The dynamics of exploitation in ensembles of source and sink

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Abstract

The ensemble is a new entity on a higher level of complexity composed of source and sink. When substrate is transferred from source to sink within the transfer space non-linearity may be observable. Saturating production functions of source and sink in combination with linear cost functions may generate superadditivity and subadditivity in the productivity of the ensemble. The combined and interdependent productivity of the ensemble forms a surface similar to the Cobb-Douglas surface in a reaction chain where the source produces a product that will be used by the sink to produce a different product. Source and sink form a harmonic ensemble. When source and sink use the same substrate there will be competition. The surface is only present in active parts of the ensemble. Both parties may have different saturating production functions, different linear cost functions and different amounts of substrates in their compartment. If substrate is now transferred following the concentration gradient in harmony or through brute force or information (education) superadditivity or subadditivity may appear. The surface within the transfer space is now in some regions above or below the Cobb-Douglas surface. When substrate is repeatedly transferred from source to sink the actual productivity of the ensemble moves along the surface to a stable point or one party is lost and the ensemble is destroyed. This movement is the dynamic aspect of the ensemble. The benefit of source and sink and the cost can be interpreted as three-dimensional, non-linear coordinates of the ensemble appearing within the transfer space.

Key words: ensemble, source, sink, superadditivity, subadditivity, symbiosis, antibiosis, wise exploitation, Cobb–Douglas production function, Michaelis-Menten equation, irrationality, brute force, education

Introduction

Biologic life and economy are characterized by consumption and production (metabolism). Both systems are open. Energy, substrates and products are taken from sources and transformed to products in sinks. Every bill has to be paid somehow by somebody (law of conservation of mass and energy). In biochemistry, the lowest level of complexity in life, there is only reaction kinetics. Substrates will flow from high concentration to low concentration or from low affinity to high affinity. At this level neither selfishness nor altruism is observable as a self - “the distinct individuality or identity of a person or thing” - as such does not jet exist. An enzyme will neither give nor take nor not give nor not take beyond the limits of reaction kinetics.

Organisms from single cells to societies of multicellular organism are ensembles of entities of a lower level. Cells are composed of many different types of molecules from water and ions to macromolecules like DNA and protein. Enzymes are a very important type of protein. They produce and consume substrates in a complex and branched reaction chain. The final product of single celled life is offspring produced by cellular division. The “parent” will be a complete part of the offspring. Multicellular organisms are composed of single cells. All phenomena of multicellular life can be completely explained from the lower level. No new laws of nature appear. Besides offspring a “body” is produced. At the end of life the body is recycled but certain components will be stable for many years. All this could be called a stable investment product. Starting at a certain body size the more investment is made into such long lasting products, the smaller the offspring number will be (Brown J.H., Marquet P.A. and Taper M.L.). This puzzles biologist as low fertility should not be a good propagation strategy on the first glance. In societies the multicellular organism is part of an even more complex entity. Again no new law of nature appears. All observed phenomena can be explainable by the behaviour of lower levels. Next to offspring the products of societies range from lime skeletons the size of mountains to cities and songs. Who pays these products and why are they reasonable?

What can we learn from the lowest levels?

General considerations:

Imagine two producing entities in close contact with a non-limiting connection between them. Both are united using either the same substrate or the substrate to the second entity is the product of the first entity.

Figure 1

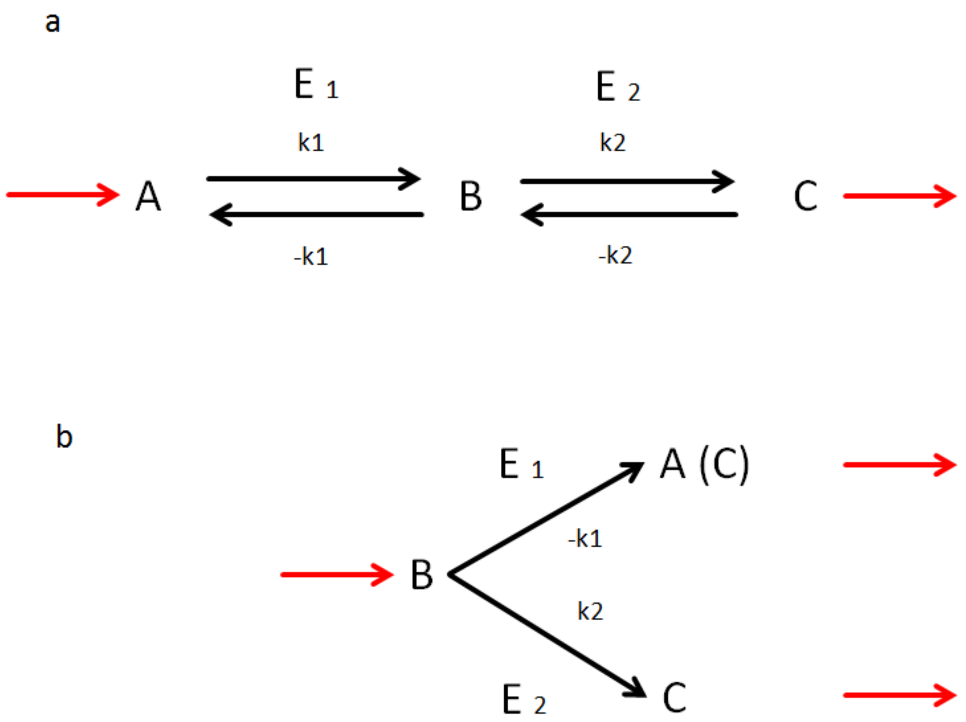

Figure 1: In figure 1a we observe a reaction chain. Entity (enzyme) E1 is using a substrate A to produce a product B. B then is used as a substrate by entity (enzyme) E2 to produce product C. The constants k1 and k2 and -k1 and -k2 are the forward and backward reaction constants. Both entities act in harmony. They produce different quantities and different qualities and depend on each other in both directions. The removal of B will increase the reaction velocity of E1 while a large concentration of B will increase the reaction rate of E2 for product C. In figure 1b we observe a branched reaction and B is the branch point. E1 and E2 are now competitors and their fate is inversely correlated. The more quantity of C will be produced by E2 from B the less B is available for E1 to produce a different quality (A) or another quantity (C). Red arrows indicate influx and efflux.

I will mainly concentrate on the case where both use the same substrate in different compartments with the possibility of exchange between the compartments. Only if affinity to the substrate, substrate concentration, product, product affinity, product concentration and production activity are identical in both entities no mass transfer will occur between them. If at least one of the properties will be different a transfer from higher to lower concentration or from lower affinity to higher affinity will occur.

The identity of the conditions is only achievable on the lowest level of complexity – in enzymes. Sequence and structural identical enzymes in a well-mixed vessel satisfy this condition. As soon as we go to more and more complex entities (composed of entities of the lower levels of complexity) it becomes more and more difficult to meet the properties of complete equality of internal and external conditions. Inequality will lead to the phenomenon of super- and subadditivity.

Ensemble:

An ensemble is defined as “a group of items viewed as a whole rather than individually”. Producing entities in close contact with possible substrate transfer should be called ensemble. The ensemble is composed of at least two parties - one source (“a place, person, or thing from which something originates or can be obtained”) and one sink (“a physical system that absorbs some form of matter or energy”). A source gives or gives not, a sink takes or takes not. Both components of the ensemble produce products (not necessarily the same) from the same or a different substrate. If both entities use the same substrate they are competitors. Competition is usually but not necessarily the cause of conflict. Within an ensemble there may be mass transfer of substrate from source to sink if conditions between both single components will not be uniformly distributed. Producing ensembles are of different complexity but the basic components and part of all entities are enzymes.

Productivity:

Many definitions exist but they all consider productivity as a rate. A rate is "a quantity measured against another quantity or measure". Usually the measure is time. The result of productivity is a product. This product could be called a benefit (b, "an advantage or profit gained from something"). The unit of productivity is amount per time (in enzymes: µmol/minute). This benefit comes at a cost (c, "an amount that has to be paid or spent to buy or obtain something"). In the characterized ensemble the benefit of one party comes at a cost to the other party. Although the mass transfer will be always from source to sink, the cost will not necessarily accumulate on the side of the source and the benefit will not always arise in the sink as I will prove later. This will be important to understand the structure of harmony and conflicts within ensembles. Productivity follows a saturating behaviour to the amount on all levels of complexity (figure 1). This has a simple physical reason, the Langmuir adsorption isotherm. Cost is usually considered of linear dependence to the amount.

