

# ECOLOGICAL ASPECTS OF SUPRASPECIFIC EVOLUTION

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## *Introduction*

The synthetic theory of evolution, or neo-Darwinism, the last ruling paradigm in evolutionary biology, was established basically by the synthesis of Mendelian genetics and population biology. A natural consequence of this descent was the orientation of most of the neo-Darwinistic research on the population/species level of biological organization while, among other things, the question of supraspecific evolution (called also evolution above the species level, transspecific evolution, macroevolution, or macrophylogeny) was almost neglected in this paradigm [70].

When the hegemony of neo-Darwinism became disturbed during late 1970s, the question of supraspecific evolution started to be, along with many other problems, re-evaluated [18, 19, 31, 32, 47, 55, 63, 65]. The present paper aims to contribute to the latter problem. In view of the fact that it is supraspecific taxa which are the units of supraspecific evolution, the best way how to do it is to begin with the analysis of the taxon notion.

Although the term taxon was applied for the first time only in 1926 [38] and became widely known only during 1950s [36], it seems apparent that the taxon notion was known to humans much earlier, even before the Ancient Era. We may deduce so from the fact that both modern laymen in biological systematics [42], and native folk taxonomists [4-6] discern, when viewing biological diversity, certain (taxonomic) fuzzy [30] entities to which terms as folk generic categories, speciemes, basic level objects, or covert categories were applied [6]. Because these entities, not unlike taxa of classical scientists, are recognized on the basis of their perceptual saliency, as psychologists call the relative perceptual distinctiveness and importance of specified units [6, 22], the notion of them can be identified with the early undifferentiated and unstructured taxon notion.

Little development of the taxon notion took place since Ancient Era until recent times. This was apparently because species became distinguished as a special kind of taxa somewhen during Medieval Ages [43] and all the respective attention was subsequently paid solely to the species notion. During the Medieval and early Modern Eras, the only disputations regarding the taxon notion were those between essentialists and nominalists [36] which did not significantly contributed to its development.

Revival of the interest in the taxon notion set in only in 1940s when Simpson [51, 52] attempted to adjust the then newly established synthetic theory of evolution with paleontological data. Like other neo-Darwinists, Simpson paradigmatically distinguished between species and supraspecific taxa. Analogously to the neo-Darwinistic view that species occupy in the *abstract* ecological space certain subspaces (niches), he suggested that supraspecific taxa also occupy in the abstract ecological space certain subspaces which he called adaptive zones.

Simpson's [51, 52] concept of adaptive zones has been soon widely accepted in neo-Darwinian biology and later reformulated in that sense that supraspecific taxa are not only taxonomical, but also ecological units [7, 10, 23, 27-29, 66, 67]. Unfortunately, Simpson's hypothesis of adaptive zones as presented by himself is tautological

[13] and has, consequently, no explanatory value in theoretical evolutionary biology.

Attempting to clarify the taxon notion I suggested [39, 40] that *counterparts of adaptive zones are not taxa, but life forms* which are the actual units of ecomorphological classification [40]. A taxon is then, generally speaking, « a part of a phyletic line bordered by the limits of an adaptive zone, or, in other words, a taxon is a monophyletic part of a life form » [40, p. 311]. I argued further [40] that of generally accepted levels of taxonomical hierarchy only the genus, family, and phylum levels correspond to levels of ecomorphological hierarchy. Taxa of the order and class level do, on the contrary, not. Species seem to be units of a quite different quality uncomparable to either of the former kinds of taxa [40, 43].

For the sake of completeness I add that also various other concepts of supraspecific taxa were proposed [1, 14, 26, 59], but they usually applied to specific kinds of them only, and it appears that they are of minor importance for the further development of the general taxon notion.

### *The process of supraspecific evolution*

Having analysed the taxon notion, we may now turn to the problems of supraspecific evolution itself. In view of conclusions achieved in the former paragraphs, the term supraspecific evolution has to be considered as a summary designation of evolution at the genus, at the family, and at the phylum levels, i.e. as a designation of three different evolutionary processes. On the other hand, however, it should be recognized that these three levels of supraspecific evolution have much in common so that the unspecified designation « supraspecific evolution » retains its heuristic value. In the following text I shall then speak of supraspecific evolution in the sense of evolution at any of the three levels listed above.

