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21 March 2013

Online at https://mpra.ub.uni-muenchen.de/45405/
MPRA Paper No. 45405, posted 22 Mar 2013 08:35 UTC

Schumpeter´s Gale

Mixing and compartmentalization in Economics and Biology

Abstract

Homogenization destroys biologic structures and social organizations or companies. Sometimes structure und sometimes mixing yields the highest productivity. Why and when will destruction be creative? We theoretically demonstrate in a simple enzyme ensemble of source and sink superadditivity and subadditivity by mixing or structured transfer (compartmentalization). Saturating production functions in combination with linear cost functions create besides superadditivity and subadditivity strong rationality and irrationality. Whenever a saturated source gives a costing substrate to an unsaturated sink where the substrate will be earning superadditivity of the ensemble of both will be observed. Such conditions characterize symbiosis and synergism. In antagonistic interactions (antibiosis) an earning substrate is taken from a source to be a costing substrate in a sink. Subadditivity will appear within the ensemble when the substrate will be more costing or less earning after the transfer. Only in superadditivity an active ensemble (with substrate transfer) will have superior productivity in comparison to an inactive ensemble (no transfer of substrate). Mixing is able to destroy irrational transfers reversing the role of source and sink. In life forms the transfer may be accompanied by brute force, a mirror of higher affinity in enzymes. The different outcomes are interrelated regions on a surface within a three dimensional transfer space or ensemble space.

Key words: ensemble, source, sink, superadditivity, subadditivity, Michaelis-Menten equation, mixing, compartmentalization

Introduction

Substrates are not equally distributed in beakers without mixing and organisms or societies. A central dogma of biochemistry is mixing of enzymatic reaction volumes to improve the productivity of biochemical reactions. Homogenisation of an organism will destroy the main features of live. A central idea of biology is compartmentalization on all levels of complexity from cells to societies. Does this contrast root in a different foundation? Enzymes produce products from substrates (educts) in tubes and cells according to saturating production functions. Enzymes may be part of a linear or branched reaction chain. In branch points two identical or different enzymes compete for the same substrate. The substrate comes always at a cost either to the biochemist or to the organism. Cost functions are considered to be of linear nature to the amount. The enzyme will produce a product that confers some benefit (b) to the organism. When a source transfers substrate to a sink superadditivity and subadditivity will be observed. The reason is that in e.g. Michaelis-Menten type of production functions the cost (c) of the substrate will be at low saturation below the productivity but at high saturation the productivity will be below the cost. Therefore, benefit cost ratios larger than one ($b/c>1$) or benefit cost ratios smaller than one ($b/c<1$) will be observed. In the eye of the economist the net profit (b-c) will be positive or negative. In 1999 Turner and Chao (1) published a paper on Prisoner´s dilemma in an RNA virus. The focus of this paper was prisoner´s dilemma and game theory. We are able to explain the observed superadditivity in this paper (1, page 442, Figure 1b). In addition, we suggest an alternative view on conflict and harmony on different levels of complexity.

Theory

We set up a system of a “source” (so), a productive entity where substrates come from, a “sink” (si), a productive entity where substrates go to and an “ensemble” (e), a productive entity consisting of source and sink. The source will “give” or “give not”, the sink will “take” or “take not” the substrate depending on the degree of the actual benefit (b) to cost (c) ratio. To change the cost a party may give or take. To keep the cost a party may give not or take not. The option to a source is to give or 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 neither take nor give at $b/c=1$. This is summarized in table 1.

