $-1$ which is impossible in our model since $\beta_1$ is a ratio and always positive. This makes sense, because for limitation by the same nutrient usually one allele is the better competitor for the limiting nutrient and will exclude the other.

However, if we have an excess of a different nutrient for each allele, there exist parameter combinations that result in $w_1^1 - w_1^2 = 0$. For an excess of nutrient $a$ for allele $Y_1$ and an excess of nutrient $b$ for $Y_2$, thus $\delta_1^1$ and $\delta_1^2$ take explicit values and with a short derivation, we calculate that the demand ratio of the consumer has to be

$$\beta_1 = \frac{g_{b1}^1}{g_{a1}^2}, \tag{21}$$

to provide an equilibrium. The result may surprise us at first, but it is sensible. Each of the alleles ingests the limiting nutrient such that the ratio of the uptake of the two limiting nutrients of both alleles matches the demand ratio of the consumer. So both alleles can utilise the same amount of nutrients and none of them is the better competitor.

Similar to (21), the demand ratio $\beta_1 = g^2_{b1}/g^1_{a1}$ provides an equilibrium for the case of an excess of nutrient $b$ for $Y_1$ and an excess of nutrient $a$ for $Y_2$. These are two degenerate cases where the allele frequency $p$ is constant for every $p(0)$. This follows from the independence of $w^1_1$ and $w^2_1$ from $p$.

For the solution of the differential equation $(20a)$ with constant fitnesses a representation in a closed-form can be found

$$p(t) = \frac{1}{e^{(w^2_1 - w^1_1)t\frac{1-p_0}{p_0}} + 1}, \tag{22}$$

where $p(0) = p_0$ and $p_0 \neq 0$.

For representing the outcome, we plotted solutions for different parameter combinations with small changes in the resource density $R_1$ and different initial allele frequencies. In Fig.11 the three distinct cases are shown, one representing an increase of the allele frequency $p$, one a decrease of $p$ and the third one a case of an inner fixed point, where the allele frequency does not change over time.

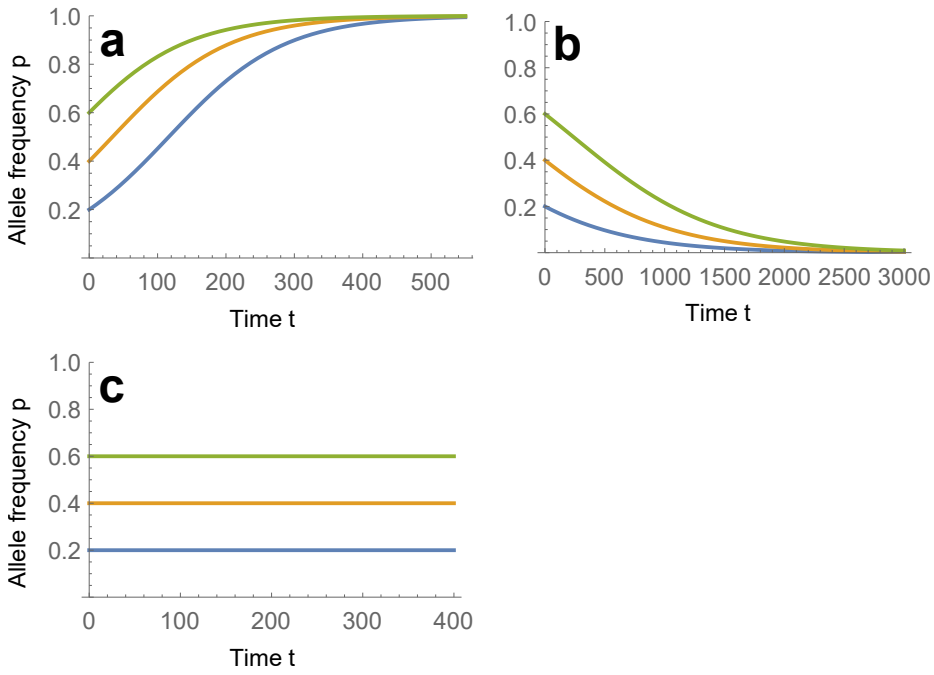


**Figure 11:** Examples of solutions for p(t) with constant resource and consumer densities for different initial allele frequencies: $p(0) = 0.2$ (blue), $p(0) = 0.4$ (orange) and $p(0) = 0.6$ (green). In **b** the inequality (23) is satisfied and for the reversed inequality of (23) the allele frequencies develop as in **a**. The degenerate cases are represented in **c**. The parameter values are as follows: $\alpha_1 = 1/3, \alpha_2 = 4.0, \beta_1 = 1/1.2, u_{11} = 0.6, u_{12} = 0.35, R_2 = 1$ and $R_1 = 3$ in **a**, $R_1 = 3.09$ in **b** and $R_1 \approx 3.078$ in **c**.

Using stability analysis, we can show that the fixed point $p = 0$ is stable if

$$\frac{w_1^1}{w_1^2} < 1. \tag{23}$$

In this case, allele $Y_1$ can utilise less nutrients than allele $Y_2$, which is consistent with our analysis. Likewise, the fixed point $p = 1$ is stable if the left hand side of (23) is greater than one.

The more interesting and also more complicated cases are the ones where ecological dynamics have an effect on the allele frequencies. We will first discuss the case where only one consumer is present, feeding on two resources, before we switch to consumers in sympatry and examine the interplay be-

tween those and the possibility of stable coexistence.

### 3.3 An Allopatric Consumer Feeding on Two Resources

The analysis becomes inevitably more difficult if we allow the resource densities and the consumer density to change over time. In the dynamics of consumer and resource abundances the allele frequencies determine the distribution of the alleles in the consumer, hence its total uptake rate, and therefore, the amount of loss of the resources. Similarly, the growth rate of the consumer is influenced by the allele frequencies because they determine the amount of nutrients that can be utilised. The resource densities, on the other hand, have an effect on the fitness of the alleles since the amount of ingested nutrients and how much of them can be utilised depends on the abundances of the resources. A change in the values of $w_1^1$ and $w_1^2$ leads to a change in the allele frequencies. In the eco-evolutionary model the four equations for an allopatric consumer, two resources, and the allele frequency $p$ are given by

$$\frac{dR_1}{dt} = D(S_1 - R_1) - R_1[u_{11}pC_1 + u_{12}(1-p)C_1], \tag{24a}$$

$$\frac{dR_2}{dt} = D(S_2 - R_2) - R_2[(1-u_{11})pC_1 + (1-u_{12})(1-p)C_1], \tag{24b}$$

$$\frac{dC_1}{dt} = C_1[p(1-\delta_1^1)(g_{a1}^1 + g_{b1}^1) + (1-p)(1-\delta_1^2)(g_{a1}^2 + g_{b1}^2) - d_1], \tag{24c}$$

$$\frac{dp}{dt} = p(1-p)(w_1^1 - w_1^2). \tag{24d}$$

Although the equation for the change in the allele frequency looks the same as in the case without ecology, the fitnesses are not constant due to the dependence on the now changing resource densities, as we can see in (12)-(14).

The following results are derived by numerical calculations, since analytical results could not be attained. This is mainly because of the maximum functions for the uptake of the resources and the corresponding non-continuous derivatives, which make the integration of the full eco-evolutionary model impossible. We used Mathematica, version 11.2, for numerical computations and for representing visualisations of our results. Explicit numerical

values are mathematically rounded to at most three decimals.

The calculations for a general fixed point were also not successful. However, if we assign real values to the parameters we can use numerical methods to get approximate solutions. We will show the results for a rather symmetric case where the composition ratios of the resources are reciprocal to each other and where the supply concentration is equal in both resources. The parameter values are analogous to those used by Fox and Vasseur in Fig.4, except that we just have one consumer instead of two and take fixed uptake rates to analyse the evolution of the allele frequencies.

We will mainly discuss this symmetric case, with parameter values: $\beta_1 = 1/1.2, \alpha_1 = 0.25, \alpha_2 = 4.0, S_1 = S_2 = 1, D = 0.1, d_1 = 0.1$ and the (fixed) uptake rates $u_{11} = 0.4$ and $u_{12} = 0.6$. After that, we will analyse the influence of other parameters on the outcome by undertaking small changes in their values.

As we already mentioned above, for ecological or evolutionary models, to find equilibria and the analysis of their stability is one of the main tasks to describe the dynamics of a model. Especially fixed points in the interior of the phase space, such that all species coexist, are of main interest.

For fixed points on the boundaries $p = 0$ or $p = 1$, we found exactly one on each boundary which lies in the state space: the resource densities can neither vanish nor be negative and the same holds for the consumer, since for an allopatric consumer there is no competition. Therefore, a fixed point is reached if one of the alleles dies out (except if a cycle in the ecological dynamics appears, but this was not detected in any of our calculations and also not mentioned by Fox and Vasseur). A polymorphism could not be calculated explicitly and as we see in the graphic analyses (Fig.12-Fig.15), we may assume that there does not exist a scenario where both alleles survive.

For the fixed point where allele $Y_1$ goes extinct ($p = 0$), we have the equilibrium resource densities $R_1 = 0.092$ and $R_2 = 0.132$ and the consumer density $C_1 = 1.651$ for the parameter values above. By analysing the Jacobian corresponding to this fixed point, we obtain four eigenvalues, and all of them are negative. This indicates a stable fixed point.

Furthermore, the equilibrium densities for the ecological dynamics for the second fixed point, $p = 1$, i.e., allele $Y_2$ dies out, are $R_1 = 0.135$, $R_2 = 0.094$

and $C_1 = 1.601$. However, for the eigenvalues of the Jacobian we get three negatives and one positive. The positive eigenvalue indicates an unstable fixed point. Hence, we obtain one stable fixed point at $p = 0$ and one unstable fixed point at $p = 1$ by numerical calculations.

If we start with both alleles present, for this parameter combination allele $Y_2$ is always the winner in the long run. But what are the explanations for this specific outcome?

First of all, let us take a look at our chosen parameters. The uptake rate $u_{11} = 0.4$ of allele $Y_1$ represents a relatively low uptake of resource $R_1$ compared to allele $Y_2$, whose effort is greater for resource $R_1$ with an uptake rate $u_{12} = 0.6$. Furthermore, resource $R_1$ contains more of nutrient $a$ than $b$, namely $k_1 = 4/5$ of $R_1$ is nutrient $a$, and similarly resource $R_2$ contains more of nutrient $b$ compared to $a$ ($k_2 = 1/5$). Since the demand ratio of the consumer $\beta_1 = 1/1.2$ expresses a higher demand of nutrient $a$ than $b$, resource $R_1$ is the more matching resource for the consumer. Therefore, allele $Y_2$ possesses an advantage in the uptake of the resources and increases in frequency as time passes. This leads to a further decrease of resource $R_1$ since more alleles are present that possess the higher uptake rate for $R_1$ and therefore consumer $C_1$ ingests a higher amount of the resource than before. As $R_1$ becomes less abundant, individuals carrying allele $Y_1$ obtain less and less utilisable nutrients and, in the end, allele $Y_1$ goes extinct.

