Self-organisation and emergent properties of the trophic structure and nutrient cycling of ecosystems

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0.1 Responsible group leader

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0.2 Composition of the research group

| name | discipline | paid by | hrs/ week |
|--------------------------------|--------------|---------|-----------|
| | | | |
| vacant | mathematics | VUA | 37 |
| Drs. L. D. J. Kuijper | biology | VUA | 5 |
| Dr. B. W. Kooi | mathematics | VUA | 5 |
| Dr. C. Zonneveld | biology | VUA | 2 |
| Prof. Dr. S. A. L. M. Kooijman | theor. biol. | VUA | 3 |
| Prof. Dr. J. A. J. Metz | theor. biol. | RUL | 1 |
| Dr. H. Dijkstra | physics | UU-IMAU | 1 |

0.3 Project Proposal

Motivation

Ecosystems, such as the open ocean, tend to be extremely diverse and complex. Many factors contribute to their complexity: biological, physical and chemical components, inflow of water, various time scales in both space and time and human influences. So far, the present models do not seem to adequately describe the complex adaptive system characteristics of an aquatic ecosystem.

Many attempts have been made in the past to model ecosystems such as estuarine environments or the sea. One of the main complications is that realistic models, which integrate biology, chemistry and physics, become very complex. Such models need many variables and parameters^{*1} to describe all the processes accounted for. For various reasons, complex models do not in general contribute much to a better understanding of ecosystem structure and functioning. They are difficult to test, parts of their structure is uncertain, and many of their parameters are poorly known. With some patience computer simulations can be tuned by

¹The * denotes the presence of an entry in the glossary at the end of the proposal

changing parameter values to fit data sets, but the predictive power remains limited. Uncertainties in the, sometimes small, amount of data add to the limitations of the usefulness of a complex model.

Important notions for characterisation of any marine ecosystem are resilience, durability and self-organisation. To reflect these notions in a model, the system is often described in terms of biological, chemical and physical interactions between a set of chosen state variables. The result is a complex dynamical ecosystem model. Examples of such models are ERSEM, the European Regional Seas Ecosystem Model [1, 2] and the GEM, a Generic Ecological Model [6].

A more straightforward way to describe an ecosystem is by considering the changes of the distribution of the different species in the system in time, the so called AMOEBE approach. However, the dynamical properties of an ecosystem cannot be described by only considering the biological components of the system. For example, the North West European Shelf Program [13] shows that the productivity in the North Sea is largely determined by the variable input of Atlantic water and the weather.

Important aspects of ecosystems are their structure, i.e. the biomass distribution over the various trophic levels^{*}, and their function, generally understood as the cycling of the various nutrients. Study of these aspects is rather difficult in complex models. The aim of this project is to study the coupling between ecosystem structure and functioning starting from more simple models that capture only the bare essentials of the system.

Aims and Methodology

We will try to reach an understanding of the function/structure coupling using a different and totally new approach. We start from a very simple single-species community of mixotrophs^{*}, and allow the community to develop into a more complex (and realistic) multi-species system following an accelerated evolutionary process. The process is realistic, autonomous and, most important, self-organising. The multi-species community will have competing producers^{*}, specialised and non-specialised decomposers^{*}, and a food web of consumers^{*}, with small and large body sizes (and associated differences in physiological time scales). The cycling of energy and nutrients in the community will be followed in a homogeneous space, and in a space with an one-dimensional spatial structure, to allow for gradients in light and redoxpotential and settling to built up sediments. Below we describe how this self-organising evolutionary process is constructed, using the DEB^{*}-model.

What we hope to find, by following this line, is a (rather) simple mathematical description for the emerging nutrient cycling and biomass distributions. Ultimately, such a model can be used in hydrodynamically explicit physical-chemical models for the description of specific systems, such as the North Sea or open ocean.

The DEB-model

The development of a mixotroph into an autotroph or a heterotroph^{*}, and a specialisation of heterotrophs into decomposers, or carnivores, is only possible if all these life forms can be captured in a single modelling framework. The DEB theory offers such a framework, and specifies the processes of substrate (nutrient, light, food) uptake and use (for the purposes of maintenance^{*}, growth^{*}, development, reproduction) of all life forms. It includes the process of aging, and body size scaling relationships. A summary of the theory is given in Section 0.4.

- Accelerated evolution The behaviour of a single-species community of mixotrophs is characterised by the parameters in the DEB-model. For instance, the ability for autotrophic assimilation^{*} is one of the parameters. The value is a measure for the efficiency of autotrophic assimilation. In the model described in the Appendix these parameters are given for the complete community. The organisms only differ in parameter values and in the values of the state variables (body size and amounts of reserves). The parameters remain fixed for each individual but the state variables change as the organisms follow their life cycles. To understand evolution over the generations, we need to distinguish the different organisms in the community. This can be modelled by specifying a set of rules:
 - 1. When the body size of an organism reaches a threshold value it will divide or start reproduction.
 - 2. The characteristics (one or more parameters) of (one of) the daughters can differ from that of the mother, even a mutation (a jump in the parameter value) might occur.
 - 3. Death occurs in a discrete manner. More precisely, every time interval, every organism has a certain probability to die. The probability depends on internal and external factors.

The characteristics that can be altered are the efficiency for autotrophic and heterotrophic assimilation. The costs for growing are related to these changes. The rules have several consequences for the model in Appendix 0.4. First, the destiny of all the individuals has to be traced separately since their behaviour is different. Second, death and parameter settings are stochastic events; as a consequence, the model is no longer deterministic.

Such an approach allows simulation of an evolutionary process. The difference in parameter values permits individuals to compete for resources in an effective way. As a consequence, reproduction is more rapid for some organisms and they are copied more frequently. In combination with death (by starvation, predation, aging) this mechanism results in selection of these organisms.

One of the questions that is interesting to us is the coexistence of individuals with different specialities. Under which conditions can these individuals coexist? In other words, can different specialised groups coexist within a single community of mixotrophs, without competitive exclusion?

We do realise that, without the ocean context, such a system is mainly of theoretical interest. However, we think that it represents the simplest ecosystem that is capable of full nutrient recycling. It is only through the understanding of such very simple artificial ecosystems, that we might hope to understand more realistic (and much more complex) ecosystems in full depth. Moreover, in simple models, the effect of parameter changes can be studied in sufficient detail.

Species-diversity and stability The increase in bio-diversity allows a specialisation of functions, which enhance metabolic* versatility. In the department of Theoretical Biology, a project parallel to this proposal is in progress. It compares the function/structure coupling in a series of simple deterministic models: an one-species community of mixotrophs, a three-species community of producers, consumers, and decomposers, and a morespecies community with a simple food web structure. We plan to compare the findings in these models with the function/structure coupling in our self-organising community. More precisely, we shall try to quantify the stability of the self-organising system. However, the standard methods to quantify stability do not apply to stochastic models, therefore new methods have to be developed and applied. If successful, the new methods are also applied to the sequence of simple deterministic models in order to compare the results.

