GENERAL MODEL OF ECOSYSTEM EVOLUTION

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Ecosystem evolution theory seeks to reveal causal links between ecosystem parameters - biomass, dead mass, diversity, stability, etc. - and the constituing population demographic parameters and adaptive strategies - density, redundancy, environmental grain, niche overlap, etc. Insofar as ecosystem is a living matter producing machine, **the biomass (B) to dead mass (M) ratio** is a major criterion of its effectiveness. In undisturbed ecosystems an increase of B/M ratio is achieved through a concomitant increase of structural - spatial, successional, trophic, mutualistic, etc. - complexity. Each species entry opens potential niches at the higher and lower structural levels, thus promoting more species entries. A growth of biological diversity is thus enhanced by the **positive feedback loop**. It is limited, however by a residual niche overlap and a redundant population density serving as a buffer against unpredictable environmental impacts. Coherent ecosystem evolution to a greater effectiveness would thus impel a reduction of the both niche overlap and redundancy. Consequently, the constituent populations would evolve towards a coarse-grained ecological strategy and minimal sustainable density, henceforth cooperative rather than competitive and less distructive to their habitats. This is what **adaptation** is supposed to be.

Adaptation can extend as far as the population redundancy can be dispensed with and the latter depends on environmental stability (the more stable environments the less a need in the redundancy buffering) which explains a positive correlation between **stability and diversity**: the more stable ecosystem - the less redundant populations - the higher diversity and vice versa. In effect, **redundancy** can serve as a negative measure of fitness.

In the course of ecological **succession** which is a condensed **reiteration** of ecosystem evolution history, the B/M ratio typically increases through seral stages and this process is accompanied by a rise of taxonomic diversity. The later appearing species are, as a rule, more effective in their use of trophic resources which makes them less distructive than their preceding seral species and even allows them to confer a stabilizing influence on their environments.

Ecosystem evolution can be **reversed** by increasing redundancy which actually happens under geological, climatic or human impacts. It was argued previously (Krassilov, 1989) that **rotational forcing** alone can produce roughly synchronous global effects inducing ecosystem restructurings via the stability/diversity regulation. The geological record of ecosystem evolution is punctuated by the falls of diversity which are known as mass extinctions and are correlated with major tectonic, eustatic and climatic events. In disturbed environments ecological successions never succeed to their potential later stages thus **cutting off their climax dominants**. This scheme is supported by the abundant fossil evidence, notably the end-Cretaceous (as well as the end-Permian) extinctions concomitant with global regressions affecting atmospheric CO_2 and terrestrial productivity.

The surviving pioneer and early successional species practise a high redundancy strategy stimulating high reproductive rates in turn impelling abbreviation and/or condensation of individual development. At the molecular level, developmental acceleration is accomplished by a reduction of the genome redundancy, notably by deletion of satellite DNA and interspersed repetitive elements affecting sequential gene activities. Such genomic events would result in **heterochronous ontogenic processes** (of which the precocious sexuality is a familiar example), abbreviation or overlap of developmental stages. Major evolutionary novelties allegedly derive from heterochronous developments. Concomitantly with a switch to coarse-grained environmental strategy a part of adaptive polymorphisms might turn **non-adaptive** by the narrowing of ecological niche and the loss of function.

Since in the pioneer stage of ecological expansion a gene pool enrichment by hybridization or nonsexual transduction of genetic material is potentially advantageous, there is no incentive for genetic insulation. Even there might be a tendency for species fusion by reciprocal genetic introgression. The species tend to be highly polymorphic and adaptively fine-grained. Subsequently, while adopting a coarse-grained strategy, they split into narrower species which are better protected from alien genetic material. A superspecies configuration of closely related but reproductively isolated species might arise from such **speciation cycles**.

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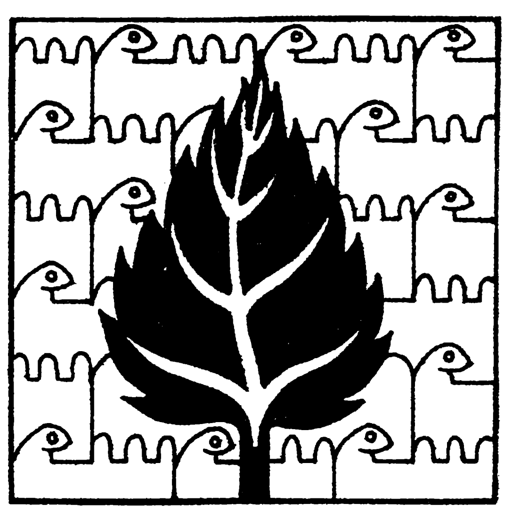
ABSTRACTS



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