

Vacant niches in nature, ecology, and evolutionary theory: a mini-review

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The use of the term “vacant niches” (unused but potentially usable resources) has recently increased in ecological literature. According to some studies, vacant niches are quite numerous in nature, especially, but not exclusively, in disturbed ecosystems. However, the concept of “vacant niche” is still controversial in ecology because of the failure to reach an agreement on how to define a situation when an ecosystem is devoid of such niches. In evolutionary biology, as distinct from ecology, this concept arouses fewer controversies and has contributed to the creation of the ecological theory of adaptive radiation. Still other evolutionists have used this concept to describe the course and mechanisms of the evolutionary assembly of ecosystems (nutrient cycles and ecological pyramids). These evolutionists attempt to prove that in the course of diversification, vacant niches are not only occupied but are also created by newly evolved organisms.

Key words: saturated communities, ecosystem evolution, succession, assembly

INTRODUCTION

Some ecologists (e. g. Cornell, 1999; Tilman, Lehman, 2001; see a survey of Rohde, 2005) tend to think that a niche can exist even without the organisms that have adapted to it to some extent. It is these ecologists who propagate the concept of vacant (= unoccupied / empty / free / unfilled) niche. In their opinion, the niche is primarily a property of the environment and not of an organism. Therefore, to emphasize the difference from the currently more widespread concept of Hutchinsonian or ecological niche, such a concept is sometimes referred to as either a non-Hutchinsonian or environmental niche. These authors define vacant niche as the resources that are unused by anyone but are potentially usable. One can also find other more sophisticated definitions of vacant niche. For instance, Lawton (1984) defines vacant niches as “evolutionarily novel suites of environmental conditions for which no species in a region are well adapted”. Rohde (2005) states that the vacant niche is the possibility that in ecosystems or habitats more species could exist than are present at a particular point in time, because many possibilities are not used by existing species. Woodley (2006, p. 30) presents a slightly different definition:

“Vacant niche is <...> defined by the absence of species along certain regions of <...> resource gradients, which has the potential to fix a species traits at the community level and affect the evolutionary trajectory of a species in a di-

rection favoring greater integration with the surrounding ecology”.

According to this author, vacant niches may be defined as negative species or species waiting to happen. The concept of negative species is based on a conceptualization of vacant niches and is appropriately used under the circumstances where it can be demonstrated to be a special case of niche theory (Woodley, 2008; see also: Copp, 2008). Additional details concerning the concept of vacant niche and the possibilities of its application may be found in a dialogue between Woodley (2007, 2008) and Rohde (2008a, 2008b).

It is difficult to say who was the first to use the term “vacant niche”. It must have been Grinnell (1924) who wrote: “...if a niche is vacated, nature hastens to supply an occupant...” Later this issue was also discussed at length by Elton (1958). Hutchinson (1957, 1959) did not consider this concept illogical, either. Hence, those who contrast his opinion with that of Grinnell and Elton can hardly be right.

Still, the concept of vacant niche seems illogical to many scientists (see Chase, Leibold 2003 and references therein). Those who find it acceptable think that it does not enjoy a wide applicability as unused resources are either non-existent in nature or extremely rare. In spite of that, this concept has become widespread in ecology, its usage in evolutionary biology being even more common (see further). The term is sometimes replaced by other analogous terms: “vacant (= empty / unoccupied) ecospace” or “ecological release”. The

latter term implies the availability of free resources and a lack of competitors. To avoid confusion, I will stick to the notion “vacant niche” in the cases when the author referred to changes only the term but not the meaning associated with this term.

In this article, I will try to briefly review cases of using the concept of vacant niche in ecology and evolutionary biology and discuss the possible prospects of this usage. In no case do I consider this survey to be an exhaustive summary of the topic. It is more likely to serve as a lead-in to the problem, the solution to which may have a significant impact on both theory and practice of ecology and evolutionary biology.

ARE THERE MANY VACANT NICHES IN NATURE?

In his well-known book *The Ecology of Invasions by Animals and Plants*, Elton (1958) concludes that invasions of alien species in species-poor communities are more likely than in saturated ones because the former abound in vacant niches. Vacant niches are abundant in agro-ecosystems, volcanogenic islands and communities at early stages of succession.

Does present-day ecology confirm these conclusions? Numerous cases of intentional and unintentional introduction have been studied over the last 50 years, therefore this question does not seem to be difficult to answer. Simberloff (1981) recorded 854 cases of successful introduction known to him. In his summary of the collected material he states:

“The most striking result is that in so many instances (678 of 854), an introduced species has no effect whatever on species in the resident community, or on the structure and function of the community. Perhaps the second most striking result is the scarcity of extinctions apparently attendant on introductions”.