Body size scaling relationships While the DEB theory deals with mechanisms, at the same time simple rules are implied for the covariation of parameter values among species. Parameter values do not vary independently, but tend to co-vary in a very special way. If the parameters of the DEB model for all species are plotted in the parameter-space, and each species is characterised by a single point, the points will scatter around a single line in this space. Many life-history features, such as maximum body sizes, reproduction rates, life spans, travelling rates and distances, can be written as functions of the parameters. As a result, these features also covary in a predictable (if sometimes complex) way [8, 10, 3]. We will allow a 'diffusion' of parameters along the line in the parameter-space, and thus allow segregation of body sizes, and the associated scales in time and space in which the organisms live. (Whales live on time/space scales that are very different from that of copepods). We expect to find that species with large body-size will be rare. It is their impact on the function and the stability of the system that we want to evaluate.

0.4 A concise description of the DEB mixotroph model

A mixotroph is an organism that has both photoautotrophic and heterotrophic capabilities to acquire energy and nutrients. This, for instance, occurs in photoautolithotrophic cyanobacteria [15, 16] and in chemoautolithotrophic bacteria [7]. We focus on the assimilation of carbon dioxide, ammonium, light, and organic compounds. In particular, we can study a non-trivial mixotroph community by analysing the situation where the organic compounds, i.e. detritus, originate from the organism itself (from aging). The organism's heterotrophic capabilities also allow uptake of organic compounds. Therefore, the mixotrophs are both a source and a sink of organic compounds, and thus we obtain resource recycling.

We are interested in the chemical elements C, H, O, and N, with ammonium as the only inorganic nitrogen source. Although nitrate is more abundant in real systems, organisms excrete ammonium, so the inclusion of nitrate requires the inclusion of ammonium as well. The carbon dioxide is represented by dissolved inorganic carbon. Water H and oxygen O are always taken to be available *ad libitum*. Therefore, the only potentially limiting compounds left are N and C, while light may also be limiting. We study a system that is closed for mass. However, the source of light is outside the system, which makes it open for energy. The temperature is taken to be constant.

Any organism is described in terms two components: structure and reserves. Each of these components has a given fixed stoichiometry^{*}. As the amount of reserves relative to structure can vary in time, overall biomass composition is not fixed. However, the scope for variation in this composition is restricted. There are several reasons for modelling an organism in this particular way, for details we refer to [10] pg. 20–23. In this approach the organism can be

characterised by two state variables^{*}: mass of reserves and structural mass (in units carbon). Due to aging individual organisms may die. As the organism is composed of structure and reserves we also delineate two types of detritus, namely dead structure and dead reserves. This yields another two state variables: mass of dead reserves and dead structure (in units carbon). The digestion efficiencies by the mixotroph for the different types of detritus might differ. The last two state variables we can introduce are mass of free carbon and mass of free nitrogen. However, it is possible to eliminate these two extra variables since the total amount of nitrogen and carbon is conserved.

The changes in the state variables are specified in terms of fluxes^{*}. Each of the fluxes represent different transformations: autotrophic and heterotrophic assimilation, growth, death and maintenance. Schematically, the different processes are shown in Figure 1. The changes in the state variables are given by a system of coupled ordinary differential equations. For the exact equations we refer to [12].



Figure 1: Schematic overview of the different transformations

As long as the mixotroph has a single type of (generalized) reserve, light, C and N are required simultaneously to growth autotrophically. Due to the spatial structure of the aquatic environment, the delineation of an N-reserve and a C-reserve must be considered. This construct allows the organism to accumulate carbohydrates at the surface, and nutrients at the bottom of the photozone, when the wind takes care for the vertical migrations.

The appendix describes some preliminary results by Claudia Mulder that might serve as a first orientation to the problem.

1 Time schedule

year 1 Literature study on DEB theory, Adaptive Dynamics theory and community physiology. Comparison of model formulations that include 0, 1 and 3 reserves. Dynamics of vertical structure with diurnal and seasonal forcing of light and temperature. (Single species). Analysis of horizontal spatial structure using ocean circulation simulation software. Orientation on software to simulate individual based dynamics.

- year 2 Adaptive dynamics studies that allow for specialization of mixotroph into auto- and heterotrophic activities. Analysis of speciation process, stability and invasibility issues. (Three species)
- year 3 Advanced adaptive dynamics studies that allow for specialization of decomposition activities, and consumer food webs subjected to body size scaling relationships. (Many species problem)
- year 4 Attempts to simplify the complex dynamics, in order to understand the observe phenomena.

Glossary

assimilation Generation of reserves from substrates (food, nutrients, light)

consumer Any organism which consumes other organisms

- **DEB** Initials of the Dynamic Energy Budget model or theory. The term 'dynamic' refers to the contrast with the frequently used Static Energy Budget models, where the specifications of the individual do not change explicitly in time
- **decomposer** Organism such as bacteria and fungi that break organic materials down into simpler compounds and eventually into inorganic materials.
- **flux** An amount of mass or energy per unit of time. An energy flux is physically known as a power
- growth Increase in structural mass or structural volume
- **heterotroph** An organism that uses organic compounds as a source of energy; Photo-autotrophs use light
- **maintenance** A rather vague term denoting the collection of energy-demanding processes that life seems to require to keep going, excluding all production processes. We also exclude heat production in endotherms
- mixotroph An organism that is both photoautotroph and chemo-heterotroph
- **nutrients** Inorganic substrates used for the synthesis of reserves; carbon dioxide and ammonia are examples, and light is also included for convenience
- **parameter** A quantity in a model that describes the behaviour of state variables. It is usually assumed to be a constant
- **producer** Any autotroph capable of synthesising organic material, thus forming the basis of the food web
- **respiration** The consumption of oxygen, or the production of carbon dioxide. Both fluxes have a relationship with the use of energy.
- **state variable** A variable which determines, together with other state variables, the behaviour of a system. The crux of the concept is that the collection of state variables, together with the input, determines the behaviour of the system completely
- **trophic level** Any of the feeding levels that energy passes through as it proceeds through the ecosystem

References

- [1] J.G. Baretta-Bekker, editor. European Regional Seas Ecosystem Model I (1991–1993), volume 33 (3–4) of Netherlands Journal of Sea Research (Special Issue), 1995.
- [2] J.G. Baretta-Bekker and J.W. Baretta, editors. *European Regional Seas Ecosystem Model II* (1993–1996), volume 38 (3–4) of *Journal of Sea Research (Special Issue)*. Elsevier, 1997.
- [3] J.D. Damuth. Taxon-free characterization of animal communities. In A.K. Behrensmeyer, editor, *Terrestrial Ecosystems through Time*, pages 183–203. The University of Chicago Press, 1992.
- [4] S.A.H. Geritz and E. Kisdi. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12:35–57, 1998.
- [5] M.H. Holmes. *Introduction to perturbation methods*. Texts in Applied Mathematics 20. Springer-Verlag, 1995.
- [6] Smits J.C.G. GEM, a Generic Ecological Model for estuaries. Technical report, delft hydraulics, 1997.
- [7] D. M. Karl. Ecology of free-living, hydrothermal vent microbial communities. In D. M. Karl, editor, *The microbiology of deep-sea hydrothermal vents.*, pages 35–124. CRC Press, New York, 1995.
- [8] S. A. L. M. Kooijman. Energy budgets can explain body size relations. J. Theor. Biol., 121:269–282, 1986.
- [9] S. A. L. M. Kooijman. The synthesizing unit as model for the stoichiometric fusion and branching of metabolic fluxes. *Biophys. Chem.*, 73:179–188, 1998.
- [10] S. A. L. M. Kooijman. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, 2000.
- [11] S. A. L. M. Kooijman. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, 2000.
- [12] S. A. L. M. Kooijman, H. A. Dijkstra, and B. W. Kooi. Light-induced mass turnover in a mono-species community of mixotrophs. J. Theor. Biol., 2001. subm 2001/02/27.
- [13] R. Laane, editor. Special Issue on NOWESP. German Journal of Hydrography, 1996.
- [14] J. Maynard Smith and G.R. Price. The logic of animal conflict. Nature, 246:15–18, 1973.
- [15] M.A. Schneegurt, D.M. Sherman, and L.A. Sherman. Growth, physiology, and ultrastructure of a diazotrophic cyanobacterium, cyanothece sp. strain atcc 51142, in mixotrophic and chemoheterotrophic cultures. *Journal of Phycology*, 33:632–642, 1997.
- [16] L. Stal. The metabolic versatility of the mat-building cyanobacteria *Microcoleus chthono-plastes* and *Oscillatoria limosa* and its ecological significance. *Algol. Stud.*, 64:453–467, 1991.

