

# Darwinian model of evolution

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**Summary.** The remarkable feature of life is its ability to self-reproduce. Self-replicating systems fit in naturally with Darwin's evolution scheme. However, I argue here that what Darwin thought was natural selection driven by the struggle for existence is indeed a manifestation of the zeroth law of thermodynamics. When this law is applied to competing self-replicating entities biological evolution appears to be a spontaneous process.

## Introduction

*Natural selection theory.* In XIX century British naturalist Charles Darwin built an innovative model to explain how life has evolved on earth (Darwin, 1876). Darwinian model consists of two propositions. First of all, evolutionary changes, or indefinite variability, occur as small spontaneous and presumably accidental events that increase the diversity of individuals. In the next place, organisms are subjected to the action of some driving force, which has been named the struggle for existence. According to Darwin natural selection takes place when a population produces more individuals than can survive in an overcrowded world. In such conditions individuals inevitably are involved in competitive interactions. Some of them fail in this struggle and, as a result, leaves less or no offspring. Darwin's model of evolution - with the natural selection principle as a cornerstone of the theory - remains as the only scientific explanation of the development of the living world. It turns out that the notion of natural selection was a deep insight into the working machinery of biological evolution. Nevertheless, the problem of modern evolutionary biology is that the natural selection theory, as it was presented by Darwin himself, is considered as describing the right mechanism that structures populations and entire communities. Probably such an attitude is not true: seemingly Darwinian selection also occurs in nonliving world (Eigen, Schuster, 1979; Lee *et al.*, 1997; Paegel, Joyce, 2008). It looks like the source of natural selection - or, more precisely, the nature of the struggle for existence - is hidden more deeply into the realm of physical principles.

## Hypothesis

*Self-replication.* Even though it may seem trivial, the most important characteristic of living things and their molecular components is their ability to make copies of themselves (Meselson, Stahl, 1958; Prusiner, 1998; Hardy, Zacharias, 2008). And maybe this phenomenon is a binding link between biological and non-living worlds (Orgel, 2004), which relates chemical reactions kinetics and biological evolution, since the reproduction of living organisms is one of the forms of chemical autocatalysis, or just a more complicated mode of simple physical division (Lee *et al.*, 1996; Lincoln, Joyce, 2009; Zhu, Szostak, 2009). Really, the relation between life and self-replication is fundamental. Such a way of multiplication is that necessary

condition that makes biological evolution possible. Without it the chance that the biosphere would arise is definitely zero (Von Neumann, 1966). In fact, reproduction acts like a ratchet, thus tremendously increasing the probability of the emergence of sophisticated organic forms.

But there is another aspect of self-replication which directly relates with the mechanism of life evolution. One side of the process of evolution is, in essence, a sequence of random steps. From point mutations to genetic material transfer between cells (Luria, Delbrück, 1943; Cosloy, Oishi, 1973; Lenski, Mittler, 1993; Zeyl, Bell, 1996) the changes of genomes are spontaneous and random. Endosymbiotic events (Okamoto, Inouye, 2005; Margulis *et al.*, 2006; Price *et al.*, 2012) are accidental as well. It is self-reproduction that gives such an uncontrolled process apparent direction, leading to seemingly organized world of living matter (Lenton, 1998). This organizing feature of self-replication reveals itself in competition.

*Competition principle.* Competition in ecological communities arises when food chains diverge or converge. As a result some populations share common resources or serve as a food to the same predators. We will refer to those relations as divergent (d-) or convergent (c-) competition respectively.

Competitors coexistence is a common naturally occurring phenomenon responsible for the complex organization of ecosystems food webs (Banašek-Richter *et al.*, 2009). Without competitors an ecological community would consist of one or more separated food chains. It is not a big exaggeration to say that the problem of competitive coexistence is one of the most important issues in ecology (Hutchinson, 1961; Richerson *et al.*, 1970; Brown, 1981; Ghilarov, 1984; Holt, 1984; den Boer, 1986; Zobel, 1992; Azovsky, 1996; Bastolla *et al.*, 2009; Neill *et al.*, 2009).

Meanwhile, long lasting coexistence of competing trophic links is not a self-evident result of species interactions. Once it has been proposed, by the way quite incorrectly, that two or more populations, exploiting exactly the same ecological niche concurrently, cannot coexist permanently - all populations but one have to die out (Gause, 1934; Hardin, 1960). This ecological rule, called the competitive exclusion principle, resembles the action of natural selection: less fitted competitors are replaced by their more successful rivals.

Later on a mechanistic approach to ecological competition - resource competition theory (Tilman, 1976; Hansen, Hubbell, 1980; Grover, 1997) - has more explicitly revealed a trivial but nevertheless important feature of competitive interactions. Namely, different species exploiting the same resources at the same time may still coexist, even if the number of competitors are greater than the number of different resources types: for a stable coexistence to occur it is *sufficient* that competitors would consume resources equally efficiently (Tilman, 1981). This, however, leaves an open question about the *necessary* conditions for enduring coexistence.