We are now interested in slight changes of parameter values and how they influence the eco-evolutionary outcome. That the demand ratio plays an important role is evident. For a reciprocal demand ratio of the former, $\beta_1 = 1.2$, the results are symmetric to those above, and allele $Y_1$ is the winner for all initial resource densities. However, there has to be a transition regarding the winner with respect to the demand ratio. Our next goal is to determine what value of $\beta_1$ leads to a change of the winning allele.

To obtain an understanding of the influence of the demand ratio, we start with a balanced demand for both nutrients expressed by $\beta_1 = 1$. Additionally, we do not want an initial advantage of one of the alleles, because we are especially interested in finding a real polymorphism, and choose $p(0) = 0.5$ for the initial allele frequencies. The other parameter values stay the same,

so we have in $R_1$ relatively more nutrient $a$ than nutrient $b$ and in $R_2$ relatively more nutrient $b$ than nutrient $a$. The eco-evolutionary outcome with dependence on the initial values of the resource densities is displayed in Fig.12.

For this parameter combination both equilibria (at $p = 0$ and $p = 1$) are locally stable, since in both cases all eigenvalues of the Jacobian are negative. Furthermore, this local stability holds for all parameter combinations that are displayed below (for an allopatric consumer). So for the cases where the eco-evolutionary outcome depends on initial resource densities, the two equilibria are locally stable.

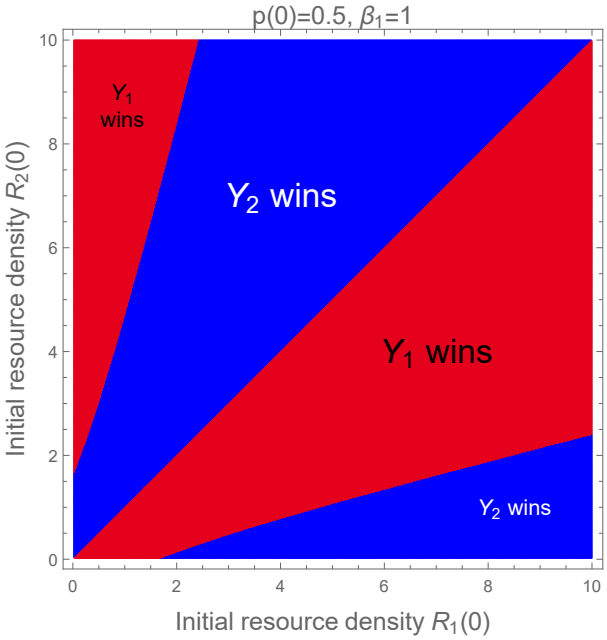


**Figure 12:** Eco-evolutionary outcome for symmetric parameters and with a balanced demand ratio, $\beta_1 = 1$, with respect to the nutrients $a$ and $b$. The initial allele frequency is $p(0) = 0.5$. The red colouring indicates a win of allele $Y_1$ ($p = 1$) and likewise, the blue colour the win of allele $Y_2$ ($p = 0$). For equal initial values for both resources the allele frequencies stay the same and none of the alleles excludes the other in the long run. The results were obtained for 6000 time steps and visual inspection of the time series ensured that this quantity was sufficient to reach equilibrium. Other parameters are as follows: $u_{11} = 0.4, u_{12} = 0.6, \alpha_1 = 0.25, \alpha_2 = 4.0, d_1 = 0.1, S_1 = S_2 = 1, D = 0.1$ and the initial consumer density is $C_1(0) = 0.1$.

The initial resource densities play an important role in the eco-evolutionary

outcome. If one resource is slightly more abundant at the beginning, the allele with a smaller uptake rate of that resource excludes the other allele. This is due to the fact, that this allele focuses on the resource which is less available and gains a comparatively greater amount of it than the other allele. Since the consumer's demand is equal in both nutrients, the winning allele can ingest more of the nutrient which is more common in the less abundant resource and due to the higher density of the other resource, it gains still enough to obtain more utilisable nutrients than its opponent.

For example, allele $Y_1$ with the uptake rate $1 - u_{11} = 0.6$ for $R_2$ ingests more of resource $R_2$ than allele $Y_2$ with an uptake rate of $1 - u_{12} = 0.4$. If resource $R_1$ is slightly more available, allele $Y_1$ can utilise the greater uptake rate of $R_2$ to ingest a higher amount of nutrient $b$ than its opponent. The larger availability of resource $R_1$ still provides allele $Y_1$ with an acceptable amount of nutrient $a$, which leads to a greater total uptake of utilisable nutrients than the one of allele $Y_2$.

Allele $Y_2$, on the other hand, ingests much more of resource $R_1$ and therefore, gains a high amount of nutrient $a$ compared to nutrient $b$. This excess of nutrient $a$ cannot be balanced through the uptake of resource $R_2$ since the allele's uptake rate for that resource is relatively small and so is the density of that resource. Hence, a high amount of nutrients must be excreted and is of no use to the allele. Therefore, the utilisable amount of nutrients is smaller than that of allele $Y_1$. This leads to a higher frequency of allele $Y_1$ which in turn increases the imbalance of the uptake of the two alleles. For an increasing allele frequency $p$, more and more of resource $R_2$ is ingested by allele $Y_1$, reducing the availability for allele $Y_2$. This leads to a further reduction of utilisable nutrients for allele $Y_2$ and, in the long run, allele $Y_1$ will exclude allele $Y_2$.

How resource densities, consumer density and allele frequency in this example develop over time is illustrated exemplary in Fig.13. The initial resource density of $R_1$ is chosen to be a little bit greater than the one of $R_2$, but both relatively small. For greater initial values the equilibrium is reached at a shorter time scale. As is the case for the initial consumer density which does not affect the eco-evolutionary outcome, but for a high value the higher density fastens the stabilisation of the dynamics.

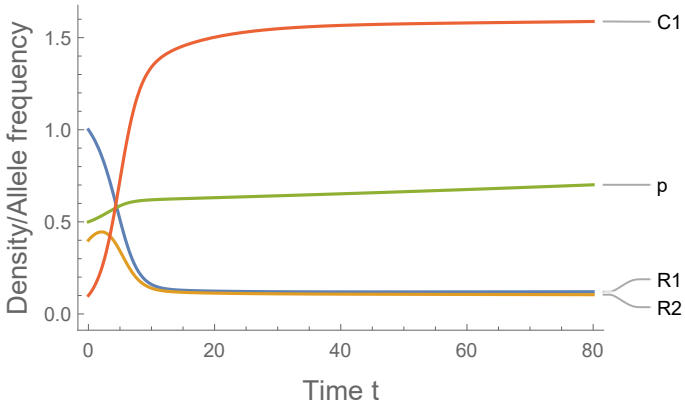


**Figure 13:** Resource densities $R_1$ (blue) and $R_2$ (orange), consumer density $C_1$ (red) and allele frequency $p$ (green) with respect to time $t$. The initial densities were $R_1(0) = 1, R_2(0) = 0.4$ and $C_1(0) = 0.1$ and both alleles are initially equally present ($p(0) = 0.5$). Other parameter values are as follows: $u_{11} = 0.4, u_{12} = 0.6, \alpha_1 = 0.25, \alpha_2 = 4.0, d_1 = 0.1, S_1 = S_2 = 1, D = 0.1$ and $\beta_1 = 1$. After approximately 1000 time steps the equilibrium is reached at $p = 1, R_1 = 0.124, R_2 = 0.086$ and $C_1 = 1.767$.

In the first few time steps we can detect a small increase in the resource density $R_2$ (orange) due to the small initial consumer density and under the assumption of a relatively small $R_2$. These small initial values result in a lower amount of ingested resource $R_2$ than is provided by the chemostat dynamics. Resource $R_1$, on the other hand, is abundant and ingested to a high extent right from the beginning such that the supply concentration $S_1$ cannot make up for the loss and we have a decrease in the density of $R_1$.

For extremely different initial resource densities, the advantage over the less common resource is lost. This is due to the rich abundance of the other resource which provides the allele with a huge amount of nutrients. After excretion there is still more of the limiting nutrient available than the other allele can gain through ingesting a higher amount of the resource containing more of the limiting nutrient, but being less abundant. In our example above with a much higher initial resource density $R_1$ than $R_2$, allele $Y_1$ cannot lean on the advantage over the uptake of resource $R_2$ and allele $Y_2$ prevails (blue area in the lower-right corner, Fig.12).

If we change the demand ratio a little bit, we detect a change in the eco-evolutionary outcome and a relocation of the extinction regions as can be seen in Fig.14. If the demand ratio $\beta_1$ is smaller than 1 and by further decreasing

its value, the red area (extinction of allele $Y_2$) below the first median becomes narrower and recedes from low values of the initial resource densities. The blue areas, one above the first median and the second for sufficiently higher initial resource densities $R_1$ than $R_2$, join in a larger region for extinction of allele $Y_1$ which pushes back the survival region of $Y_1$. This receding "loop" (red), defining combinations of initial resource densities where allele $Y_1$ wins, soon becomes very small and vanishes for $\beta_1$ just below $\beta_1 < 0.942$. The red region in the upper-left area recedes upwards until it vanishes for reasonable initial values of $R_2$ for $\beta_1 < 0.924$. (We consider initial resource densities up to $R_1(0), R_2(0) = 10$ as reasonable, since we take a relatively low consumer density $C_1$ and do not want to consider oversized resources.)

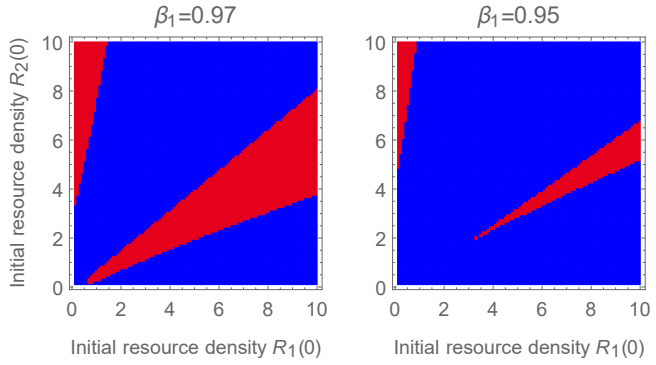


**Figure 14:** The change in the eco-evolutionary outcome for demand ratios $\beta_1 < 1$. The colour coding is described in Fig.12 and the same parameters are taken, except for $\beta_1$ which takes the values 0.97 (left graphic) and 0.95 (right graphic): $u_{11} = 0.4, u_{12} = 0.6, \alpha_1 = 0.25, \alpha_2 = 4.0, d_1 = 0.1, S_1 = S_2 = 1, D = 0.1$ and the initial consumer density $C_1(0) = 0.1$ and allele frequency $p(0) = 0.5$.