Various approaches to the problem of supraspecific evolution have been proposed, but the recently most frequently supported one is Simpson's [51, 52] view that supraspecific evolution is reducible to microevolution, i.e. to the evolution at the species level, or speciation [8-10, 12, 20, 25, 35, 37, 50, 58]. Arguments cited by propo-

nents of classical neo-Darwinism in support of this view are so vague that one may be inclined to conclude that their desire to save their neo-Darwinism prevented them from seeing the matter of the problem. It is notable that most of the recent advocates of this view are either geneticists or population geneticists.

Interestingly enough, cladists arrived at similar conclusions as neo-Darwinists. They likewise consider supraspecific evolution as reducible to speciation phenomena [24, 68], although they derive this conclusion from Hennigian axioms of cladistics. No commentary upon their views is needed here, because the cladistic approach to the problem of supraspecific evolution is nothing more than a nice example of what can produce a wrong application of a set of methods on problems for which they are not designed.

Another important hypothesis, the saltationist one, means that supraspecific taxa originate by some kind of macromutations ([16], and many others), a view which is still supported by a minority of authors [11, 60]. In accordance with the recently revised gene and heredity notions [69, 71], it seems possible that changes in single characters may occur very quickly, but no change in any single character can be identified with an origin of a supraspecific taxon. The saltationistic hypothesis of the origin of supraspecific taxa was already often criticized [36, 50-52], and it is certainly nothing in modern genetics what could even distantly supported any type of saltationistic hypotheses regarding the origin of supraspecific taxa.

Stanley [53-56] and others [13, 15, 17] developed another hypothesis, according to which discontinuities observed between supraspecific taxa originate by species selection. Vrba's [62-65] effect hypothesis may be regarded as a variant of species selection hypothesis in this respect. Although this hypothesis seems to be acceptable as an explanation of the origin of supraspecific taxa at least at the phenomenological level, there are two major objections to it. First, computer simulations showed that taxonomic diversity comparable to that observed in nature can arise from random events [48, 49], i.e. without any effects of species selection and, second, it has been shown that such selection models as proposed by Stanley [53-56] and others can be valid only in non-hierarchical one-level systems [2, 3] which is evidently not the case here.

Before outlining in the following text my own view of the

process of supraspecific evolution, I add for the sake of completeness that there is a lot of morphological hypotheses related to this problem, but they are in fact only descriptive, not explanatory, and hence not relevant to problems discussed here.

In the following I shall describe my own view of the process of supraspecific evolution. Before doing so, however, I have to point out that adaptive zones as recognized here are slightly intergrading into one another, i.e. they are « fuzzy » in the sense of mathematical logics. If then a phyletic line (at any level of supraspecific evolution) moves not within an adaptive zone, but crosses its borders, it fuzzy enters in another adaptive zone. At that given level, then, the incipient new taxon is still not separated from its maternal taxon. (See [57] for a nice example). Note that this process is not reducible: a genus originates from a genus, a family originates from a family, a phylum originates from a phylum. It is impossible from the methodological point of view to derive, e.g., a genus or a family from a species, although it could be actually only one species which, as *representative of a given phyletic line*, crossed borders of an adaptive zone and caused later origin of a new genus, or a new family.

In the course of evolutionary time the phyletic line entering a new adaptive zone becomes subsequently more and more adapted on it. Parallely, it usually diversifies by subsequent occupation of various subzones and/or niches of the given adaptive zone. This process, known as adaptive radiation [46], is still less understood. It is probable that it follows, mathematically, logistic curve [60]. Nevertheless, the subsequent numbers of subtaxa of the given taxon may considerably vary [44]. The same seems to be true also for diversity of the whole life forms (cf. [21]). Morphologically, new taxa are very diversified at first, and their morphological diversity declines later in that sense that only few (more favourable?) solutions of problems posed by the new adaptive zone to the new taxon are used by more progressive subtaxa [33, 34, 41, 61]. The latter phenomenon seems to be explainable in the terms of epigenetics [41]. From this brief review is evident that our knowledge of the process of supraspecific evolution is still quite insufficient. I hope, nevertheless, that the analysis of properties of adaptive zones (see below) may constitute an usable basis for respective investigations.

So far as I know, nobody attempted to investigate the properties of adaptive zones thus far. I wish to start such analyses by proposing here three properties of adaptive zones which I consider to be fundamental from the evolutionary point of view. It will not be said by this, however, that adaptive zones do not have more properties than these ones. The three fundamental properties of adaptive zones which I shall consider here are 1) accessibility, 2) perspectivity, and 3) permeability. They are defined here as follows: Accessibility is the ease with which a given adaptive zone can be invaded by phyletic lines. Perspectivity is the ease with which a given adaptive zone can be left by phyletic lines. Permeability is a difference between accessibility and perspectivity, defined as accessibility minus perspectivity.