A Adaptive dynamics applied to the DEB mixotroph model by Claudia Mulder

A.1 Introduction

Ecosystems generally consist of various species. These species represent three basic functions: Producer, consumer and decomposer. In modelling ecosystems one may either focus on species level or on the functional level. The disadvantage of the species level is that such models rapidly become very complex. Because ecosystem normally consists of many species, a species-based model will have a large number of parameters and variables. As a consequence, the analysis is difficult and few general insights are to be expected.

Models based on the functional approach tend to be much simpler as only a small number of functions is involved. Although general insights can be expected this approach also has its drawbacks. First, species-specific results are not possible because species are not considered explicitly. Second, the choice of the functional variables implies that the different functions are given beforehand. Moreover, it is possible that different functions co-occur in a single organism. The modeller should decide whether or not such an organism is part of the model. Therefore, the model cannot explain why such an organism should exist.

To understand the co-occurrence of different functions in a single organism one can model in an evolutionary context. Suppose a model organism is in principle able to perform all the basic functions. Furthermore, suppose that these basic functions may vary quantitatively in their contribution to the total metabolism. In such a model organisms may evolve that specialise in one of the basic functions. This model may therefore explain which conditions lead to the evolution of producers, consumers and decomposers. Also, the model may indicate key characteristics of these functions. For example, decomposers are often bacteria, characterised by their small size. If the model indicates that the decomposition functions is always linked to small cell size, the model would explain the role of the bacteria.

This study explores the possibility to model ecosystems in an evolutionary context. We start with a mono-species ecosystem in which the single species combines all basic functions. The species is allowed to evolve and may loose one or two of the basic functions. Evolution of a mono-species population may lead to a poly-species ecosystem. The original population splits in two or more subpopulations where each subpopulation specialises in certain functions. The aim of this study is to explain under which conditions such specialisation might occur.

First, we discuss part of the formal framework developed for modelling adaptive dynamics and evolutionary strategies, Section A.2. Next, we apply this theory to the Dynamic Energy Budget model for a mixotroph community, Section A.3. We end with the results and conclusions obtained by applying the the adaptive dynamics theory to this specific model, Section A.4.

A.2 Adaptive dynamics

In [4] the concept of evolutionarily singular strategies is introduced as a generalisation of ESS-concept [14]. Here, we shortly recall the important ideas for modelling adaptive dynamics. We confine ourselves to the notions that are needed to understand the application of this theory to the DEB-mixotroph model, cf. Section A.3

Consider a population with state-vector $N \in \operatorname{Re}^{n}$, for instance the different physiological states of the individuals. In such a population state-vector different types can be distinguished. We assume that the difference in type are characterised by a vector $x \in \operatorname{Re}^{k}$. Such a vector is referred to as **strategy**. A strategy is simply a collection of parameters by which the behaviour of the individual, and therefore of the population, is represented. Assume that the dynamics of the population is given by

$$\frac{\partial E}{\partial t} = f(N, E, x)$$

$$\frac{\partial N}{\partial t} = M(x, E)N$$
(1)

where $E \in \operatorname{Re}^{m}$ stands for the different environmental state variables. These can be for instance the available nutrients. Assume moreover that the system has only one equilibrium (E_x, N_x) .

The concept of evolution and mutation is brought in via the strategy x. We formulate the following question: What is the destiny of an initially rare mutant with a (different) strategy y that appears in an equilibrium population of x-strategists, does the mutant survive or does it go extinct? It is this question we aim to answer.

Since the mutant is rare the (equilibrium) environment E_x , determined by the x-strategists, is not modified by the presence of the mutants. Therefore, as a first order approximation, the growth of the mutant is determined by the leading eigenvalue $\rho(y, E_x)$ of the matrix $M(y, E_x)$. Moreover, because the mutant is rare, we can also assume that during invasion the environment is still in equilibrium and therefore constant $E = E_x$. Although the mutant grows or goes extinct the effect of this does not affect the environment significantly. Until of course the mutants reached a considerable size. Right after the mutant is introduced its growth will exhibit transient behaviour. After the transient phase the specific growth rate becomes constant. This constant is called 'the mutants fitness'. If the mutants fitness is positive the mutant can maintain itself and invade in the resident population, if it is negative the mutant goes extinct.

To formally define the mutants fitness one needs to distinguish two different time scales [5], Chapter 2. A global time scale t in which the environment does not change, and a smaller time scale τ , $\tau \ll t$ in which the transient behaviour right after mutation is described. In terms of the smaller time scale τ one should consider the long-term behaviour of the growth rate to obtain the mutants fitness. In this context the mutants fitness is defined by

$$s_x(y) = \lim_{\tau \to \infty} \rho(y, E_x).$$
⁽²⁾

In Section A.3.2 we show how this definition applies to our model. The sign of $s_x(y)$ determines the behaviour of the mutant. If $s_x(y) < 0$ the mutant dies out, whereas if $s_x(y) > 0$ it will spread.

A.2.1 Evolution and the fitness' gradient

During evolution mutations are small, i.e. $\|\rho_{mut} - \rho_{res}\| \ll 1$. An approximation of the mutants fitness is obtained by expansion.

$$s_{\rho_{res}}(\rho_{mut}) = s_{\rho_{res}}(\rho_{res}) + \nabla_{\rho_{mut}}s_{\rho_{res}}(\rho_{mut}) \Big|_{\rho_{mut}=\rho_{res}} \cdot (\rho_{mut} - \rho_{res}) + \mathcal{O}(\|\rho_{mut} - \rho_{res}\|^2), \quad (\rho_{mut} \to \rho_{res})$$

$$\approx \nabla_{\rho_{mut}}s_{\rho_{res}}(\rho_{mut}) \Big|_{\rho_{mut}=\rho_{res}} \cdot (\rho_{mut} - \rho_{res}).$$
(3)

Hence, the gradient field $\nabla_{\rho_{mut}} s_{\rho_{res}}(\rho_{mut})|_{\rho_{mut}=\rho_{res}}$ determines the direction in which the population evolves. When the population reaches the neighbourhood of a 'singular strategy' x^* , where the gradient becomes zero, the evolutionary behaviour of the population is determined by the second derivative. Depending on the properties of the second derivative in x^* the evolutionary behaviour can be characterised. In the case of an one-dimensional strategy parameter the possible behaviour is completely classified in [4]. In particular, in the one-dimensional case it is possible to obtain evolutionary branching in a singular strategy.