Stability:

Stability ("The state or quality of being stable, especially: Resistance to change, deterioration, or displacement; constancy of character or purpose and reliability") is measured over a wide range of time scales and is a prerequisite for observability within and beyond the considered timescale. The benefit/cost ratio (b/c) is a very important measure for the stability and success of a system. Benefit/cost ratios of 1 indicate stability. Benefit/cost ratios smaller 1 indicate a decline and benefit/cost ratios larger 1 indicate growth. A living system from cells to societies will be stable if the benefit/cost ratio is 1 (figure 2). The unit of the benefit/cost ratio (amount/time/amount) is Hertz (sec^{-1}). As living systems are open, the stability is to be understood as steady state equilibrium. A single party will grow from b/c>1 or shrink from b/c<1 to b/c=1. An ensemble may possess a stable point but this may lead to instability in source and sink as I will show. The benefit/cost ratio within the source may be: b/c>1; b/c=1 and b/c<1. The benefit/cost ratio within the sink may be: b/c>1; b/c=1 and b/c<1.

Figure 2

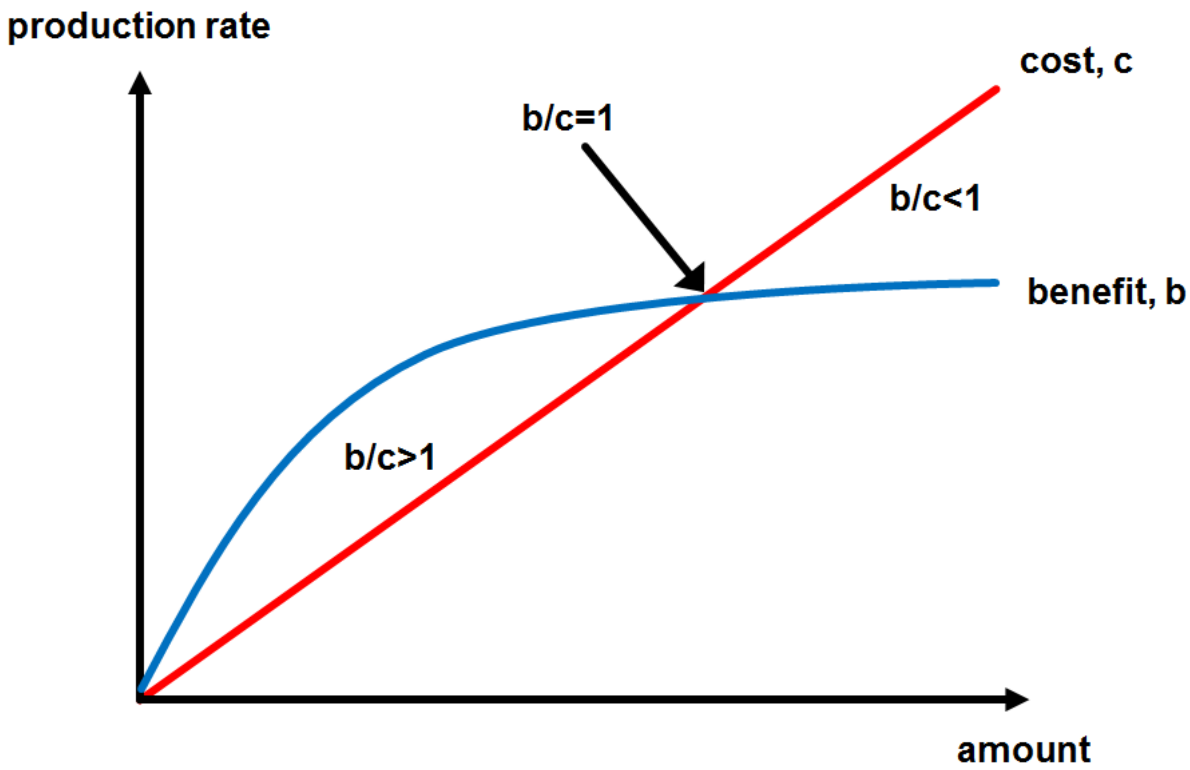

Figure 2: Linear cost functions (red) and saturating production functions (blue) lead to three different benefit/cost ratios when the amount is increased.

In organisms the productivity of enzymes will be of genetically fixed size. Therefore, to achieve the optimal benefit/cost ratio b/c=1 only the change of cost on a short timescale is an option. This may be different in other productive entities where a change of productivity is a fast and easy option. To change the cost a party can give or take. To keep the cost a party will not give or will not take. The option to a source is to give and give not. The option to a sink is to take or take not. At b/c>1 a source will not give the valuable substrate. At a ratio of b/c<1 the source will give to reduce costing substrate. The sink will take at b/c>1 but will not take at a ratio of b/c<1. Both parties will neither take nor give at b/c=1. This leads to table 1.

Table 1

source	sink	behaviour of the single party	
b/c ≥ 1	b/c >1	The source will not give. The sink will take.	conflict
b/c < 1	b/c >1	The source will give. The sink will take.	harmony
b/c < 1	b/c ≤ 1	The source will give. The sink will not take.	conflict
b/c ≥ 1	b/c ≤ 1	The source will not give. The sink will not take.	no conflict

Simple selfish behaviour will lead to “conflict”, “no conflict” and “harmony” within the ensemble. The picture becomes more complicate if we look at the consequences for the ensemble in the case of conflict. Here I assume for simplicity identical functions in source and sink and a small transfer.

Table 2

source	sink	behaviour of the single party	use of brute force (investment)	outcome for the ensemble
b/c >> 1	b/c >1	The source will not give. The sink will take.	transfer after conflict	decreased productivity
b/c > 1	b/c >>1	The source will not give. The sink will take.	transfer after conflict	increased productivity
b/c << 1	b/c < 1	The source will give. The sink will not take.	transfer after conflict	increased productivity
b/c < 1	b/c << 1	The source will give. The sink will not take.	transfer after conflict	decreased productivity
b/c = 1	b/c > 1	The source will not give. The sink will take.	transfer after conflict	increased productivity
b/c < 1	b/c = 1	The source will give. The sink will not take.	transfer after conflict	increased productivity
b/c > 1	b/c = 1	The source will not give. The sink will take.	transfer after conflict	decreased productivity
b/c = 1	b/c < 1	The source will give. The sink will not take.	transfer after conflict	decreased productivity

The combination of different behaviour of the single parties and the outcome for the system can be best understood in a three dimensional space, the transfer space (Friedrich, T., figure 3). The exploitation of the source by the sink or vice versa will be called productive wise if the increased productivity will pay the investment of brute force and education to realize a transfer in the case of conflicts. The only conflict free increase in productivity will be realized in the case of source: b/c<1 and sink: b/c>1. This condition is called symbiosis.