Since all parameters are symmetric and so is the initial allele frequency, for $\beta_1 > 1$ the change in the eco-evolutionary outcome is analogous. The blue area (extinction of allele $Y_1$) shrinks until allele $Y_1$ is the winner for all reasonable initial resource densities.

Now we will briefly examine how a starting advantage of one of the alleles influences the outcome. Naturally, the presence of more alleles of one type promotes its survival, but how much influence it actually has is explored below.

In the total symmetric case, where we started with an allele frequency of $p(0) = 0.5$ and otherwise symmetric parameter values, the range where the outcome depends on initial conditions was around $\beta_1 = 1$. If we now have a favoured allele $Y_1$, with a starting advantage $p(0) = 0.95$, this range shifts to smaller $\beta_1$-values. Since allele $Y_1$ is present to a great extent, they demand a large amount of the resources and less is available for allele $Y_2$. So even for a demand ratio, which better matches the uptake rates of allele $Y_2$, allele $Y_1$ can capitalise the higher amount of ingested nutrients. Nevertheless, for rather small demand ratios expressing a higher demand of nutrient $a$, allele $Y_1$ is still not able to win against its competitor.

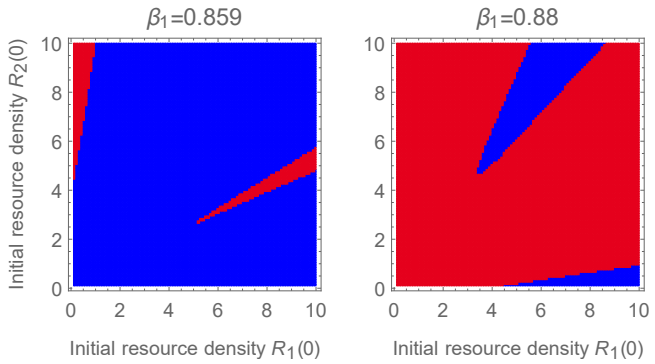


**Figure 15:** The change in the eco-evolutionary outcome for a starting advantage of allele $Y_1$ with $p(0) = 0.95$. The colour coding is as described in Fig.12. The demand ratio has the values $\beta_1 = 0.859$ (left graphic) and $\beta_1 = 0.88$ (right graphic). Otherwise, parameters are again chosen to be symmetric: $u_{11} = 0.4, u_{12} = 0.6, \alpha_1 = 0.25, \alpha_2 = 4.0, d_1 = 0.1, S_1 = S_2 = 1, D = 0.1$ and the initial consumer density $C_1(0) = 0.1$.

The value of $\beta_1$ is now smaller, a little bit greater than 0.856, compared to the symmetric case where allele $Y_1$ first has the chance to prevail for certain initial resource densities. If we compare Fig.15 to Fig.14 (illustrating the outcome for balanced initial allele frequencies), we see that the transition between the win of allele $Y_2$ and the win of allele $Y_1$ for all considered initial resource densities happens in a shorter interval of the demand ratio $\beta_1$. If allele $Y_1$ has a chance for some initial resource densities, it soon prevails for all reasonable initial resource densities if the demand ratio takes a slightly higher value (for $\beta_1$ slightly above 0.896). For the demand ratio $\beta_1 = 1$, allele $Y_1$ is the winner for all initial resource densities, in contrast to the

symmetric outcome in Fig.12 for balanced initial allele frequencies, where both alleles had the chance to prevail.

Next, we will discuss the influence of the uptake rates on the dynamics. With the chosen uptake rates $u_{11} = 0.4$ and $u_{12} = 0.6$; the alleles divide their effort on the resources contrarily but well-balanced. Allele $Y_1$ takes up resource $R_1$ with a rate of 0.4 and resource $R_2$ with a rate of 0.6, for allele $Y_2$ its effort is exactly the other way around with respect to the resources. If we now perturb this balance a little bit, the eco-evolutionary outcome changes accordingly. For instance, uptake rates $u_{11} = 0.4$ and $u_{12} = 0.7$ decrease the critical value of $\beta_1$ where a similar symmetric outcome appears as in Fig.12 (to approximately $\beta_1 = 0.908$). This means that allele $Y_1$ starts to prevail for an even smaller demand ratio and certain initial resource densities. This is because allele $Y_2$ has more extreme uptake rates than its opponent and for an equal demand of both nutrients the uptake is less balanced and more of the ingested nutrients cannot be utilised. So even for a slightly higher demand of nutrient $a$ than $b$, allele $Y_2$ cannot prevail in the long run even though it is the better competitor for resource $R_1$, containing proportionally more of nutrient $a$. Only for a relatively unbalanced demand in both nutrients, favouring nutrient $a$, it can take advantage of the greater uptake rate of resource $R_1$.

For more extreme uptake rates for both alleles, the transition from fixed point $p = 0$, such that this fixed point is reached for all reasonable initial resource densities, to the fixed point $p = 1$ happens in shorter intervals of the demand ratio $\beta_1$. The same effect is detected for a higher initial consumer density, since the greater number of alleles enforces the evolutionary dynamics.

What happens when the availability of the nutrients is changed in each resource, is discussed further below. The composition of the resources plays an important role, since it determines how much of each nutrient can be ingested through the uptake of each resource. In the symmetric case with composition ratios $\alpha_1 = 0.25$ and $\alpha_2 = 4.0$, the proportioning of the nutrients in the overall distribution is equal although they are distributed unevenly

across the resources.

We examine the changes in the outcome for an increased overall proportional availability of one nutrient. If we have in resource $R_1$ a ratio of 3/5 of nutrient $a$ instead of 4/5 and the composition in resource $R_2$ remains the same, nutrient $b$ is proportionally more abundant than nutrient $a$. Of course the actual availability depends on the resource densities. Consequently, more of nutrient $b$ than $a$ is ingested compared to the uptake with the former composition ratios in the same situation. This favours allele $Y_2$, since it concentrates on the resource which possesses more of the rarer nutrient $a$ ($R_1$). For allele $Y_1$ it is even harder to prevail with the smaller amount of nutrient $a$ in resource $R_1$ than before. A demand ratio expressing a much higher demand of nutrient $b$ than of nutrient $a$ is required for allele $Y_1$ to be able to use its preference for resource $R_2$ and win over its opponent. How extinction regions regarding initial resource densities develop with respect to the demand ratio is shown exemplarily for $\beta_1 = 1.538$ in Fig.16. For relatively higher demand ratios ($\beta_1 > 1.64$), allele $Y_1$ is the winner over the whole phase plane of initial resource densities (red colouring). For relatively lower demand ratios ($\beta_1 < 1.5$), it is the other way around and allele $Y_2$ prevails (blue colouring).

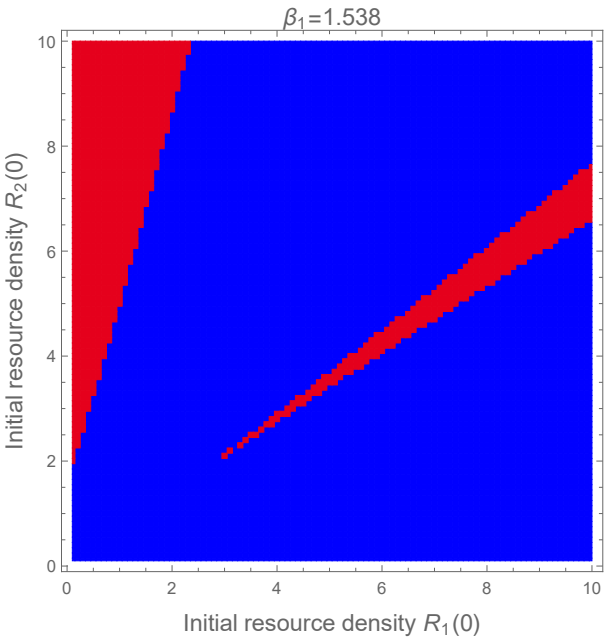


**Figure 16:** The change in the eco-evolutionary outcome for asymmetric composition ratios of the resources. The colour coding is as described in Fig.12. Except the composition ratios, other parameters are again chosen to be symmetric: $u_{11} = 0.4, u_{12} = 0.6, \alpha_1 = 2/3, \alpha_2 = 4.0, d_1 = 0.1, S_1 = S_2 = 1, D = 0.1$ and $\beta_1 = 1.538$ and the initial consumer density $C_1(0) = 0.1$ and allele frequency $p(0) = 0.5$.

We can see, that the "loop" is thinner than in the symmetric case in Fig.14. The parameter range of initial resource densities that lead to a win of allele $Y_1$ is smaller than the one for a symmetric distribution of the nutrients, if resources are present to a similar amount at the beginning. The diminished occurrence of nutrient $a$ and the thus more available nutrient $b$ requires better matched resource abundances to support the win of allele $Y_1$. For relatively low initial resource densities, allele $Y_2$ is still the winner, even for similar proportions of $R_1(0)$ and $R_2(0)$ than the one taken in the "loop". Only for higher demand ratios, allele $Y_1$ starts to prevail for smaller initial resource densities with $R_1(0) > R_2(0)$.

The area in the upper-left corner allows a relatively greater initial resource density of $R_1$ than for symmetric composition ratios. The large availability of resource $R_2$ provides allele $Y_1$ with a greater total amount of utilisable nutrients than its opponent even for a slightly higher resource density $R_1$. That resource $R_1$ can be a little bit larger compared to the symmetric

case is due to the new composition ratios. They induce a diminished ratio of nutrient $a$ that allows allele $Y_1$ a greater uptake of utilisable nutrients for higher $R_1(0)$ than allele $Y_2$ wins through the more balanced diet of nutrient $a$ and $b$. This diet is more balanced due to the higher uptake rate $u_{11}$ for $R_1$ of allele $Y_2$, but to a smaller degree than in the symmetric case because of the lower availability of nutrient $a$ in resource $R_1$ ($k_1 = 3/5$).

For higher values of $\beta_1$, the region for survival of $Y_1$ pushes back the area where $Y_2$ is the winner more and more until its extinction region spreads over the whole phase plane of initial resource densities. Above a critical value of $\beta_1$, allele $Y_1$ is the only winner for all initial resource densities, as we mentioned above.

