# A BRIEF SKETCH OF THE ECO-DARWINIAN PARADIGM

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## Abstract

Species diversity is supported by trophic specialisation and the variability of environmental conditions in space and time, in other words, it is a form of the division of labour (a);Biodiversity helps to stabilise the functions (essential variables) of individuals, populations, and ecological communities (b);The emergence of biodiversity is determined by heritable variation and the advantage of specialised (more effective) structures over non-specialised ones (c);Biodiversity is characterised by its ability to increase itself and to organise itself during succession and/or evolution into relatively consistent structures, which we call production pyramids and nutrient cycles; in a certain sense, the ‚ontogenesis' of communities recapitulates their ‚phylogenesis'. (d).

## Introduction

Already Darwin encountered the paradox of primitive life forms: they co-exist with more complex organisms and do not seem to be less adapted to their environment than the latter. In the 20th century, a few more paradoxes have been discovered: the paradox of the plankton, of a meadow, of the tropical forest and, finally, the paradox of genetic diversity (Lekevičius 2018a). Researchers were uncertain what forces maintain diversity of genotypes and species.

Unfortunately, the project to incorporate the latest progress in ecology into Darwinism has never been properly implemented. I am convinced that this was the main reason why, up till now, we still do not have anything that could be called eco-Darwinism, or a general biodiversity theory. The theory should answer the following questions (Lekevičius 2018a, 2019): What forces maintain biodiversity (1); What is the function (if any) of biodiversity (2); How does biodiversity occur and attain an organised form that we usually call an ecological pyramid, an ecological community, and a nutrient cycle (3)?

## Biodiversity: maintenance and function

The paradoxes mentioned above were caused by overestimation of the importance of antagonistic relationships. Biotic attraction (cooperative, mutualistic, facilitatory or complementary relations) to be an equally widespread force which remains in a dynamic equilibrium with repulsion (e.g. Lekevičius 1986, 2002, 2018a; Begon et al. 2006; Taylor et al. 2009; Guimarães et al. 2016). Species are not functionally independent, so they cannot be autonomous in evolution also. In the long-term perspective, only an ecosystem with its nutrient cycle is alive. In other words, guilds and species are merely specialised units of 'the economy of nature'. The paradox of primitive forms has been resolved with the discovery that most of them not only do not compete with highly organized beings but are involved in indirect mutualism with them (Odum, Barrett 2005; Loreau 2010). Thus, the lack of autonomy of species, guilds and even 'functional kingdoms' should be considered one of the key factors that ensure and maintain biodiversity. In terms of trophic relations producers, consumers and decomposers perform defined functions, which become more specific at the tier of trophic levels and guilds, and are narrowed down even further to the very specific roles of individual species. The greatest challenge is to explain the coexistence of plant species, especially in tropical communities. Nonetheless, some insight has been gained even there. There is a broad agreement that diversity of species is self-maintaining due to the

differentiation of niches and numerous negative feedback links (e.g. Ellenberg 1974; Sommer 1984; Kelly and Bowler 2002; Tilman 2004; Levine and HilleRisLambers 2009; McIntire and Fajardo 2014). The variability of abiotic conditions, both in space and in time, creates a huge diversity of niches and sub niches for species.

There are reasons to believe (e.g. Hairston et al. 1960: Paine 2002; Bell et al. 2006; Bagchi et al. 2014;) that species diversity at a lower trophic level is maintained by the 'top-down' impact produced by the next higher trophic level ('exploiter-mediated coexistence').

It seems that these days very few experienced ecologists would doubt that species diversity not only stabilises the functional parameters of a guild (production, total biomass, etc.) but also tends to maximise these parameters in the process of self-arrangement, of course, to the extent possible with the available limited range of responses to environmental changes and limited speed of restructuring (e.g. Tilman et al. 2001; Loreau 2010; Huang et al. 2018).

Organisms live in a rather unstable environment, with regard to both time and space. However, they are capable of adjusting to the environmental conditions, and the process seems to be endlessly going on. They invoke various adaptation mechanisms: individual, populational, community-level, and genetic, or evolutionary. The basis of non-genetic mechanisms is the diversity of structures (genes, macromolecules, metabolic pathways, genotypes, species, etc.): the structures that reach optima are multiplied and thus activated, while the functioning of those which lost their optima is suppressed (Lekevičius 1986, 2011, 2018a; Lekevičius, Loreau 2012). In this way, life maintains its essential variables (biomass and productivity) as stable as possible under given conditions.


## Biodiversity: origin and self-organisation

Traditionally, evolutionary biologists are not too interested in succession, while most ecologists show limited interest in the evolution and diversification of life. Just the other way about, my concept of 'conditionally complete (= synthetic) explanation' (Lekevičius 1985) recommends any researcher aiming to understand the occurrence of biodiversity and its development to start with the increase of biodiversity and its self-organisation during ecological succession, and only then to address the problems of evolution. In metaphorical language, the laws of the evolution of life are laid right at our feet, they can be found in daily phenomena, one just has to bring them out into the light.

