

Biophysical causality in Volterra competition systems, including *Homo sapiens*

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I. Introduction

This study is the continuation of an effort to come to a biophysical understanding of competition (Walker 1983, 1984, 1987). Competition involves macroscopic energies and bodies in space and in time and is therefore a kind of process that ought to be understandable in terms of classical physics. Yet, little progress has been made in this sense since Volterra (1926) proposed his equations to assist Italian fisheries. Attempts to relate concrete biological parameters of resource uptake and limitation to the Lotka (1932) / Volterra (1926) equations (Vance 1985; Tilmann 1977, 1982) remain under heavy debate (Thompson 1987, Tilmann 1987). There does still not exist a generally accepted definition of competition, and biological diversity, maintaining itself in nature and in computer models despite all principles of competitive exclusion, keeps bewildering theoretical ecology (Hutchinson 1959, Wangersky and Wangersky 1983, May 1976).

In classical physics phenomena are causally connected. Water, for example, boils because its internal vapour pressure exceeds

atmospheric pressure. Thus established predictabilities approach 100%. The argument of competition seems to belong to a similarly deterministic category. Resources/space are limited and demonstrably shared by various consumer populations with variable growth rates. Hence, the population with the largest growth rate will eventually replace all other consumers. Yet we find 235 tree species belonging to 43 families in a hectare of amazonian rain forest (Prance et al 1976), all utilizing the same pools of light, water and minerals. Analogous situations one finds in mountain prairies and their herbacious cover and in the fauna of coral reefs, to mention just some of the most extreme conditions. There can be only one possible conclusion: competition in the sense of the above, seemingly logical argument, is inoperative, because of at least one of three possible reasons: either resources/space are not limiting, or they are not shared, or the various consumer populations have the same average growth rates. Neither of the three criteria opposes insuperable obstacles to verification.

The obstacle materialised in the form of Darwin's (1859) "Struggle for the Life" and "War of Nature", glorified in the title and in the last paragraph of his "Origin of Species"¹⁾. Now, humanity in general, and of Darwin's period in particular, is- and was- intimately aware of famine, disease and death, and since earliest childhood we all wanted things that are hard to get. The term "competition" in its meaning of contest is much older than any competition theory. Competition as struggle is therefore a universal, human, intuitive truth, which is accepted as a basic mode of operation, and Darwin has verbalized this intuition. But intuitions are not scientific concepts; this is the root of the problems in competition theory.

1) Title of the third edition: Of the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.

Citation from last paragraph of "The origin of species": Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely the production of the higher animals, directly follows.

The struggle is won by the fittest, and, in mathematical terms, the fittest is the one with the highest growth rate. Whence the pervasive conviction, from traditional biology to modern economics, that systems must engage in contest, that growth rates must be maximized by production and re-production, that competition guarantees maximum quality of systems, and that, quite generally, successful existence is the result of "strategy" (a term borrowed from military science).

As competition implies shortage of resource (in its widest sense) as an initial condition, the maximized growth rate of the winner presents the classical case of a positive feed-back mechanism, which leads, inevitably, to the disruption of any organization in its sense of consistent, biophysical interaction between different, identifiable components of the system. "Famine and death" eventually catches up with the fastest growing winner. The anxiety generated by shortage of resource leads, in addition, to the modern obsession with efficiency. The fastest growing winner is, supposedly, also the most efficient user of the resource, an intuition that is in blatant opposition to the present state of affairs: today the world is economically dominated by societies with maximum consumption of energy per person. The "struggle for life" not only permeates, but actually dominates traditional biology. Thus, plants evolve strategies to defend themselves against herbivory. It is not quite clear why species have survive in the first, and to be palatable in the second place, and the successful existence of the vegetation that supports the fauna of the earth is hardly ever mentioned. This, in the face of the fact that agriculture resorts since hundreds of years to artificial herbivory (pruning fruits trees, cutting grass etc) in order to maximize plant production/reproduction. Sexual reproduction is the topic of repeated symposia because of the bewildering existence of males, which, in the higher evolved animals means a 50% loss of reproductive fitness. That the evolution of compulsory, sexual reproduction is accompanied by the systemic, genetic mortalization of 99,99...% of biomass (only fertilized gametes retains the potential of reproduction, Walker 1978)

remains unmentionable. Male existence, so runs the argument, is the cost that must be paid for some other, more than compensating fitness gains, such as defense against parasites (Brenemann 1980; Hamilton 1990) for example. Rare species present a much pondered problem, because what is growing ought to get numerous, and what is not growing, should not exist. These are just some of the best known cases which shall serve as examples for how the intuition of "struggle" and obsession with growth guides reasoning and obfuscates the obvious. This does not mean to say that all this reasoning is wrong, nor indeed, that the results of research done on these premises are invalid. It *does* mean, though, that argumentation is single-tracked and lop-sided and as such leads to inconsistencies with opinion-free observation, and that the underlying intuitions successfully suppress all other points of view.

It is the objective of this paper to analyse the section of Darwin's "War of Nature", that is commonly understood as competition, in terms of the classical, physical parameters of space, time and mass/energy, and to come to a clear formulation of the biophysical causes that allow for, or preclude the coexistence of diverse, self-reproducing species. This attempt includes the species *Homo sapiens* as an ordinary part of nature. If, as far as competition is concerned, Man *does* occupy a special position in the biosphere, this must be expressible in biophysical terms.

II. The premises underlying competition theory

Logic, original Darwinism and contemporary, general biology (including molecular genetics) allow for the formulation of the following premises which underly the argumentation of this analysis:

1. For a population to exist successfully, i.e. to be observable by *Homo sapiens* for long periods (including scientific extrapolation into the past), it is necessary and sufficient that this population maintains itself; that is, restitution of individuals (reproduction) must balance losses (mortality). Reproduction in this sense means *redundancy*, rather than growth.
2. This principle is independent of the number of individuals in the population; rare species present no special problem (special interests in special mechanisms that allows for sufficient redundancy notwithstanding!).
3. The faculty of redundant reproduction results in positive population growth in environments with excess resources and/or space; discovery of new types of resources thus allows for the expansion of the respective population system.
- 4: Considering the known order of magnitude of mutation rates (including DNA base pair mismatch and genetic tinkering at large; Jacob 1983), population systems, whether growing or just maintaining themselves, are subject to incessant, generation-wise diversification in time and in space ("quasi-species", Eigen and Schuster 1979).
5. If population system (taxons) remain relatively invariant over relatively prolonged time periods, mechanisms that suppress/eliminate variation must be in operation (for instance genetic repair, sexual reproduction, selection of specific phenotypes; sexual reproduction, for instance, permits reproduction then only, when two similar individuals are involved, as such it creates and conserves "the species" (Walker 1978)).
6. The eventual inevitable limitation of space and/or resources, together with inevitable fluctuations of the growth rates

within and between varieties, leads to a continuous loss of varieties with relatively low growth rates. This *general, numerical competition* is thus a mechanism that *reduces potential diversity*.

