Recycling and growth in early evolution and today.[*]

Autocatalysis without recycling comes inevitably to an end – not only in early evolution.

Peter Schuster[†]

Robert Malthus[1] seems to have been the first who stressed the exceptional role and the consequences of geometric progressions in growth. Today we commonly adopt continuous time and use Leonhard Eulers exponential function to model unlimited growth through autocatalytic multiplication:

$$(\mathrm{A}) + \mathrm{X} \;\rightarrow\; 2\,\mathrm{X}\,,$$

with A put in parentheses because unconstrained growth assumes infinite resources. The best illustration of the power of exponential growth is the metaphor of water lilies covering the surface of a pond: "*Assume, the lilies are doubling the surface they cover on the pond every year. Three years ago they extended over one eights of the water surface and accordingly were hardly noticed, one year ago the coverage was one half, and today the pond is completely covered and all light dependent life in the pond except the lilies is doomed to die.*" Malthus compared the expected growth of agricultural production of food that he assumed to increase linearly in time with a human population growing according to a geometric progression, and made the simple and up to date correct prediction of the occurrence of hunger catastrophes unless birth control is introduced. Although technology driven increases in crop yields like the "green revolution" of the nineteen sixties and seventies were unforeseeable, they did not change the principle behind the problem: More food causes population sizes to increase until the starvation limit is reached again at the level of larger population numbers. The Malthus model is so simple that it can't be wrong, and regulation of growth by birth control is the only way out of the dilemma. We shall come back to the "green revolution" later in pointing out that one of the causes of its success is the introduction of a new process of recycling nitrogen compounds.

Biological evolution, on the other hand, is based upon multiplication of individuals in populations of species. How can natural selection work if exponential growth can only be maintained for a limited span of time? A general answer can be given in mathematical terms, since Darwin's principle is easily converted to a mathematical theorem:[2]

$$\frac{dx_k}{dt} = f_k\, x_k\,; \quad k = 1,\ldots,n \;\text{ and }\; \sum\nolimits_{j=1}^{n} x_j = 1 \quad \Rightarrow \quad x_k(t) = \frac{x_k(0)\exp(f_k\, t)}{\sum\nolimits_{j=1}^{n} x_j(0)\exp(f_j\, t)} \quad \text{with}$$

$$\lim\nolimits_{t\to\infty} x_k(t) = 1 \text{ if } k = m \quad \text{and} \quad \lim\nolimits_{t\to\infty} x_k(t) = 0 \text{ if } k \neq m \text{ with } f_m = \max\left\{ f_j\,;\; j = 1,\ldots,n \right\},$$

where the variables x_j are the normalized concentrations of different variants $\mathrm{X_j}$. Darwinian evolution selects for the variant of highest fitness, f_m.[‡] Without normalization

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the population or the individual variant would grow with the simple exponential in the numerator of $x_k(t)$. Among other properties the dynamics of exponential growth has one unique feature: The process of selection – when normalized to population size, $\sum_{j=1}^{n} x_j = 1$, as in the equation above – is identical in growing, constant and even decaying populations as long as the species does not die out.[3,4] In other words "selection of the fittest" occurs also in populations of constant population size and the outcome of the selection process is the same as we would expect to see in growing populations. Successful competition with exponential growth is only possible for variants that grow exponentially with higher fitness parameters f_k or with hyper-exponential or "hyperbolic" growth.