Cases of competitive exclusion were extremely rare (3 cases). Local communities were most strongly affected by alien predators and parasites. However, their impact was related to the extermination of prey or hosts respectively rather than the displacement of local competitors (predators or parasites). According to Walker and Valentine (1984), these data suggest that the number of vacant niches in nature is probably much greater than it was suspected. Surveys (Mack et al., 2000; Davis, 2003; Sax et al., 2007) that have appeared in recent years in fact confirm Simberloff’s conclusion that cases of competitive exclusion are rather rare.

Explaining why introduced species often turn into the invasive ones, Elton (1958) arrives at a conclusion that due to introduction these species often get rid of their enemies – predators and parasites. Owing to this fact, they gain advantage over other species in a novel range. The newly gathered facts seem to support this idea (e. g. Mack et al., 2000; Torchin, Mitchell, 2004). Introduced species lose about 75% of parasites and pathogens they had in their native habitats, which can become one of the decisive factors facilitating invasion (Torchin, Mitchell, 2004). On the other

hand, as it follows from the above-mentioned definitions, introduced species themselves turn into niches occupied only partly. How does this fact affect introduced species and local communities? Facts prove (Torchin, Mitchell, 2004) that with time alien species acquire newer and newer parasites from the species exploiting local communities.

When the parasites (or even predators) that can exploit alien species increase in number, host (or prey) populations should decrease and become stable eventually. However, this process (Mooney, Cleland, 2001) is likely to be related to unavoidable microevolutionary changes, host–parasite co-evolution, and therefore it is rather slow. It is quite probable that the self-suppression of many invasive outbreaks observed in the 19th century can be explained by the fact that this microevolution is actually over. However, it seems that there is no proof of it.

Southwood et al. (1982) demonstrated that trees introduced into South Africa and Great Britain have much fewer arthropods feeding on them than conspecific trees in their homeland. The authors conclude that communities of herbivores feeding on these introduced tree species are still not saturated with species. Such saturation can be achieved both by colonization and evolution, but both ways are time-consuming.

Lawton (1982) investigated communities of insects feeding on bracken *Pteridium aquilinum* L. in G. Britain and the south-western part of the USA. The study has shown that the diversity of these insects in America is much smaller: some (gall-formers) of the four main ecological groups characteristic of G. Britain (chewers, suckers, miners and gall-formers) were not found in America at all, while diversity in other insect groups was also smaller. The author maintains that these insect communities are not saturated with species in America, i.e. bracken as a resource is not used to the full. In Lawton’s (1982) opinion, a similar situation must have developed among other herbivores as well, because they, as is well known, make use of only a small part of the primary production.

Rohde (1991, 2005) has shown that parasites have not occupied all trophic niches that are open to them, either. He found that the number of species parasitizing gills of the investigated marine fish fluctuate between 0 and 30, although the fish did not differ much in body size and their habitats. The author presumes that the maximum possible number of species is 30 (or even higher, since there is no evidence that 30 cannot be exceeded). If that is the case, then, according to the author’s estimate, only 16% or less of all the niches for ectoparasites of marine fish are occupied.

Rohde (2005) relates his approach to the so-called “non-equilibrium paradigm” which, in his opinion, is gaining in popularity among ecologists. The origin of this “paradigm” should be traced to works by Price (e. g. 1984) and Chesson and Case (e. g. 1986). In our context, this paradigm is interesting in that its supporters reject the idea that organisms and communities are in equilibrium with the environ-

ment. The latter is constantly changing, and organisms are forced to adapt to these changes in one way or another. As soon as organisms adapt to altered conditions, new changes take place and this process goes on incessantly. Disturbances, uncertainty and suboptimal states are more likely to be the rule than the exception. Factors that are difficult to predict affect ecological communities much more than customarily thought until the 1980s. That is why, as Rohde (2005) and many other representatives of this paradigm assert, natural communities are not and cannot be saturated with species. As an unavoidable consequence of continuous and usually unpredictable disturbances, vacant niches should always exist in natural communities. Disturbances can be caused by droughts, fires, climate change, impacts of cosmic origin, anthropogenic activity and other factors. According to Rohde (2005), representatives of the traditional (equilibrium) paradigm believe that, in natural ecosystems, all accessible resources are usually (at least in climax communities) used in one way or another, while trophic niches of species belonging to one guild are very often overlapping. This fact, in their opinion, proves the importance of competition in nature.