Elton (1958) has once emphasised that vacant niches stimulate not only evolution but also the increase of species diversity during ecological succession. As the number of vacant niches is reduced to the minimum at the end of succession, immigrants find it harder to settle in the community. These insights have planted a logical conclusion into some heads that significant similarities exist between evolution and ecological succession (Odum 1969; Whittaker 1975). The idea has become even stronger after the ecosystem concept was created. The authors of this concept (Odum 1971) discovered that local ecosystems share many common features. Despite the fact that Earth's ecosystems vary significantly in their species composition, their functional portraits are similar. The greatest similarities are observed between the material turnover (cycles) and production pyramids (the 10 % rule). Ecologists clearly understood that these similarities have evolved despite the fact that some local communities have been formed almost exclusively by succession (immigration), while others – for instance, those on remote islands – have been mostly produced *in situ*. This implies that in both cases, succession and evolution, similar factors delimiting and shaping diversification are in play. The common features shared by all local communities and ecosystems I named a functional convergence of ecosystems not so long ago (Lekevičius 2002). On top of that, we could add thousands of ecological equivalents – not closely related but convergent species found in different geographical regions and occupying similar ecological niches (see Odum 1971; Pianka 2000).The conviction is growing that even in distant geological past, e. g. in the Mesozoic, the structure of communities already attained the form very close to the present one (Odum 1971; Wilson et al. 1973; Richardson 1977; Lekevičius 2002, 2018b)

Primary succession is a rather strictly determined and partly predictable process (e.g. Odum 1969; Thornton 1996; Hagwar et al. 2017). It starts with the immigration of producers and decomposers, which not only fill the pre-existing niches but themselves become vacant niches for the arriving consumers. A vacant niche hereafter should be understood as potentially suitable energetic or material resources not used by any consumer ( Lekevičius 2002, 2009a). Such resources could be light, inorganic nutrients, detritus or other living organisms, provided they are not exploited by other consumers. When vacant niches are abundant, the concept of adaptive zone is usually used.

Succession proceeds at an increasing rate and ends with the establishment of the top predators. Species diversity induces its own increase according to the autocatalytic model. The assembly stages characteristic of the Hawaiian communities have no principal differences from those observed in a typical primary succession (Carlquist 1965; Ziegler 2002; Lekevičius 2018b).

Colonisation starts with producers and/or detritus, followed by herbivores and decomposers, and finally, predators. The stages might have been similar, but not the mechanisms of assembling. Vacant niches – and they were abundant on Hawaii – promoted evolution, so it took the form of adaptive radiation. The inclination of communities to achieve a predefined organisational structure (the phenomenon of the functional convergence of ecosystems) is so strong that the missing chains can be hastily produced by evolution from ill-suited material, resulting in numerous peculiar ersatz species. This is what happened with Hawaiian nature.

Vacant niches have played the key role in the assemblage of nutrient cycles also, they promoted and directed diversification (Lekevičius 2002, 2003, 2009b, 2019). One of the mechanisms was the accumulation of metabolic by-products, e. g. the metabolic waste of chemo- or photosynthetic organisms. After a certain evolutionary period, the very same producers would acquire the ability to use these waste products for respiration, as more efficient final electron acceptors. Another mechanism might have been related to the depletion of some pre-existent nutrients in the environment. At the early stage, $H_2$ and $NH_3$ might have been among these nutrients. Once the reserve of a vital nutrient had been depleted, the growth of total biomass would inevitably come to a halt, and life would tumble into a global crisis. Nevertheless, the selection pressure would produce new species capable of utilising other, usually more abundant, albeit less readily available, sources of certain chemical elements, energy or electrons (light, $H_2S$, $Fe^{2+}$, $N_2$, $H_2O$). Basically, there are reasons to believe that, some 2.5-2.0 billion years ago, the aerobic carbon, nitrogen and oxygen cycles had already attained their present form.

During the period between 4 and 2 billion years ago, biomass was not subject to direct exploitation as a resource. Thus, it turned into a huge adaptive zone open for potential users. Once the primary consumers had evolved the course of events started to accelerate – diversification of multicellular organisms in the Cambrian and Ordovician led to the formation of other trophic levels, and the ecological pyramids in the ocean acquired an almost modern shape (Lekevičius 2002, 2003, 2009b). The lower trophic levels produced the upper ones (see **figure**).