A.2.2 Coexistence

Two strategies x and y in a population do not always (in the long term) give rise to a dimorphic population. Suppose a population initially consists of two different strategies, say x and y. If $s_x(y) > 0$ the x-strategists cannot push out the y-strategists because once the ystrategists are rare the positive mutants fitness guarantees their survival. In the same manner we see that $s_y(x) > 0$ implies that the x-strategists can never go extinct. A sufficient condition for coexistence of two different strategies in one population can therefore be expressed in terms of the mutants fitness.

A sufficient condition for polymorphism is not straightforward from the mutants fitness. If n strategies x_1, \ldots, x_n have the the property that $s_{x_i}(x_j) > 0$ for all i and j then polymorphism is not guaranteed. Because when there are n strategies the environment for one of them is determined by the other n - 1 strategies. Whereas the mutants fitness $s_x(y)$ assumes that the environment for y is determined by x only. It might therefore happen that in a population with the strategies x, y, z, the x and y-strategists establish an equilibrium in which the z-strategists cannot survive, although $s_x(z) > 0$ and $s_y(z) > 0$.

A.3 The DEB mixotroph model

The dynamic energy budget theory provides a simple model for growth of a facultative photoautotroph with chemo-heterotrophic capabilities. The organism is described by only one reserve component and one structural component. Both components are taken to be generalized compounds. The rules of Synthesizing Units are used for interactions among the uptake processes. Parallel processing is used for the uptake of the various nutrients and light. Whereas, the merging of autotrophic and heterotrophic activities is modelled by sequential processing.

We focus on the assimilation of carbon dioxide, ammonium and light. The two organic compounds that can be assimilated are dead reserves and dead structure, these organic compounds originate from aging. The DEB mixotroph model describes the process of resource recycling in a closed environment, as driven by light. A simple diagram of the metabolism of the mixotroph is given in Figure 2

To understand how the assimilation is modelled we refer to [11, 9]. The assimilation and other fluxes as well as the precise equations are given in Appendix B.



Figure 2: Diagram of the metabolism of a mixotroph. Resources (light L, carbon dioxide C, ammonium N, detritus D_E and D_V), reserves, E, and structural mass, V, and the basic transformations (assimilation A, growth G, and maintenance M) are indicated. Water H and di-oxygen O are assumed to be non-limiting. The excretion of ammonium and carbon dioxide in association with the basic transformations is not indicated. The death process H that converts reserves E into detritus D_E , and structural mass V into detritus D_V is also not indicated. The gray area indicates the assimilation apparatus of the cell, a subset of the structural mass where no compounds accumulate.

A.3.1 Strategy

As strategy parameters we introduce ρ_{E_E} , ρ_{E_V} and $\rho_{E_A} \in (0, 1]$. In Appendix B these parameters occur in the different uptake fluxes. The parameter ρ_{E_E} is concerned with the uptake of reserve detritus, the parameter ρ_{E_V} with the uptake of structure detritus and the parameter ρ_{E_A} with the uptake via the autotrophic route. These parameters are a measure for the efficiency of the different uptake routes. Moreover, we model the maximal uptake fluxes to depend on the values of $\rho = (\rho_{E_E}, \rho_{E_V}, \rho_{E_A})$ according

$$j_{E_A,Am} = j_{E_A,A}^A \rho_{E_A}$$

$$j_{E_E,A_{HE}m} = j_{E_E,A_{HE}}^E \rho_{E_E}$$

$$j_{E_V,A_{HV}m} = j_{E_V,A_{HV}}^V \rho_{E_V}.$$
(4)

The new parameters $j_{E_A,A}^A$, $j_{E_E,A_{HE}}^E$ and $j_{E_V,A_{HV}}^V$ represent the absolute maximal fluxes that can be reached (when $\rho = 1$).

By modelling the strategy in this way it is obvious what happens in the long term when mutations are allowed. Since, the higher the values of ρ the better the uptake of nutrients and detritus. Therefore, the growth rate will be larger, and the 'best' organisms are those which have $\rho = 1$. As a consequence, one can show that allowing mutants in a population of ρ -strategists will ultimately lead to a population with strategy more or less $\rho = 1$.

The three different strategies of obtaining resources require different biochemical machinery. For instance, the autotrophic route demands the presence of an electron transport chain, which consists of several enzymes. Likewise, the dependence on heterotrophic resource acquisition involves specialised enzyme systems. Increased efficiency in a particular uptake route can be accomplished by increasing the amount of machinery involved. In other words, there is price tag attached to an increase in efficiency. In the context of DEB theory we represent this price tag by the conversion parameters y_{EV}^A , y_{EV}^E and y_{EV}^V . The conversion efficiency, which is modelled in DEB by the parameter y_{EV} , represents how many units of reserves are needed to obtain one unit of structure. The higher the value the less efficient growth is. We model the conversion efficiency to depend on the ρ -strategy of the population according

$$y_{EV}(\rho) = y_{EV} + y_{EV}^A \rho_{E_A} + y_{EV}^E \rho_{E_E} + y_{EV}^V \rho_{E_V}.$$
(5)

The parameter y_{EV} represents the basic conversion efficiency (it can be seen that $y_{EV} \ge 1$ should be chosen). The higher the values of ρ the less efficient conversion from reserves to structure is. This is the price that is payed for increasing the efficiency. As a result, higher values of ρ lead to smaller growth rates.

Modelling the maximal uptake fluxes according to 4 and the conversion efficiency to 5 it is a priori not clear what the evolutionary behaviour of a population of ρ -strategists is. Higher values of ρ are both good and bad for the populations growth rate, as well as lower values of ρ .

A.3.2 The fitness of mutants

As explained in Section A.3.1 we consider a population whose characteristics are determined by the parameters $\rho = (\rho_{E_E}, \rho_{E_V}, \rho_{E_A})$. We are interested in the effect of a rare mutant with different strategy, which we denote by ρ_{mut} . More precisely, can such an mutant manifest itself or will it get extinct? In Section A.2 we explained that the mutants behaviour can be characterised by the sign of the mutants fitness $s_{\rho_{res}}(\rho_{mut})$.

To understand how the mutants fitness relates to a mixotrophic organism we look at its growth. A mixotrophic organism as modelled by DEB consists of two components (state variables), reserves X_E and structure X_V . The growth of the organism is reflected in both these components. The environment E introduced in Section A.2 is, in the mixotroph model, given by the remaining state variables

$$E = \{X_N, X_C, X_{D_V}, X_{D_E}\}.$$

The Equations $(11)^{1-4}$ describe the dynamics of the environment E, cf. $(1)^1$. From the Equations $(11)^{5,6}$ we obtain that the specific growth rate for reserves s_E and structure s_V , as a function of the strategy ρ and the environment E, is given by

$$s_{V} = s_{V}(m, \rho)$$

= $j_{V,G}(m, \rho) + j_{V,H}(m, \rho)$
$$s_{E} = s_{E}(m, \rho, E)$$

= $\frac{1}{m}(j_{E,A}(m, \rho, E) + j_{E,G}(m, \rho) + j_{E,M}(\rho) + j_{E,H}(m, \rho)),$ (6)

where

$$m = \frac{X_E}{X_V}.$$

Equation (6) shows that the growth rates do not depend on the reserves X_E and structure X_V explicitly but only on their quotient, the reserve density, m.