Figure 3

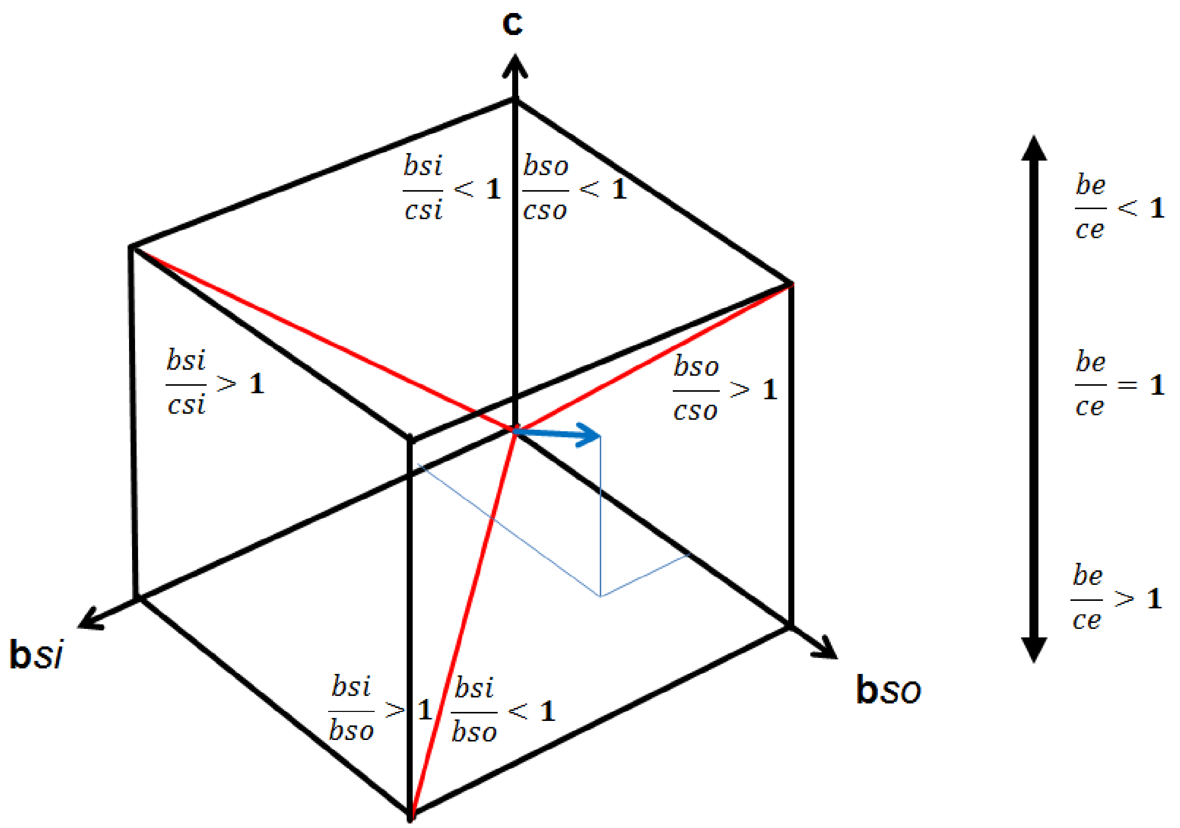

Figure 3: The transfer space has the coordinates cost (c, cost of source and cost of sink), benefit to the source (bso) and benefit to the sink (bsi). The ensemble manifests within the space. The benefit/cost ratio of the ensemble (be/ce) will increase when the cost to both sides will decrease (arrow on the right side). The benefit/cost ratios to source (bso/cso) and sink (bsi/csi) are indicated on the side of the space. The ground of the space shows the benefit-sink/benefit-source ratio (bsi/bso) and separates productive (left) from consumptive (right) exploitation. The red lines on the side of the cube are benefit/cost ratios equal to one. On the ground the benefit-sink to benefit-source ratio (bsi/bso) equal to one is marked as a red line. An ensemble vector (blue) points at the coordinate bso – bsi – c. This specific ensemble would be irrational and not stable.

To judge the outcome for the ensemble (benefit/cost ratio) will be even more difficult if we go to different (maybe even non-linear) cost functions, different production functions and different amounts of substrate. The production functions may differ in many ways. The maximal productivity, the steepness of the initial increase and even the shape (sigmoid behaviour, monotonous saturating) may be different. Therefore, a general mathematic understanding should be used to model the whole ensemble of source and sink. The benefit of the ensemble (be) is the productivity of the ensemble (Pe). The productivity of the ensemble is also a saturation function. Therefore, the benefit of the ensemble is proportional to the productivity of the single components (benefit of source, bso; benefit of sink, bsi).

$$be \sim bso + bsi$$

The cost to the ensemble is the sum of the cost to source (cso) and sink (csi) because these functions are linear

$$ce = cso + csi$$

The benefit cost ratio (b/c) of the ensemble is:

$$\frac{be}{ce} \sim \frac{bso}{cso} + \frac{bsi}{csi}$$

Benefit b, productivity P and reaction velocity V will be used interchangeable in the following considerations.

Productivity within ensembles of enzymes:

Enzymes are basic to life and a good model for saturating productivity. The Michaelis-Menten kinetics is a simple model of productive behaviour in enzymes.

The reaction velocity V or productivity P are part of the maximal reaction velocity V_{max} or maximal productivity P_{max}.

$$\frac{P}{\mathrm{Pmax}} = \frac{V}{\mathrm{Vmax}}$$

The source has a reaction velocity (productivity) V_{so} with the substrate concentration $[S]_{so}$ and the sink has a reaction velocity V_{si} with a substrate concentration $[S]_{si}$. According to Michaelis-Menten the reaction velocity in the source is:

$$Vso = \frac{[S]so}{(Kmso + [S]so)} * Vmax\ so$$

The reaction velocity in the sink is:

$$Vsi = \frac{[S]si}{(Kmsi + [S]si)} * Vmax\ si$$

If all reaction parameters are identical no transfer between the parties takes place. The ensemble (V_e) of both parties has the productivity. The ensemble is not active.

$$\mathrm{Ve} = \mathrm{Vso} + \mathrm{Vsi}$$

A single transfer:

In an inactive ensemble and the condition “no conflict” no transfer will be observable. A rational and reasonable ensemble will not be active. If a transfer would be made nevertheless it could be called active irrational ensemble. As soon as there is a transfer both parties become really source and sink and a transfer of substrate [ΔS] will be observable.

$$Ve = \frac{[S]so - [\Delta S]}{(Kmso + ([S]so - [\Delta S])} * Vmax\ so + \frac{[S]si + [\Delta S]}{(Kmsi + ([S]si + [\Delta S])} * Vmax\ si$$

This is the case when harmony between the two parties is observable (table 1). In the case of conflict both sides invest (Iso, investment of the source; Isi, investment of the sink) to avoid to give or to take and to be able to give or to take.

$$Ve = \frac{[S]so - [\Delta S] - Iso]}{(Kmso + ([S]so - [\Delta S] - Iso])} * Vmax\ so + \frac{[Ssi + \Delta S - Isi]}{(Kmsi + ([S]si + [\Delta S] - Isi])} * Vmax\ si$$

The investment I is a substrate equivalent. It is either the same substrate S used in a different process with a different cost and benefit function or a different substrate in the same or different process.

Besides “harmony”, “no conflict” and “conflict” there are three outcomes for the ensemble:

1. consumptive transfer: Ve (be) < Vso (bso) + Vsi (bsi) (table 2, decreased productivity)
2. productive transfer: Ve (be) > Vso (bso) + Vsi (bsi) (table 2, increased productivity)
3. productive wise transfer: Ve (be) > Vso (bso) + Vsi (bsi) - Iso - Isi
   Wise refers here to the fact that the investment “I” (brute force or education) is overcompensated in the ensemble by the gain in productivity after the transfer from source to sink.

The effect of the investment brute force and education is that the cost function or the production function or both is re-evaluated by source and sink. The investment by the not saturated sink has the effect that the source is changed from not giving to giving. The counter force used by the source is aimed to move the sink from taking to not taking. A saturated source will use force to move the sink from not taking to taking. The counter force by the sink is used to change the behaviour of the source from giving to not giving. A different interpretation is that the whole transfer space is deformed. The use of education and counter-information has the same purpose. The size of the investment in comparison to the size of possible superadditivity after the transfer will be discussed in more detail later (wise exploitation).

The transfer space (figure 4) represents on the surface of the cube source and sink and within the transfer space the ensemble. Harmony, conflict and no conflict depend on the shape of the production function, size of the cost (actual saturation with substrate) and size of the transferred amount of substrate.

Figure 4

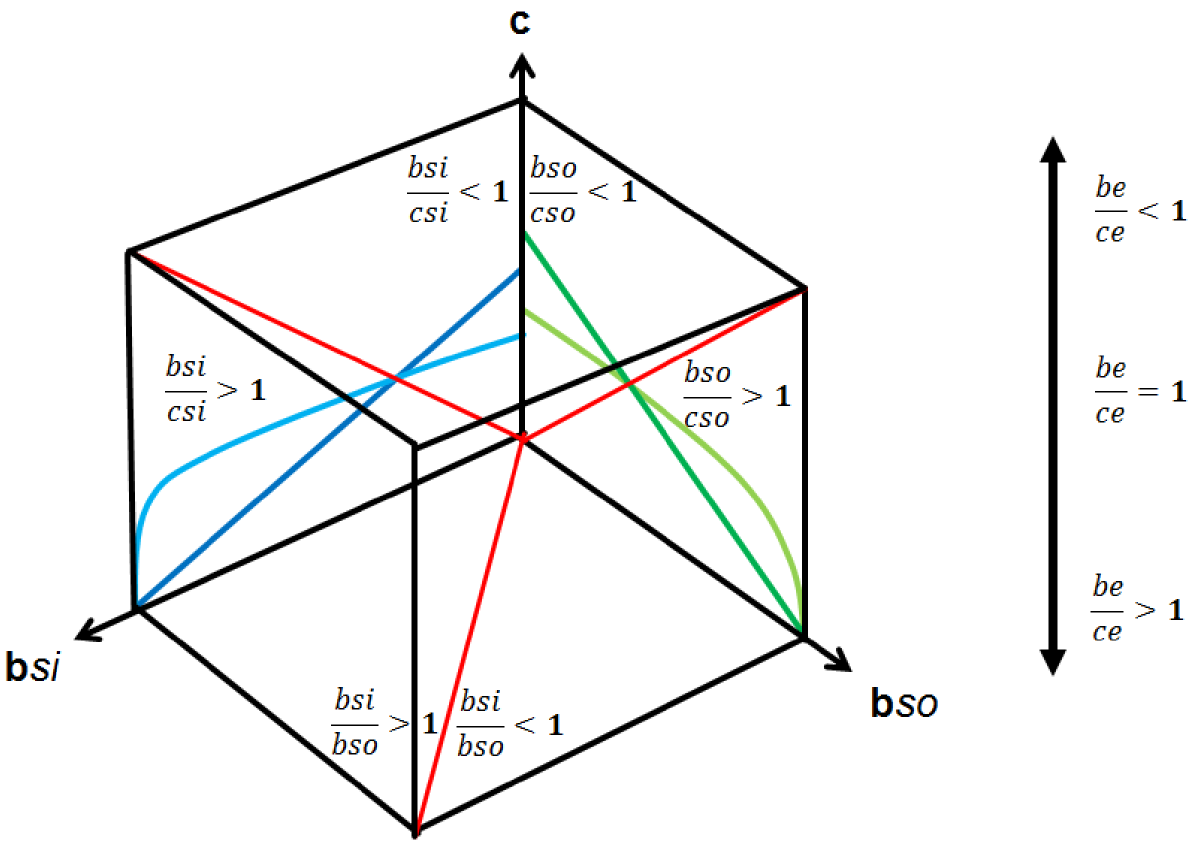

Figure 4: Source (green curves, so) and sink (blue curves, si) possess a different monotonous saturating productivity with different linear cost functions. On the side of the transfer space the benefit cost relationship of the ensemble is depicted.