For these losses to occur there is no necessary energetic, causal link between the variety in decline and its physical/biophysical environment, or between specific varieties with different growth rates.

7. Where such specific interactions *do* occur, the process of elimination results in specification of the varieties that remain in the population system. It follows (from paragraphs 6 and 7) that selection of specific phenotypes by a specific and limiting environment is, in fact, a competitive process. (Whether phenotype corresponds to genotype, i.e. the evolutionary aspect, is not the topic of this study).

8. Competition may be interpreted as "contest", if the reduced growth rate of one particular population (variety, taxon) is demonstrably a direct, physiological function of the presence of individuals of the same or/and of different populations, over and above the mere effect of resource/space limitation. (Aggression, defense, pheromonal effects, chemical, acoustic, visual interactions etc). The term "strategy" should not be used, because it implies finalistic, purposeful action, in contradiction to objective, scientific analysis which is confined to deterministic and probabilistic interpretation.

Summarizing points 1-8 we find that from the mathematical point of view competition is a mere number game which is determined by the limitation of the respective system (ΣN_i is limited; $N_i =$ number of individuals in the i^{th} population), and by the presence of diverse, self-reproducing populations with various and variable growth rates. Physical aspects enter with energetic interactions between the populations and their limiting environment, and between the individuals within and between populations, and

which thus determine the actual growth rates of the populations. In principle, two kind of processes may be distinguished that allow for the maintenance of diversity:

1. The rate of diversification by mutations is balanced by the rate of loss of varieties as a consequence of limitation. This applies primarily to *intra-specific competition* which contributes to a relatively slow rate of morphological/physiological change of the species through time.

2. Maintenance of diversity between such relatively conservative species (eucaryotes with sexual reproduction) as a result of resistance against competitive elimination (*inter-specific competition*); this necessitates biophysical interactions of individuals within and/or between species.

In reality, this separation of the two kinds of mechanisms is not consistent. Species, too, diversify and may die out, and biophysical interactions between genetic varieties within species may occur. Important, though, is the hierarchization of the system, specially with regard to time. Species diversification occurs through geological times while intraspecific variation changes with each generation. We may thus formulate the apparent paradox that *evolution of species depends on maintenance of species*.

In the following, we are only concerned with coexistence and competitive elimination of established species. Thereby the term "species" is used in the liberal sense of "identifiable, more or less closed population", particularly where *Homo sapiens* is concerned. To the extent of arbitrariness in the definition of "species" (and this includes taxonomy, notably in asexually reproducing organisms), the conclusions will also implicate *intraspecific competition*.

III. Limitation of population systems.

1. Survival of the fittest: pure number game competition.

Self-reproducing populations under non-limiting conditions grow exponentially, accordingly (N_i = number of individuals):

$$\dot{N}_i = r N_i; \quad r = b - d \quad (1)$$

r = intrinsic growth rate (Malthusian parameter or Malthusian fitness) = genetically determined maximum growth rate in a given environment; b = rate of reproduction (birth rate); d = system-specific death rate; hence, r is a measure of redundancy, i.e. of the potential to balance additional, extrinsic accidents. With positive r -values, systems grow to infinity, therefore, mathematical models and real populations alike, are subject to limitation. Thus, in the Eigen-Schuster model (1978) on pre-cellular evolution, a mixed population of autocatalytically replicating macromolecules, with species-specific replication rates, is confined to a given space with the condition, that the total number of molecules is constant ($\sum N_i = c$). An input flow of metabolites allows for the various r_i within the box, while an output flow carries away excess production and metabolic waste. For every molecule produced in excess of c , one molecule must leave the space. This emigration is randomized between the various (i) species, and therefore, the species with lower growth rates (r_i) are "crowded out"; eventually, the *one* species with the largest r -value will occupy the systemic space. Randomized emigration means that the output flow carries away the same fraction of individuals of each population at any one time. In other words, all species suffer (or react with) the *same* additional death rate as a consequence of the imposed limitation. We may call this process "pure number game competition". In

fact, the model is akin to the thermodynamic systems, in that the dynamic behaviour in space of various types of molecules is basically non-specific.

An analogous, macroscopic model was presented by Steiner (1990). Fishing from a lake with a variety of fish species removes all fish above a certain total number c , hence, within the lake $\sum N_i = c$. Each species then contributes the same percentage of N_i to the fishing quota. Eventually, the fish species with the largest r -value will be the only species left, with its population number $N = c$. If diversity is to be preserved, wildlife authorities must impose *species-specific* quotas which protect the species with lower r -values.

Steiner's (1990) fish pond is analogous to any spacelimited consumer system with a variety of resource organisms and generalist consumers (insect prey of birds, grass species of large herbivores for example). The theoretical consequence is a single, surviving resource species. The model has also serious implications for mixed social systems. Imposing the same limitations on all sectors (ethnic/social/production units etc) may threaten plurality without any gain in return; the growth rate r is not necessarily associated with a quality parameter - it means growth and nothing else.

From the pure number game (i.e. mathematical) competition models we can derive a *fundamental principle*:

Assuming that different populations (species, genotypes, traditional populations, etc) are characterized by different r -values, and that are subject to limiting conditions common to all populations, population diversity can be maintained if, and only if, populations *can react type-specifically* to the limiting conditions and/or to the presence of the component populations. The Eigen-Schuster (1979) and Steiner (1990) models represent, in fact, merely the authors' initial conditions to explore the possible maintenance of species diversity as a function of population interaction.

2. Growth limitation; the logistic equation.

The logistic equation adds a species-specific reaction term which relates the growth rate to the limiting condition:

$$\dot{N}_i = (r_i - a_i N_i) N_i \quad (2)$$

a_i = reduction of potential growth r_i per individual already present in the system.