At the early stages of land colonisation by life in the Paleozoic, the process of filling the pre-existing niches was prevailing. The organisms that occupied them would themselves automatically become vacant niches. Therefore, species diversity tended to increase with acceleration. Vacant niches not only promoted diversification but also set its course. This course had eventually (by the late Carboniferous or early Permian) led towards the formation

of the nutrient cycles and production pyramids (see **figure**) pretty similar to the modern ones (Lekevičius 2002, 2003, 2009a,b, 2018b). Once communities had been more or less assembled, evolution progressed mostly by way of niche partitioning and differentiation, which resulted in the production of many highly specialised forms (Pfennig and Pfennig 2010; Ding et al. 2015). In addition to that, the common Darwinian evolution was taking place by way of exclusion of the weaker competitors, as well as maladapted prey or hosts. In this process, old life forms were being replaced by new, more advanced ones.
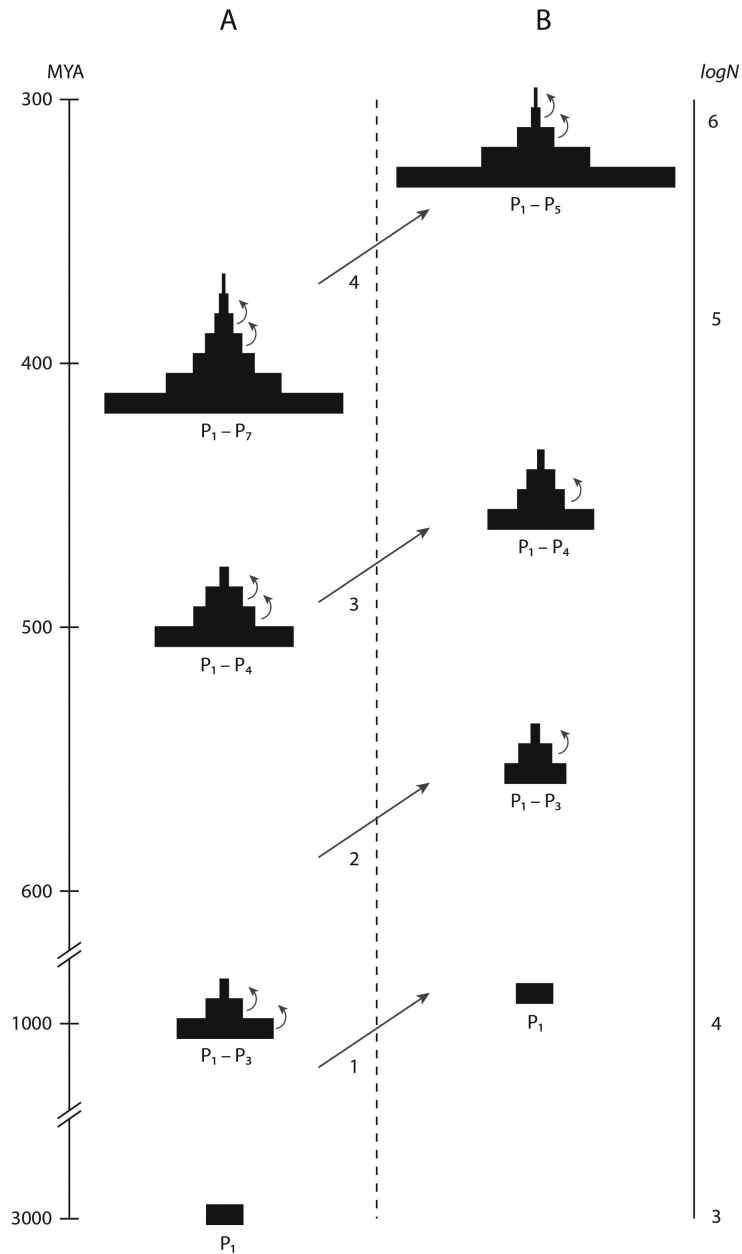
## Summing-up

So, the sequence of stages is hardly dependent on the way this process has taken: through succession, evolution, or, in Hawaii, a combination of both. In a certain sense, the `ontogenesis` of communities recapitulates their 'phylogenesis'. By occupying a vacant niche, species not only avoid competition but also increase species diversity in the community. Moreover, by occupying such a niche, they increase the stability of the community and bring it closer to the «mandatory» organization. Thus, in the course of evolution species accumulate two different types of traits. Whereas one group enhances their competitive capacities, the other one benefits not only individual species but also the entire community. Due to the dualistic nature of accumulated traits, it is appropriate to recognize the existence of two evolutionary pathways: the evolution of species and the evolution of ecosystems.

Species diversity is *supported* by trophic specialisation and the variability of environmental conditions in space and time, in other words, it is a form of the division of labour (a);

Biodiversity helps to *stabilise the functions* (essential variables) of individuals, populations, and ecological communities (b);

*The emergence* of biodiversity is determined by heritable variation and the advantage of specialised (more effective) structures over non-specialised ones (c);

Biodiversity is characterised by its ability to increase itself and to *organise itself* during succession and/or evolution into relatively consistent structures, which we call production pyramids and nutrient cycles (d).

**Figure.** The likely assemblage stages of aquatic and terrestrial production (energy) pyramids. *MYA* – million years ago; *N* – approximate number of species in the biosphere; $P_1$ - $P_n$ – the levels of production pyramid. The long arrows represent the phases in the terrestrial expansion of aquatic organisms ('raw materials'): the presumed appearance of unicellular producers and decomposers in wetlands and coastal areas (1); the emergence of primary consumers and primary predators on land (2); the subsequent diversification of consumers and the emergence of secondary (3) and tertiary (4) predators on land. The short arrows pointing from the lower to the higher trophic levels represent *in situ* production of the new level from the organisms in the lower level.

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