Assume that the resident population, of which the strategy is denoted by $\rho = \rho_{res}$, reached its equilibrium. In particular this implies $s_V = s_E = 0$ for the ρ_{res} -strategists. Assume, moreover, that the mutant population is rare, i.e.,

$$\begin{aligned} X_{V\rho_{mut}} \ll X_{V\rho_{res}}, \\ X_{E\rho_{mut}} \ll X_{E\rho_{res}}. \end{aligned}$$

Then the equilibrium is, in a first order approximation, determined by the resident population, In particular, the environment equilibrium only depends on the strategy of the resident population, i.e. $E = E_{\rho_{res}}$. Therefore, a good approximation of the specific growth rates of the mutant population are, cf. (6),

$$s_{V} = s_{V}(m_{\rho_{mut}}, \rho_{mut}) = j_{V,G}(m_{\rho_{mut}}, \rho_{mut}) + j_{V,H}(m_{\rho_{mut}}, \rho_{mut}) s_{E} = s_{E}(m_{\rho_{mut}}, \rho_{mut}, E_{\rho_{res}}) = \frac{1}{m_{\rho_{mut}}} (j_{E,A}(m_{\rho_{mut}}, \rho_{mut}, E_{\rho_{res}}) + j_{E,G}(m_{\rho_{mut}}, \rho_{mut}) + j_{E,M}(\rho_{mut}) + j_{E,H}(m_{\rho_{mut}}, \rho_{mut})),$$
(7)

where

$$m_{\rho_{mut}} = \frac{X_{E\rho_{mut}}}{X_{V\rho_{mut}}}.$$

Hence, the specific growth rates of the mutants depend on the reserve density $m_{\rho_{mut}}$, the strategy ρ_{mut} itself and the equilibrium environment values of the ρ_{res} -strategists, $E_{\rho_{res}}$. We derive an expression for the mutants fitness $s_{\rho_{res}}(\rho_{mut})$ in three steps

- 1. In Appendix C we prove that the long-term specific growth rate of reserves and structure of a mutant ρ_{mut} in a resident environment ρ_{res} are the same. In other words: if the reserves of a mutant grow, so does its structure and vice versa. This allows us to derive the mutants fitness by only considering one of the two components (reserves or structure) of the organism since they grow the same anyway. Otherwise it might happen that the reserves of the mutant grow, whereas the structure decays. In this case we do not know if the mutant grows or not.
- 2. From Appendix C we find that in a good approximation

$$m_{\rho_{mut}} = \frac{j_{E,A}(\rho_{mut}, E_{\rho_{res}})}{\dot{k}_E}.$$
(8)

From which we see that $m_{\rho_{mut}}$ can be expressed in terms of ρ_{mut} and $E_{\rho_{res}}$

3. In Appendix D we show that we do not have to calculate the equilibrium values of the environment $E_{\rho_{res}}$ explicitly. We prove that

$$j_{E,A}(\rho_{mut}, E_{\rho_{res}}) = j_{E,A}(\rho_{mut}, \rho_{res}).$$
(9)

We can express the assimilation flux of a rare ρ_{mut} -strategist in a ρ_{res} -population by only knowing the strategies and, of course, the remaining parameters, none of the state variables is needed. We believe this purely has to do with the type of model.

From 1, 2 and 3 it follows that

$$s_{\rho_{res}}(\rho_{mut}) = s_E(m_{\rho_{mut}}, \rho_{mut}, E_{\rho_{res}})$$

$$= s_V(m_{\rho_{mut}}, \rho_{mut})$$

$$= s_V(\frac{1}{\dot{k}_E} j_{E,A}(\rho_{mut}, E_{\rho_{res}}), \rho_{mut})$$

$$= s_V(\frac{1}{\dot{k}_E} j_{E,A}(\rho_{mut}, \rho_{res}), \rho_{mut})$$

$$= \frac{(\dot{k}_E - \dot{h}_{\dagger})j_{E,A}(\rho_{mut}, \rho_{res}) - \dot{k}_E \dot{k}_M y_{EV}(\rho_{mut})}{j_{E,A}(\rho_{mut}, \rho_{res}) + \dot{k}_E y_{EV}(\rho_{mut})},$$
(10)

which, together with (5), (17) and (24) yields an analytic expression for the mutants fitness.

A.4 Results and Conclusions

The mutants fitness depends only on the values of ρ and the limited amount of parameters summarised in Table A.4. The evolutionary behaviour is fully characterised by the values of these parameters. In particular, we find that the evolutionary behaviour is independent of the total amount of carbon X_{C+} and nitrogen X_{N+} . However, the total amount of carbon and nitrogen determines which of the nutrients is limiting. We conclude that neither nitrogen nor carbon limitation does affect the evolutionary behaviour.

| \dot{k}_{E_A} | [mol/mold] | y_{EV} | [mol/mol] |
|-----------------|------------|---------------------|------------|
| \dot{k}_{E_H} | [mol/mold] | y_{EV}^A | [mol/mol] |
| \dot{k}_{E_V} | [mol/mold] | y_{EV}^E | [mol/ mol] |
| \dot{k}_{E_E} | [mol/mold] | y_{EV}^V | [mol/ mol] |
| $ \rho_{E_H} $ | [-] | \dot{h}_{\dagger} | [1/d] |
| $y_{D_V E}$ | [mol/mol] | \dot{k}_E | [1/d] |
| $y_{D_E E}$ | [mol/mol] | \dot{k}_M | [1/d] |

Table 1: Relevant parameters for the mutants fitness function.

A.4.1 Evolution

The gradient of the fitness function is used to study the evolutionary behaviour of our system, cf. Section A.2. If mutations are small, i.e. $\|\rho_{mut} - \rho_{res}\|$ is small, the vector field $\nabla_{\rho_{mut}} s_{\rho_{res}}(\rho_{mut})|_{\rho_{mut}=\rho_{res}}$ gives the directions in which the resident population on the long term evolves. The mathematica notebook 'FitnessFunction.nb' calculates the mutants fitness (10) and its gradient $\nabla_{\rho_{mut}} s_{\rho_{res}}(\rho_{mut})|_{\rho_{mut}=\rho_{res}}$ given the parameter values in Table A.4. As an example consider Figure 3 that is produced by 'FitnessFunction.nb'.



Figure 3: Vector field $\nabla_{\rho_{mut}} s_{\rho_{res}}(\rho_{mut})|_{\rho_{mut}=\rho_{res}}$ for the parameters in Appendix B and $y_{EV}^A = y_{EV}^E = y_{EV}^V = 0$.

Figure 3 shows the behaviour when there is no price tag attached to an increase in efficiency. As we already predicted in A.3.1 this situation evolves to $\rho = (1, 1, 1)$.

Suppose we choose a large value for y_{EV}^A , which means that the biochemical machinery involved in uptake via the autotrophic route is 'expensive'. We expect evolution to a strategy with a smaller ρ_{E_A} value. This is indeed the case as can be seen from Figure 4. Large and small values of ρ_{E_A} turn out to be evolutionary unfavourable.

The gradient of the mutants fitness shows how a population of ρ -strategists evolves in time when small mutations are allowed. However, it is not possible to see if a population with a certain ρ -strategy can even exist with the given choice of parameters. For example: In the parameter setting chosen for Figure 4 it can be shown that not a single population ρ -strategists can maintain themselves, they simply all go extinct! The evolutionary behaviour and the survival of a population ρ -strategists are completely different issues.