To conclude, no stable polymorphism of the two alleles could be found and always one of the alleles went extinct.

There even is only a very small range for the demand ratio where both alleles have a chance to be the better competitor depending on initial values for the resource densities. This range is shifted and shortened by slight changes of other parameter values. More extreme uptake rates allow the allele with the less extreme uptake rates to compete successfully for a rather unfavoured demand ratio, since it better balances its effort on the two resources. The compositions of the resources have an effect on the proportional availability of each nutrient and influence the efficiency of the uptake rates. If one nutrient is proportionally more available, the allele which lays more of its effort on the uptake of the resource which contains the limiting nutrient to a greater extent has an advantage over its competitor. As is the case for a starting advantage of one of the alleles, since it helps this allele to establish itself for conditions which rather favours the other allele.

A higher frequency of one allele at the beginning fastens the transition between the winning alleles and shortens the range of $\beta_1$ where the outcome depends on initial conditions. The same holds true for higher initial consumer densities, since the greater number of individuals enforces the evolutionary dynamics.

However, the crucial parameter is the demand ratio.

## 3.4 Sympatric Consumers Feeding on Two Resources

We see that also the relatively simple case of one consumer and two resources bears interesting dynamics. If we now consider two consumers living in sympatry the eco-evolutionary interplay gets inevitably more difficult.

In the case of an allopatric consumer, we only investigated the fate of one or the other allele and not the survival of the consumer itself. This was due to the fact that the consumer had no competitor and could not go extinct. For two consumers living in the same habitat the situation is different. Now a consumer can actually go extinct due to the shared resources and exclusion by the other consumer.

Therefore, we are not only interested in the development of the allele frequencies, but also if both consumers can survive. The range of possible outcomes reaches from the maintenance of one allele to four alleles. In the first case one consumer dies out and in the other consumer one allele can exclude the other. If two alleles survive and two die out, either one allele in each consumer can prevail or one consumer dies out and the other stays polymorphic. In the case of survival of three or four alleles, both consumers coexist and at least one consumer stays polymorphic.

Recalling the notation of the alleles in consumer 1, $Y_1$ and $Y_2$, and of the alleles in consumer 2, $Z_1$ and $Z_2$, we are interested in the allele frequency $p$ for $Y_1$ and the allele frequency $q$ for $Z_1$. These are given by (20):

$$\begin{aligned}\frac{dp}{dt} &= p(1-p)(w_1^1 - w_1^2),\\ \frac{dq}{dt} &= q(1-q)(w_2^1 - w_2^2),\end{aligned}$$

where $w_j^1$ and $w_j^2$ are the fitnesses of allele 1 and allele 2, respectively, in consumer $j$.

Of course we are only interested in these frequencies as long as the regarding consumer is present. We have to keep this in mind, since the consumer densities do not have an explicit effect on the allele frequencies. These frequencies could still be positive even though the consumer is extinct. Obviously, this is not something we want to consider and if one consumer goes

extinct we do not examine its allele frequencies any further.

The ecological dynamics are as in (15):

$$\begin{aligned}
\frac{dR_1}{dt} &= D(S_1 - R_1) - R_1[(u_{11}p + u_{12}(1-p))C_1 \\
&\qquad + (u_{21}q + u_{22}(1-q))C_2], \\
\frac{dR_2}{dt} &= D(S_2 - R_2) - R_2[((1-u_{11})p + (1-u_{12})(1-p))C_1 \\
&\qquad + ((1-u_{21})q + (1-u_{22})(1-q))C_2], \\
\frac{dC_1}{dt} &= C_1[p(1-\delta_1^1)(g_{a1}^1 + g_{b1}^1) + (1-p)(1-\delta_1^2)(g_{a1}^2 + g_{b1}^2) - d_1], \\
\frac{dC_2}{dt} &= C_2[q(1-\delta_2^1)(g_{a2}^1 + g_{b2}^1) + (1-q)(1-\delta_2^2)(g_{a2}^2 + g_{b2}^2) - d_2].
\end{aligned}$$

As we can see already, the number of parameters increased compared to the allopatric case, and it is more difficult to analyse the dynamics with respect to single parameter choices. Our main interest will lie on different combinations of uptake rates for the alleles and when one or more alleles can prevail.

Since we were not even successful in the simpler case of an allopatric consumer, an analytical solution could not be found in the eco-evolutionary model of sympatric consumers. The results were again obtained by numerical methods using Mathematica and iterating for sufficiently many time steps in NDSolve. The dependence of the survival of the alleles on the choice of uptake rates was determined by holding the uptake rates of consumer 1 fixed and running through all different combinations of the uptake rates for the second consumer in steps of 0.02. To detect dependences on initial conditions, we considered three different initial consumer densities, two where either the first or the second consumer is initially more present and one where both consumers are similarly present at the beginning with a slight starting advantage of consumer 2. Unlike in the allopatric case, the initial resource densities play no crucial role in the eco-evolutionary outcome in sympatry. At most slightly shifted boundaries between two distinct outcomes appear. We will, therefore, restrict our analysis to initial resource densities $R_1(0) = 1$ and $R_2(0) = 1$.

As in the allopatric case, we first analyse the case of rather symmetric parameters. The resources have reciprocal composition ratios $\alpha_1 = 0.25$ and $\alpha_2 = 4.0$, such that resource $R_1$ contains relatively more of nutrient $a$ than $b$ and $R_2$ relatively more of nutrient $b$ than $a$. The demand ratios of the consumers are also reciprocal and given by $\beta_1 = 1/1.2$ and $\beta_2 = 1.2$, expressing a relatively higher demand of nutrient $a$ for the first consumer and of nutrient $b$ for the second consumer. The supply concentrations are chosen to be equal for both resources, as is the death rate for the consumers, $d_1$ and $d_2$. The resources are equally present at the beginning and likewise the alleles, starting with allele frequencies $p(0) = 0.5$ and $q(0) = 0.5$, since we try to find polymorphisms. Although we are not really interested in the same uptake rates for both alleles in one consumer, we do not explicitly exclude them in our graphical analysis, but they will not be discussed any further.

We will especially examine two cases of fixed uptake rates for consumer 1: first, the relatively balanced uptake rates $u_{11} = 0.4$ and $u_{12} = 0.6$, and then the more unbalanced rates, $u_{11} = 0.2$ and $u_{12} = 0.7$. The first case will be discussed in more detail and afterwards we will analyse the changes occurring for the more unbalanced uptake rates. For that purpose, we explain the outcome for specific initial values first and its dependence on the uptake rates of the second consumer. Subsequently, we are interested in the influence of initial consumer densities and what outcome depends on initial conditions.

In Fig.17 the eco-evolutionary outcome is displayed in dependence on the uptake rates $u_{21}$ and $u_{22}$, where the uptake rates of consumer 1 are $u_{11} = 0.4$ and $u_{12} = 0.6$. The initial consumer density $C_1$ is relatively small ($C_1(0) = 0.2$) compared to that of its competitor ($C_2(0) = 2$).

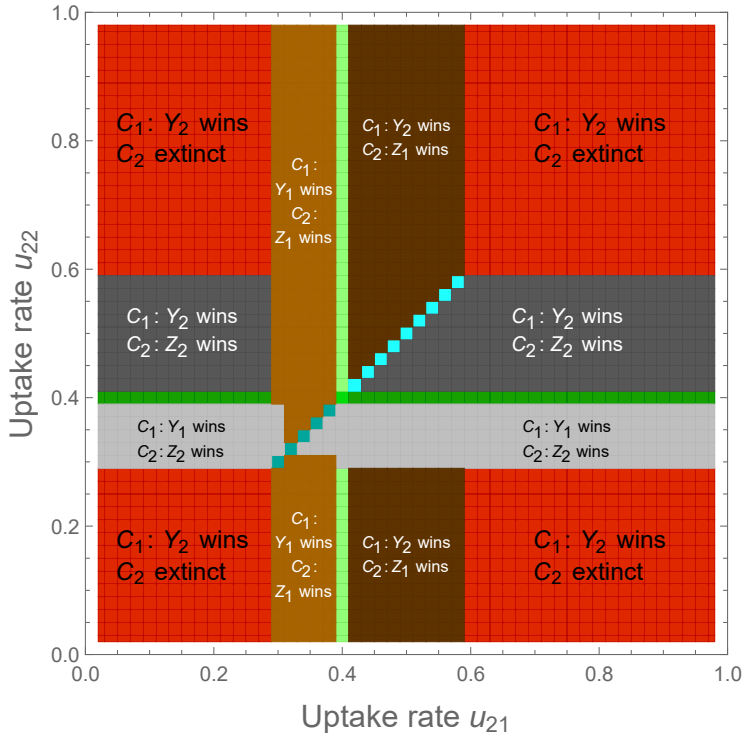


**Figure 17:** The eco-evolutionary outcome of two consumers living in sympatry. In the red region consumer 2 goes extinct and in consumer 1 just allele $Y_2$ is present. In the grey and brown regions, both consumers survive, but in each consumer one allele dies out: $Z_1$ is the winner and $Y_1$ (light brown) or $Y_2$ (dark brown), or $Z_2$ prevails just as $Y_1$ (light grey) or $Y_2$ (dark grey). The green areas represent combinations where consumer 1 goes extinct and either allele $Z_1$ wins (light green) or allele $Z_2$ (dark green). The other colours appear for equal uptake rates for consumer 2 ($u_{21} = u_{22}$) and are not of special interest (light blue: $C_2$ is polymorphic and $Y_2$ wins; medium green: $C_2$ is polymorphic, but $C_1$ goes extinct; viridian: $C_2$ is polymorphic and $Y_1$ wins). The parameters are chosen to be rather symmetric: $u_{11} = 0.4, u_{12} = 0.6, \alpha_1 = 0.25, \alpha_2 = 4.0, \beta_1 = 1/1.2, \beta_2 = 1.2, d_1 = d_2 = 0.1, S_1 = S_2 = 1, D = 0.1$. The outcome of the eco-evolutionary model was derived for initial consumer densities $C_1(0) = 0.2$ and $C_2(0) = 2$, resource densities $R_1(0) = 1$ and $R_2(0) = 1$ and balanced allele frequencies $p(0) = 0.5$ and $q(0) = 0.5$, so that no allele has an advantage at the beginning.

In the following paragraphs we explain each region explicitly and how the uptake rates determine the outcome.