Different forms of growth are compared in figure1, which illustrates well the special feature of the functions for exponential and logarithmic growth: The exponential function represents the borderline between growth functions approaching infinity at finite time – commonly called "hyperbolic growth" curves – and "parabolic growth" functions that become infinite only in the limit of infinite time. Hyperbolic, exponential, and parabolic growth exhaust quickly the reservoirs of required materials and, in particular, exponential growth and hyperbolic growth empty all forms of resources highly efficiently. Accordingly, the only way to cope with particularly fast growing systems is recycling because more growth of individuals with finite life time leads to more death and more recycled material. Recycling is a prerequisite for efficient growth but it is, of course, not a sufficient condition, since other resources that cannot be recycled like, for example, energy may also be diminished and eventually dissapear. Linear growth approaches infinity at infinite time and this is also true for all forms of sublinear growth above the lower borderline in the figure that is given by logarithmic growth, which represents the slowest growing function reaching infinity at infinite time. Below logarithmic growth we have sublogarithmic growth curves, which stay finite at infinite time, and it is important to stress that only these very slow growing curves are compatible with finite reservoirs and can be sustained for longer times. These slow growing curves are characterized by diminishing rates with increasing time. All forms of unlimited growth – hyperbolic, exponential, parabolic, linear, and sublinear – can be continued only for some time. Needless to say, economists who preach that economies can grow for ever at constant rate must be cheating in one way or another. At constant population size, recycling is nevertheless sufficient to sustain Darwinian selection. In principle all forms of growth can be constrained to finite population size and then recycling helps to sustain populations, but only exponential growth guarantees that selection in growing and constant populations progresses in the same way.

Theoretical and experimental models for the origin of life commonly focus on one or more of three different issues: (i) creation, storage and maintenance of information in genes, (ii) harvesting and transforming energy in form of a metabolism, and (iii) creation of a local environment by means of a container.[5] Autocatalysis commonly viewed as multiplication is, as said, the basis of Darwinian evolution and it is thought to be

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[‡] Acknowledging the pioneering contribution of Robert Malthus fitness is often denoted as the Malthusian parameter, r, of a population.

indispensible in early evolution too. The main task to be solved by a prebiotic metabolism is to provide building blocks for the synthesis of the most important biopolymers, proteins and nucleic acid molecules through canalizing the enormous wealth of organic compounds into a relatively small set of key molecules.[6,7] Possible forms of early metabolism have been frequently discussed but only recently the view was directed also towards recycling of materials.[8] Already in the year 1997 Shneior Lifson indicated the importance of recycling in a paper on crucial stages at the origin of life[9]: *"… . Here suffice it to recognize that adaptation of autocatalysts to their changing environments by incorporating sequels into the autocatalytic process yields a great selective advantage. …"*[§] In the reaction mechanism,

$$A + X \rightarrow 2\,X \quad \text{and} \quad X \rightarrow D\,,$$

the molecule X is the autocatalyst as before and the degradation product D is a sequel of X. The system achieves a new quality in case D is converted by some energy driven recycling reaction $D \rightarrow A$ back into A. A recycling system driven by a photochemical reaction has been suggested already some time ago[2] and interestingly, the first protocell with an internal metabolism – often called the Los Alamos bug" –makes use of a light-driven reaction of a ruthenium complex.[1011] Photochemistry, apparently, is the most convenient strategy for enabling energetically uphill reaction, and light as a source of energy is – still – almost non-exhaustible.[**] Indeed photoreactions may be easily coupled to membrane bioenergetics, which is currently thought to be the first and until now most efficient form of recruitment of chemical energy in prebiotic and early prokaryotic scenarios.[12] In this context it should be remarked that the oldest fossils are possibly remnants of ancient photosynthetic cyanobacteria.[13] The recycling process need not be – and by the rules of standard chemistry cannot be – a single compound involved in a single reaction. There is, however, a problem with large cycles of metabolic reactions in a primordial world where protein catalysts did not exist: Uncatalyzed reactions are neither sufficiently specific nor efficient enough to allow for substantial yields after several steps.[14] Also in this aspect photochemical reactions may be useful, since they can be quite specific and lead to high amounts of product when the quantum yield plays no role.