A.4.2 Singular strategy

As we discussed in Section A.2.1 the behaviour in the neighbourhood of a singular strategy ρ^* , i.e. where the gradient is zero, depends on the properties of the second derivative of the mutants fitness function in ρ^* . A program was written to find zero's of the gradient vector



Figure 4: Vector field $\nabla_{\rho_{mut}} s_{\rho_{res}}(\rho_{mut})|_{\rho_{mut}=\rho_{res}}$ for the parameters in Appendix B and $y_{EV}^E = y_{EV}^V = 0$ and $y_{EV}^A = 15$.

field for different choices of the parameters in Table A.4. We did a random search in feasible intervals for the different parameters. So far we did not manage to find a parameter setting for which a singular strategy ρ^* lies within the cube. Evolution always seems to 'hit' the lateral faces of the ρ -cube.

The evolutionary behaviour at the boundary of the cube is not a priori clear. In the two examples of Figure 3 and 4, evolution leads to a population with one or more of the strategy values maximal. As an example consider Figure 3, suppose that evolution leads to a population of ρ -strategists with $\rho_{E_A} = 1$. Since the gradient field at the lateral face $\rho_{E_A} = 1$ points outwards, the ρ_{E_A} strategy resides at one. Therefore, the behaviour of the population is determined by the projection of the gradient onto the lateral face $\rho_{E_A} = 1$, the component of the gradient in ρ_{E_A} -direction does not affect the evolutionary behaviour. Thus, we can reduce to a two dimensional domain, as is illustrated in Figure 5.

There is no singular strategy for the projection of the gradient vector field in this lateral face. We see that evolution leads to a population with either $\rho_{E_V} = 1$ or $\rho_{E_E} = 1$. Suppose that evolution leads to a population of ρ -strategists with $\rho_{E_V} = 1$. The vector field points outwards at $\rho_{E_V} = 1$, so the ρ_{E_V} strategy resides at one. Thus, we can reduce the dimension once more by considering the lateral edge $\rho_{E_A} = 1 \cap \rho_{E_V} = 1$. The components in ρ_{E_A} and ρ_{E_V} direction do not affect the evolutionary behaviour. We obtain the one dimensional vector field in Figure 6.

Finally, the population ends up at $\rho = (1, 1, 1)$, for this particular choice of parameters. However, it might also occur that evolution hits a lateral face or edge of the cube where the projection of gradient field has a zero and therefore a singular strategy. In that case one can expect interesting evolutionary behaviour depending on the behaviour of the second derivative of the mutants fitness in the plane or edge of projection. It is reasonable to expect evolutionary branching or perhaps some of the other phenomena described in [4].



Figure 5: Projection of the gradient of the mutants fitness for the vector field in Figure 3 on the lateral face $\rho_{E_A} = 1$.



Figure 6: Projection of the gradient of the mutants fitness for the vector field in Figure 5 on the lateral edge $\rho_{E_A} = 1 \cap \rho_{E_V} = 1$.

B The DEB mixotroph model equations

The system has 6 state variables: the concentrations of 2 minerals and 4 organic compounds. The changes are specified in terms of 22 fluxes; the 6 compounds (labelled C, N, D_V , D_E , V, E) partake in 6 transformations (labelled A_A , A_{HV} , A_{HE} , G, M, H). The changes are given by

$$\frac{d}{dt}X_{C} = X_{V}(j_{C,A_{A}} + j_{C,A_{HV}} + j_{C,A_{HE}} + j_{C,G} + j_{C,M})$$

$$\frac{d}{dt}X_{N} = X_{V}(j_{N,A_{A}} + j_{N,A_{HV}} + j_{N,A_{HE}} + j_{N,G} + j_{N,M})$$

$$\frac{d}{dt}X_{D_{V}} = X_{V}(j_{D_{V},A_{HV}} + j_{D_{V},H})$$

$$\frac{d}{dt}X_{D_{E}} = X_{V}(j_{D_{E},A_{HE}} + j_{D_{E},H})$$

$$\frac{d}{dt}X_{V} = X_{V}(j_{V,G} + j_{V,H})$$

$$\frac{d}{dt}X_{E} = X_{V}(j_{E,A} + j_{E,G} + j_{E,M} + j_{E,H})$$
(11)

Specification of fluxes

Auxiliary variables

$$\begin{split} f_{C_{H}} &= \frac{(1+z_{C}^{-1})}{1+z_{C}^{-1}f_{C}^{-1}+\frac{jL_{,FK}}{-jL_{,F}}} - \left(z_{C}f_{C}+\frac{-jL_{,F}}{jL_{,FK}}\right)^{-1}}, \quad f_{C} = \frac{1}{1+x_{C}^{-1}}; \quad x_{C} = \frac{X_{C}}{K_{C}} \\ j_{E_{A},A_{A}} &= \frac{j_{E_{A},Am}\left(1+z_{N}^{-1}+z_{C_{H}}^{-1}-(z_{N}f_{N}+z_{C_{H}}f_{C_{H}})^{-1}\right)}{1+z_{N}^{-1}f_{N}^{-1}+z_{C_{H}}^{-1}f_{C_{H}}^{-1}-(z_{N}f_{N}+z_{C_{H}}f_{C_{H}})^{-1}}, \quad f_{N} = \frac{1}{1+x_{N}^{-1}}; \quad x_{N} = \frac{X_{N}}{K_{N}} \\ j_{E_{E},A_{HE}} &= j_{E_{E},A_{HE}m}\left(1+x_{N_{E}}^{-1}+x_{D_{E}}^{-1}-(x_{N_{E}}+x_{D_{E}})^{-1}\right)^{-1}, \\ x_{N_{E}} = X_{N}/K_{N_{E}}; \quad x_{D_{E}} = X_{D_{E}}/K_{D_{E}} \\ j_{E_{V},A_{HV}} &= j_{E_{V},A_{HV}m}\left(1+x_{N_{V}}^{-1}+x_{D_{V}}^{-1}-(x_{N_{V}}+x_{D_{V}})^{-1}\right)^{-1}, \\ x_{N_{V}} = X_{N}/K_{N_{V}}; \quad x_{D_{V}} = X_{D_{V}}/K_{D_{V}} \\ j_{E_{H},A_{H}} &= \left(\dot{k}_{E_{H}M}^{-1}+\left(\rho_{E_{E}}j_{E_{E},A_{HE}}+\rho_{E_{V}}j_{E_{V},A_{HV}}\right)^{-1}\right)^{-1}, \\ \dot{k}_{E_{H}M} = \alpha_{E_{E}}\dot{k}_{E_{E}}+\left(1-\alpha_{E_{E}}\right)\dot{k}_{E_{V}}; \quad \alpha_{E_{E}} = \left(1+\frac{\rho_{E_{V}}j_{E_{V},A_{HV}}}{\rho_{E_{E}}j_{E_{E},A_{HE}}}\right)^{-1} \\ j_{E,A} &= \left(\dot{k}_{EM}^{-1}+\left(\rho_{E_{A}}j_{E_{A},A_{A}}+\rho_{E_{H}}j_{E_{H},A_{H}}\right)^{-1}\right)^{-1}, \\ \dot{k}_{EM} = \alpha_{E_{A}}\dot{k}_{E_{A}}+\left(1-\alpha_{E_{A}}\right)\dot{k}_{E_{H}}; \quad \alpha_{E_{A}} = \left(1+\frac{\rho_{E_{H}}j_{E_{H},A_{H}}}{\rho_{E_{A}}j_{E_{A},A_{A}}}\right)^{-1} \end{split}$$