A problem arises when one wish to estimate values of these properties. It is evidently impossible to measure them directly, so that only approximative methods have to be used, one of which I shall propose here. At first I have to point out that the recognition and characterization of particular adaptive zones is based on the analysis of locomotor and feeding behavior and, correspondingly, of locomotor apparatus and feeding apparatus [42]. The method itself consists in recording aberrant behavior of individuals belonging in taxa of certain adaptive zone, i.e. of those individuals which used behavior strange for their adaptive zone, but typical for another one. We could, e.g., record as aberrant a behavior of a swallow feeding in gait, because its typical locomotion during feeding is flight.

Using this method I tried to investigate adaptive zones of the genus level in a selected taxon, the waterfowl (Aves: Anseridae) [42]. This selection was influenced by the fact that waterfowl belongs to best known animal taxa, and that it is at the same time sufficiently, but not excessively diversified. Note, that it is not possible to apply this method on inadequately known taxa — at least in the present state of its development. Based on the above statements I identified three locomotion types (1. gait, 2. swimming, 3. diving), and five feeding methods (1. filtering, 2. individual collecting, 3. preying, 4. plucking, 5. nipping). A combination of these types gives a matrix of adaptive zones  $AZ_1 = [\text{locomotion type, feeding method}]$ , which shows the designation of the individual waterfowl adaptive zones:

	11	12	13	14	15
AZ <sub>1</sub> =	21	22	23	24	25
	31	32	33	34	35

An analysis of the ecological position of individual waterfowl species [42] yielded then another matrix (AZ<sub>2</sub>), which shows which of potential adaptive zones listed in the matrix AZ<sub>1</sub> are presently actually occupied by waterfowl. The resulting matrix is AZ<sub>2</sub> = [locomotion type, feeding method], where 0 stands for unoccupied, and 1 for occupied adaptive zones. Note, that because adaptive zones 12 and 22 were not discernable in practice, I lumped them into one adaptive zone designated as 12/22.

	1		0	0	1
		(1)			
AZ <sub>2</sub> =	1		0	1	0
	1	1	1	1	0

The matrix AZ<sub>2</sub> can be quantified by substituting the binary coding used in the matrix AZ<sub>2</sub> by numbers of genera which occupy each of the recognized adaptive zones. I repeat that number of Recent genera occupying an adaptive zone (which are recorded here) is identical with the number of phyletic lines which invaded that adaptive zone and which still survive in it. By the quantification we become the matrix AZ<sub>3</sub>:

	4		0	0	11
		(6)			
AZ <sub>3</sub> =	4		0	2	0
	4	8	4	2	0

As a result of this analysis I recognized 9 currently occupied adaptive zones of the genus level in the waterfowl family which are correspondingly occupied by 9 life forms, which I designed with the names of typical genera belonging in them, as follows: Tadorna, Cairina, Anser, Anas, Cygnus, Biziura, Somateria, Mergus, and Nyroca. See Table I for their matrix identification.

At this stage of investigation it was possible to count aberrant locomotor and feeding behavior, and to construct matrices  $T_1 =$  [initial locomotion, subsequent locomotion], and  $T_2 =$  [initial feeding behavior, subsequent feeding behavior], designed for recording changes in locomotion types ( $T_1$ ), and in feeding methods ( $T_2$ ). The coding is binary with 0 standing for unrecorded changes, and 1 standing for recorded changes. The matrices are

$$T_1 = \begin{array}{ccc} \text{---} & 1 & 0 \\ 1 & \text{---} & 1 \\ 0 & 1 & \text{---} \end{array}$$

and

$$T_2 = \begin{array}{ccccc} \text{---} & 1 & 0 & 0 & 1 \\ 0 & \text{---} & 1 & 0 & 1 \\ 0 & 1 & \text{---} & 0 & 0 \\ 1 & 1 & 0 & \text{---} & 0 \\ 1 & 1 & 0 & 0 & \text{---} \end{array}$$

Using Boolean algebra we can derive from the matrices  $T_1$  and  $T_2$  a general transition matrix  $T_3 =$  initial adaptive zone, subsequent adaptive zone, where adaptive zones are ordered as in Table I.

$$T_3 = \begin{array}{ccccccccc} \text{---} & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \text{---} & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 1 & \text{---} & 1 & 0 & 0 & 0 & 0 & 0 \\ 1 & 1 & 1 & \text{---} & 0 & 1 & 1 & 0 & 0 \\ 1 & 1 & 0 & 1 & \text{---} & 1 & 1 & 0 & 1 \\ 0 & 0 & 0 & 1 & 0 & \text{---} & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \text{---} & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & \text{---} & 0 \\ 0 & 0 & 0 & 1 & 1 & 1 & 1 & 0 & \text{---} \end{array}$$



The final matrix  $T_3$  includes all data necessary for the calculation of the three fundamental properties of adaptive zones introduced above. They are summarized in Table I.