In the red area, only one allele survives: consumer 2 goes extinct and in $C_1$ just allele $Y_2$ persists. Since the uptake rates of consumer 1 are relatively balanced, $u_{11} = 0.4$ and $u_{12} = 0.6$, for more extreme uptake rates for the

two alleles in $C_2$ (the red regions in each corner) none of them can survive in the long run. This is due to their high specialisation on one resource. The demand ratios of both consumers are relatively close to one and therefore, the difference of the demand of the two nutrients is relatively small. Since the nutrients are proportionally evenly distributed over the two resources, a more balanced uptake rate for both resources is advantageous if they are similarly available. Consequently, $C_1$ can exclude its competitor. The reason why allele $Y_2$ is the winner over the first allele is the fact that $Y_2$ has a higher uptake rate for resource 1 which consists of relatively more nutrient $a$ than $b$. Consumer 1 has a demand ratio smaller than one ($\beta_1 = 1/1.2$) and hence, requires relatively more of nutrient $a$. Supported by the absence of $C_2$, the uptake rates of allele $Y_2$ matches these conditions to a higher extent and it can prevail over $Y_1$.

For combinations of uptake rates for $C_2$ where at least one of the alleles possesses a relatively balanced uptake rate, the two consumers are able to coexist (with a small exception: the green strips represent extinction regions of consumer 1). Nevertheless, only one allele in each consumer has the chance to survive. To analyse how the winning allele is selected, let us take a closer look at those combinations.

If allele $Z_1$ has relatively balanced uptake rates, where the range is slightly shifted to a smaller uptake rate for resource 1, so $u_{21}$ lies between $0.3 \leq u_{21} < 0.6$, it can prevail over its opponent for most of the choices for $u_{22}$. This outcome is marked by brown colouring. Only if the uptake rate $u_{22}$ of $Z_2$ also takes a value between $0.3 \leq u_{22} < 0.6$, $Z_1$ can go extinct (grey regions). In this situation, where for both alleles the uptake rates lie between 0.3 and 0.6, the allele which has a slightly greater uptake rate for resource 2 has an advantage. The slight specialisation on resource 2 supports the higher uptake of nutrient $b$, which is more abundant in $R_2$. This on the other hand, better matches the demand ratio of consumer 2, since $\beta_2 = 1.2$ expresses a higher demand of nutrient $b$ than nutrient $a$. Therefore, the allele with a slightly greater uptake rate for resource 2, but otherwise relatively balanced, is able to exclude its competitor.

As we can see in Fig.17, the outcome is symmetric about interchanged uptake rates of $u_{21}$ and $u_{22}$ and the explanations for allele $Z_2$ are the same

as for $Z_1$ with interchanged roles.

In the outcome of consumer 1 we notice that only a very small area of uptake rates allows allele $Y_1$ to prevail over allele $Y_2$. Just in the light grey and light brown regions, allele $Y_1$ is the winner. But let us first analyse the outcome of the green areas, representing uptake rates for which consumer $C_1$ dies out. For exact same uptake rates for the first alleles in each consumer $u_{11} = u_{21} = 0.4$, the light green region expresses extinction of $C_1$ and the winning of allele $Z_1$ in consumer 2. The reason is the smaller initial consumer density of $C_1$ ($C_1(0) = 0.2$) compared to $C_2$ ($C_2(0) = 2$). At the time where allele $Z_1$ has established itself, both alleles in $C_1$ are still present. As the density of $C_2$ continues to grow (after a short up and down due to the initial conditions), because $Z_1$ provides a high amount of utilisable nutrients, the abundance of the resources shrinks for the other consumer. Since the uptake rates of allele $Y_1$ are the same as of consumer 2 ($Z_1$ is now the only allele present in $C_2$), the effort for the uptake of the two resources is equal. Due to the relatively high consumer density of $C_2$ compared to $C_1$, allele $Y_1$ has always a disadvantage which is transferred to its consumer. Although the allele frequencies in $C_1$ change in favour of the allele which better matches its consumer's demand ($Y_2$), this cannot help to recover from the already low density and the consumer goes extinct. These dynamics are shown exemplarily for uptake rates $u_{21} = 0.4$ and $u_{22} = 0.18$ in Fig.18.

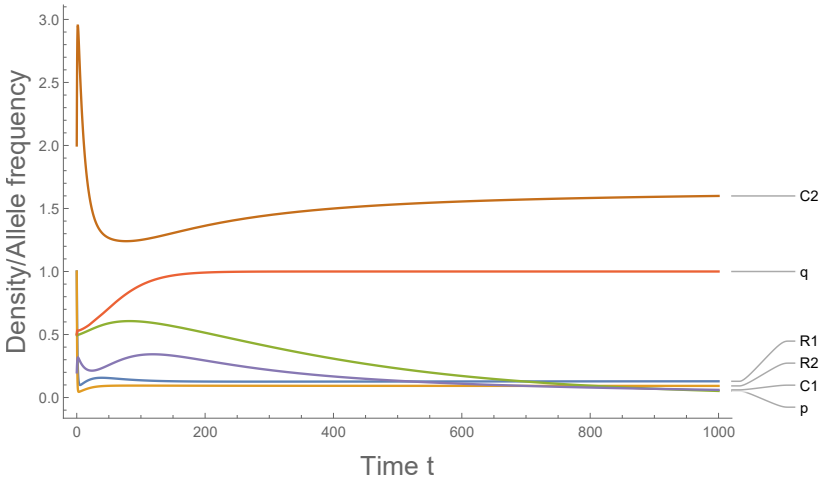


**Figure 18:** Resource densities $R_1$ (blue) and $R_2$ (orange), consumer densities $C_1$ (purple) and $C_2$ (brown) and allele frequencies $p$ (green) and $q$ (red) with respect to time $t$ for uptake rates $u_{21} = 0.4$ and $u_{22} = 0.18$ for the second consumer (light green region in Fig.17). The equilibrium $C_1 = 0, C_2 = 1.651, q = 1, R_1 = 0.132, R_2 = 0.092$ is reached after approximately 10000 time steps. The initial densities were given by $C_1(0) = 0.2, C_2(0) = 2.0, R_1(0) = R_2(0) = 1$, and the allele frequencies by $p(0) = 0.5$ and $q(0) = 0.5$. Other parameter values are as in Fig.17.

For slightly smaller uptake rates $u_{21}$ than $u_{11} = 0.4$, so for $0.3 \leq u_{21} < 0.4$ and located in the light brown region, the consumer density of $C_1$ in equilibrium can still be low but consumer 1 can persist. In consumer 2, allele $Z_1$ again excludes allele $Z_2$ while both alleles in $C_1$ still exist. With the now smaller uptake rate $u_{21}$, allele $Z_1$ puts a little bit less effort on resource $R_1$ than allele $Y_1$ and $Y_1$ can obtain more utilisable nutrients than in the case of equal uptake rates. The reason why allele $Y_1$ can prevail over $Y_2$ is again the unequal initial consumer densities. Allele $Y_2$ specialises more on $R_1$ and cannot uphold enough of $R_2$ due to the higher consumer density of $C_2$ and its relatively greater uptake rate for $R_2$. To obtain enough utilisable nutrients to survive it is necessary to put a high effort in the uptake of resource 2 to maintain one's share, even though the demand ratio of $C_1$ expresses a higher demand of nutrient $a$ (which is more abundant in $R_1$). The uptake rates $u_{11} = 0.4$ for $R_1$ and $1 - u_{11} = 0.6$ for $R_2$ of allele $Y_1$ fulfil these requirements to a higher extent than those of allele $Y_2$. Therefore, allele $Y_1$ is the winner in consumer 1. This outcome is shown for uptake

rates $u_{21} = 0.36$ and $u_{22} = 0.18$ in Fig.19.

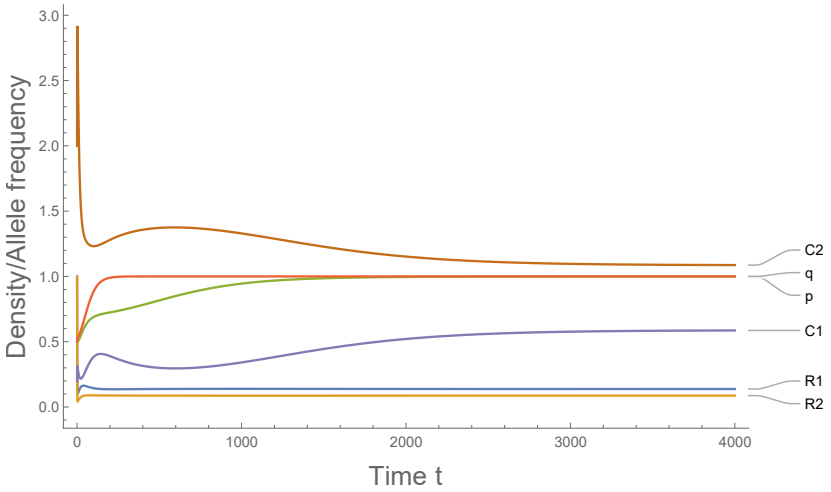


**Figure 19:** Resource densities $R_1$ (blue) and $R_2$ (orange), consumer densities $C_1$ (purple) and $C_2$ (brown) and allele frequencies $p$ (green) and $q$ (red) with respect to time $t$ for uptake rates $u_{21} = 0.36$ and $u_{22} = 0.18$ for the second consumer (light brown region in Fig.17). The equilibrium $C_1 = 0.588, C_2 = 1.085, p = 1, q = 1, R_1 = 0.138, R_2 = 0.087$ is reached after approximately 8000 time steps. The initial densities were given by $C_1(0) = 0.2, C_2(0) = 2.0, R_1(0) = R_2(0) = 1$, and the allele frequencies by $p(0) = 0.5$ and $q(0) = 0.5$. Other parameter values are as in Fig.17.

For even smaller uptake rates $u_{21}$, the allele divides its effort too unevenly on the two resources and cannot gain enough utilisable nutrients. These more extreme uptake rates lead us into the red region marking the extinction of consumer 2.

This light brown strip is only interrupted by the light grey area displaying a win of allele $Z_2$ instead of $Z_1$. The change in the winning allele of consumer 2 happens for similar uptake rates of $Z_1$ and $Z_2$, where $Z_1$ has a slightly higher uptake rate for resource 1. Since $\beta_2 = 1.2$, consumer 2 demands more of nutrient $b$ relative to nutrient $a$ and for these rather balanced uptake rates $Z_2$ is the better competitor. Similarly, the light green strip is interrupted. Since in the light grey area, allele $Z_2$ prevails over $Z_1$ the allele with the same uptake rate as $Y_1$ goes extinct and does not exclude consumer 1.

For the dark brown strip the explanations are similar to those above. To be located in this region, allele $Z_1$ possesses an uptake rate that expresses a relatively higher specialisation on resource 1 than the one of allele $Y_1$

($0.4 < u_{21} < 0.6$). This diminishes the abundance of $R_1$ and for most uptake rates $u_{22}$, the smaller uptake rate for $R_1$ of $Y_1$ does not provide enough nutrients. In this region, allele $Y_2$ uses its advantageous uptake rates to exclude allele $Y_1$.