In case we would calculate all possible benefit-source and benefit-sink combinations depending on all possible sizes of [ΔS] we would obtain a surface within the transfer space. The surface would look like the Cobb-Douglas functional form of production functions widely used in economics to represent the relationship of output to inputs. In its standard form for production of a good Y with two factors L and K, the function is $Y = AL^{\propto}K^{\beta}$:

Y = total production, L = labour input, K = capital input, A = total factor productivity. α and β are the output elasticity of labour and capital, respectively. The values are constants and determined by observation. Output elasticity measures the responsiveness of output to a change in levels of either labour or capital used in production. Interestingly there is a further similarity between the transfer space and the Cobb-Douglas production function. If $\alpha + \beta = 1$ the production function has constant returns to scale. This is similar to a benefit/cost ratio of 1 in the transfer space. In a symmetric ensemble (figure 5a) a straight line between a convex and a concave part of the ensemble surface connecting bso/cso=1 and bsi/csi=1.

If $\alpha + \beta < 1$ returns to scale are decreasing. In the transfer space this is a be/ce ratio < 1. The surface in the transfer space will be concave in relation to the origin. Finally if $\alpha + \beta > 1$ returns to scale are increasing. Here the transfer space is convex in relation to the origin (be/ce>1). This completely symmetric space may be superadditive depending on the distribution of substrates. When the source would start to give at a benefit cost ratio of bso/cso<<1 and the sink would start to take at a bsi/csi ratio>>1 the outcome for the ensemble would be greater than 1.

The initial conditions have been set in a way that the source is giving and the sink is taking. Therefore, the rational ensemble will not be active in all parts of the surface. The surface is the result of two pairs of functions. If we now consider that there are many different curve pairs of cost functions with production functions (b/c=1) going through the same point at the same straight line (red in figure 5a) we obtain an endless number of surfaces united by the same property. These surfaces fill the transfer space and the active regions of these ensembles form a subspace. This will be discussed later in more detail.

Symmetric ensembles: If the ensemble is symmetric in all aspects nothing will happen. A transfer of substrate will start when the substrate concentration is different in source (high, b/c<1) and sink (low, b/c>1) or the affinity is different (source low, sink high); a first asymmetry.

There are two types of harmonic ensembles. In the first type (figure 5a) the source will produce a product that is consumed by the sink to form a second product. Such behaviour is usually observed in (enzymatic) reaction chains (figure 1 a).

Figure 5a

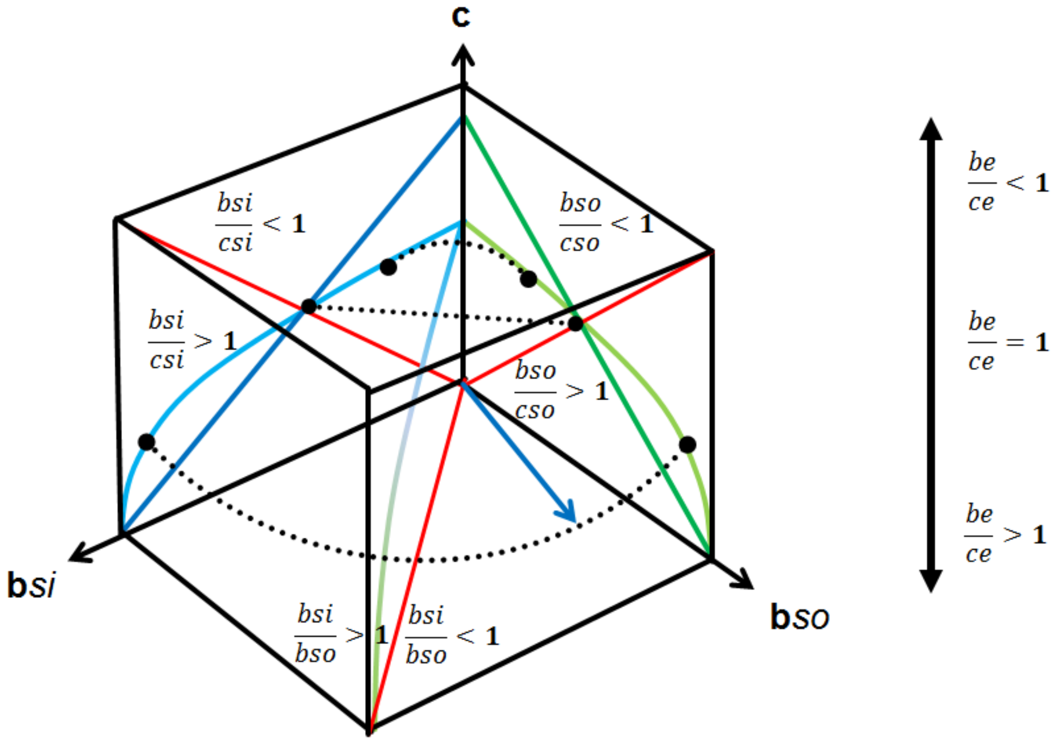

Figure 5a: This symmetric ensemble illustrates the similarity between the Cobb-Douglas production function and the ensemble surface of the transfer space. The dotted lines indicate the convex, linear and concave ensemble surface. In the convex area more of an earning substrate is better. In the concave area less of a costing substrate is better. This ensemble is harmonic. The source produces a product consumed by the sink. No super- or subadditivity is observable. The ensemble is active everywhere. Though its vector (blue) points on the side bsi/bso<1 the ensemble is a stable reaction chain.

The symmetric ensemble of figure 5b will use the same substrate in source and sink (branched reaction, 1b). Here we observe conflict, no conflict (no surface will appear) and harmony. Harmony here differs from harmony in ensemble of 5a. Harmony in the ensemble 5b occurs when the saturated source with a bso/cso ratio smaller than one will get rid of the costing substrate to a not saturated sink where the same substrate will be earning (bsi/csi>1). Substrate may be transferred freely from source to sink in the harmonic case or by means of brute force and education, which will be discussed later. The use of the same substrate will lead to superadditivity when the recipient can produce more from the substrate than the sender loses. In the case of subadditivity the recipient will produce even less from the substrate than the sender lost as productivity.

Figure 5b:

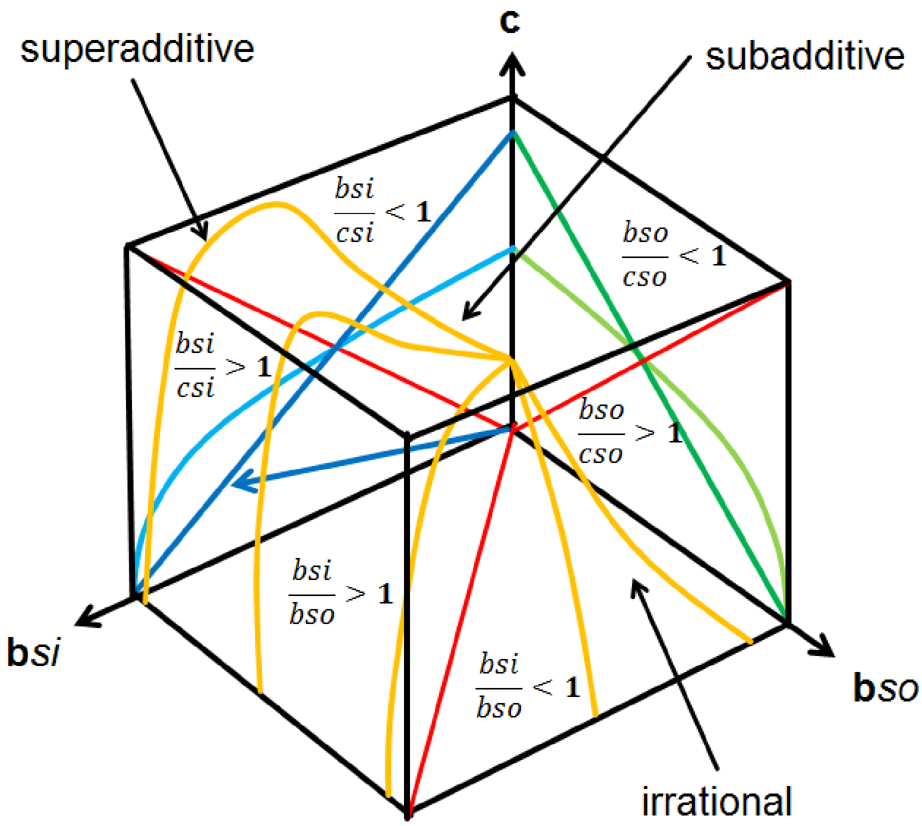

Figure 5b: This symmetric ensemble illustrates qualitatively what happens when source and sink compete for the same substrate. We observe superadditivity in the front and subadditivity in the back of the space. The ensemble is not active in the irrational region. This is an additional aspect of asymmetry in the symmetric ensemble. A vector (blue) characterizes a specific ensemble and points to the surface of the productive side. A necessary condition for stability but no sufficient condition.

Again a surface appears. The surface is above the surface in figure 5a when superadditivity is observed and below in the case of subadditivity. A vector originates also here at c=bso=bsi=0. This vector points towards the actual productivity of the ensemble at the surface and is called ensemble vector.

Asymmetric ensembles: Ensembles may be completely asymmetric with respect to the production function, the cost function, affinity and the actual saturation and substrate concentration. In figure 6 the sink may start everywhere in the observed region. The source may start at a point bso/cso<1. We observe harmony.

Figure 6

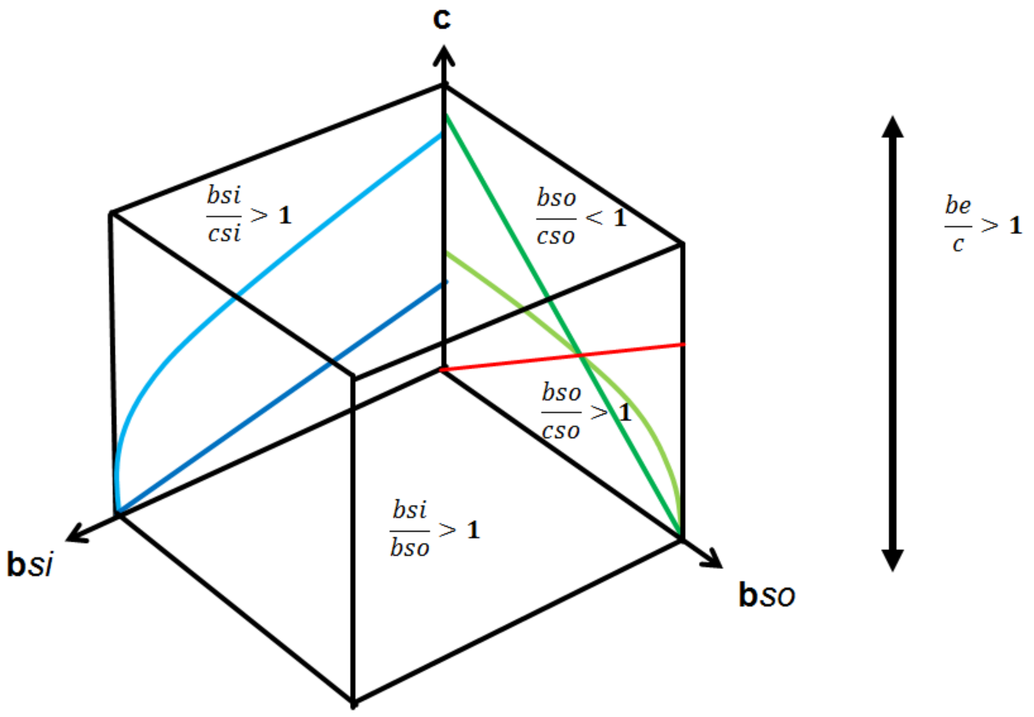

Figure 6: This asymmetric ensemble is productive, superadditive and harmonic at bso/cso<1. And the ensemble is productive and superadditive but with conflicts at bso/cso≥1 (on cost of the source). Continuing transfer of substrate from source to sink will increase the ensemble productivity and the productivity in the sink until the ensemble breaks down.

The transfer will decrease the saturation of the source and will increase the saturation in the sink. The cost function is so flat in the sink that bsi/csi=1 is not visible. The sink will not stop to take as taking will always pay. Is stability in reach? This productive and harmonic asymmetric ensemble (figure 6) may be stable in case the source is able to stop giving at bso/cso=1. The productivity is on cost of the source but in bso/cso<1 it is reasonable to give. If the source is neither able to stop giving nor able to regenerate at a loss identical velocity from anywhere else the source will become exhausted and the ensemble will break down. The ensemble could be also stable at other points. Investments in brute force and counter force or education and counter-information will change the points of possible stability. At those points the investments will compensate each other. Under those conditions the source may start to suffer because bso/cso<1 (also the sink may suffer if forced to stand the condition of bso/cso<1 in other cases).

The ensemble surface in figure 6 will no longer be symmetrically as in figure 5a. The surface will have a more convex shoulder on the side bsi/bso>1. In symbiosis both parties share the gain of superadditivity. In this neighborhood we still observe a productive ensemble but the productivity is no longer owned by the ensemble. The productivity in figure 6 would be owned and controlled by the sink. We observe a type of wise exploitation.

Wise exploitation: Only in asymmetric ensembles with superadditivity the ensemble can pay the investment brute force or education. In productive wise exploitation the investment brute force or education are overcompensated by the gain due to superadditivity. In the ensemble of figure 7a we again observe an asymmetric ensemble. This time the cost function in the source is very flat and very steep in the sink.

There are many production functions and cost functions in source and sink having bso/bso=1 and bsi/cso=1 in the same point at the red line shown in picture 7a. From these different pairs active surfaces can be calculated. These surfaces will form a subspace within the transfer space. These subspaces are symbiosis, antibiosis, wise exploitation type I and wise exploitation type II (figure 7b).

Figure 7a

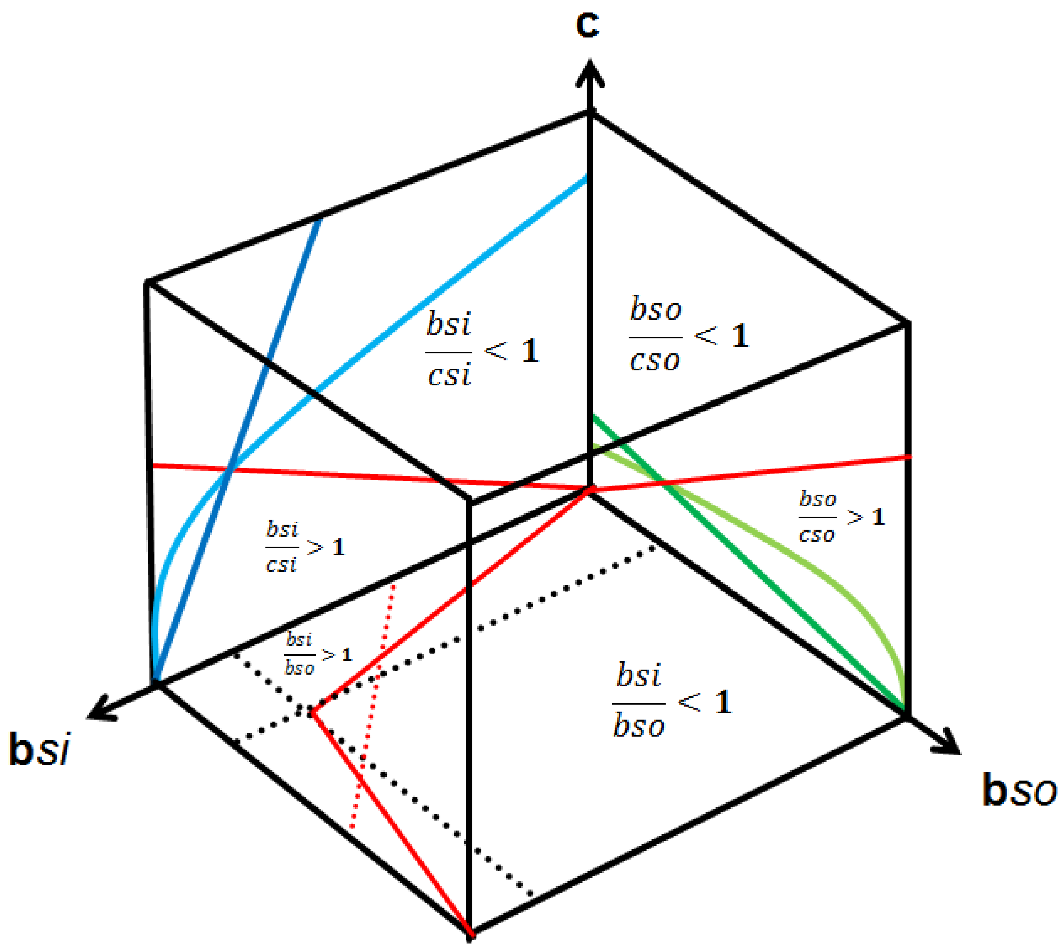

Figure 7a. On the ground of this space we find three dotted lines. The black lines mark the position of bso/cso=1 and bsi/csi=1. The space is asymmetric. Left of the position of the dotted red line the bsi/bso ratio has become so big that the cost of brute force or education will be paid completely by superadditivity. The red solid line separates bsi/bso<1 (consumptive region) from bsi/bso>1 (productive region). This line is due to the asymmetry of the space bent.