For the former, space-limited system, this means that each species reduces growth in relation to its own density only, and stops growing when $r_i - a_i N_i = 0$. Eventually, all component

populations would have the same growth rate $\dot{N}_i = 0$.

In this case, maintenance of species diversity is possible. The logistic equation stands for negative feed-back regulation, and, in this example, self-regulation depends on the faculty of species to recognize their own kind as different from all others. Thus enters *information* as a causal factor in competitive systems. We will persevere this aspect later and first turn attention to resource-limited systems.

Resource, henceforth referring exclusively to mass/energy, is different from space in that it may itself be a function of the user populations. Resource limitation is a physical process and imposes certain constraints on mathematical procedure.

Related to resource limitation, the logistic equation was presented by Verhulst in 1838, 35 years after Malthus (1803) came to the conclusion that late marriage was a much more efficient check on populations than famine and death, and 21 years before Darwin's "Origin of Species" (1859).

In Verhulst's equation,

$$a = \frac{r}{R} h \quad (3)$$

R = total resource at disposition; h = resource removed from the system per individual (and, as it diminishes growth, meaning mere maintenance quantity); consequently, $\frac{r}{R} =$ reduction of potential growth r per unit of resource (spent on mere maintenance or, inversely, growth permitted per unit of resource not spent on maintenance). Substituting in (1), $\dot{N} = 0$ if $hN = R$, i.e. when total resource is spent on mere maintenance. At this instant, $N = N^*$, and $N^* = K$ for carrying capacity. As resource consumed (hN) cannot exceed resource available (R), growth, in the Verhulst equation, cannot assume negative values, although, in reality, organisms continue to reproduce with less than h until internal reserves (fats, proteins) are spent. This results in famine and excessive death rates ($d > b$) in the following generation (= overshooting carrying capacity).

In 1926 Volterra introduced the double-logistic equations to calculate population numbers of two consumer populations limited by a common resource supply.

The following analysis of causality in competitive systems is based exclusively on the parameters of the double-logistic equations. Mathematical manipulation is restricted to the equilibrium form of the equations and is therefore accessible to all interested biologists. Repetition from earlier papers (Walker 1983, 1984, 1987, 1988) is kept to the minimum necessary to follow the arguments; this is also valid for the citation of literature.

IV. Resource-limited systems

1. The original Volterra (1931) equations

The equations and basic conditions. The growth of two consumer populations of different species (N_1, N_2) shall be limited by a constant input flux (R) of a given resource. In principle, any one resource unit is available to the individuals of both populations, whence arises the state of *interspecific competition: mutual deprivation of resource with a correlated reduction of the growth rates* (N_1, N_2). The resource flow R is renewable in the sense that consumption has no effect on its input. This condition is realized in all inorganic resources (light, rain, mineral); and in case of organismic resources, if consumption occurs after the period of resource reproduction. Furthermore, as for maintenance of the resource populations each individual must, in the average, leave behind a single reproductive offspring only, all reproduction above one per parent and generation is available for the food chains without affecting the input R . In all following considerations, R refers to this excess reproduction only. If not stated otherwise, space is not limiting. Initial population growth

N_1^0, N_2^0 shall be > 0 , and as the populations grow, the density of resource diminishes, although its input flow R is constant. For convenience, (N_1) and (N_2) stand for the name of the populations (species), while N_1 and N_2 stand for the number of individuals in the respective populations. Volterra's (1931) original equations read:

$$\begin{cases} \dot{N}_1 = [r_1 - \gamma_1 (h_1 N_1 + h_2 N_2)] N_1, & N_1(0) = N_1^0 \\ \dot{N}_2 = [r_2 - \gamma_2 (h_2 N_2 + h_1 N_1)] N_2, & N_2(0) = N_2^0 \end{cases} \quad (4)$$

N_1, r_1 and h_1 as in (2) and (3); h_1 as maintenance quantity includes the normal metabolism of maintenance and reproduction, because every dying individual must leave behind a fertile offspring.

γ_1 = mean reduction of the growth rates r_1 per unit of resource removed for maintenance. As deceleration of growth depends on total resource available per individual at time zero, γ_1 establishes the relation between total resource flow R and r_1 , that is, in

according with (3), $\gamma_1 = \frac{r_1}{R}$, and $\gamma_2 = \frac{r_2}{R}$ and hence,

$$\frac{r_1}{\gamma_1} = \frac{r_2}{\gamma_2} \quad (5)$$

Population growth is zero when the terms in the angular brackets reduce to zero, i.e. if

$$\begin{cases} \gamma_1 (h_1 N_1^* + h_2 N_2) = r_1 \\ \gamma_2 (h_2 N_2^* + h_1 N_1) = r_2 \end{cases} \quad (6)$$

N_1^*, N_2^* : population numbers when N_1 and N_2 respectively are reduced to zero.

Substituting for γ_1 we find that two equations are identical, that $N_1^* = N_1$ and $N_2^* = N_2$, and that

$$h_1 N_1^* + h_2 N_2^* = R \quad (7)$$

Both populations are reduced to zero growth simultaneously when total resource available is utilized for mere maintenance. That the physical form of the equations in (6) is correct is also seen from a dimension control: setting resource in calories we find:

$$\frac{r^{-1}}{\text{cal}} \left(\frac{\text{cal}}{N_1} (N_1) + \frac{\text{cal}}{N_2} (N_2) \right) = r^{-1} \quad (8)$$

and analogously for the second equation in (6). It is important to note that the various (N_i) enter as different dimensions, because we cannot add different species. Solving (6) for population numbers we find:

$$\begin{cases} N_1^* = \frac{R}{h_1} - \frac{h_2}{h_1} N_2^* \\ N_2^* = \frac{R}{h_2} - \frac{h_1}{h_2} N_1^* \end{cases} \quad (9a)$$

which may be written in the conventional form

$$\begin{cases} N_1 = K_1 - \alpha N_2 \\ N_2 = K_2 - \beta N_1 \end{cases} \quad (9b)$$

$$\alpha = \frac{1}{\beta} = \frac{K_1}{K_2} \quad (10)$$

K_i = carrying capacities, α and β are the traditional competition coefficients. As obvious from (8) and (9) they are, in fact, simple conversion factors which transform individuals of species 2 into individuals of species 1 and vice-versa, as required for physical reasons. The graphical representation of (9) is a single, straight line which links all possible points of (unstable) population equilibria, where the translations on the axes are set by the carrying capacities and the angles of the slope by the reciprocal conversion factors α and β . The equilibrium points on this single line depend on the initial conditions N_i^0 and the r_i -values. The

nearest to the axis a point lies, the more probable is extinction of the competitor as a result of random accidents. As genetic redundancy $r = b - d$, a relatively large reproductive rate b allows for fast recovery, while a low death rate b means resistance against extinction.