Although the leading role of competitive interactions in the evolution of ecological communities has been disputed (Wiens, 1977; Patten, Odum, 1981; Walter, 1988), nevertheless an old and fruitful idea in ecology is that competitive interactions itself somehow determines the conditions for competitors coexistence (MacArthur, Levins, 1967; Grant, Abbott, 1980; Tilman, 1997; Loreau, 1998; Chesson, 2000; Bonsall *et al.*, 2004; Levine, HilleRisLambers, 2009), which other relationships between individuals may help to fulfill. In other words, exploitative

competitive interactions probably have some intrinsic fundamental property which makes competition exceptionally important in organizing ecological communities. We could refer to this property as the principle of competition. It states that competitors coexist *if and only if* they use common resources, or are exploited by the same consumers, equally efficiently (Balciunas, 2009). And the reason for this requirement lies in the zeroth law of thermodynamics.

*Zeroth law.* According to the zeroth law in the form of the thermodynamic transitive property (Planck, 1903; Bergthorsson, 1977), if a subsystem exchanges energy with two other subsystems, which are in turn inter-isolated, then all three subsystems come into equilibrium with each other; subsystems are characterized by some set of parameters which gain the same values for all subsystems at equilibrium respectively. The two isolated subsystems we call competitors. As an instance of the implementation of this law we consider concurrent reversible chemical reactions; we identify a stationary state of reversible reactions with the state of thermodynamic equilibrium. In this case the parameters which characterize subsystems are chemical potentials. However, populations of self-reproducing elements get in trouble when they are involved in competitive interactions. Indeed, when competitors are self-replicators, i.e. if we deal with two concurrent autocatalytic chemical reactions, they are intrinsically incapable to always reach equilibrium: different energy transfer routes may not be in equilibrium at the same time. As a result, in this particular case of autocatalytic reactions, coexistence of competitors cease and one of them must be excluded from the system. Survives that competitor which minimizes the free energy of the resulting system.

The above formulation of the zeroth law implies that all three subsystems make an isolated system. More important is that the thermodynamic transitive property applies even if the whole system is open. True, this extension of the zeroth law means that a more general principle may exist from which the zeroth law follows as a special rule applicable to isolated thermodynamical systems.

Now let's return to chemical reactions. In the case of the open system, instead of equilibrium the system may reach a stationary state or even be in a state which changes over time. However, the coexisting competitors always evolve to an equilibrium condition: their corresponding parameters reach the same value; at least they must remain at equilibrium on average. We say that coexisting competitors are identical. Very likely that this property of the zeroth law makes the core of the natural selection principle: it is the reason for the "struggle for existence".

Open systems, consisting of branching energy transfer routes, bring in a certain dichotomy. If energy flows through the system then the two cases are possible: the paths of energy transfer may diverge or converge. The zeroth law applies in both cases. These two possibilities of energy transfer are exploited in the food webs of ecological communities.

*Tendency of evolution.* Ecosystems organization, as a result of evolution, is a reflection of the zeroth law. As we noted above, an ecological community is a highly complicated food web with a lot of competitive interactions (Martinez, 1991; Williams, Martinez, 2000; Michio *et al.*, 2010). Its biodiversity for the most part is maintained due to coexisting competitors, as the number of trophic levels in communities is limited and small (Pimm, Lawton, 1977; Pimm, Kitching, 1987). Because c-competition strives to enhance the density of consumers, meanwhile d-

competition minimizes resources densities (Holt *et al.*, 1994), thus, in conformity with the zeroth law, evolution leads to a higher effectiveness of energy transfer routes in food chains by replacing less efficient populations with those who make more effective trophic links. This is the essence of both the competitive exclusion and natural selection principles. As a matter of fact, these two biological principles are only different formulations of the same phenomenon, tightly related with self-replication.