If we look from the top down on the transfer space in figure 7a we lose the cost dimension but we get a better look at the active surfaces of the asymmetric ensemble (figure 7b). As the cost dimension is lost the active surfaces are not curved and are no longer separated by a different height in the transfer space.

Figure 7b

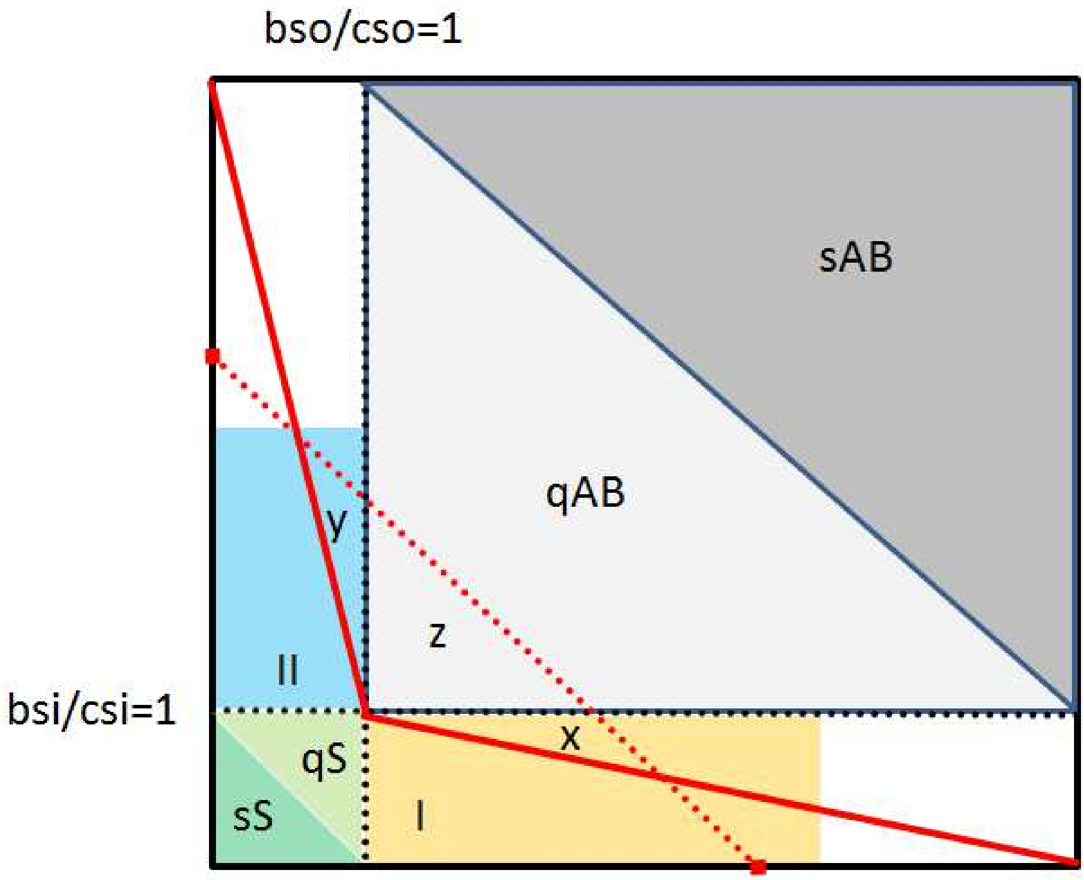

Figure 7b. Here we have a bird`s-eye view of the ensemble. The green surface (S) is the area of symbiosis. Symbiosis is divided in strict symbiosis (sS) and qualified symbiosis (qS). Strict refers to the fact that both parties start giving and taking from an earning point. In the qualified condition one party starts not from a gaining point. The orange area (I) is the area of productive wise exploitation of the source. The smaller surface x is consumptive exploitation of the source. The blue area (II) is productive wise exploitation of the sink. The small blue area y is consumptive exploitation of the sink. The grey area is the surface of irrationality and could be named antibiosis (sAB, strict and qAB, qualified antibiosis). The strong asymmetry shifts a part of the qualified antibiosis to the left side of the red dotted line. Both parties harm each other but it can be paid for although it is irrational. The red line is bsi/bso=1. The curvature of the surface is very asymmetric and convex in direction of bsi/csi=bso/cso. The surfaces are separated in the third dimension (cost). Symbiosis is sandwiched sideways between wise exploitation I and II. The ensemble is not active in most of the area of antibiosis but can be active in z. A source for the whole ensemble is a prerequisite to be stable and active on the consumptive side. Someone has to pay the bill.

The non-linear ensemble: Depending on the distribution of substrates, cost functions and production functions in source and sink many different outcomes are possible. The ensemble as new entity appears within the transfer space and will be stable (be/ce=1) or growing (be/ce>1) or shrinking (be/ce<1) on cost of source and/or sink for the benefit of source and/or sink (figure 8).

Figure 8

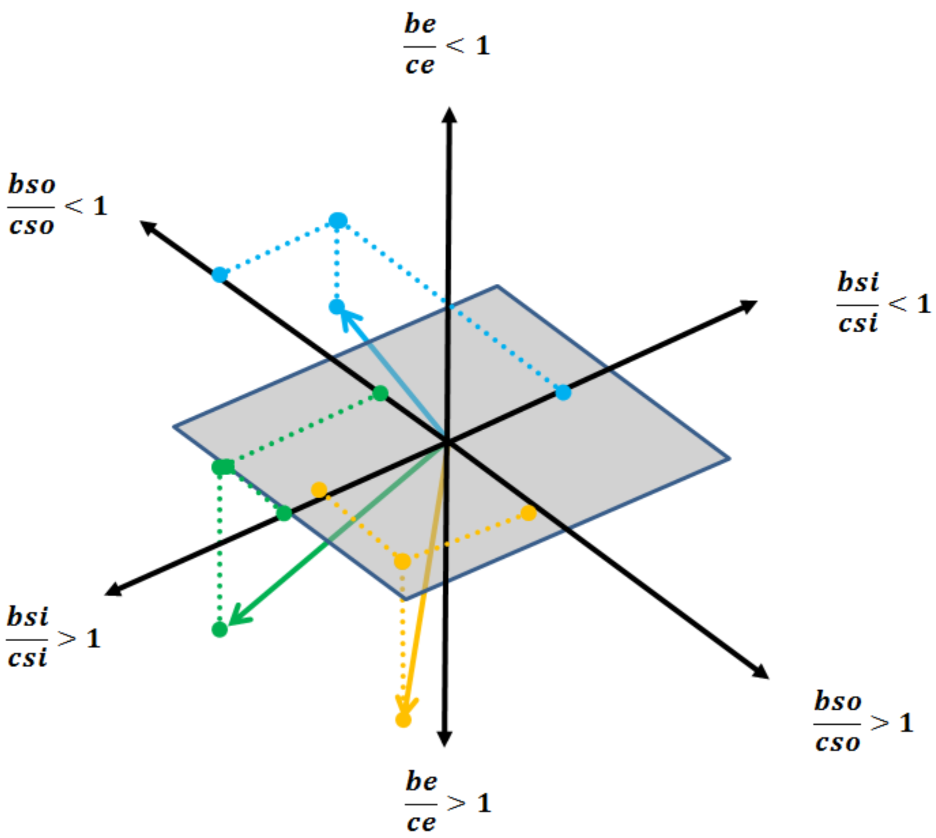

Figure 8. The ensemble appears within the transfer space. The origin of this coordinate system is on a diagonal line running through the volume of the transfer space, be/ce=bso/cso=bsi/csi=1. The green arrow is a productive ensemble (be/ce>1) in symbiosis. The orange arrow is wise exploitation of the source (type I) and the blue arrow is wise exploitation of the sink (type II). The space is non-linear.