Table 1

source	sink	behaviour of the single party	result
$b/c \geq 1$	$b/c >1$	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
$b/c < 1$	$b/c \leq 1$	The source will give. The sink will not take.	conflict
$b/c \geq 1$	$b/c \leq 1$	The source will not give. The sink will not take.	no conflict or irrationality

Simple selfish behaviour of both parties leads to “conflict”, “no conflict” and “harmony” within the ensemble. In harmony a transfer of substrate will always be superadditive (a win-win situation, strong rationality). In case of conflict (win-lose; lose-win) the result of a transfer may be superadditive (win exceeds loss) or subadditive (loss exceeds win). In case of “no conflict” strong irrationality appears when an exchange is realized against all reasonable behaviour. Irrationality is an extreme form of subadditivity (a lose-lose situation). A b/c ratio of 1 is considered an optimal b/c ratio in our system (b-c=0). This contrasts with the general expectation that b/c ratios greater than 1 are desirable as they produce profit (b-c>0, net profit ($) = sales revenue ($) - total costs ($)). The amount of substrate is a Janus-like thing. On one side the substrate has a cost attribute. Cost should be avoided or reduced. On the other side it has a benefit attribute as a benefit will be produced from the substrate. Benefits should be sought and increased. At b/c=1 a stable equilibrium between both types of aims is reached. In our model profit seems better comparable to superadditivity. For example in a hunting ensemble glucose (cost) will be used during the hunt preferentially in muscles and brain to catch the prey (benefit) and not in intestines. A rational transfer from glucose from the intestines to brain and muscles takes place. During digestion glucose (cost) will be redirected via blood flow to the intestines to energize nutrient (benefit) uptake. The profit of this ensemble on glucose basis will be positive. The profit would be negative if glucose would be preferentially used in intestines during the hunt and in muscles and brain during digestion (an irrational transfer). Benefit and profit should not be mixed. Benefit (an advantageous gain or return) is a complex concept. Benefit and cost have quantitative and qualitative aspects. In the transfer space and in the ensemble space

we compare benefits relative to costs in different distribution of the same substrate between two enzymes (productive entities). Enzymes are well understood productive entities in cells. The enzyme is a fix cost to the cell. This fix cost is for simplicity not included in our model. In organisms the productivity of enzymes is of genetically fixed size. Therefore, to achieve the optimal benefit/cost ratio b/c=1 only the change of cost on a short time scale is an option - a mutation is considered to be on a longer time scale as an improved or reduced productivity will be realized in a future enzyme version. This may be different in other productive entities where a change of productivity is a fast and easy option. We treat the cost attribute of the substrate in transfer and homogenisation differently. Structure and information correlate. Structured transfer preserves the connection of the substrate and its cost attribute. Homogenisation destroys this connection as structure and information are lost. The cost always precedes the benefit. The cost is a benefit of a preceding step. The benefit will be a cost to a following step. A setting like this is known in biochemistry as a reaction chain and in biology as the food chain. In biology the input by the source exceeds the output by the sink by far. This results in the interpretation of a pyramid. The system of source and sink is an open system. The observed source was a sink to an earlier source and the observed sink will be the source to a later sink. Sources and sinks may be an ensemble, too. The whole setting is primarily powered by the sun or chemical energy sources (dark, extreme environments). Source, sink and the ensemble of both share the transfer space and the ensemble space (2, and figure 1).