For uptake rates $u_{21}$ and $u_{22}$ that are both between 0.3 and 0.6, but with a slightly greater uptake rate $u_{22}$ than $u_{21}$, allele $Z_2$ can exclude $Z_1$ as we discussed above (grey areas). Nevertheless, $Y_2$ is the winner for most of the choices of $u_{22}$. Only a small strip (light grey) represents an area where allele $Y_1$ can yet outcompete $Y_2$ in consumer 1. That allele $Y_1$ can prevail is due to the high utilisation of resource 2 by consumer 2 ($Z_2$ is the remaining allele) owing to the high consumer density and the selected uptake rates. The higher specialisation on $R_2$ of allele $Y_1$ is necessary to ingest sufficient utilisable nutrients so that consumer 1 can maintain itself. For an uptake rate $u_{22}$ greater than 0.4 this advantage of allele $Y_1$ is lost, because $Z_2$ puts its effort more on resource $R_1$ and it is no longer beneficial for $C_1$ to specialise on resource $R_2$.

This explains the eco-evolutionary outcome for sympatric consumers and with rather symmetric parameters, neglecting uptake rates that are equal for both alleles in one consumer ($u_{21} = u_{22}$).

As we already mentioned, the outcome does not only depend on the chosen uptake rates, but also on initial values for the consumer densities. How they influence the outcome is briefly discussed in the following paragraph. The previous explanations were based on a small initial consumer density of $C_1$ ($C_1(0) = 0.2$) and a respectively larger density of $C_2$ ($C_2(0) = 2$). In Fig.20 the outcome is displayed once for more similar initial conditions of the two consumers, but still with a small starting advantage for $C_2$ ($C_1(0) = 0.9$, $C_2(0) = 1.1$), and once for a distinctly greater initial consumer density of $C_1$ than $C_2$ ($C_1(0) = 2$, $C_2(0) = 0.2$).

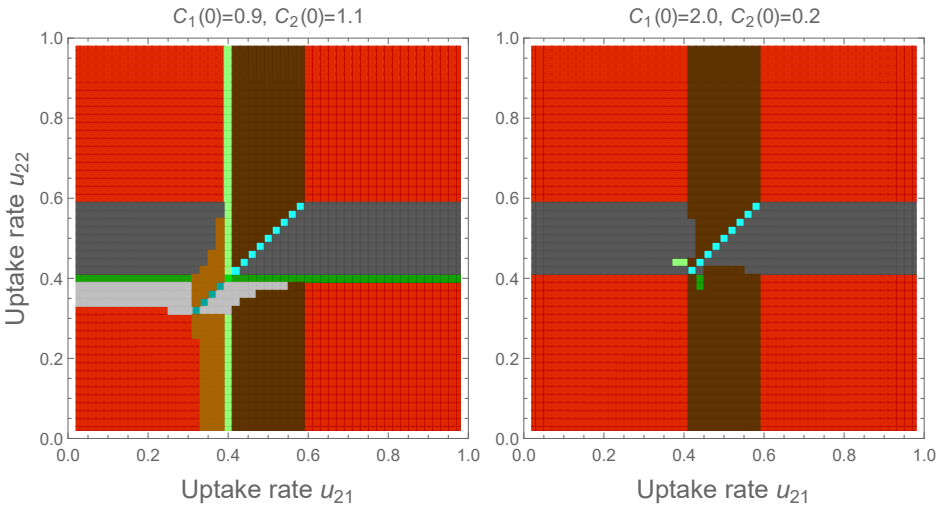


**Figure 20:** The eco-evolutionary outcome for the same symmetric parameters as in Fig.17, but different initial consumer densities. The colour coding is as described in Fig.17. On the left hand side the initial consumer densities are $C_1(0) = 0.9$ and $C_2(0) = 1.1$, the ones for the right hand side $C_1(0) = 2.0$ and $C_2(0) = 0.2$.

We can see, that if we reduce the initial density of $C_2$ compared to $C_1$ and increase the one for $C_1$, the light grey and light brown regions recede. As we already mentioned in the previous analysis of the eco-evolutionary outcome with initial consumer densities $C_1(0) = 0.2$ and $C_2(0) = 2.0$, that allele $Y_1$ in consumer 1 can prevail over its competitor for these uptake rates was due to the high initial density of $C_2$. For an overrepresented consumer 2, with an uptake rate for the winning allele between 0.3 and 0.4, it was necessary to put enough effort on the uptake of $R_2$ to defend one's share on that resource. Since the demand ratios are relatively close to one and the composition ratios of the two resources reciprocal to each other, it is essential to obtain enough of both resources to survive. When the initial consumer density of $C_2$ is chosen to be smaller than $C_2(0) = 2.0$, the total uptake of $R_2$ is also smaller and a higher amount is left for consumer 1. The more advantageous uptake rates regarding the demand ratio of $C_1$ provide allele $Y_2$ with a sufficient amount of nutrients of resource 2 and $Y_2$ can prevail over $Y_1$.

This receding of the two regions for uptake rates of one allele between 0.3 and 0.4 starts for high uptake rates for the second allele. The extreme

uptake rates for the second allele lead to its extinction on a faster time scale. The remaining allele provides $C_2$ with little nutrients and the higher initial consumer density of $C_1$ ensures that $C_2$ is excluded by its competitor. Since consumer 2 goes extinct while both alleles in $C_1$ are still present, allele $Y_2$ can use its better matching uptake rates to succeed in outcompeting allele $Y_1$. For even more deviating initial consumer densities in favour of consumer 1, $C_2$ can only prevail if at least one allele possesses even more balanced uptake rates than $C_1$ and allele $Y_2$ is the winner for almost all combinations of uptake rates for $C_2$.

Only the combinations in the green area lead to an extinction of consumer 2. This exceptional outcome results from an instability of the internal equilibrium (coexistence of the two consumers). Although, the temporary development shows a similar result as for combinations in the brown or grey region, as one allele in $C_2$ has almost asserted itself a sudden decrease in its frequency leads to its extinction. This entails a decrease in the density of $C_1$, since $Y_2$ is the only present allele in $C_2$ at that time and the uptake rate $u_{12} = 0.6$ is a little bit less profitable than the uptake rate of the now prevailing allele in $C_1$ regarding consumers' demand ratios. Eventually, consumer 1 goes extinct and either allele $Z_1$ (light green) or allele $Z_2$ (dark green) in consumer 2 is the only surviving allele.

As in the case of an allopatric consumer, we will now analyse the impact of other parameters. First, we identify the dependence of the eco-evolutionary outcome on the demand ratios of the consumers. Apparently, this outcome is independent of initial consumer densities and displayed in Fig.21. We analyse the effect of demand ratios that express a more extreme ratio of the two required nutrients and examine the outcome for $\beta_1 = 1/2$ and $\beta_2 = 2$.

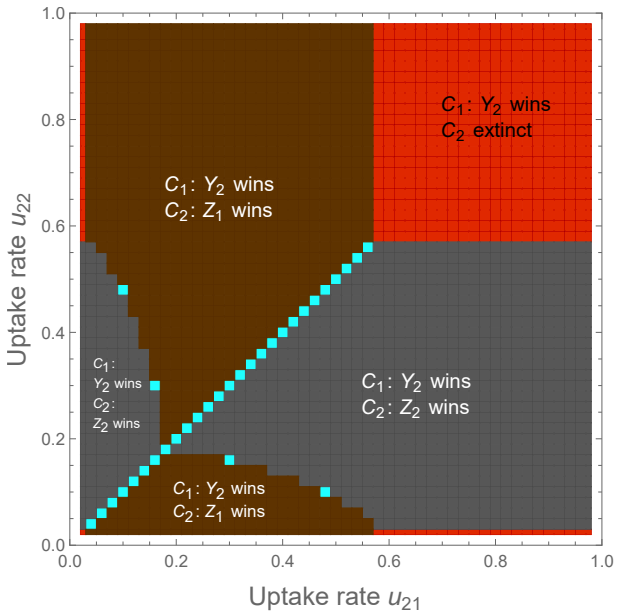


**Figure 21:** The eco-evolutionary outcome for more extreme demand ratios for both consumers, but which are again chosen to be reciprocal to each other. The demand ratio of consumer 1 takes the value $\beta_1 = 1/2$ and accordingly $\beta_2 = 2$ is the demand ratio for consumer 2. The colour coding is as described in Fig.17 and most of the regions are additionally labelled. Only the light blue region is left unlabelled and represents an equilibrium where $C_2$ is polymorphic and allele $Y_2$ is the winner in consumer 1. The parameters are still rather symmetric and still the same as in the preceding graphics except for the demand ratios: $u_{11} = 0.4, u_{12} = 0.6, \alpha_1 = 0.25, \alpha_2 = 4.0, d_1 = d_2 = 0.1, S_1 = S_2 = 1, D = 0.1$. The outcome does not depend on initial consumer densities and in that example is displayed for $C_1(0) = 0.2$ and $C_2(0) = 2.0$. The initial resource densities are again equal and given by $R_1(0) = R_2(0) = 1.0$, as are the initial allele frequencies $p(0) = 0.5$ and $q(0) = 0.5$, expressing no starting advantage of one of the alleles.

Fig.21 shows that allele $Y_2$ in $C_1$ is always the winner. This is due to the high demand for nutrient $a$ compared to $b$ and the more matching uptake rates of $Y_2$. For the demand ratio closer to one, allele $Y_1$ was able to prevail for certain combinations of uptake rates for the second consumer and appropriate initial consumer densities. As the demand ratio becomes more unbalanced, allele $Y_1$ has no chance to survive for the rather unsuitable uptake rates $u_{11} = 0.4$ for $R_1$ and $1 - u_{11} = 0.6$ for $R_2$.

If we compare the outcome for more extreme demand ratios with Fig.17, we can see, that the dark grey and dark brown strips become broader for

smaller uptake rates. That consumer 2 survives for relatively extreme uptake rates, where at least one uptake rate is relatively low, is a result of the more distinct demand ratios of the two consumers and the even better matching composition of one resource. So each of the consumers (or at least one allele in each) can ingest enough nutrients from its favoured resource. This holds true for almost all of these combinations, except if one uptake rate equals 0.02 and the second uptake rate is greater than 0.58. In this case, one allele ingests almost nothing of resource 1 which is in contrast to the other allele. Particularly, consumer 1 can exclude its competitor for these combinations of uptake rates for $C_2$.