Organic fluxes

$$j_{E,A_{A}} = \alpha_{E_{A}}j_{E,A} \qquad j_{E,G} = -y_{EV}j_{V,G}$$

$$j_{E,A_{HE}} = \alpha_{E_{E}}(1-\alpha_{E_{A}})j_{E,A} \qquad j_{E,G} = -y_{EV}\dot{k}_{M}$$

$$j_{E,A_{HV}} = (1-\alpha_{E_{E}})(1-\alpha_{E_{A}})j_{E,A} \qquad j_{V,H} = -\dot{h}_{\dagger}\frac{m}{y_{EV}+m}$$

$$j_{D_{E},A_{HE}} = -y_{D_{V}E}j_{E,A_{HE}} \qquad j_{D_{V},H} = \dot{h}_{\dagger}\frac{m}{y_{EV}+m}$$

$$j_{V,G} = \frac{m\dot{k}_{E}-y_{EV}\dot{k}_{M}}{m+y_{EV}} \qquad j_{E,H} = -\dot{h}_{\dagger}\frac{m^{2}}{y_{EV}+m}$$

$$j_{D_{E},H} = \dot{h}_{\dagger}\frac{m^{2}}{y_{EV}+m}$$

Mineral fluxes

| Parameters and | provisional | val | lues |
|----------------|-------------|-----|------|
|----------------|-------------|-----|------|

| X_{C+} | 1000 | $\mu \mathbf{M}$ | $j_{L,F}$ | -5 | mol/ mol d | n_{NE} | 0.2 | - |
|-------------|-------|------------------|---------------------|------|------------|-------------|-----|------|
| X_{N+} | 150 | $\mu \mathbf{M}$ | $j_{L,FK}$ | 25 | mol/ mol d | n_{NV} | 0.1 | - |
| K_C | 500 | $\mu \mathbf{M}$ | $j_{E_A,Am}$ | 2.5 | mol/ mol d | z_C | 10 | - |
| K_N | 0.1 | $\mu \mathbf{M}$ | $j_{E_V,A_{HV}m}$ | 1.5 | mol/ mol d | z_N | 10 | - |
| K_{N_E} | 0.001 | $\mu \mathbf{M}$ | $j_{E_E,A_{HE}m}$ | 2 | mol/ mol d | z_{C_H} | 10 | - |
| K_{N_V} | 0.001 | $\mu \mathbf{M}$ | \dot{k}_{E_A} | 10 | mol/ mol d | $ ho_{E_A}$ | 0.9 | - |
| K_{D_V} | 2500 | $\mu \mathbf{M}$ | \dot{k}_{E_H} | 10 | mol/ mol d | $ ho_{E_H}$ | 0.8 | - |
| K_{D_E} | 1000 | $\mu \mathbf{M}$ | \dot{k}_{E_E} | 5 | mol/ mol d | $ ho_{E_E}$ | 0.9 | - |
| $y_{D_V E}$ | 4 | mol/ mol | \dot{k}_{E_V} | 5 | mol/ mol d | $ ho_{E_V}$ | 0.7 | - |
| $y_{D_E E}$ | 2.5 | mol/ mol | \dot{h}_{\dagger} | 0.45 | 1/ d | \dot{k}_M | 0.1 | 1/ d |
| y_{EV} | 1.0 | mol/ mol | | | | \dot{k}_E | 0.6 | 1/ d |
| | | | | | | | | |

C Kinetics of the reserve density

Concentrating on de reserve density m we find that the Equations (11) and the explicit expressions for the fluxes in Appendix B imply that m follows a first order kinetics given by

$$\frac{dm}{dt} = (s_E(m,\rho) - s_V(m,\rho)m)$$

$$= -\dot{k}_E(m - \frac{j_{E,A}}{\dot{k}_E}).$$
(14)

In Appendix B we find that $j_{E,A} = j_{E,A}(\rho, E)$. Therefore:

- 1. The flux $j_{E,A}$ does not depend on X_E and X_V (or *m*).
- 2. In equilibrium the flux $j_{E,A}$ can be considered constant since the environment state variables *E* are time-independent.

Hence, the solution m of (14) converges to the constant value

$$m \longrightarrow \frac{j_{E,A}(\rho, E)}{\dot{k}_E} \qquad (t \longrightarrow \infty).$$

The positive parameter $\frac{1}{k_E}$ determines a characteristic time scale for the speed of convergence. It can be thought of as the ratio of the maximum assimilation capacity and the maximum storage capacity. In Figure 7 the convergence to the new reserve density after mutation is shown. As a result we find that in the long-term the reserve density m of a rare mutant population (characterised by ρ_{mut}) invading in an equilibrium resident population of ρ_{res} -strategists is

$$m_{\rho_{mut}} = \frac{j_{E,A}(\rho_{mut}, E_{\rho_{res}})}{\dot{k}_E}.$$

The reserve density of the mutant converges to a constant value and consequently the reserves X_E and structure X_V of the mutant change equally fast because $X_E \sim X_V$, $(t \longrightarrow \infty)$, this is illustrated in Figure 7.



Figure 7: Reserve densities, reserves and structure for resident and mutant strategists. At time t = 40 a small fraction of the total reserves and structure mutates. After mutation the reserve density rapidly changes to the new equilibrium value. The reserves and the density of the resident population hardly changes. The reserves and structure of the mutant grow equally fast in the 'long' term.

D The assimilation flux $j_{E,A}$

For further convenience we define the shorter notations for the expressions in Equations $(12)^{2,3,4}$.

$$j_{E_A,A_A,max} = \frac{j_{E_A,A}^A \left(1 + z_N^{-1} + z_{C_H}^{-1} - (z_N + z_{C_H})^{-1}\right)}{1 + z_N^{-1} f_N^{-1} + z_{C_H}^{-1} f_{C_H}^{-1} - (z_N f_N + z_{C_H} f_{C_H})^{-1}},$$

$$j_{E,A_{HE},max} = j_{E_E,A_{HE}}^E \left(1 + x_{N_E}^{-1} + x_{D_E}^{-1} - (x_{N_E} + x_{D_E})^{-1}\right)^{-1},$$

$$j_{E,A_{HV},max} = j_{E_V,A_{HV}}^V \left(1 + x_{N_V}^{-1} + x_{D_V}^{-1} - (x_{N_V} + x_{D_V})^{-1}\right)^{-1}.$$
(15)

The purpose of this notation is to show that these fluxes $j_{E_A,A_A,max}$, $j_{E_A,A_A,max}$ and $j_{E_A,A_A,max}$ only depend on the environment E and not on any of the strategies. The advantage of these auxiliary variables (15) is that we can, using (4), write the assimilation fluxes $(12)^{2,3,4}$ for either mutant / or resident strategists in a resident population as

$$j_{E_A,A_A} = \rho_{E_A mut/res} j_{E,A_A,max}(E_{\rho_{res}}),$$

$$j_{E,A_{HE}} = \rho_{E_E mut/res} j_{E,A_{HE},max}(E_{\rho_{res}}),$$

$$j_{E,A_{HV}} = \rho_{E_V mut/res} j_{E,A_{HV},max}(E_{\rho_{res}}).$$
(16)

These assimilation fluxes depend linearly on the strategy, and further only on the environment determined by the resident strategists.