Figure 1

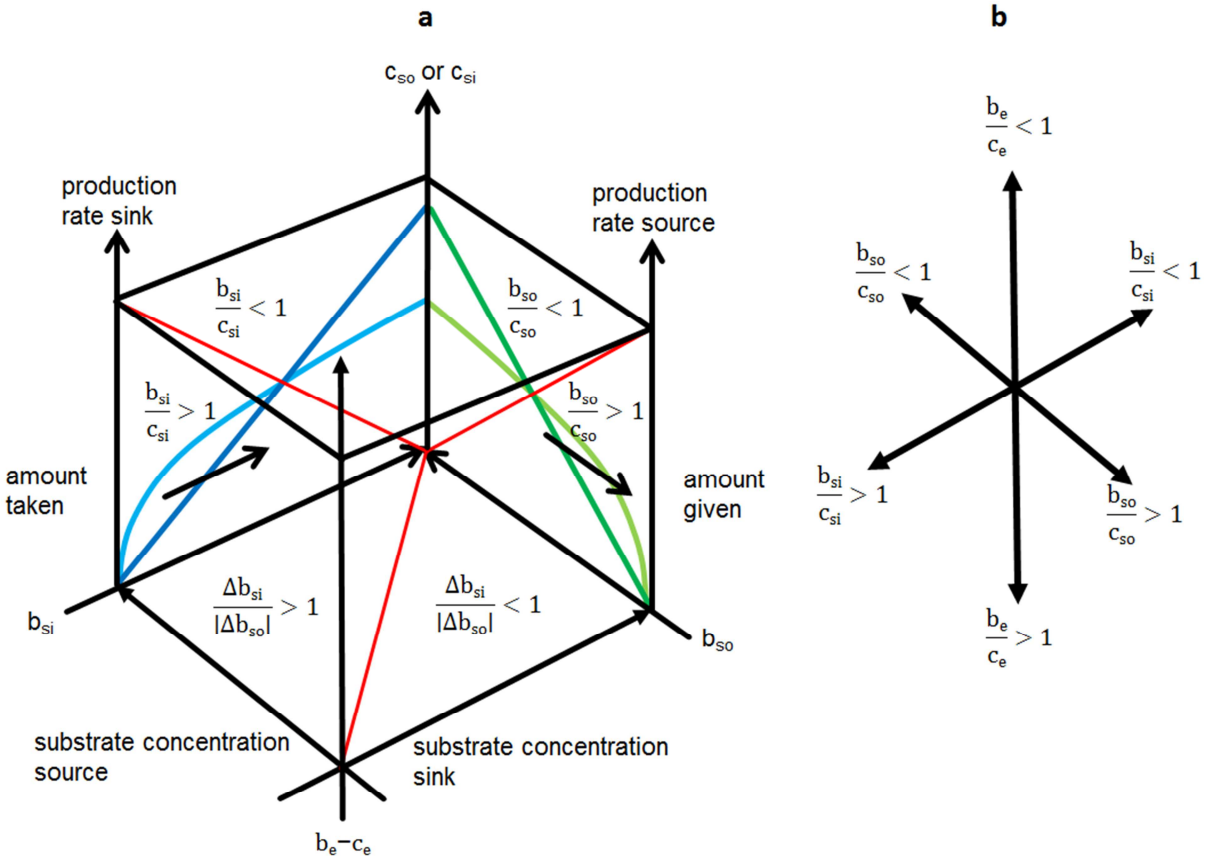

Figure 1

a. The transfer space. Source and the sink appear as two dimensional projections to the outside of the ensemble. The dark blue and dark green straight lines are the linear cost function of source and sink. The light green and light blue saturating curves are the Michaelis-Menten type production function of the benefit in source and sink. The red lines on the side separate b/c<1 from b/c>1 (benefit source b_{so}, cost source c_{so}, benefit sink b_{si}, cost sink c_{si}). The red line on the ground separates the outcome for the system ($\Delta b_{si}/|\Delta b_{so}|>1$, production; $\Delta b_{si}/|\Delta b_{so}|<1$ consumption). Δb is benefit before transfer minus benefit after transfer. Δb_{so} is benefit lost in source and Δb_{si} is benefit gained in sink. The coordinates of the space are substrate concentration in source and sink and b_e-c_e= z. The linear amount given or taken corresponds to a non-linear benefit lost or gained.
b. The ensemble space. The coordinates are b_{so}/c_{so}; b_{si}/c_{si} and b_e/c_e (benefit of the ensemble b_e, cost for the ensemble c_e). The origin of this space is 1. The ensemble space appears within the transfer space in an upside (large quotients b/c) down manner.

Calculations

The concentration of the substrate is ideally kept constant in steady state equilibrium. No product inhibition is observed. The reaction velocity v is interpreted as productivity - the production of some benefit. $v= [S]/(K_m+[S])*V_{max}$ according to (3). The cost is a linear function to the amount of substrate. The cost accrues before the benefit. Transfer of substrate transfers cost. Mixing equalizes the substrate concentration after the cost has been paid for. Our investigation takes into account three different cases of enzyme ensembles, all producing according to a Michaelis-Menten productivity function:

1. *The symmetric ensemble:* We assume both enzymes have V_{max} of 5 µmol/min and K_m of 0.25 mmol/l substrate concentration and substrate ownership involves a linear cost factor of 3.5 per mmol/l substrate concentration.