The system, however, is unrealistic, because it is determined by direct resource shortage. The model stands for "famine and death", particularly for the generation that is born when the parents start starving (overshooting carrying capacity). Natural populations, particularly in relatively pristine conditions as in the amazonian ecosystems, for example, do not present a picture of habitual famine and death. In the benthic habitat of forest streams, for instance, the relation between the standing stocks of the various predators and their potential prey organisms is at least 300 prey/predator (Walker 1990).

The resource-bound eggs in (4), however, can be applied to space, if space is truly the limiting factor, and if space occupation by the individuals of the competitor species is mutually exclusive; h_i then represents individual space cells (sessile organisms that cover the ground such as pastures, forests and reef faunae; territorialism between species, which is, however, rather infrequent). In large systems with many species (i equations for i species), the model approaches reality and represents cases of "non-equilibrium coexistence", where the occasional loss of species is balanced by immigration of species (tropical forest dynamics, Whitmore 1982; Guillaumet and Kahn 1982; reef fauna, Paine and Levine 1981).

In my first competition paper (Walker 1983) I argued that the *single-line system* of unstable equilibria is the only possible, biophysical outcome of Volterra competition system, in which resource (or mutually exclusively occupied space) is the limiting factor, while Volterra himself stated that unstable coexistence represents a mathematically possible, but extremely improbable case.

Volterra (1931), in fact, did not specify the γ_i -factors in Verhulst's

(see (3) above) sense. Apart from being positive constants, reducing the growth rates, they can assume any value. The normal case is therefore

$$\frac{r_1}{\gamma_1} \neq \frac{r_2}{\gamma_2} \quad (11)$$

and the equality in (5) is a rare exception. Now, γ_i is dependent on total resource, while r_i is a physiological constant. Thus, if anything in nature satisfies the inequality in (11), it must be species-specific resource quantities R_1 and R_2 . Let us assume, then, that, although all resource units are potentially available to both consumers, the portions they at best can get hold are different for reasons that will be discussed later. Thus, resource availability for (N_1) is a certain fraction q_1 of the total resource flow R , and for (N_2) it is q_2 ; q_i being dimension-less, positive numbers ≤ 1 . Therefore,

$$q_1 R = R_1, \quad \text{and} \quad q_2 R = R_2 \quad (12)$$

$$\gamma_1 = \frac{r_1}{R_1}, \quad \text{and} \quad \gamma_2 = \frac{r_2}{R_2} \quad (13)$$

Substituting γ -values in (6) we find

$$\begin{cases} h_1 N_1^* + h_2 N_2 = R_1 \\ h_1 N_1 + h_2 N_2^* = R_2 \end{cases} \quad (14)$$

$N_1 \neq N_1^*$ and $N_2 \neq N_2^*$ and there are now *two different, parallel lines* representing (14), resolved for N_1^* and N_2^* respectively. There is no common point of zero growth. The winning population will possess the whole resource while the looser will become extinct.

This is *Volterra's principle of competitive exclusion*.

The so-called competition coefficients α and β remain the same as in the single-line system, and resource limitation is the essential, determining factor in both systems. Intrinsic growth (r_i) does not even appear in (7) and (14), while the h_i -values, which represent metabolic efficiency, remain unaltered. Whence the *inevitable conclusion for resource-* (including mutually exclusively utilized space)- *limited systems:*

In the switch from (unstable) coexistence to compulsory, competitive exclusion neither resource limitation, nor intrinsic growth rates, nor efficiency of resource utilization are causally involved. There must be other biophysical reasons which reside in the q_i -values. If anything in this model satisfies the idea of "competition coefficient", it is the q_i -factor. The coefficients α and β are simple unit-conversion factors.

2. Species-specific, critical resource density

Critical resource density as cause for competitive exclusion was shown by Tilman et al (1977, 1982), Tilman and Sterner (1984) and was discussed by Thompson (1987) and Tilman (1987). The experimental system consists of various algae species which compete for a limiting nutrient input. For explanation of the situation, though, I choose a purely theoretical example: Two algae species (N_1), (N_2), with the same cell volume and with the same values of h , r , b and d ($(b-d) > 0$), are limited by a controlled phosphate input (R). Species

(N_1) has spherical cells, while (N_2) is lamelliform and has thus a much larger surface. (N_1) is therefore reduced to zero growth at a higher phosphate concentration, while (N_2) continues growing, thus reducing phosphate density to below maintenance level for (N_1). Eventually, $N_1=0$ and $N_2=N_2^*$, when its lower critical

phosphate density permits merely for its maintenance. In reality the physiological parameters (h_1, r) are usually different, and different rates of resource flow and absorption complicate mathematical elaboration. The essential point, however, is valid, namely that the effort to obtain the resource determines a critical, specific resource density that just permits for population maintenance.

In a multispecies system, the species with the lowest critical density is the winner with its $q_c=1$.

The species-specific, critical resource density is determined by the physiology of the respective consumer species and is independent of the number of other consumer populations that operate in the system. The critical density of resource species allows the prey organisms to recover when their predators overshoot carrying capacity and thus enter a phase of negative growth (these time lag effects are not expressible by (2),(3)).

The physiological necessity of critical resource density allows for the conclusion that resource is not the limiting factor in systems in which diverse consumer species sustain themselves on *the same resource supply*. If anything justifies Volterra's (1931) principle of competitive exclusion, it is species-specific *resource density*.

3. Aggressive resource prevention

Competitive replacement may be the result of interference between the consumer species in that they prevent the competitor from successfully absorb/ingest/catch a resource unit. At critical, relative population numbers $\frac{N_1}{N_2}$, the weaker competitor (say N_1) will just maintain itself ($N_1 = N_1^*$), while the more successful

aggressor will continue to grow; thus reducing N_1 to below zero; this population decline liberates resource units for (N_2), until $N_1 = 0$ and

$N_2 = N_2^* = K_2 = \frac{R}{h_2}$ (neglecting probable, critical densities).