We claim that we only need an analytic expression for the fluxes (15) in terms of ρ_{res} to find an analytic expression for $j_{E,A}(\rho_{mut}, E_{\rho_{res}})$. To understand why we combine the Equations (12)^{5,6} and (16) for the mutants strategy and find indeed that

$$j_{E,A}(\rho_{mut}, E_{\rho_{res}}) = \frac{1}{\dot{k}_{EM}^{-1} + \frac{1}{\rho_{E_{Amut}}^{-1} j_{E_{A},A_{A},max}(E_{\rho_{res}}) + \rho_{E_{H}} j_{E_{H},A_{H}}(\rho_{mut}, E_{\rho_{res}})}},$$

$$\dot{k}_{EM} = \alpha_{E_{A}} \dot{k}_{E_{A}} + (1 - \alpha_{E_{A}}) \dot{k}_{E_{H}},$$

$$\alpha_{E_{A}} = \left(1 + \frac{\rho_{E_{H}} j_{E_{H},A_{H}}}{\rho_{E_{Amut}}^{2} j_{E_{A},A_{A}},max}}\right)^{-1},$$

$$j_{E_{H},A_{H}}(\rho_{mut}, E_{\rho_{res}}) = \frac{1}{\dot{k}_{EH}^{-1} + \frac{1}{\rho_{E_{Emut}}^{2} j_{E_{E},A_{HE},max}(E_{\rho_{res}}) + \rho_{E_{Vmut}}^{2} j_{E_{V},A_{HV},max}(E_{\rho_{res}})}},$$

$$\dot{k}_{E_{H}M} = \alpha_{E_{E}} \dot{k}_{E_{E}} + (1 - \alpha_{E_{E}}) \dot{k}_{E_{V}},$$

$$\alpha_{E_{E}} = \left(1 + \frac{\rho_{E_{Vmut}}^{2} j_{E_{V},A_{HV},max}}{\rho_{E_{Emut}}^{2} j_{E_{E},A_{HE},max}}\right)^{-1}.$$
(17)

Remains to be shown that (15) can be expressed explicitly in terms of ρ_{res} and other parameters. This we show in a series of steps: Assume the system is in Equilibrium and the resident population consists of ρ_{res} -strategists. Then, (11)⁵ gives $j_{V,G} + j_{V,H} = 0$ from which we obtain using (13)^{6,9}

$$m = \frac{y_{EV}\dot{k}_M}{\dot{k}_E - \dot{h}_{\dagger}}.$$
(18)

We expressed m in terms of the known parameters, which implies that $j_{V,G}$ can be expressed in known parameters, yielding

$$j_{V,G} = \frac{\dot{k}_M \dot{h}_{\dagger}}{\dot{k}_M + \dot{k}_E - \dot{h}_{\dagger}}.$$
(19)

Equations (18) and (19) imply that we can express other several fluxes in terms of known parameters, namely the organic fluxes $(13)^{7,9,10,11,12}$. As a result, first, we can, by using $j_{E,A} + j_{E,G} + j_{E,M} + j_{E,H} = 0$, cf. (11)⁵, express $j_{E,A}$ in terms of standard parameters. This gives in terms of *m* and $j_{V,G}$

$$j_{E,A} = y_{EV}(\dot{k}_M + j_{V,G}) + \frac{\dot{h}_{\dagger}m^2}{y_{EV} + m}.$$
 (20)

And second, we find $j_{E,A_{HV}}$ and $j_{E,A_{HE}}$ explicitly from $j_{D_V,A_{HV}} + j_{D_V,H} = j_{D_E,A_{HE}} + j_{D_E,H} = 0$, cf. (11)^{3,4}, which gives

$$j_{E,A_{HV}} = \frac{\dot{h}_{\dagger}}{y_{D_V E}} \frac{m}{y_{EV} + m},$$

$$j_{E,A_{HE}} = \frac{\dot{h}_{\dagger}}{y_{D_E E}} \frac{m^2}{y_{EV} + m}.$$
(21)

From Equations $(13)^{2,3}$, (20) and (21) we find

$$\alpha_{E_A} = 1 - \frac{j_{E,A_{HE}} + j_{E,A_{HV}}}{j_{E,A}},$$

$$\alpha_{E_E} = \frac{j_{E,A_{HE}}}{j_{E,A_{HE}} + j_{E,A_{HV}}}.$$
(22)

Since we know α_{E_A} , α_{E_E} and $j_{E,A}$ we are nearly done. We can use the Equations (12)^{5,6} to find expressions for j_{E_A,A_A} , $j_{E,A_{HE}}$ and $j_{E,A_{HV}}$. Therefore, we obtain

$$\dot{k}_{EM} = \alpha_{E_A} \dot{k}_{E_A} + (1 - \alpha_{E_A}) \dot{k}_{E_H},
\dot{k}_{E_HM} = \alpha_{E_E} \dot{k}_{E_E} + (1 - \alpha_{E_E}) \dot{k}_{E_V},
j_{E_A,A_A} = \frac{1}{\rho_{E_{Ares}}} \frac{\alpha_{E_A}}{j_{E_A}^{-1} - \dot{k}_{EM}^{-1}}
j_{E_H,A_H} = \frac{\rho_{E_{Ares}}}{\rho_{E_H}} j_{E_A,A_A} (\alpha_{E_A}^{-1} - 1),
j_{E_E,A_{HE}} = \frac{1}{\rho_{E_{Eres}}} \frac{\alpha_{E_E}}{j_{E_H,A_H}^{-1} - \dot{k}_{EHM}^{-1}},
j_{E_V,A_{HV}} = \frac{\rho_{E_{Eres}}}{\rho_{E_{Vres}}} j_{E_E,A_{HE}} (\alpha_{E_E}^{-1} - 1).$$
(23)

Finally, combining (15), (16) for the resident strategists and $(23)^{3,5,6}$ we obtain the required expressions

$$j_{E_{A},A_{A},max} = \frac{j_{E_{A},A_{A}}}{\rho_{E_{Ares}}} = \frac{1}{\rho_{E_{Ares}}^{2}} \frac{\alpha_{E_{A}}}{j_{E,A}^{-1} - \dot{k}_{EM}^{-1}}, j_{E,A_{HE},max} = \frac{j_{E_{A},A_{HE}}}{\rho_{E_{Eres}}} = \frac{1}{\rho_{E_{Eres}}^{2}} \frac{\alpha_{E_{E}}}{j_{E_{H},A_{H}}^{-1} - \dot{k}_{E_{H}M}^{-1}}, j_{E,A_{HV},max} = \frac{j_{E_{A},A_{HV}}}{\rho_{E_{Vres}}} = \frac{\rho_{E_{Eres}}}{\rho_{E_{Vres}}^{2}} j_{E_{E},A_{HE}} (\alpha_{E_{E}}^{-1} - 1).$$
(24)

Note that the strategy of the resident population is indeed represented in these expressions. They do not depend however on the specific environment E equilibria but only on the parameters. When we substitute the explicit equations (24) in (17) we find $j_{E,A} = j_{E,A}(\rho_{mut}, \rho_{res})$ explicitly.