Eventually, we come back to our initial problem of feeding the human population and consider recycling at present. Precious metals are not too hard to recycle and most of the metal producing companies have processes for recovering all kinds of metals from waste in their repertoire, which they can take up into their portfolio whenever the prices on the world-market are sufficiently high. The yield of crop is worldwide increased by using modified plant species and fertilizers. Here we consider two crucial elements, which are a *conditio sine qua non* for life and accordingly for agriculture too: nitrogen and phosphorous. Gaseous molecular nitrogen (N_2) is ubiquitous and we find it in almost non-exhaustible amounts in the atmosphere. It is quite inert and can't be assimilated by plants or animals, only a few bacterial species metabolize molecular nitrogen and convert it into nitrogen containing molecules that are useful for the other organisms. Until the beginning of the twentieth century practically there were only two sources of useful

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[§] Shneior Lifson uses the term "sequel" for the reaction products in the degradation of autocatalysts.
[**] This is of cause not always true for the biosphere where the rain forests present an instructive example of the struggle for light.

nitrogen: (i) legume plants that live in symbiosis with bacteria of the species *Rhizobium* which assimilate molecular nitrogen,[15] and (ii) guano, the excrements of birds, which lived and are still living in huge colonies on islands along the coastline of Chile and Peru. Using guano as fertilizer is recycling in a way but the cycle time is incredibly long. The invention of a chemical process converting molecular nitrogen and molecular hydrogen in a catalyzed reaction into ammonia by the two German chemists, Fritz Haber und Carl Bosch, changed the situation completely. Despite the fact that the Haber-Bosch process is extremely energy intensive the nitrogen components of guano were almost completely replaced by chemically synthesized nitrogen fertilizers, and this was one, presumably the most important basis providing food for an enormously increased and further increasing human population. The importance of the chemical ammonia production is illustrated by a statement taken from Robert Horwath:[16] *"…The rate of change is astounding, and half of all of the synthetic nitrogen fertilizer ever used on Earth has been produced since 1985. Today, over 80% of the nitrogen in the protein of the average human on Earth is derived originally from the Haber-Bosch process."* Four out of five nitrogen atoms in our bodies have seen a Haber-Bosch plant from inside. The nitrogen cycle is an excellent example of recycling with a huge reservoir, production of synthetic nitrogen encounters practically no limits except energy supply and environmental problems caused by the high-density of food production and fertilizers in waste waters.

The second biological recycling problem concerns another essential element in biopolymers: phosphorous. High agricultural production requires phosphate fertilizers and, in addition, phosphate is an indispensible ingredient of modern detergents. The conventional source of phosphate are phosphate-rich rocks but new lodes become harder and harder to find and some experts speak of "peak phosphorous" in analogy to the frequently discussed "peak oil".[17] Meanwhile, phosphorous industry has developed recycling strategies and processes to recover phosphorous from sewage and other waste waters.[18] The major difference between nitrogen and phosphorous recycling is the existence of a practically inexhaustible reservoir of pure nitrogen whereas phosphate has to be isolated and purified from highly diluted solutions enriched with impurities. In addition, phosphate that reaches the rivers and the sea becomes so highly diluted that it is practically lost for any affordable recycling process.

Finally, we repeat the relation between exponential growth and recycling: Exponential growth exhausts all reservoirs and after an essential reservoir has been lost and no refill is possible the population dies out. In particular, the realistic experimental implementation of prebiotic models is jeopardized by precisely this problem. Recycling provides a solution, because the amount of recycled material is coupled to the level of autocatalysts, and the efficiency of the recycling process determines together with other factors the amount of autocatalysts that can be sustained. This is likewise true for primodial autocatalysis, for biological evolution as well as for the development of the human population.

References:

[1] Malthus, T.R. An essay of the principle of population as it affects the future improvement of society. J. Johnson: London 1798.

[2] Schuster, P.; Sigmund, K. Dynamics of evolutionary optimization. Ber. Bunseges. Phys. Chem. 1985, 89, 668-682.

[3] Eigen, M.; Schuster, P. The hypercycle. A principle of natural self-organization. B. The abstract hypercycle. Naturwissenschaften 1978, 65, 7-41.