Mathematically, the process is the same as in the case of critical densities. The loser can at best get at $q_1 R$ resource units, while $q_2=1$ for the winner (N_2). However, as the reduced resource availability of the loser is the result of the presence of the

aggressor (N_2), the realistic carrying capacity of (N_1) is $\frac{R}{h_1}$, and

not $\frac{q_1 R}{h_1}$ (always neglecting critical density!).

Zero growth of the loser population is determined by the relative population numbers $N_1(t)/N_2(t)$ at that particular moment (t). To be a consistent winner, the (stronger) rather than its own. In other words: *successful, aggressive resource prevention by a consistent winner relies on information*, that is, on the faculty of the winner to distinguish between its own and other species.

Aggressive kill of competitor individuals, however, is not covered by this model, because the effect on the loser's growth rate

(N_1) is not mediated by the term $\gamma_1 h_1$ in equations (4) (Walker 1983).

In both types of competitive exclusion, either by specific, critical densities or by aggressive prevention of resource acquisition, (14) stand for two parallel lines. The winner is represented by the outer line, but, as seen from Fig.1, the winner may be the population with higher or lower carrying capacity, i.e. higher or lower resource efficiency (h_1).

In reality, the two mechanisms are likely to be involved together. A well-informed winner, for example, may lower its critical, specific resource density (which, however, aggravates pathological population oscillation in case of overexploitation of resources).

As both mechanisms are expressed by the q_i -values, the lines of zero population growth (eqs (12),(13),(14)) remain parallel. The crucial point with respect to causality in competitive exclusion is, that these biophysical factors are the irreducible cause for exclusion, and that *the winner is the one species that does not permit the loser(s) to maintain itself (themselves)*, and not the species with the larger growth rate (r_i). *The decisive criterium is maintenance*, not growth. Whence the importance of the concept of r_i as *redundancy* that can balance population losses that are extrinsic to the definition of the system under consideration.

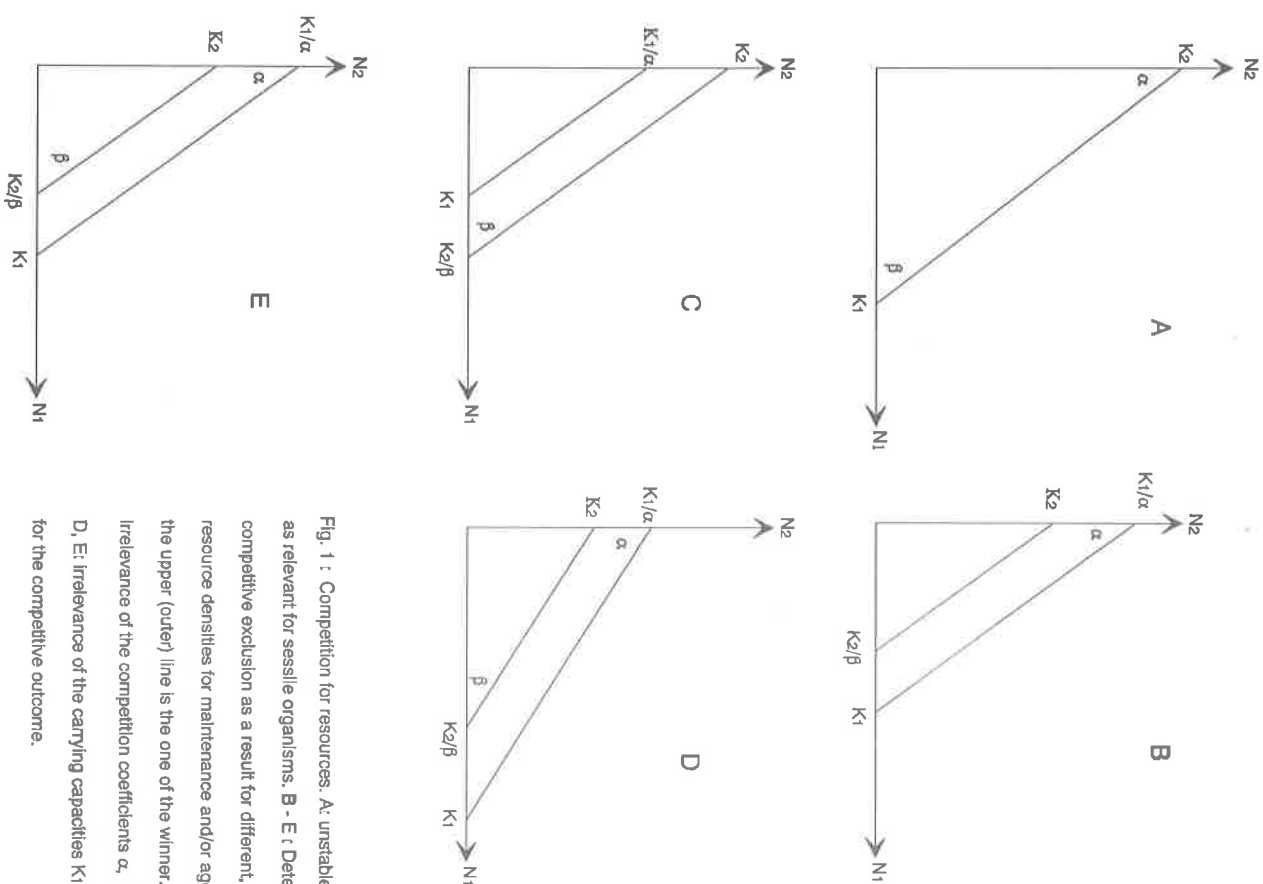


Fig. 1 : Competition for resources. A: unstable equilibria as relevant for sessile organisms. B - E : Deterministic, competitive exclusion as a result for different, critical resource densities for maintenance and/or aggression, the upper (outer) line is the one of the winner. A - C: Irrelevance of the competition coefficients α , β . D, E: Irrelevance of the carrying capacities K_1 and K_2 for the competitive outcome.