2. *The first asymmetric ensemble:* Here we assume V_{max} to be 5 µmol/min for source and 15 µmol/min for sink. K_m in source set to be 0.25 mmol/l and in sink K_m is 0.1 mmol/l. Substrate ownership costs 3.5 per mmol/l substrate for source and is doubled in sink.

3. *The second asymmetric ensemble:* Here source and sink change roles compared to the first asymmetric ensemble. For each of these three cases we examine three kinds of behaviour:

a.) Inactive (red): Both enzymes produce separately.

b.) Transfer (green): Source transfers a very small amount of substrate to sink.

$v_{so}= [S_{so}-\Delta S]/(K_m+[S_{so}-\Delta S])*V_{max}$; $v_{si}=[S_{si}+\Delta S]/(K_m+[S_{si}+\Delta S])*V_{max}$

c.) Homogenisation (blue): The total substrate is shared equally between both enzymes, but costs remain with the original contributor.

For all nine combinations we have two 3D-diagrams each:

A: Substrate concentration of source and sink as independent variables produce a total net productivity (productivity minus cost) which is displayed on the vertical axis

B: productivity/cost quotients for source and sink produce a total productivity/cost quotient for the ensemble.

The diagram of type B is produced by calculating the substrate concentration S from a given quotient x of productivity/cost in an intermediate step: $S= V_{max}/(cx)-K_m$. All diagrams were created by MuPAD Pro 4.0.6 computer algebra system.

Results

We calculate the combined cost normalized productivity (b-c; b/c) of source and sink with transfer of substrate (active ensemble) or without transfer of substrate (inactive ensemble). Besides transfer we investigated simple mixing or no mixing (inactive ensemble). We obtain surfaces in the transfer space and the ensemble space. In symmetric ensembles both enzymes have identical K_m, V_{max} and cost values. In two types of asymmetric ensembles V_{max}, K_m and cost values in source and sink are different. Neither transfer cost nor mixing cost or fix cost is considered. The size of K_m and V_{max} compare to known lactic dehydrogenases, a cofactor is not considered.

In figure 2 we compare inactive ensembles (red surfaces, compartments are isolated) to active ensembles (connected compartments with transfer, green surfaces or mixing, blue surfaces).