We are not going to discuss the strong and weak points of these paradigms here. Each of them has its own pros, and most probably they are not mutually irreconcilable. It is quite probable that in the future these paradigms will complement one another and, as a result, both will benefit.

Woodley's (2008) proposed a potential compromise between the non-equilibrium and saturation paradigms, which is based on the idea that the resource space is globally unsaturated, but locally saturated in places. The majority of species will tend to converge on a thermodynamically optimal set of resources, which results in competition and drives ecosystem evolution; however, much resource space is empty simply because the majority of species cannot make use of it. According to Woodley, this is evident from the relative rarity of extremophilic species.

The non-equilibrium approach may become more popular among ecologists with time because it emphasizes the importance of disturbances. Due to anthropogenic activity this importance is increasing year by year. Many of the authors addressing the issue of vacant niches acknowledge that man has created innumerable vacant niches by destroying natural communities and decreasing species diversity in the biosphere (e. g. Tilman, Lehman, 2001; Rohde, 2005). The first two authors state: "Anthropogenic changes in environmental limiting factors are likely to cause significant loss of plant diversity, leaving many niches empty and creating plant communities dominated by weedier species (poor competitors but good dispersers)".

Attractive as the idea of vacant niches is, it seems to be facing serious difficulties of theoretical character. The question as to when a community is to be considered as saturated with species, i. e. devoid of vacant niches, seems to be one of the most complicated problems. As Whittaker (1972, p. 217) once pointed out, "there is no evident intrinsic limit on the

increase in species number, with increased packing and elaboration of axes of the niche hyperspace". Moore and his colleagues (Moore et al., 2001) hold the following opinion on this issue:

"Many of (...) coexistence mechanisms do not lead to saturated communities or assemblages; indeed in many of the models there are no theoretical limits to species richness".

The theoretical discussion of this problem may be found in publications by Loreau (2000), Moore et al. (2001) and Russel et al. (2006).

Bambach, Bush and Erwin (2007) faced a similar problem. Using environmental niches of marine animals and respective "modes of life" as a guide, the authors devised a theoretical ecospace or, to be more exact, a theoretically feasible combination of tiering positions, motility levels and feeding strategies. They distinguished six categories on each of the three ecospace axes. As a result of free in-between combination of these categories, $6 \times 6 \times 6 = 216$ "modes of life" are obtained. Empirical data show that at present only 92 of these environmental niches are used by marine animals. In the authors' opinion, a wider use of niches is impeded by constraints of functional and energetic character. They make some "modes of life" either impossible or less efficient, so they will hardly ever come into existence. This conclusion is undoubtedly preliminary and somewhat speculative, and the authors perceive that. The fact that deductive methodology, widespread in physics but unpopular among biologists (Murray, 2001), is widely used in this publication is rather astonishing. The theoretical "ecospace" is a peculiar kind of ecological analogue of the periodic system of chemical elements. If this "table of niches" has unoccupied squares, it is possible to surmise that these niches are probably either "forbidden" or unoccupied yet. Another possibility is that they are occupied, but the respective organisms have not been described yet. Bambach, Bush and Erwin (2007) understand the advantages of such a methodology perfectly:

"Ecospace, as defined in this paper, gives us a theoretical construct in which to track ecosystem change and attempt to answer not just what changed and when, but how, why and to what effect".

By the way, Pianka (1978, Ch. 7) also cherished the hope of constructing a "periodic table of niches" with a similar purpose in mind.

Palaentological data show (Benton, 1990; Foote, 2000) that biodiversity grew up all the time during the last 550 million years till the Quaternary, though there were some interruptions. Rohde (2005) treats this circumstance as a solid argument that natural communities are yet not saturated with species completely. The number of vacant species should be especially high in temperate and cold climate zones (Rohde, 1992; Rohde, Stauffer, 2005) as the speed of diversification was much slower here than in tropics (the hypothesis of effective evolutionary time).

To sum up, in the near future ecologists are not likely to reject the concept of vacant niche for the reason that unused

(but potentially usable) and not fully used resources do exist in nature. On the other hand, even those ecologists who use the concept of vacant niche undoubtedly face certain difficulties, a great part of which is of a theoretical character. What is missing is, first of all, more defined and fit for use concepts of vacant niche and saturated community. The fact that both of these concepts are also widely used by evolutionists (see further) makes this problem even more acute.