Besides saturating Michaelis-Menten kinetics there are saturating logistic (sigmoid) shapes of the production observable. In enzymology we observe sigmoid behaviour when enzymes are oligomers of subunits each carrying a catalytic site. In addition, the different binding sites will influence each other in a way that the binding of the first substrate will increase the binding of a second substrate and so on. This type of enzyme is called allosteric. A simplified velocity equation for allosteric enzymes is the Hill Equation. Four binding sites with very high cooperativity between them results in the following equation:

$$\frac{V}{Vmax} = \frac{\frac{[S]^4}{a^3b^2cKs^4}}{1 + \frac{[S]^4}{a^3b^2cKs^4}}$$

This equation can be reduced to an equation similar to the Michaelis-Menten equation. K is a constant containing the interaction factors a, b and c and the intrinsic dissociation constant Ks.

$$V = \frac{[S]^n}{(K+[S]^n)} * Vmax \quad (K = a^3b^2cKs^4)$$

The ensemble productivity of a source and sink with sigmoid production functions will be therefore:

$$Ve = \frac{([S]so - [\Delta S])^n}{Kso + ([S]so - [\Delta S])^n} * Vmax\ so + \frac{([S]si + [\Delta S])^n}{Ksi + ([S]si + [\Delta S])^n} * Vmax\ si$$

Now we can calculate the benefit cost ratio of the ensemble in harmony with simple monotonous productivity:

$$\frac{Ve}{ce} = \frac{\frac{[S]so - [\Delta S]}{(Kmso + ([S]so - [\Delta S])} * Vmax\ so}{cso} + \frac{\frac{[S]si + [\Delta S]}{(Kmsi + ([S]si + [\Delta S])} * Vmax\ si}{csi}$$

and in conflict with monotonous saturating productivity:

$$\frac{Ve}{ce} = \frac{\frac{[S]so - [\Delta S] - Iso}{(Kmso + ([S]so - [\Delta S] - Iso)} * Vmax\ so}{cso} + \frac{\frac{[S]si + [\Delta S] - Isi}{(Kmsi + ([S]si + [\Delta S] - Isi)} * Vmax\ si}{csi}$$

in harmony with sigmoid saturating productivity:

$$\frac{Ve}{ce} = \frac{\frac{([S]so - [\Delta S])^n}{Kso + ([S]so - [\Delta S])^n} * Vmax\ so}{cso} + \frac{\frac{([S]si + [\Delta S])^n}{Ksi + ([S]si + [\Delta S])^n} * Vmax\ si}{csi}$$

and in conflict with sigmoid saturating productivity:

$$\frac{Ve}{ce} = \frac{\frac{([S]so - [\Delta S] - Iso)^n}{(Kso + ([S]so - [\Delta S] - Iso)^n} * Vmax\ so}{cso} + \frac{\frac{([S]si + [\Delta S] - Isi)^n}{(Ksi + ([S]si + [\Delta S] - Isi)^n} * Vmax\ si}{csi}$$

But source and sink may also differ in the shape of the production function like in the following harmonic behaviour (figure 9):

$$\frac{Ve}{ce} = \frac{\frac{[S]so - [\Delta S]}{(Kmso + ([S]so - [\Delta S])} * Vmax\ so}{cso} + \frac{\frac{([S]si + [\Delta S])^n}{Ksi + ([S]si + [\Delta S])^n} * Vmax\ si}{csi}$$

Figure 9

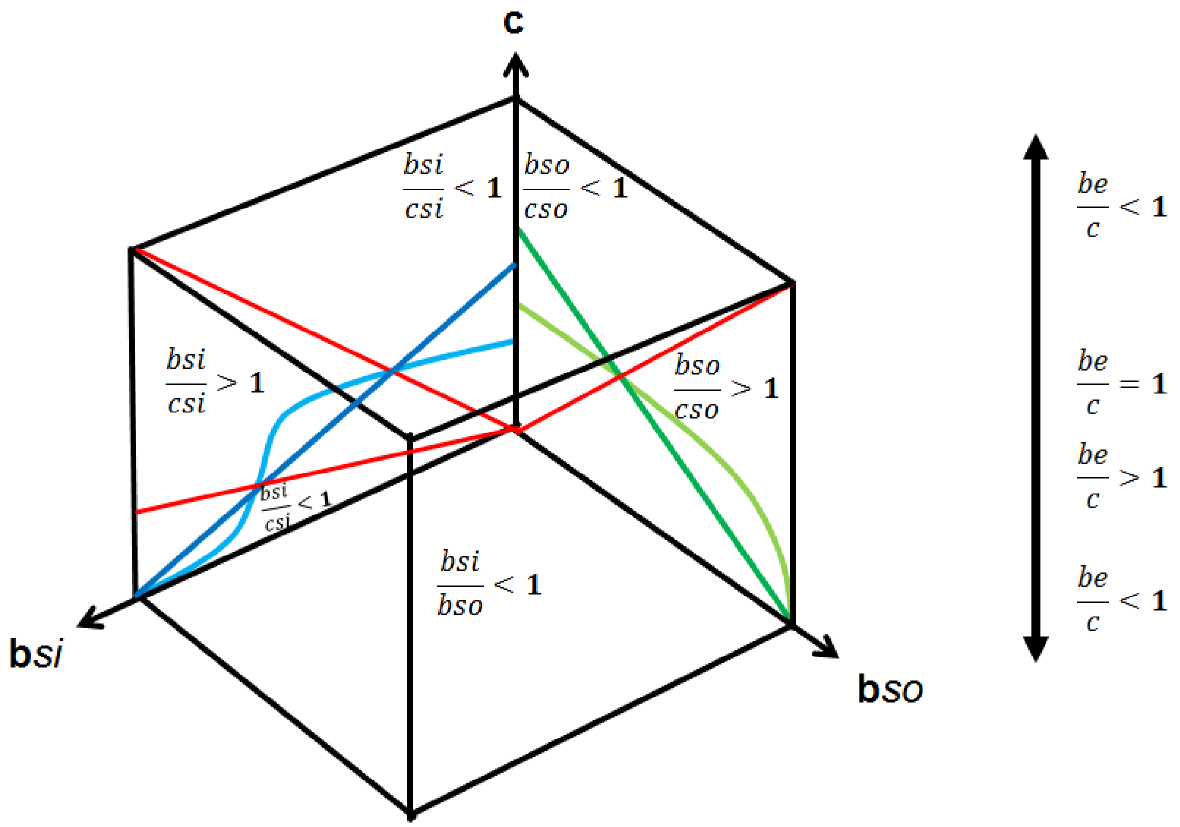

Figure 9: The transfer space with different production functions and cost functions in source and sink. In the source there is a saturating production function (light green) and a linear cost function (dark green). The sigmoid production function in the sink (light blue) and a linear cost function (dark blue). The side of the sink has an additional red line separating bsi/csi<1 from bsi/csi>1. The benefit ratio comparing sink over source is smaller than one at the ground. This will change when the cost is rising.

All combinations including several sources and several sinks in harmony and conflict with different behaviours can now be modelled.

Repeated transfers and dynamics:

If the transfer [ΔS] for example in wise exploitation is repeated because one side does not stop to take or give the source or the sink will sooner or later be exhausted and the ensemble will fall apart. The Lotka-Volterra equation is a model for an autocatalytic ensemble.

$$A + X \overset{k1}{\rightarrow} 2X$$

$$X + Y \overset{k2}{\rightarrow} 2y$$

$$Y + B \overset{k3}{\rightarrow} E + B$$

A is an endless external source for the source within the ensemble. B is an endless external sink for the ensemble internal sink. A and B are considered constant. A enters the ensemble and is transformed to X; Y leaves the ensemble being transformed to E with the help of B.

$$\frac{dx}{dt} = k_1AX - k_2xy$$

$$\frac{dy}{dt} = k_2xy - k_3BY$$

This system is well understood and a good model for cyclic population behaviour in predator-prey and parasite-host systems (Prigogine, I.). Let us take it as an orientation.