Figure 2

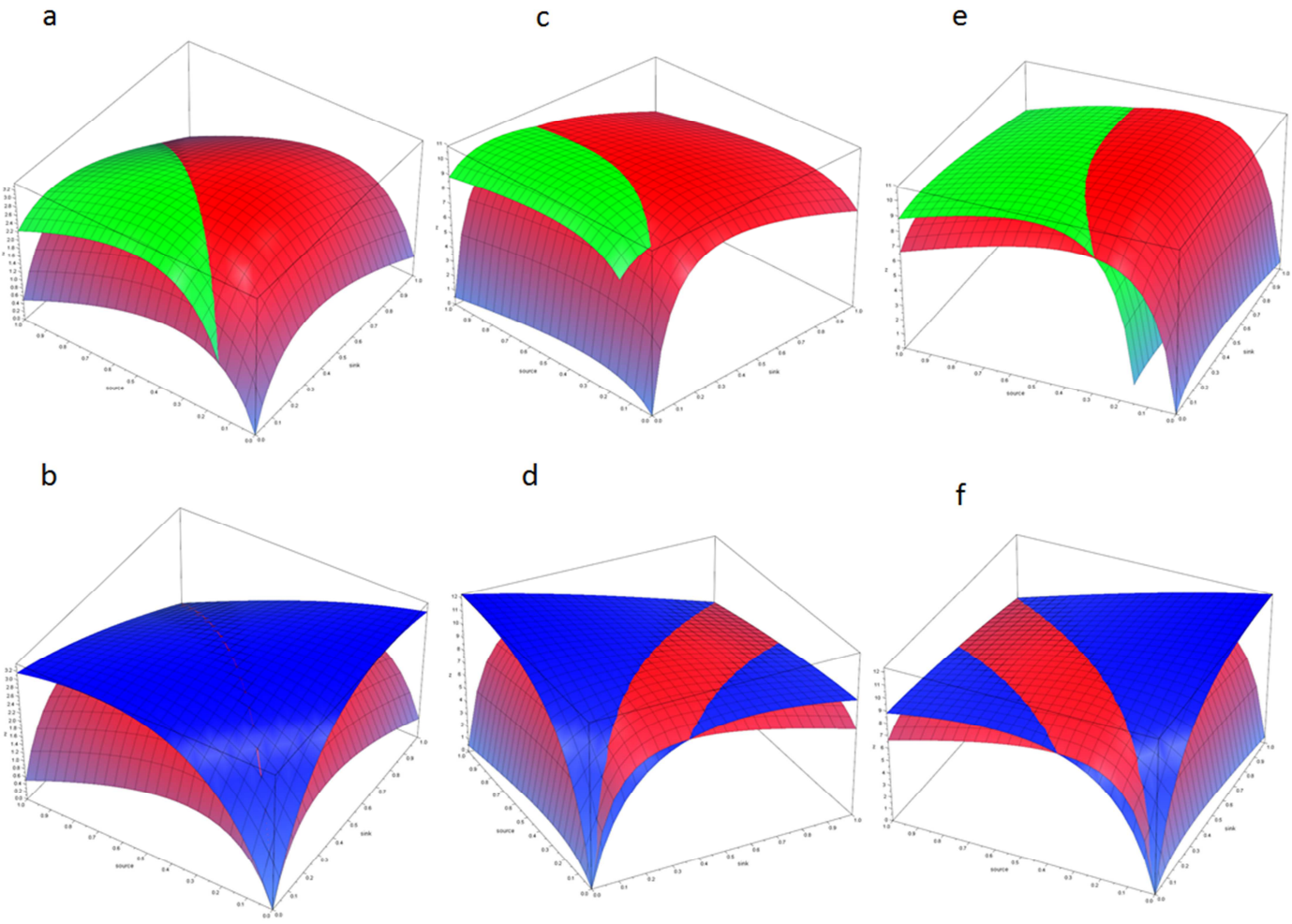

Figure 2

In the transfer space we compare transfer (a, c, e; green surfaces) and mixing (b, d, f; blue surfaces) in symmetric (a, b) and asymmetric (c, d, e, f) ensembles with an ensemble of two neither mixing nor transferring compartments (all red surfaces). The values for the symmetric ensemble a, b: V_{max} source and sink 5 µmol/min, K_m source and sink 0.25 mmol/l, cost source and sink 3.5 times amount substrate. The values for the asymmetric ensembles c, d: V_{max} source 5 µmol/min, K_m source 0.25 mmol/l, cost source 3.5 times amount substrate, V_{max} sink 15 µmol/min, K_m sink 0.1 mmol/l, cost sink 7 times amount substrate and asymmetric ensemble e, f: V_{max} source 15 µmol/min, K_m source 0.1 mmol/l, cost source 7 times of the substrate amount V_{max} sink 5 µmol/min, K_m sink 0.25 mmol/l, cost sink 3.5 times amount substrate. In case of a transfer the source will give 0.15 mmol substrate to the sink. Concentrations below 0.15 mmol/l are therefore not considered. The cost is calculated according to the substrate concentration after transfer. In case of mixing the cost is paid before mixing.

It is clearly visible that movement of substrate by transfer or mixing from a compartment of low productivity because of high saturation and high cost to a compartment of better productivity because of low saturation and low cost results in superadditivity (figure 2a, 2b, green or blue surface above red surface). Transfer in a symmetric ensemble (2a) results in superadditivity, however there are also regions of mild or severe subadditivity (irrationality). In these regions ($b-c<0$; $b/c<1$) the red surface is above the green surface. Mixing in a symmetric ensemble (2b) is always causing superadditivity (blue surface always above red surface). The exception is at identical substrate concentration in both compartments with simple additivity (red broken line). Subadditivity is not observed.