Paying too much attention to the exclusion, however, we turn away from the other scenario which follows from the zeroth law - the coexistence of concurrent energy transfer routes. This outcome is, maybe, even more important in ecology and evolutionary biology. From competitors point of view three states of communities are possible. Denote them by  $\beta_0$ ,  $\beta_1$  and  $\beta$ .  $\beta_1$  means that only one competitor presents.  $\beta$  denotes the system of nonidentical competitors.  $\beta_0$  identifies a community of identical competitors ( $\beta_1$  is a special case of  $\beta_0$ ). From one point of view all three states are unstable because of errors occurring in the process of biological reproduction that leads to the divergence of populations, thus enhancing the number of competitors. On the other hand, regarding competitors coexistence, only states  $\beta_1$  and  $\beta_0$  are stable. We look at  $\beta_0$  as the special stationary state of an evolving community, consisting of self-replicating competitors. Such communities should be the most stably functioning composition of species. On the whole, the stability of the  $\beta_0$  state is attained due to growing biological diversity (Naeem, Li, 1997; Schindler, 2010). Communities which have plenty of species and high intraspecific biodiversity are able to maintain competitors identity more easily, because of more numerous and versatile ecological interactions. In this way, random events, coupled with competition, lead to organized ecological networks (Shinbrot, Muzzio, 2001). Although we should notice here that random and continuous variations are not the essential point of Darwinian theory. For instance, it is supposed that mutations are not entirely random (Rosenberg, 2001). Such a standpoint, however, does not undermine the foundation of contemporary evolution theory. In any case the final decision is in the hands of the zeroth law.

The network of coexisting identical competitors is the most probable result of evolution - in the case it proceeds long enough as we have on Earth. The identity of competitors is evaluated on the level of energy transfer in ecosystems food webs. How this identity is achieved is another question. On the whole, it does not matter what behaviour modes species possess. Intra- and interspecific relationships may cover the entire spectrum of interactions - from negative to positive ones. Such characteristics of organisms as mutual help, and cooperative behaviour in general, are not an argument against Darwinian model and do not rise the question about the compatibility between Darwinian evolution and the emergence of altruism.

## Conclusion

Despite the fact that the appearance of organic matter and its subsequent blooming out may seem unlikely at first superficial sight, the biological world is not only in agreement with thermodynamical principles but is a direct consequence of some of those laws. Indeed, organisms are open systems, and they are far from thermodynamic equilibrium. Therefore, living things permanently seek to obtain free

energy to support their existence, thus, satisfying the entropy requirements (Schrödinger, 1945). But even being in a nonequilibrium state probably is not enough to create and sustain biological organization. Most likely is that another thermodynamical principle - the zeroth law - is a direct cause of life evolution: the zeroth law, combined with competitive self-replication, provides a general mechanism for evolution. It follows from here that evolution itself takes place spontaneously. And because of its spontaneous nature, this process is capable of maintaining biological organization.

## References

- Azovsky, A.I. 1996. The effect of scale on congener coexistence: can molluscs and polychaetes reconcile beetles to ciliates? *Oikos*, 77: 117-126.
- Balciunas, D. 2009. The driving force of life evolution. *NeuroQuantology*, 7: 176-180.
- Banašek-Richter C. *et al.* 2009. Complexity in quantitative food webs. *Ecology*, 90: 1470-1477.
- Bastolla, U. *et al.* 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, 458: 1018-1020.
- Bergthorsson, B. 1977. Temperature, transitivity, and the zeroth law. *Am. J. Phys.*, 45: 270-271.
- Bonsall, M.B., Jansen, V.A.A., Hassell, M.P. 2004. Life history trade-offs assemble ecological guilds. *Science*, 306: 111-114.
- Brown, J.H., 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. *Am. Zool.* 21, 877-888.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31: 343-366.
- Cosloy, S.D., Oishi, M. 1973. Genetic transformation in *Escherichia coli* K12. *Proc. Natl. Acad. Sci. USA*, 70: 84-87.
- Darwin, C.R. 1876. *The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* John Murray, London; (<http://darwin-online.org.uk>).
- den Boer, P.J. 1986. The present status of the competitive exclusion principle. *Trends Ecol. Evol.*, 1: 25-28.
- Eigen, M., Schuster, P. 1979. *The hypercycle. A principle of natural self-organization.* Springer-Verlag, Berlin.
- Ghilarov, A.M., 1984. The paradox of the plankton reconsidered; or, why do species coexist? *Oikos*, 43: 46-52.
- Grover, J.P. 1997. *Resource competition.* Chapman and Hall, London.
- Hansen, S.R., Hubbell, S.P. 1980. Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes. *Science*, 207: 1491-1493.
- Hardy, P.A., Zacharias, H. 2008. Walther Flemming und die Mitose: Der Beitrag seiner ersten Kieler Jahre. *Schr. Naturwiss. Ver. Schlesw.-Holst.*, 70: 3-15.
- Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.*, 124: 377-406.
- Holt, R.D., Grover, J.P., Tilman, D. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am. Nat.*, 144: 741-771.
- Hutchinson, G.E. 1961. The paradox of the plankton. *Am. Nat.*, 95: 137-145.
- Lee, D.H., Granja, J.R., Martinez, J.A., Severin, K., Ghadiri, M.R. 1996. A self-replicating