4. The role of information in competition for resources

Consistent, aggressive competitive exclusion relies on information: distinction between individuals of ones own and the other populations; realization that ones own resource is also the one of the competitor, and, to help efficient operation (maximization of resource units "stolen"), knowledge of time and place of resource supply, so that one can get at the resource before the others arrive. This is, where "Biophysics" begins. *Movement of relatively large bodies becomes non-random, not because some force vector drives them in a given direction (as in the case of stones rolling down a mountain slope), but because they are programmed* (Walker 1972, 1991). Living bodies have essentially two separate, but interacting, types of energy systems: a low-energy information system (neuro-endocrine, hormonal, genetic systems) that *determines* the course of action, and a high-energy system (general metabolism, muscular and other motor systems) that *allows* for the execution of the thus determined actions. Mobile animals have a central nervous system that receives, processes and stores information and that determines their movement in space and time. This is why animals are *potentially successful competitors*. Sessile animals and plants are subject to the phase-spatial play of random movement of their propagules. Therefore it is far more probable that monocultures get "weedy" and diversify than that single species eradicate complex communities (non-equilibrium coexistence, "single-line" Volterra-system), this quite beside the fact that patchiness stabilizes coexistence for mere geometrical reasons (intra-patch, intra-specific competition being severer than interspecific competition along the circumference; Walker 1988). Programmed movement as a result of information on kind and phase-spatial parameters of resource supply has its effect on the "sameness" of resource. Same resource means that every resource

unit is potentially available to every consumer. Trees, for example, cannot compete for light in the horizontal plane, because each tree has its own, vertical input of radiation; only along the vertical axis can a higher grown tree deprive a lower one, because light moves downward. This to mention just one case in point that the only effective niche is the phase-spatial niche (Walker 1987).

The more information one consumer (say (N_1)) has on kind, time and space of anothers (say (N_2)) resources, the more (N_1) "assimilates" the resources of (N_2) , while the relative ignorance of (N_2) leaves (N_1) with an exclusive resource compartement. Competition exclusion, therefore, is the result of "asymmetrical, informative resource assimilation".

On the other hand, perceptual differentiation of essentially similar resources (carbohydrates, proteins, fats etc) may render resources dissimilar: "tasty" resource species are accepted, while other, equally valuable food organisms are rejected. Inversely, under duress or by sheer curiosity, animal consumers break through this information barrier and accept new species of resource organisms, thus engaging in competition with the respective food specialists. Of special interest is the situation in which the information system renders predation independent of prey density. This condition is realized when the predator has information on more prey items than it has time or energy to catch. Predators of small mammals are probably well informed on the population of their prey, which, however, tend to remain in their burrows when the predators are on their prowl. A similar situation applies to dangerous prey animals, such as zebras and large gazelles for lions or the moose for wolves. The limiting factor in these situations is the effector system of the consumers. (Anybody in doubt on this matter can convince himself by watching dogs and kids catching pigeons in urban parks!). The number of prey taken in these consumer systems is probably a function of the conflict between laziness, fear and hunger. As warmblooded animals cannot simply pass excess food to increased reproduction, this mechanism avoids

disease from overfeeding.

Limitation of predation success combined with ample information on prey and other potential predators may lead to "fictitious competition", i.e. to competitive aggression despite the fact that the prey is not limiting. This is important for the interpretation of field research: squabbles over food items are not conclusive for resource limitation and may express entertainment rather than starvation. In higher animals the borderline between fight and play is exceedingly narrow, and all have 24 hours per day to fill with their activities.

5. Incomplete resource sharing

The necessity that all resource units must potentially be accessible to the competing consumers means that this criterium of "same resource" as same phase-spatial supply is almost unrealizable. Preference of certain qualities of resource (larger or smaller items etc), partially preferred areas of feeding on relatively stationary resource organisms; relative movement between predators and prey in and out of areas of consumption, and, above all, resource renewal between feeding periods, results usually in an exclusive portion of resource for each consumer species, although the bulk may be shared (Walker 1987; always assuming, that these preferences are upheld when resources get short!). Thus, again, resource availability is q_1R for (N_1) and q_2R for (N_2) , and $q_1R = R_1$ (see (12),(14)). But, unlike the case of deterministic, competitive exclusion, these are initial conditions, and not conditions resulting from consumer/resource interaction. Hence, the resource compartment $(1-q_2)R$ remains exclusive for consumer (N_1) , and $(1-q_1)R$ for (N_2) , and therefore, the consumers are, in fact, not suffering the complete weight of interspecific competition: (N_1) suffers the effect of p_2N_2 only and (N_2) the effect of p_1N_1 only; $0 < p_i \leq 1$. The equations for the lines of zero

population growth ($\dot{N}_i=0$; (4),(6),(9)) are then

$$\begin{cases} N_1^* = \frac{q_1R}{h_1} - \frac{h_2}{h_1} p_2 N_2 = K_1 - \alpha N_2 \\ N_2^* = \frac{q_2R}{h_2} - \frac{h_1}{h_2} p_1 N_1 = K_2 - \beta N_1 \end{cases} \quad (15)$$

$$\alpha \neq \beta \quad (16)$$

Depending on the feeding conditions, p_2N_2 means that not all competitors (N_2) are feeding on the resource of (N_1) , or p_1h_2 means that the competitors (N_2) remove less than the maintenance quantity h_2 per individual; and vice-versa for the second in (15). Under the reasonable assumption that the impact not suffered by (N_1) , i.e. $1 - p_2$, is equal to the fraction of resource (N_2) has to its own use, $1 - q_1$,

$$q_1 = p_2 \quad \text{and} \quad q_2 = p_1 \quad (17)$$

As the p_i -values are reducing the angles α and β in (9), this leads of necessity to an intersect of the two lines above the line K_1 , K_2 (Fig. 2), and thus satisfies the traditional inequality conditions for stable equilibrium (Smith 1974).

$$\begin{cases} K_1 < \frac{K_2}{\beta}, & \text{i.e. } p_1 < \frac{q_2}{q_1} \\ K_2 < \frac{K_1}{\alpha}, & \text{i.e. } p_2 < \frac{q_1}{q_2} \end{cases} \quad (18)$$

large multiple of the body volume of the consumer. Hence, space occupation is not mutually exclusive, usually many species operate within the area that is worked over by single individuals. This spatial overlap is paralleled by specific rates of consumption. Space occupied is therefore not necessarily proportional to resource obtainable; depending on local species composition, local resources, and/or specific resources, may be scarce in one place and abundant in others. Such a system is untractably complex and dynamically erratic, if, namely, we adhere to the view that resources are limiting and thus determine the growth rates (N_i).

To avoid this situation, we make following assumptions:

1. Mobile animals have a certain perception of the momentaneous abundance of their resources within the area in which they operate. Newcomers settle, if this abundance is satisfactory; already established individuals extend/contract their operational space according to this abundance.