In the two types of asymmetric ensembles we observe basically the same. In addition, we now learn that mixing may also create subadditivity (red area above blue area). Subadditivity will appear when smaller concentration differences are aligned in a way that expensive substrate in a high productive compartment is mixed with a low productive compartment. The reason is that the cost is paid in the order of events before the mixing event by each side separately. A large red area emerges (figure 2d, 2f) in the middle. Here simple additivity of the inactive ensemble dominates. At large concentration differences the effect of the different cost and productivity is lost and superadditivity (blue) of the active ensemble is observed again. In transfer (2c, 2e) the superadditive area shifts towards the side with smaller productivity.

It is obvious that mixing or transfer may free productivity potentials. The active ensemble (transfer or mixing) is in some areas superior to the inactive ensemble. To judge what is better - transfer or mixing - we compared the active surfaces of transfer (green) and mixing (blue) in figure 3. In a symmetric ensemble there is only a line (blue-

green) where transfer (green) is equal to mixing (blue). Along this line the concentration difference between source and sink equals two times (0.30mmol/l) the amount transferred (figure 3a). In the direct neighbourhood of this line mixing is marginally better than transferring 0.15mmol/l. If we take into account different cost and productivity in source and sink in asymmetric ensembles an area appears here with true superadditivity of transfer (green) over mixing (blue).

Figure 3

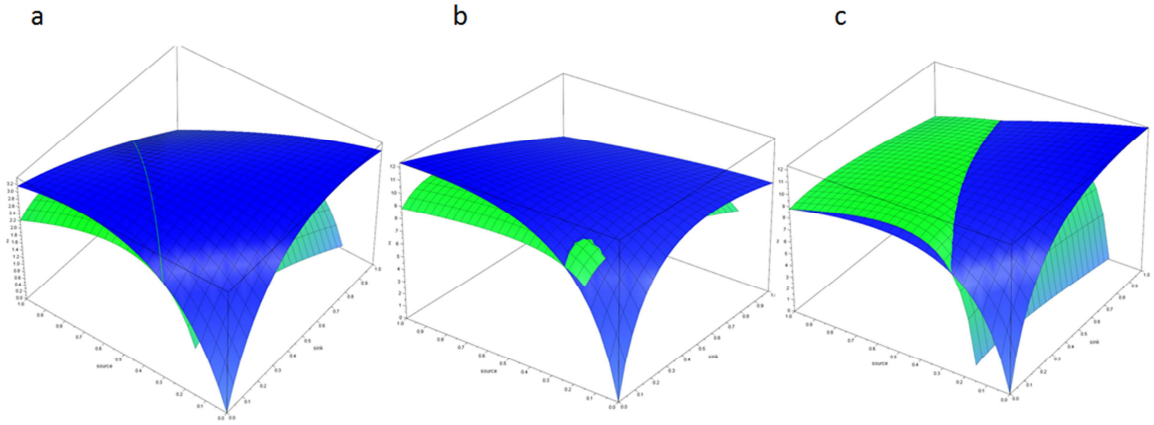

Figure 3

The calculation of an active ensemble with transfer (green) or mixing (blue) is identical to figure 2 and results in the same surface. Symmetric ensemble a: V_{max} source and sink 5 µmol/min, K_m source and sink 0.25 mmol/l, cost source and sink 3.5 times amount substrate; asymmetric ensemble b: V_{max} source 5 µmol/min, K_m source 0.25 mmol/l, cost source 3.5 times amount substrate, V_{max} sink 15 µmol/min, K_m sink 0.1 mmol/l, cost sink 7 times amount substrate and asymmetric ensemble c: V_{max} source 15 µmol/min, K_m source 0.1 mmol/l, cost source 7 times of the substrate amount V_{max} sink 5 µmol/min, K_m sink 0.25 mmol/l, cost sink 3.5 times amount substrate. In case of transfer source will give 0.15 mmol substrate to sink. The cost is calculated according to the substrate concentration after transfer. In case of mixing the cost is paid before mixing.