[4] Schuster, P. Mathematical modeling of evolution. Solved and open problems. Theory Biosci. 2011, 130, 71-89.

[5] Rasmussen, S.; Chen, L.; Nilsson, M.; Abe, S. Bridging nonliving and living matter. Artificial Life 2003, 9, 269-316.

[6] Morowitz, H.J.; Kostelnik, J.D.; Yang, J.; Cody, G.D. The origin of intermediary metabolism. Proc.Natl.Acad.Sci.USA 2000, 97, 7704-7708.

[7] Copley, S.D.; Smith, E.; Morowitz, H.J. How life began: The emergence of sparse metabolic networks. Journal of Cosmology 2010, 10, 3345-3361.

[8] Braakman, R.; Smith, E. The compositional and evolutionary logic of metabolism. Phys.Biol. 2013, 10, e011001.

[9] Lifson, S. On the crucial stages in the origin of animate matter. J.Mol.Evol. 1997, 44,1-8.

[10] DeClue, M.S.; Monnard, P.-A.; Bailey, J.A.; Maurer, S.E.; Collis, G.E.,; Ziock, H.-J.; Rasmussen, S.; Boncella, J.M. Nucleobase mediated, photocatalytic vesicle fornation from an ester precursor. J.Am.Chem.Soc. 2009, 131, 931-933.

[11] Rasmussen, S.; Bedau, MA.; Chen L.; Deamer, D.; Krakauer, DC.; Packard, NH.; Stadler, PF. Protocells: Bridging nonliving and living matter. MIT Press: Cambridge, MA, 2009.

[12] Lane, N.; Martin, W.F. The origin of membrane bioenergetics. Cell 2012, 151, 1406-1416.

[13] Schopf, J.W. Fossil evidence of Archaean life. Phil.Trans.Roy.Soc.London B 2006, 361, 869-855.

[14] Orgel, L.E. The implausibility of metabolic cycles on the prebiotic Earth. PLoS Biology 2008, 6, e18.

[15] Bernhard, A. The nitrogen cycle: Processes, players, and human impact. Nature Education Knowledge 2012, 3(10), 25