2. As a result of reproductive functions, (mating, offspring raising etc) mobile organisms have a definite recognition of individuals of their own species.

3. Breeding units (individuals, pairs, colonies) of a particular population/species maintain specific, average distances within their population space (which may vary with resource abundance). The average reproductive rate is a function of this distance (density): short distances (high density) result in mutual inhibition (or possible eviction); larger distances (low density) release reproductive inhibition. Perception of nearest neighbours (density) relies on biochemical effector substances (smell, pheromones etc), on acoustic and visual signals.

Density-dependent, mutual inhibition of reproduction and/or emigration as mechanisms of intra-specific competition for space

(breeding sites, niches etc) are known from unicellular organisms to birds and monkeys. They include reduced and/or delayed reproduction, change in sex ratios, appearance of dispersal forms and, in higher organisms, they involve everything that is known on home ranges, territorialism, social status etc. The biochemical pathways from perception via neurotransmitters and hormones to gonads are described for diverse organisms (Coulson 1970, Wilson 1975, Karlson 1980, further references see Walker 1984). The most effective inhibitors are the successful breeders; this secures mutually effective function within the population. This system has a number of biophysical and conceptual advantages:

1. Unlike resource, space is not a function of consumption; space can be occupied, but not consumed. Thus, the negative feed-back mechanism implied by the logistic equation is effective without time lags and precludes pathological population oscillations.

2. A lower carrying capacity in relation to space than to resource guarantees resource redundancy.

3. Density-dependent, reversible, physiological inhibition of reproduction guarantees reproductive redundancy (r_i not fully in operation).

4. Recognition of ones own species, perception of ones mates in the vicinity and for the immediate abundance of ones own resources are far more credible animal faculties than brainstorming over what, when and where other folks eat. Above all, there is no biophysical necessity to recognize other organisms as consumers of one's resource, mere reaction to actual abundance is sufficient.

The practical result of these functions is *relatively even species packing* (while population numbers fluctuate in relation to food abundance) and a conspicuous *absence of interspecific, competitive interference*. This is pretty close to what we observed in nature (MacArthur and Wilson 1963; Walker 1988).

The system depends entirely on its information input, on the *preponderance of information on one's own species*, and on *relative ignorance of other species' necessities* and activities.

Apart from its influence on the size of operational space, resource plays a merely permissive role.

As regards the Volterra equations, resource-bound coefficients are substituted by coefficients of growth as a direct measure of intraspecific and interspecific inhibition of growth. In this way we arrive at the Gause-Witt form of the equations (Gause and Witt 1935).

$$\begin{cases} \dot{N}_1 = N_1 (r_1 - a_1 N_1 - b_1 N_2) \\ \dot{N}_2 = N_2 (r_2 - a_2 N_2 - b_2 N_1) \end{cases} \quad (22)$$

a_1 = intraspecific effects;
 b_1 = interspecific effects;
 physical dimension = $(t)^{-1}(N_1)^{-1}$.

Solving for population numbers at zero growth we find

$$\begin{cases} N_1^* = \frac{r_1}{a_1} - \frac{b_1}{a_1} N_2 = K_1 - \alpha N_2 \\ N_2^* = \frac{r_2}{a_2} - \frac{b_2}{a_2} N_1 = K_2 - \beta N_1 \end{cases} \quad (23)$$

The two lines represented by the equations may, or may not intersect.

In accordance with the inequalities in (18), the conditions for stable equilibrium are

$$\frac{r_1}{a_1} < \frac{r_2}{b_2} \quad \text{and} \quad \frac{r_2}{a_2} < \frac{r_1}{b_1} \quad (24)$$

which, for the sake of interpretation may be written

$$\frac{a_1}{r_1} > \frac{b_2}{r_2} \quad \text{and} \quad \frac{a_2}{r_2} > \frac{b_1}{r_1} \quad (25)$$

meaning that the relative (to r) intraspecific competitive effect must exceed the competitive effect imposed on the other species.

This agrees with the physiologically probable, apparently realistic, state of affairs described above. The lines of zero growth intersect above the line K_1 , K_2 , thus indicating overlap in the utilization of space, while the reverse relation with an intersect below the K_1 , K_2 -line stands for unstable equilibrium and for under-utilization of space as a result of intense, interspecific inhibition, which may include direct killing. Absence of a point of intersection stands for competitive exclusion.

It is important to note that, although the K -values may allow for calculation of density in space, they give no information on the area exploited *per individual*. In fact, all individuals may forage over the whole systemic space; the same is true for interspecific utilization of space in equilibrium populations; territorial organization may, or may not, be realized, and any degree of overlap between the species may occur.

Relations between food and space competition are discussed in Walker (1983).

VI. General conclusions and discussion

Pure number game competition (pp. 7, 8) applies to the extent populations *cannot react type-specifically* to limiting conditions, and hence, operates mostly between *intraspecific*, genetic variation (genetic drift, different r -values with regard to physical and ecological limitations)

Interspecific competitive exclusion with the survival of "the fittest" (maximum r_i -value) is inoperative, because:

1. Species react species-specifically to their own density in space; high density represses, low density de-represses growth *i*. This intra-specific competition for space maximizes intra-specific r -values which stand for redundancy that repairs losses (Steiner and Walker 1990). (Rare species are rare because this redundancy/repair mechanism is not under sufficient selection pressure, as in the case of toxic or otherwise unattractive organisms, which thus suffer low rates of predation!) This mechanism reduces the average long-term growth rates (\bar{N}_i) of most populations (species) to zero irrespective of their r_i -values (short-term fluctuations notwithstanding).
2. The carrying capacity of space is, as a rule, smaller than the potential carrying capacity of resources.
3. The phase-spatial structure of resource supply and consumption does usually not permit for complete resource deprivation, even if resources are directly limiting (uniformly structured, small experimental systems notwithstanding).

In short: quite generally, resources are neither limiting, nor the

same, and the rates of population growth (\bar{N}_i) are equal .

These are the conditions sine qua non for the continuous evolution of species as we know it. Catastrophs which exceed the resilience of systems do occur, and leave their marks in the evolutionary process, but these are accidents. "Famine and war" are not basic mechanisms of evolution.

Coexistence or competitive exclusion are *determined by the information input*, while *resources play a permissive role*. The more information a species has on the resources of other species, the greater becomes potential similarity of supplies between species, and the more increases potential deprivation between competitors, and this quite regardless of whether or not the resources in question are truly limiting. The better informed will not permit the less informed to maintain itself, either by aggressive deprivation or by lowering its own critical resource density to below the one of the other consumers (in case resources *are* limiting).