At high cost and high productivity in the sink a small region of superadditivity created by transfer is superior to mixing. Here source and sink are not saturated (figure 3b) and the ensemble rearranges productivity. Low saturation is a condition often observed in nature. At high cost as well as high productivity in the source and saturated productivity in source and sink a large area of superadditivity by transfer is observed. Here the saturated ensemble rearranges cost (figure 3c). Transfer will be suspended by mixing if the following limits are exceeded: a. the concentration difference is more than two times the size of the amount transferred (symmetric ensemble); b. in case the transfer would be irrational; c. transfer costs are larger than superadditivity through substrate transfer (the costs of mixing are generally considered negligible small); d. if the velocity of the formation of the concentration difference is similar to the velocity of the transfer. The limit d points to an additional strength of transfers - repeatability. The effect of superadditivity of a transfer is reinforced by repetition and its internal time scale. Mixing will force a system to adjust to the external time scale of the build-up of concentration differences. Therefore, even in areas where a single mixing event will generate more productivity than a single transfer, repeated transfer may be superior to single mixing. In symmetric ensembles a single transfer will never be better than mixing.

The benefit to cost ratios of source, sink and the ensemble of source and sink in figure 4 teach the same. In addition, we better see that the superadditivity created in asymmetric ensembles by mixing and transfer is much stronger than in symmetric ensembles. The ensemble space is highly non-linear. A small linear change of substrate in the transfer space will have a big effect on the benefit to cost ratio in the ensemble space, especially at low saturation. The three different surfaces (red, inactive; blue, mixing; green,

transfer) in figure 4 appear in different areas on top of the other areas. A patchwork of different optimal behaviours is in some points in direct neighbourhood.

Figure 4

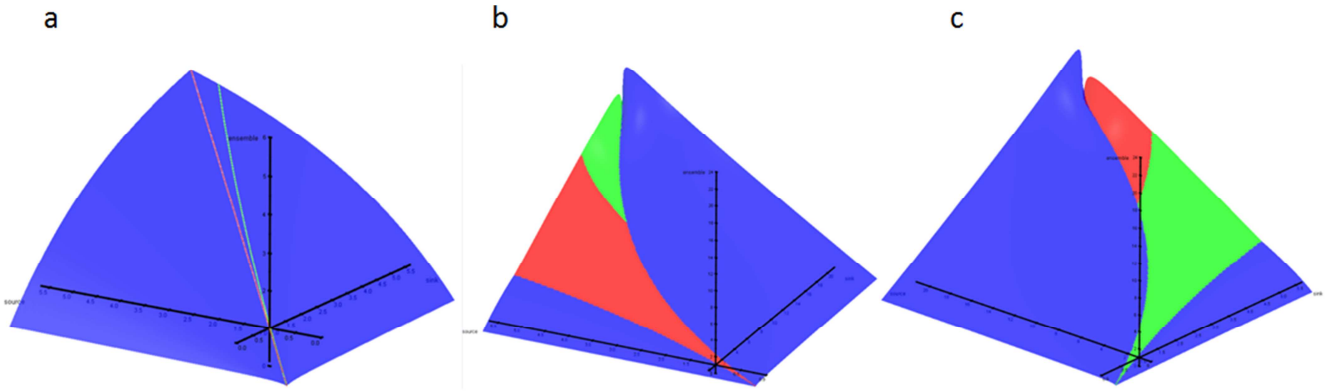

Figure 4

The ensemble space: The orientation of this presentation is in contrast to figure 1eeb upside (large quotients b/c) up. The benefit to cost ratios of source and sink are displayed on x and y axis. Although mixing (blue) transfer (green, here 0,015mmol) and inactive ensemble (red) form a complete surface we only show the highest values for the ensemble in a source and sink pair. The surfaces are partially transparent to make the three axes visible. In the symmetric ensemble (4a) we only see two lines where inactivity (red) or transfer (green) is as good as simple mixing. In the asymmetric case with a low productivity, low cost source (4b) transfer is only the best at high b/c ratios i.e. at low saturation in source and sink. In the second asymmetric case with a low productivity, low cost sink (4c) transfer is better at low and medial b/c values.