Case 1:

The source obtains the substrate S at a certain rate k1 from the endless external source A.

$$A \overset{k1}{\rightarrow} [S]so$$

From this substrate the source will have the productivity:

$$Vso = \frac{k1 * [S]so}{(Kmso + k1 * [S]so)} * Vmax\ so$$

The sink has also the basic source A where the substrate S is produced from at a rate k2:

$$A \overset{k2}{\rightarrow} [S]si$$

The productivity of the sink is:

$$Vsi = \frac{k2 * [S]si}{(Kmsi + k2 * [S]si)} * Vmax\ si$$

The productivity of the inactive ensemble would be again

$$\mathrm{Ve} = \mathrm{Vso} + \mathrm{Vsi}$$

As soon as the ensemble becomes active substrate is transferred from source to sink. But this time the transfer would be repeated over and over again at a certain rate k3 (amount of substrate within a time interval).

$$[S]so \overset{k3}{\rightarrow} [S]so - [\Delta S]$$

$$[S]si \overset{k3}{\rightarrow} [S]si + [\Delta S]$$

$$Ve = \frac{k1 * [S]so - k3 * ([S]so - [\Delta S])}{(Kmso + k1 * [S]so + (k3 * ([S]so - [\Delta S]))} * Vmax\ so + \frac{k2 * [S]si + k3 * ([S]si + [\Delta S])}{(Kmsi + k2 * [S]si + (k3 * ([S]si + [\Delta S]))} * Vmax\ si$$

Case 2

The situation is similar to case 1 but the sink regenerates completely on cost of the source. Again the source obtains the substrate S at a certain rate k1 from the endless external source A

$$A \overset{k1}{\rightarrow} [S]so$$

From the substrate A the source will have the productivity:

$$Vso = \frac{k1 * [S]so}{(Kmso + k1 * [S]so)} * Vmax\ so$$

This time the sink obtains the used substrate completely from the source.

$$[\Delta S] = [S]si$$

The sink has a basic given saturation BS witch will not be used if a source is present. The productivity of the sink alone is:

$$Vsi = \frac{BS}{(Kmsi + BS)} * Vmax\ si$$

The productivity of the inactive ensemble would be again:

$$\mathrm{Ve} = \mathrm{Vso} + \mathrm{Vsi}$$

The ensemble becomes active when substrate is transferred from source to sink. But this time the transfer must be repeated over and over again at a certain rate k2.

$$[S]so \overset{k2}{\to} [S]so - [\Delta S]$$

$$[S]so \overset{k2}{\to} [\Delta S]$$

$$Ve = \frac{k1 * [S]so - k2 * [\Delta S])]}{(Kmso + k1 * [S]so + k2 * ([\Delta S])} * Vmax\ so + \frac{BS + k2 * [\Delta S]}{(Kmsi + BS + k2 * [\Delta S]))} * Vmax\ si$$

Similar considerations can be made for sigmoid or mixed behaviour including the investments of brute force and education.

The ensemble vector will move with every ΔS to a new location at a certain velocity along the surface within the transfer space. This will result in a path from start of the transfer to the equilibrium of source and sink or to the end of the ensemble. The velocity v depends on the frequency of the transfer of small substrate portions from source to sink.

$$v = \frac{d[\Delta S]}{dt}$$

But the velocity of development of the ensemble is also the change of ensemble productivity Ve over time.

$$v = \frac{d[Ve]}{dt}$$

As the space is non-linear

$$\frac{d[\Delta S]}{dt} \sim \frac{d[Ve]}{dt}$$

In case the change of Ve does not take place in harmony, there will be force and counterforce of source and sink. The force F to move the vector is necessary to overcome the counterforce. The counterforce could be interpreted as viscosity of the transfer space.

$$F = \mu A \frac{du}{dy}$$

The force is equal to the dynamic viscosity factor (μ, in this case a property of the transfer space), the area A (in this case a property of the ensemble vector) and the shear velocity.

In the beginning the system was set up with a non-limiting connection between source and sink. This simple assumption avoids external limitations. The viscosity of the space and properties of the ensemble vector are internal limitations combining features of source and sink. The vector may even show signs of inertia forcing the vector out of the optimum although it had been reached.

Discussion:

Live is based on the DNA/RNA/Protein complex including other groups of organic and inorganic molecules. All components of life are important but enzymes and enzyme complexes contribute basically and directly to productivity. Organisms compete for similar substrates like carbohydrates, amino acids, lipids, light, water, oxygen, carbon dioxide and many other building blocks of live. Most of the conflicts are handled with brute force within and between species. The romantic game theory suggests that the best solution for conflicts is “cooperation” because this has the highest productivity and long term stability. The transfer space can better explain on all levels of complexity (from enzymes to societies) the behaviour of living entities and in which way unexpected dynamics will arise. Superadditivity has been observed in experiments solely designed to investigate ideas develop in game theory ((Turner, P.E. and Chao, L.; 1999). What is generally regarded as cooperation is either wise exploitation where on side stops at b/c=1 or harmony of giving and taking in symbiosis. Source and sink may be tied together by accident falling in all generations into the same pit or by brute force and education which makes a process of recognition for the gaining party necessary. To be source and sink may be a fixed fate but may also depend on the point of view. Especially in wise exploitation the sink may become a source for the exploited primary source like in breeding and farming. Therefore, the idea of “reciprocity” of classic game theory seems to be naïve as is the idea of “altruism”. There is only selfishness in all actions of source and sink. We no longer need to explain the development of altruism with “haystacks” in “group selection” as there is no altruism.

The suns energy is handed over from sources to sinks in the food chain. In all life forms substrate surplus is finally transformed into offspring. In many species offspring is fed and taken care of by the parents. The reason is not altruism. Altruism does not exist even in the basic biologic sense. Additional substrate could be either used to produce more sperm and eggs (more new offspring) or used to feed or care for the already existing offspring. Depending on the effectiveness and productivity additional substrate is used where it will have the biggest impact on productivity. The mechanism to decide what has the biggest impact is “survival of the fittest”. Productivity is an important part of fitness. Fitness means in some species more offspring (quantity) and in other species higher quality offspring. The quality increase is due to low saturation and high productivity during growth in comparison to the saturated parents with low productivity and shorter residual lifetime.

The food chain does not end when the suns energy arrives in man. The transfer space has additional consequences for the interpretation of human behaviour in societies. Frederick Solt published in 2011 (Solt, F.) a working paper on “Diversionary Nationalism: Economic Inequality and the Formation of National Pride”. Solt´s model clearly indicates that nationalism correlates directly to inequality within societies. How can enzymes help to understand this finding? The explanation would be again the transfer space. The poor (the source) and the rich (the sink) form an ensemble. The more the sink invests in cheap education towards cheat pride (nationalism) the more the sink can take away without risking to overcome expensive physical counterforce. In some nations this behaviour is connected to productive exploitation, a further argument for pride. The role of emotions in combination with brute force and education has already been discussed (Friedrich, T.) The success of ensemble and sink however is always on cost of the source living proudly in trailer parks. Wise exploitation with the use of cheap education (in comparison to harming brute force and counter force) seems to be a central component of human associations. Especially important is education in certain political and religious systems. There the elite will enjoy the work of a controlled majority. The gain for the ensemble may be knowledge like casting bells and canons or building cathedrals and fortresses. Education is also important in egalitarian, modern, productive societies. Maybe it would be worth to investigate the history of man and civilisation on the background of the transfer space under consideration of brute force and education with the result of productive or consumptive exploitation.

The high economic productivity in modern industrial societies is accompanied by a sharp decrease in offspring (Myrskylä, M. et al). The transfer space is able to explain this also. The productivity of the source is transformed into consume and production of goods while reproduction suffers. To be rich in children is synonymous for being poor in material goods on the average from individuals to societies (conservation law of mass and energy). If the data of Myrskylä, M. et al would have been not been linearized with a hitherto unknown method it would be easy to see that the system follows an indifference curve where less (of a costing good) is better. This is in contrast to usual indifference curves in economics where "more is better". Both shapes are part of the transfer space (figure 5a).

Summary:

Source and sink transfer substrates and form an ensemble, a new entity. The transfer may lead to super- and subadditivity. This non-linearity in the productivity results in unusual dynamics and behaviours of ensembles in comparison to single parties. Ensembles of lower complexity may become source or sink of an ensemble of higher complexity. In highly complex ensembles we use to observe only the fate of the single parties. The result of linear activities on the level of a single party will lead to non-linear, unexpected observations on the level of the ensemble. In neighbourhood to symbiosis where source and sink own the gain together wise exploitation appears. The gain is here is owned by the sink (type I) or the source (type II). Antibiosis is an irrational consuming behaviour. Highly productive ensembles start in inequality of resources (high in the source, low in the sink) and affinities (low in the source and high in the sink). The success is the ability to realize superadditivity but the result will be new inequality and suffering if the parties are not able to find b/c=1 at the same moment. The transfer space is a tool to be used on all "levels of selection". Therefore, surprising behaviours and the omnipresence of inequality in societies of featherless bipeds with broad flat nails could be of chronic nature. The answer to the question of the introduction can now be given. The bill is paid by the source and superadditivity in the sink. In case the ensemble is stronger than one or two single parties it is reasonable and will survive.

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