It is naturally impossible to derive general conclusions from a study of a single taxon, but because no comparable studies have been published, I shall point here towards some possible interpretations of the empirical results obtained here.

TABLE 1

Properties of the waterfowl adaptive zones.  $AZ_{ij}$  = matrix code of adaptive zones from the matrix  $AZ_1$ ; A = accessibility, P = perspective, P-A = permeability, n = number of Recent genera occupying the given adaptive zone.

nominal designation	$AZ_{ij}$	A	P	P-A	n
TADORNA	11	3	3	0	4
CAIRINA	12/22	4	3	-1	6
ANSER	15	3	3	0	11
ANAS	21	5	5	0	4
CYGNUS	24	1	6	5	2
BIZIURA	31	3	2	-1	4
SOMATERIA	32	5	1	-4	8
MERGUS	33	1	1	0	4
NYROCA	34	1	4	3	2

1) Spearman's nonparametric correlation test with Kendall's correction for supernumerary ties showed that, as expected, accessibility is not correlated with perspective ( $r_s = -0.164$ ,  $p > 0.1$ ). On the contrary, permeability is correlated both with accessibility ( $r_s = -0.723$ ,  $0.025 > p > 0.01$ ), and perspective ( $r_s = 0.728$ ,  $0.025 > p > 0.01$ ). These correlations are, however, probably a mathematical artifact, because due to the calculation mode of permeability the two compared variables are not fully independent, as required by Spearman's  $r_s$  test.

2) Spearman's modified correlation test indicated that there is a positive correlation between the number of Recent genera occupying an adaptive zone and accessibility of adaptive zones ( $r_s = 0.641$ ,  $0.05 > p > 0.025$ ), and a negative one between them and permeability of adaptive zones ( $r_s = 0.716$ ,  $0.025 > p > 0.01$ ). On the contrary, no such correlation could be revealed between the number of Recent genera and perspectivity ( $r_s = 0.540$ ,  $0.1 > p > 0.05$ ). The meaning of these results remains to be studied in the future.

3) A close correlation seems to exist between the morphological definability of life forms and the properties of adaptive zones.

a) The higher are both accessibility and perspectivity of an adaptive zone, the less clearly definable (i.e. the more fuzzy) is it itself, and the life form which occupies it. b) The degree of distinctiveness between filial and maternal taxon is probably caused by the process of competition between subtaxa of the given taxa. When the accessibility of the subsequent adaptive zone is low, the transitory forms in the given phyletic line cannot survive when « attacked » by better adapted forms from both sides. When the accessibility is higher, the differences of competitive abilities are not so high, and even transitory forms may survive for long periods. c) Low perspectivity means that life form which occupies the given adaptive zone is specialized to a high degree. d) The matrix  $T_3$  is not symmetrical. It means that the transition between between two adaptive zones need not be equally complicated when going from adaptive zone A to B, and when going from B to A.

4) It seems incorrect to assume that ancestral forms of supraspecific taxa are always rather generalized, and that more specialized forms originate only in the process of the further evolution of that taxon. In the waterfowl, for example, the ancestral life form seems have been *Tadorna* which occupies the adaptive zone [11]. Although it is certainly not too specialized life form, it is by far not the most generalized one among waterfowl life forms (see Table I).

Relatively much attention has been recently paid to the problem of supraspecific evolution, and two symposia were entirely devoted to it — the first one in Kjaeriku, Estonia, in September 1980 [47], the second one in Chicago, Illinois, in October 1980 [32]. Most of the pertinent research, however, has been considering merely the question of reducibility of supraspecific evolution to microevolution. On the contrary, the present paper aimed also at studying the characteristics of supraspecific evolution. Due to place limitations, many relevant problems were mentioned only succinctly, and other ones even remained unmentioned. For this reason, some results of this paper may appear as unsubstantiated and other ones as insufficiently analyzed. Nevertheless, it is hoped that new aspects presented here will serve as a basis for more concrete investigations of supraspecific evolution than were previous ones, and that this will in future lead to incorporation of supraspecific evolution in the modern theory of evolution (cf. [70]).

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