In contrast to this is the upper-right red region, where both alleles in $C_2$ ingest a high amount of resource 1 that contains more of nutrient $a$ than $b$. Since the demand ratio of $C_2$ expresses a comparatively higher demand for nutrient $b$ than $a$, this uptake is rather unprofitable. Additionally, allele $Y_2$ in $C_1$ is the surviving allele with a corresponding high uptake rate for $R_1$ which further diminishes the abundance of $R_1$ and consumer 2 goes extinct.

In the other regions, the decision which of the alleles in consumer 2 is the winner depends, of course, on the uptake rates. As we already mentioned, the two strips (dark grey/brown) became broader for very small uptake rates for both alleles in $C_2$ compared to the outcome for demand ratios closer to 1. In the former analysis, we argued that for rather balanced uptake rates for one allele, this allele is the winner over its competitor except if the other allele possesses equally balanced uptake rates, then a higher uptake of resource $R_2$ was required. These arguments extend from balanced uptake rates to including small uptake rates for $R_1$ because the demand ratio $\beta_2 = 2$ stands for an even better matching resource $R_2$.

That the transition between the winning alleles in the lower-left corner is concave compared to a straight line at a critical value as in the previous case, is due to the more extreme uptake rates. For a low uptake rate for resource 1 of both alleles, the allele which puts considerably more effort on the uptake of $R_1$ can outcompete its opponent. Even though resource 2 is more favourable for consumer 2, if the uptake rate for $R_1$ is too small the allele cannot obtain as much utilisable nutrients as the allele with a slightly more balanced uptake of the two resources. This interaction is not linear,

but the higher this small uptake rate gets, the less advantageous is the more balanced uptake rate.

Special emphasis should be placed on the light blue areas apart from the diagonal for equal uptake rates of both alleles. In this area, allele $Y_2$ is still the winner in consumer 1 but furthermore, consumer 2 stays polymorphic in equilibrium. The combinations of uptake rates for this remarkable outcome are $u_{21} = 0.3$, $u_{22} = 0.16$ and $u_{21} = 0.48$, $u_{22} = 0.1$, and for reasons of symmetry the same uptake rates for interchanged roles of the two alleles. These seem to be the combinations that allow allele $Z_1$ and $Z_2$ to coexist for evolving abundances of the two resources. The resources are available at a certain extent that balances out the advantage of one uptake rate over the other for exact those uptake rates and none of the alleles in $C_2$ has an advantage.

As the demand ratios become more asymmetric, the regions for survival of the consumer with the more unbalanced requirements of the two nutrients recedes. For example $\beta_1 = 1/1.2$ and $\beta_2 = 2$, then the dark grey and dark brown strips in Fig.21 become thinner and in each corner the red region, expressing extinction of consumer 2, appears. On the other hand, if $\beta_1$ is more extreme, as for example $\beta_1 = 1/2$ and $\beta_2 = 1/1.2$, then the red region recedes towards each corner. Alongside the dark grey and dark brown areas, there even emerge regions for extinction of consumer 1.

Besides the demand ratios of the consumers, the composition of the resources plays an important role in the eco-evolutionary outcome. In the next paragraph we will examine the impact of these composition ratios in our example of uptake rates $u_{11} = 0.4$ and $u_{12} = 0.6$ for consumer 1 and with the previously chosen demand ratios ($\beta_1 = 1/1.2$, $\beta_2 = 1.2$). For this purpose, we change the composition ratios such that the resources contain a more balanced amount of both nutrients, but with still a little bit more of nutrient $a$ in $R_1$ and $b$ in $R_2$. Therefore, the composition ratios are closer to one and we set $\alpha_1 = 2/3$ and $\alpha_2 = 3/2$.

This has a similar effect on the eco-evolutionary outcome as more extreme demand ratios of the consumers, but for some other reason. For demand ratios that are more deviating from the value one, the consumers require much

more from one nutrient than from the other and a higher specialisation on the more matching resource is advantageous. In the case of similar resource compositions, both resources provide the consumer with a similar amount of both nutrients. Since allele $Y_2$ with a higher uptake rate for $R_1$ is the winner in consumer 1, $C_2$ with a rather small uptake rate for $R_1$ of at least one allele obtains enough utilisable nutrients from $R_2$ which is the (slightly) better matching resource anyway. Since the compositions of the resources are more balanced, a high uptake of resource 2 provides $C_2$ still with enough of the less abundant nutrient $a$. Again, if both alleles in $C_2$ have a relatively small uptake rate for resource 1, the allele with a slightly higher uptake rate for $R_1$ is the winner. This is due to the high uptake of $R_2$ and the resulting decrease of the resource abundance. The allele which obtains more of $R_1$ survives this shortage of $R_2$ while the other allele goes extinct.

As for more unbalanced demand ratios, there exist combinations of uptake rates for $C_2$ that lead to a polymorphism in consumer 2. The two combinations are given by $u_{21} = 0.36$ and $u_{22} = 0.2$ and, vice versa, $u_{21} = 0.2$ and $u_{22} = 0.36$.

If we change the composition ratios asymmetrically, one nutrient is proportionally more abundant than the other. For a certain higher availability of nutrient $a$, consumer 2 has no chance to survive, independent of the uptake rates of its alleles. The demand of proportionally more nutrient $b$ than $a$ leads to a malnutrition of the consumer and entails the extinction of $C_2$. Since nutrient $a$ is more abundant, consumer 1 has to make sure to obtain enough of nutrient $b$. Allele $Y_1$ has the better matching uptake rates in this case and consequently is the winner. If nutrient $b$ is more available, the phase space for the outcome with respect to the uptake rates of $C_2$ shows a different pattern. As the more required nutrient becomes proportionally more abundant in both resources, consumer 2 can even exclude its competitor for a certain set of uptake rates. For these exclusion regions, one allele in $C_2$ just has to have a relatively high uptake rate for $R_1$ (between 0.44 and 0.88) to reduce enough of the amount of the better fitting resource for $C_1$. In these regions, there even exist relatively large areas where allele $Z_1$ and $Z_2$ can coexist. Nevertheless, for extremely high uptake rates for $R_1$ of both alleles in $C_2$, consumer 1 can outcompete its opponent and for few combinations it

even stays polymorphic.

The above results were obtained for chosen fixed uptake rates for consumer 1, namely $u_{11} = 0.4$ and $u_{12} = 0.6$. These provided consumer 1 with rather balanced uptake rates for both resources. How the outcome changes if we assume more extreme uptake rates for $C_1$ is the final topic in our discussion.

For this purpose, we assign the values $u_{11} = 0.2$ and $u_{12} = 0.7$ to the uptake rates of the alleles in $C_1$. For an allopatric consumer, these uptake rates would rather favour allele $Y_2$ if the demand ratio is still $\beta_1 = 1/1.2$ and the composition ratios of the resources are again $\alpha_1 = 0.25$ and $\alpha_2 = 4.0$. In sympatry the outcome is more complicated since the second consumer influences the abundances of the resources, which on the other hand can change the more profitable allele.

If we again consider otherwise symmetric parameters, the outcome displayed in Fig.17 changes to Fig.22 for the altered uptake rates of consumer 1. We again start to discuss the eco-evolutionary outcome for a small initial consumer density of $C_1$ ($C_1(0) = 0.2$) and a higher initial consumer density of $C_2$ ($C_2(0) = 2.0$).

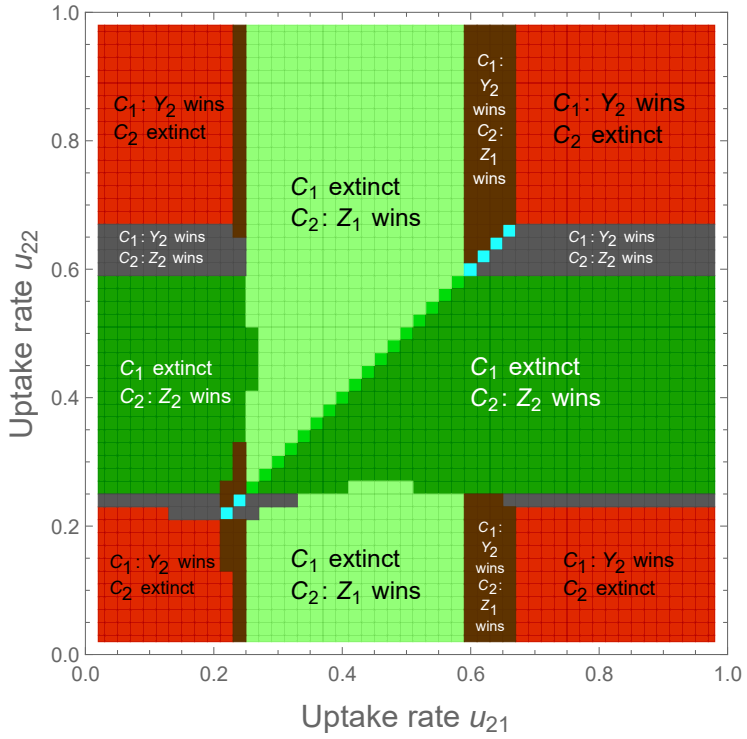


**Figure 22:** The eco-evolutionary outcome for more extreme uptake rates for consumer 1 and two consumers living in sympatry. The colour coding is as in Fig.17 with additional colours: in the green regions, consumer 1 goes extinct and either allele $Z_1$ (light green) or $Z_2$ (dark green) is the winner in consumer 2. The uptake rates for consumer 1 are $u_{11} = 0.2$ and $u_{12} = 0.7$. Other parameters are again chosen to be rather symmetric: $\alpha_1 = 0.25, \alpha_2 = 4.0, \beta_1 = 1/1.2, \beta_2 = 1.2, d_1 = d_2 = 0.1, S_1 = S_2 = 1, D = 0.1$. The outcome of the eco-evolutionary model was derived for initial consumer densities $C_1(0) = 0.2$ and $C_2(0) = 2$, resource densities $R_1(0) = 1$ and $R_2(0) = 1$ and balanced allele frequencies $p(0) = 0.5$ and $q(0) = 0.5$.

Immediately, the green area catches our eye. For the more balanced uptake rates for $C_1$, there was always at least one of the alleles in consumer $C_1$ that could prevail in the end (again with the small exception of the green strips in Fig.17). Now the situation is different: for uptake rates for consumer 2 that take intermediate values (at least for one of the alleles), $C_2$ is able to exclude its competitor. These more balanced uptake rates prevent the reliance on one resource and since the initial consumer density of $C_2$ is considerably high, both resources are utilised to a great extent, leaving no chance for consumer 1 to gain enough utilisable nutrients. This extinction

region extends over almost the whole range between 0.2 and 0.7, the uptake rates for the alleles in $C_1$.