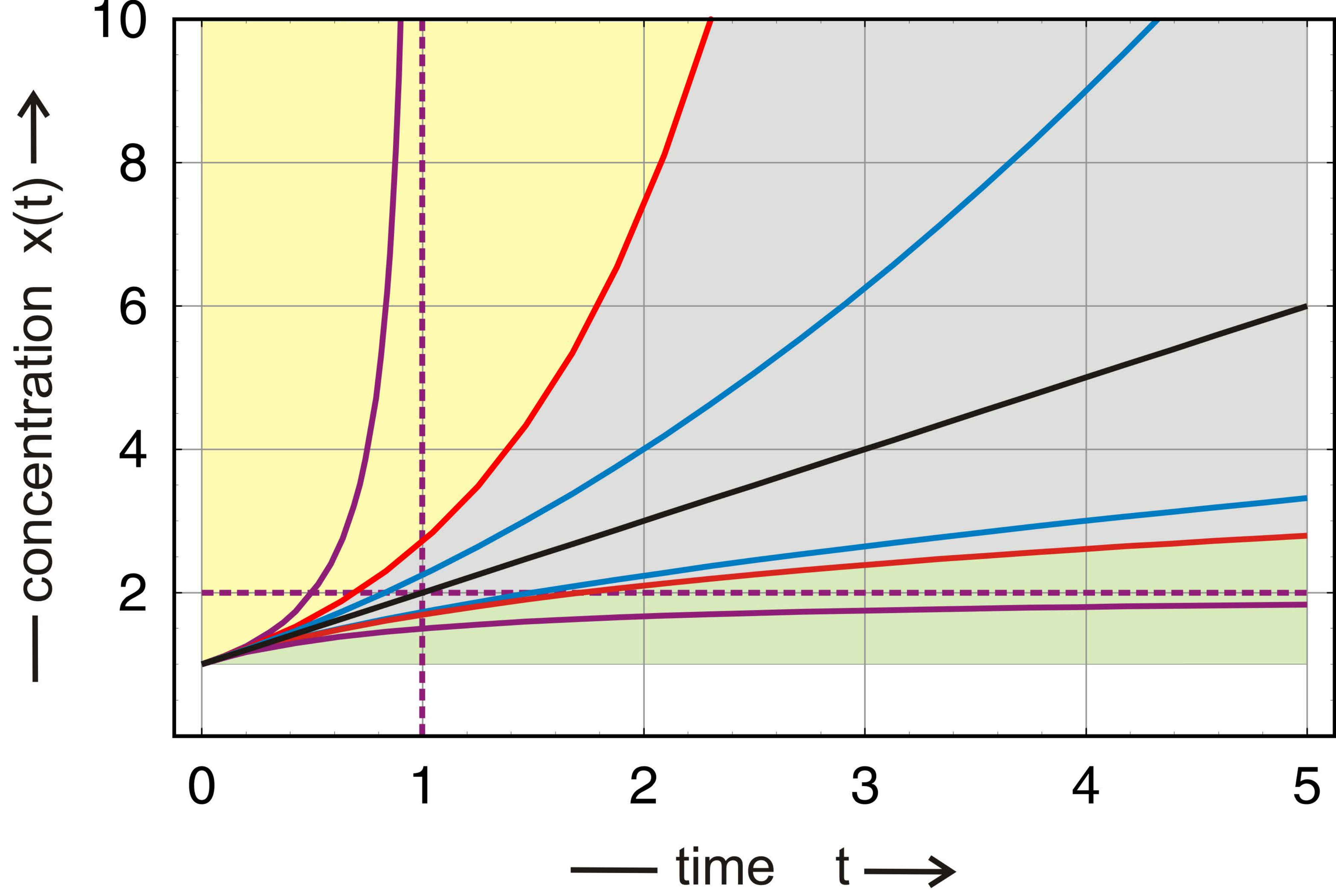
[16] Howarth, R.W. Coastal nitrogen pollution: A review of sources and trends globally and regionally. Harmful Algae 2008, 8, 14-20.

[17] Beardsley, T.M. Peak phosphorous. BioScience 2011, 61, 91.

[18] Schipper, W.J.; Klapvijk,A.; Potjer, B.; Rulkens, W.H.; Temmink, B.K.; Kiestra, F.D.K.; Lijmbach, A.C.M. Phosphate recycling in the phosphorous industry. Phosphorous Research Bulletin 2004, 15, 47-51.

Figure caption:

Figure 1: Idealized functions for unconstrained growth. All functions are normalized in order to fulfill the conditions $x(0) = 1$ and $dx/dt|_{x=0} = 1$. The individual curves (from upper left to lower right corner) show (i) hyperbolic growth ($x(t) = 1/(1 - t)$; violet; the dotted line shows the position of the instability), (ii) exponential growth ($x(t) = \exp(t)$; red), (iii) parabolic growth ($x(t) = (1 + t/2)^2$; blue), (iv) linear growth ($x(t) = 1 + t$; black), (v) sublinear growth ($x(t) = \sqrt{(1 + 2t)}$; blue), (vi) logarithmic growth ($x(t) = 1+\log(1+t)$; red), and (vii) sublogarithmic growth ($x(t) = 1+t/(1+t)$; violet; the dotted line indicates the maximum value x_{max}: $\lim_{t\to\infty} x(t) = x_{max}$). The two red curves separate regions of different qualitative behavior: (i) growth curves in the yellow region grow to infinity at finite times, (ii) growth curves in the grey region approach infinity at infinite time, and (iii) growth curves in the green region stay finite in the limit $t\to\infty$. The black line separates concave and convex curves.



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