High information of one's own, and relative ignorance of other species' conditions, on the other hand, strengthens intra-specific competition (population regulation in case of space limitation) and weakens interspecific competition. These are the mathematical conditions for stable coexistence (inequalities (18), (22)), which conform, on the whole, to the state of affairs in the animal kingdom.

Essential is that *information determines magnitude and direction* (towards (N_1) or (N_2)) of *resource flow*, thus prevailing over randomness of interference between the relevant units (encounters between resource items and consumers, probability of absorption, ingestion etc), just as gravity overrides the intermolecular movement in a waterfall. Probabilistic elaborations on the level of consumer-resource interactions results in a single isocline of unstable equilibria ((6), (7)). Only nonrandom vectors, affecting the resource flow as a whole, can provoke deterministic

competitive exclusion, such as conditions of critical resource density for consumer maintenance, specific information, and *a-priori* directed resource flows (the down-stream receivers being deprived; Walker 1987).

The most important conclusion of this analysis might be, therefore, that information play a role that is analogous to the force fields in classical physics (gravity, electromagnetic fields), in that it directs mass/energy flows in relation to specific absorption centers (consumers of (N_1) , (N_2) , ... (N_i) etc.). The Shannon-Weaver concept of information, which is analogous to the thermodynamic gas model, can thus not cater for the analysis of deterministic, biological systems. Theoretical physics will eventually have to explain how small-energy information input vectors can determine the high-energy vectors of the permissive Erfolg systems (Walker 1991).

The species Homo sapiens: The general conclusion for the position of Man in competitive systems is implied throughout this paper: as a consequence of neural development, *Homo sapiens* is the consistent winner of interspecific competition which he himself promotes to the extent of his knowledge.

Recognition of ever more plant and animal species as resource, eventually culminating in the discovery of the chemical sameness of all biomass (carbohydrates, proteins, minerals etc.; microscopic sameness), together with increasing knowledge of the ecological conditions of potential resource species, involving ever better transport and communication systems (macroscopic sameness, Walker 1987), eventually transformed the entire planet Earth into a single resource space with Man as the universal winner against all other species.

At least since early post-glacial times the ascent of Man is accompanied by an increasing rate of extinction of plant and animal species. This accelerated reduction of biological diversity is paralleled by precipitated cultural uniformization as a result of inter-population, notably economic, competition, for the sake of which national organization and social infrastructure are

abolished, the safeguards of cultural diversity and autonomy of life styles.

The invention and universal convertibility of money means universal, phase-spatial homogenization of all resources. True physical/biophysical conditions which resist such homogenization are losses. Thus appear efficiency, economy and institutionalized greed. Other species are either parasites/weeds or resources. Seasonal and geographic interruptions of resource flows are overcome by continuous breeding of livestock and vegetables in stables and greenhouses the world over. Factories operate day and night. Time lags of transport are minimized by jet planes and by money transfer via telecommunication. The stock market is the purest expression of the principle underlying the evolution of *Homo sapiens* as the universal competitor: the winner is the one with more information which is transmitted fastest worldwide.

Transformation of ever more and new kinds of matter into resource resulted in unprecedented population explosions with abject misery on the one hand and unmanageable waste on the other, while war and violence developed into Man's preferred entertainment (boredom is the strongest root of war). Money and transport allow for large cities with accumulations of inhabitants that are entirely disconnected from the physical distribution of their resources. These circumstances lead to the deterioration of Man's relation to space, to the complete sacrifice of free action and free movement. Preconstructed apartments impose where one eats and sleeps. One queues for elevators to enter and to leave the place. One walks on side walks and crosses roads when traffic lights turn green. Recreation is confined to public places and to established foot paths. Density-induced irritation has reached the pitch where dogs are not allowed to bark and church clocks have to be stopped at night. Absurd population density is countered with the refusal to take notice of each other (try to catch somebody's eye in the London metro!), which explodes into aggression whenever this privacy is disturbed. Within the last few decades, scarcity of living space atomized the last vestiges of

primate-type clan/family structure: teenagers must have their own, however small, apartment, and grandparents are removed into "old peoples' homes".

In short, *exuberance and management of resources abolished spatially determined population regulation.*

Time and again, Man's information-driven frenzy outstripped the permissiveness of space and/or resources, involving cities, states and, eventually, continents, in the misery of wars and famines. This time, though, mankind is approaching global limits.

And still, competition is the celebrated dogma for the creation of the best of all worlds: access for everybody, at any time, at any place, to everything: equal opportunity and survival of the fittest, which, according to the Volterra model, means the *one* that can deprive the others regardless of all other falcuties.

Darwin's "struggle for life" and "war of nature" thus reveals itself as an anthropomorphism, as a projection of Man's own, peculiar situation onto the biosphere as a whole.

The tale of the destabilizing and disastrous effects of excessive information is an old one. Some four or five thousand of years ago, after Man had burnt firewood for thousands of years already, when the forests of the Mediterranean Region and of Asia Minor receded and the deserts spread; when Cain, the jealous agriculturist slew Abel the hunter and sheep farmer; when the first large cities flourished with academies and museums (Babylon had an art museum), wise men resumed the situation in a few lines: Lucifer (the "light/fire-bringer"!) tempted Man with god-like omniscience.

It was the end of paradise, of Man's peaceful coexistence with other creatures and with his own kind. Henceforth, it was the struggle for life and the war of nature (Genesis 3 and 4). The suggestion might not be far-fetched, that this remarkable story (beside aspects not considered here) includes a first written record of environmental problems: scarcity of energy (fire wood) near at hand, drying up of agricultural land, overgrazing, social/ethnic problems (nomads, agriculture, cities etc). Abraham and his clan,

for example emigrated from Mesopotamia in search of a promised, better land, and he decided to proceed to Egypt because a grave famine afflicted Canaan (Genesis 12).

To end this study on a somewhat more hopeful note it may be pointed out that - from macromolecules to *Homo sapiens* - biophysical interactions in general, and information in particular, are also determining cooperative processes, and that analysis of cooperative systems (Eigen and Schuster 1979, Steiner 1990, Arrigoni 1990, Pini 1990, Walker and Williams 1976) might uncover a healthier basis for human and biosphere organization than growth and competition.

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