Discussion

Two compartments containing productive entities may stay separated or transfer substrates preserving the concentration difference or mix and equalize the substrate concentration. Destructive homogenisation or mixing seems to be antagonistic to structured organisation of substrate transfer. However, mixing and structure may both lead to optimized productivity under certain constraints. Mixing will improve the productivity of a symmetric ensemble (identical enzymes) abolishing asymmetric distribution of substrates. A small window exists where mixing and transfer are equal. Mixing will destroy all forms of irrational transfers or transfers that are too small and increase in that way productivity in asymmetric ensembles. This brings back the idea of Schumperter´s gale in economics. Transfer within an asymmetric ensemble may lead to strong superadditivity under asymmetric distribution of the substrate. Mixing and equal concentration would here destroy the ability to generate superadditivity in small concentration differences. The evolution of the first cells must have been predated by less structured precursors. It is difficult to imagine that in the course of evolution from biochemistry to biology the driving force would suddenly change. We interpret evolution as a process where increasing superadditivity (or decreasing subadditivity) is generated by productivity compartmentalized in space and time. A self-copying process seems to be comparable to perfect mixing as the product is its own substrate. To copy a different molecule which in return will copy the first molecule would be a compartmentalization at least in time. This may have started in the window of symmetric ensembles where the effect of mixing and transfer is comparable, enhanced by repeated copying. The hypercycle would be an ensemble compartmentalized in time (4, 5) and cells in space

and time. We suggest that molecular organization, division of labour and specialisation will start with superadditivity of an ensemble of source and sink. In the progressing specialisation neither the sink nor the source will be lost. In a fully integrated ensemble the source will finally serve as a collector and supplier for the better productive sink or the sink will become a valve and a disposer for the better productive source. A branch point becomes a reaction chain. A different type of ensemble integration will be observed in stable branch points when transfer costs consume the product of superadditivity and neither source nor sink gain while the ensemble gains. In a third type of fully integrated ensembles the productivity of the single party will be zero (e.g. the male-female ensemble). Finally, we want to emphasize that our considerations have nothing in common with cooperative game theory. The superadditivity of the ensemble has a biochemical reason. Linear cost functions in combination with saturating production functions are responsible for both - superadditivity and subadditivity. The whole may be more (Aristotle) but also less than the sum of the single components. The superadditivity of the grand coalition however is a theoretical construct. Superadditivity in our model is not violating the conservation laws because it is only better efficiency.

Conclusions

We suggest that mixing and compartmentalization are two sides of the same coin. Mixing is reasonable in symmetric ensembles to avoid concentration differences. Compartmentalization is reasonable in asymmetric ensembles utilizing small concentration differences to produce superadditivity and achieve that mixing and concentration differences coexist. As all members of a species compete basically for

identical substrates (energy, building blocks, money) we think that the transfer space and the ensemble space are also tools to look in a new way on interactions between organisms and to understand the continuum of harmony, conflict, rationality and irrationality and the resulting success (production and superadditivity $\Delta b_{si}*|\Delta c_{so}|/|\Delta b_{so}|*\Delta c_{si}>1$ or consumption and subadditivity $\Delta b_{si}*|\Delta c_{so}|/|\Delta b_{so}|*\Delta c_{si}<1$; Δb_{so} is benefit lost in source and Δb_{si} is benefit gained in sink. Δc_{so} is cost lost in source and Δc_{si} is cost increased in sink) of an ensemble, the invisible but always present third party. Observing a successful ensemble makes us forget that there may be a hidden source giving an earning substrate or a sink taking a costing substrate on the one hand, and on the other hand observing a growing source or sink may obscure observations of a doomed ensemble. In contrast, suffering sources or sinks within a successful ensemble may be stable as long as they are able to regenerate in the open system at a sufficient rate.

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