- peptide. *Nature*, 382: 525-528.
- Lee, D.H., Severin, K., Yokobayashi, Y., Ghadiri, R. 1997. Emergence of symbiosis in peptide self-replication through a hypercyclic network. *Nature*, 390: 591-594.
- Lenski, R.E., Mittler, J.E. 1993. The directed mutation controversy and neo-Darwinism. *Science*, 259: 188-194.
- Lenton, T.M. 1998. Gaia and natural selection. *Nature*, 394: 439-447.
- Levine, J.M., HilleRisLambers, J. 2009. The importance of niches for the maintenance of species diversity. *Nature*, 461: 254-257.
- Lincoln T.A., Joyce, G.F. 2009. Self-sustained replication of an RNA enzyme. *Science*, 323: 1229-1232.
- Luria, S.E., Delbrück, M. 1943. Mutations of bacteria from virus sensitivity to virus resistance. *Genetics*, 28: 491-511.
- MacArthur, R., Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, 101: 377-385.
- Margulis, L., Chapman, M., Guerrero, R., Hall, J. 2006. The last eukaryotic common ancestor (LECA): Acquisition of cytoskeletal motility from aerotolerant spirochetes in the Proterozoic Eon. *Proc. Natl. Acad. Sci. USA*, 103: 13080-13085.
- Martinez, N.D. 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Monogr.*, 61: 367-392.
- Naeem, S., Li, S. 1997. Biodiversity enhances ecosystem reliability. *Nature*, 390: 507-509.
- Meselson, M., Stahl, F.W. 1958. The replication of DNA in *Escherichia coli*. *Proc. Natl. Acad. Sci. USA*, 44: 671-682.
- Michio K., Satoshi K., Yoshikuni S. 2010. Food webs are built up with nested subwebs. *Ecology*, 91: 3123-3130.
- Neill, C., Daufresne, T., Jones, C.G. 2009. A competitive coexistence principle? *Oikos*, 118: 1570-1578.
- Okamoto, N., Inouye, I. 2005. A secondary symbiosis in progress? *Science*, 310: 287.
- Orgel, L.E. 2004. Prebiotic chemistry and the origin of the RNA world. *Crit. Rev. Biochem. Mol. Biol.*, 39: 99-123.
- Paegel, B.M., Joyce, G.F. 2008. Darwinian evolution on a chip. *PLoS Biol.*, 6: e85.
- Patten, B.C., Odum, E.P. 1981. The cybernetic nature of ecosystems. *Am. Nat.*, 118: 886-895.
- Pimm, S.L., Kitching, R.L. 1987. The determinants of food chain lengths. *Oikos*, 50: 302-307.
- Pimm, S.L., Lawton, J.H. 1977. Number of trophic levels in ecological communities. *Nature*, 268: 329 - 331
- Planck, M. 1903. *Treatise on thermodynamics*. Longmans, Green, and Co., London.
- Price, D.C. *et al.* 2012. *Cyanophora paradoxa* genome elucidates origin of photosynthesis in algae and plants. *Science* 335: 843-847.
- Prusiner, S.B. 1998. Prions. *Proc. Natl. Acad. Sci. USA*, 95: 13363-13383.
- Richerson, P., Armstrong, R., Goldman, C.R. 1970. Contemporaneous disequilibrium, a new hypothesis to explain the "paradox of the plankton". *Proc. Natl. Acad. Sci. USA*, 67: 1710-1714.
- Rosenberg, S.M. 2001. Evolving responsively: Adaptive mutations. *Nature Rev. Genet.*, 2: 505-515.
- Schindler, D.E. *et al.* 2010. Population diversity and the portfolio effect in an exploited species. *Nature*, 465: 609-612.
- Schrödinger, E. 1945. *What is life? The physical aspect of the living cell*. Cambridge University Press, Cambridge.
- Shinbrot T., Muzzio, F.J. 2001. Noise to order. *Nature*, 410: 251-258.
- Tilman, D., 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science*, 192: 463-465.
- Tilman, D. 1981. Tests of resource competition theory using four species of lake Michigan

- algae. *Ecology*, 62: 802-815.
- von Neumann, J. 1966. *Theory of self-reproducing automata*. University of Illinois Press, Urbana.
- Walter, G.H. 1988. Competitive exclusion, coexistence and community structure. *Acta Biotheor.*, 37: 281-313.
- Wiens, J.A. 1977. On competition and variable environments. *Amer. Sci.*, 65: 590-597.
- Williams R.J., Martinez N.D. 2000. Simple rules yield complex food webs. *Nature*, 404: 180-183.
- Zeyl, C., Bell, G. 1996. Symbiotic DNA in eukaryotic genomes. *Trends Ecol. Evol.*, 11: 10-15.
- Zobel, M. 1992. Plant species coexistence – the role of historical, evolutionary and ecological factors. *Oikos*, 65: 314-320.
- Zhu, T.F., Szostak, J.W. 2009. Coupled growth and division of model protocell membranes. *J. Am. Chem. Soc.*, 131: 5705-5713.