If the alleles in consumer 2 take even more extreme values for the uptake rates than $C_1$, $C_2$ is again not able to persist against $C_1$. This outcome is marked with a red colour and is found in each corner of the phase space (Fig.22) with respect to the uptake rates of consumer 2. The consumer with the more balanced uptake rates is most probable also the winner over its competitor and only in the transition regions, both consumers can prevail (dark grey and dark brown regions).

We also notice that if consumer 1 is able to survive, allele $Y_2$ is always the winner. This is due to the higher uptake rate for resource 1, the better matching resource for $C_1$. For consumer 2, the allele with the more balanced uptake rates for both resources prevails over its opponent, unless both alleles have similar uptake rates. Then the allele with the higher uptake rate for resource 2 is the winner, which is owned to the demand ratio, expressing a higher demand of nutrient $b$ than $a$.

As the initial consumer densities change in favour of consumer 1, the red regions in the upper-left, lower-left and lower-right corner expand, forcing the regions of extinction of $C_1$ to recede. Otherwise the outcome is very similar to the one discussed for $C_1(0) = 0.2$ and $C_2(0) = 2.0$.

The impact of slight changes of other parameter values is, of course, similar to the one for more balanced uptake rates for $C_1$ ($u_{11} = 0.4$ and $u_{12} = 0.6$). For the altered demand ratios, the areas of extinction of consumer 2 recede, which leaves more space for the regions where consumer 2 can survive and sometimes even exclude its competitor.

The effect of changes in the composition ratios depends on the proportionally more available nutrient. If we increase the proportion of nutrient $a$ in $R_2$, the area where consumer 1 excludes its competitor is now polymorphic. Both resources contain enough of nutrient $a$ to survive and since the alleles in $C_1$ specialise on different resources, they are able to coexist. A higher proportion of nutrient $b$ in resource 1 is disadvantageous for consumer 1 and the region where $C_1$ could exclude $C_2$ recedes for the more extreme uptake rates of $C_1$. In the case, that both resources contain very similar proportions of both nutrients, the outcome is almost the same as for the more balanced

uptake rates. Only the region where consumer 1 excluded $C_2$ and allele $Y_2$ was the winner changes to a coexistence region for $Y_1$ and $Y_2$ in consumer 1 and a small transition region appears where $C_1$ stays polymorphic and either allele $Z_1$ or $Z_2$ prevails.

So far we only considered demand ratios that fall on opposite sides of the nutrient supply ratio ($\alpha_S$). These allowed a greater variety of eco-evolutionary outcomes. Nevertheless, we want to briefly discuss the impact of the nutrient supply ratio since it played an important role in the sympatric outcome of the Fox-Vasseur model.

In our model, both consumers are able to coexist even if both demand a relatively higher amount of nutrient $a$ ($b$) compared to $b$ ($a$). The actual outcome depends on the chosen uptake rates, but the range of parameter combinations that provide a coexistence region is smaller than for demand ratios on opposite sides of $\alpha_S$.

For consumers with adaptive uptake rates (Fox-Vasseur model), a higher demand of the same nutrient always leaded to an exclusion of one consumer. Recall that if both consumers became limited by the same nutrient, the consumer which could make the most of the non-limiting nutrient was prevailing over its competitor. This was due to the reduction of the availability of the limiting nutrient for the second consumer such that it could not ingest enough utilisable nutrients.

We have seen that for consumers living in sympatry the analysis becomes inevitably more difficult. Since there are many different parameters, it is more difficult to understand their interplay. For this reason, we partitioned the analysis into smaller sections where we discussed the influence of each parameter separately. When we have understood their effect on the outcome, we can combine the explanations to understand the full eco-evolutionary dynamics including parameter changes.

In sympatry, we note that more balanced uptake rates are advantageous for the consumer. In the case of two consumers, the resources are less abundant for a single consumer than in allopatry and each allele has to "fight" for enough nutrients. A specialisation on one resource diminishes the chance to

obtain sufficient utilisable nutrients. Unless either the demand ratios or the composition ratios take more extreme values, then it could be profitable to have a rather unbalanced uptake of the two resources.

For most combinations of uptake rates for $C_2$, not more than one allele in each consumer can survive. There is just a small parameter range, where a polymorphism appears in one consumer. We found no combinations where both consumers stay polymorphic and therefore, at most three alleles could coexist.

# 4 Discussion

To conclude, we compare the two eco-evolutionary models, the Fox-Vasseur model and the alternative model with the population-genetics approach, and point out their main differences.

If we restrict our analysis to the pure ecological dynamics, both models have the same ecological outcome. For fixed allele frequencies in our population-genetics model, the average uptake rates have the same properties as fixed uptake rates in the Fox-Vasseur model. As soon as we include evolutionary dynamics in our analysis, the results of the two models are quite different.

Whereas in the Fox-Vasseur model the adaptive dynamics of the uptake rates and how resource abundances influence them is the subject of the analysis, in our population-genetic model, we are interested under which conditions consumers can be maintained polymorphic. Unfortunately, we did not find a case, where both consumers stayed polymorphic. At most one consumer was able to maintain its genetic diversity, whereas in the other consumer one allele went extinct or the second consumer was not able to survive at all. In the Fox-Vasseur model, the consumers can alter their diet to maintain enough utilisable nutrients and adapt to the ecological conditions. In our alternative model, the average uptake rates of the consumers also change according to the allele frequencies. The alleles, on the other hand, have fixed uptake rates and we examine how allele frequencies develop and if both alleles can persist. In the case of extinction of one of the alleles, the average uptake rate evolved to the uptake rate of the prevailing allele.

One main difference in the two eco-evolutionary models is the analysis of the allopatric case. In the Fox-Vasseur model the question if an unbalanced diet or a colimitation by the two nutrients is advantageous is of main interest. Since one consumer has always enough resources due to the chemostat dynamics, it can never die out. So in allopatry the goal of the consumer is to maximize its density by adapting the uptake rates such that it gains as much utilisable nutrients as possible. This can even include a higher ingestion of the rather unfavoured, but more abundant, resource and excreting the excess nutrient. In this case, the demand ratio would promote a specialisation on

one resource if provided ad libitum, but as this resource is driven to a very low density a higher uptake of the more abundant resource is advantageous.

In our population-genetic model we also assumed chemostat dynamics for the growth of the resources and therefore, the survival of the consumer in allopatry is ensured. Compared to the Fox-Vasseur model, the consumer can only change its uptake rate to a certain extent. Since the average uptake rate depends on the allele frequencies, the most extreme values it can take are the uptake rates of the alleles if one allele goes extinct. For an allopatric consumer, we were not able to find a polymorphism and therefore, the uptake rate of the consumer evolves to one of the uptake rates of the alleles. The given uptake rates decide which allele can make the most of the current conditions and further prevails over its opponent. For most of the demand ratios the outcome is decided merely by the choice of uptake rates. Only for a small range of the demand ratio, the outcome depends on initial conditions. Consequently, we were mainly interested in those transition regions where the outcome depends on the initial resource abundances. So, compared to the Fox-Vasseur model where the adaptive uptake rates play an important role, we investigated which allele could provide more utilisable nutrients and exclude its competitor.

Another significant difference of the two models is the role of the nutrient supply ratio in a sympatric habitat. In the Fox-Vasseur model, if the two consumers have demand ratios on opposite sides of the nutrient supply ratio ($\alpha_S$) the coexistence in sympatry is stable whenever they were able to persist under allopatric conditions. The contrary is the case for demand ratios that fall either both above or both below the nutrient supply ratio, where the better competitor for the non-limiting nutrient can always exclude its opponent.

In our population-genetic model, the outcome does not depend solely on the nutrient supply ratio. Even though the range of parameter combinations for coexistence of the two consumers becomes smaller when both demand ratios are either greater or smaller than $\alpha_S$, coexistence is still possible. On the other hand, demand ratios that fall on opposite sides of $\alpha_S$ do not guarantee a stable coexistence. It rather depends on the chosen uptake rates, which of the consumers can prevail. More balanced uptake rates promote

the survival of its consumer, except for an extremely uneven distribution of the nutrients over the resources or a much higher demand of one nutrient compared to the other. Then it may be advantageous to possess rather unbalanced uptake rates in favour of the consumer's demand. In our analysis, we investigated the outcome primarily for the uptake rates $u_{11} = 0.4$ and $u_{12} = 0.6$ for consumer 1 and explore the impact of other parameters by slightly varying their values. The conclusion, that more balanced uptake rates promote the survival of its consumer, was drawn by comparing the outcome for the case of rather balanced uptake rates for consumer 1 ($u_{11} = 0.4$, $u_{12} = 0.6$) to the outcome for more extreme uptake rates $u_{11} = 0.2$ and $u_{12} = 0.7$.

Additionally to the survival of the consumers, we investigated which of the alleles could prevail in an existing consumer. Especially, we tried to find a polymorphism where in both consumers both alleles would be able to survive and for this purpose, we always started with balanced allele frequencies $p(0) = 0.5$ and $q(0) = 0.5$. As we already mentioned above, we were not able to find a polymorphism in both consumers at the same time. Since the consumer's demand ratio applies for both alleles, for most combinations of uptake rates, usually one allele has the better matching trait and is the winning allele in its consumer. However, the complex dynamics of two consumer and two resource abundances provide, in some cases, small ranges of parameter combinations where a polymorphism in one consumer appears. This is in contrast to a consumer in allopatry, where always one allele went extinct and just one allele could prevail in the end. Still, we found no parameter combinations where stable polymorphisms in both consumers were the case and hence, not more than three alleles could be maintained.

In the Fox-Vasseur model, not only the adaptation of a single uptake rate was investigated, but also how the two uptake rates evolved compared to each other. So, for a stable coexistence of the two consumers the question arose if this coexistence was achieved either by character convergence, divergence, or parallel shifts of the traits. The answer was found by investigating the adaptation of the uptake rates in the allopatric case for both consumers. If they were both colimited, character convergence was the result. Since the second consumer diminishes the abundance of the resources,

the consumer has to maintain enough of the preferred resource of its opponent which leads to converging uptake rates. For a single-nutrient limitation of both consumers, the advantage of the more abundant resource is lost due to the shared resources and a specialisation on the more matching resource is beneficial. Since the demand ratios have to be on opposite sides of the nutrient supply ratio to provide stable coexistence, for each consumer another resource is the better option and character divergence is the result. In the case that one consumer was colimited and the other one nutrient-limited, the consumers' uptake rates both change in the same direction which was referred to as parallel shifts by Fox and Vasseur.

So, while in the Fox-Vasseur model the adaptation of the uptake rates and the selected diets were the main subjects, for the population-genetic approach, we investigated under which conditions consumers can be maintained polymorphic. Hence, besides the survival of the consumers and if both consumers were able to coexist, we were additionally interested if the genetic diversity in the consumers can be preserved.

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