EVOLUTION AS A NICHE-FILLING PROCESS

Mayr (1942), Simpson (1944, 1953) and MacArthur (1955) must have been the first to use the vacant niche concept in the evolutionary context. These authors had no doubts that vacant niches stimulate diversification, in the course of which niches are filled. When vacant niches are numerous (in that case it is possible to speak about a new adaptive zone), diversification, as a rule, proceeds much faster than normally. In that case we face adaptive radiation. When an adaptive zone is occupied, evolution decelerates. In the authors' opinion, there are sufficient paleontological data to substantiate these ideas.

This view has not changed much up to now. Summarizing the experience gained over more than fifty years, Meyer (2001) states:

"The "modern synthesis" in evolutionary biology has included a range of traditional explanations for the origin of adaptive radiations. The principal focus of these models is on divergent natural selection, under which species come to occupy different ecological niches and thereby avoid direct competition. Other models stress the colonization of a new habitat, usually an island or a lake, with few competitors and hence many new ecological opportunities (i. e., a wide resource spectrum with many adaptive peaks). The extinction of a previously domineering group offers another means of opening up ecological opportunities and facilitating diversification. Lastly, adaptive radiations may be initiated when a group acquires a "key innovation", enhancing its ecological opportunities by enabling it to exploit a different set of resources".

So, it seems that the "modern synthesis" has successfully adopted and is still exploiting the idea of vacant niches (here they are often referred to as ecological opportunities). It must have been a difficult decision to make, especially if we recall what Lewontin (1978), one of the then most influential specialists in population genetics and evolution theory, wrote about vacant niches three decades ago:

"In the absence of organisms in actual relation to the environment, however, there is an infinity of ways the world can be broken up into arbitrary niches".

Lewontin (1978) stated that the existence of a niche is impossible without an organism because a niche is first of all a property of an organism and not of the environment. Therefore, the vacant niche concept cannot contribute to the theory of evolution. It is both vain and illogical. However, evolution-

ists of the new generation seem to have ignored this advice, although some of them, Meyer among them (see above), for the sake of "diplomacy" tend to replace the vacant niche concept by the term "ecological opportunity"

I do not wish to review the numerous empirical and theoretical studies dealing with the role of vacant niches or ecological opportunities in adaptive radiation. Therefore, we will focus on two quite detailed reviews of recent years (Schluter, 2000; Dieckmann et al., 2004), and in more detail we will discuss only some of the generalizations made as a result of these studies. Now that more than half a century has passed since the appearance of studies by the above-mentioned authors (Mayr, 1942; Simpson, 1944, 1953; MacArthur, 1955), evolutionists seem to be even less inclined to doubt that vacant niches emerging after mass extinction or created after the emergence of a new island or lake are powerful stimuli for diversification (see e. g. Solé et al., 2002; Gillespie, Roderick, 2002; Streebman, Danley, 2003; Seehausen, 2006). Through efforts of these authors and those not mentioned herein, an "ecological theory of adaptive radiation" (further ETAR) was developed. According to it, in many cases evolution can be defined as a process of vacant niche filling. The presence of vacant niches can be viewed as permissions and their absence as prohibitions of diversification. Therefore, adaptive radiation produces assemblages of species with the properties that allow for the utilization of all unused but available resources. The number of vacant niches is finite. Therefore, waves of adaptive radiation are always followed by periods of a relative stasis.

ETAR incorporated not only the notion of evolution as a niche-filling process, but also another rather old idea (e. g. Simpson, 1953; Liem, 1973; Nitecki, 2000; Schluter, 2000) that adaptive radiation can occur even when there are no vacant niches. Sometimes it may be triggered by "key innovations", i. e. such evolutionary changes that turn a species into a supercompetitor.

As Schluter (2000, p. 70) notes:

"Sometimes a change in traits possessed by a lineage, a single 'key character' or a whole block of characters, would confer access to an array of new niches or would bestow competitive superiority over taxa already using them. The extent of diversification initiated by the trait was viewed as 'the extent of adaptive opportunity provided by the change' (Simpson, 1953, p. 223). As an example, Simpson suggested that the huge diversification of rodents <...> may be explained by one new feature: their 'persistently growing, chisel-like incisors' (Simpson, 1953, p. 346)".

The diversification of cichlids, which occurred in the large lakes of Eastern Africa (Danley, Kocher, 2001; Salzburger, Meyer, 2004), is often given as an example of evolution which proceeded in accordance with ETAR predictions. This is perhaps the most widely discussed case of adaptive radiation at present. These lakes came into existence 9–12 mill. (Tanganyika), 2–5 mill. (Malawi) and 250.000–750.000 years ago (Victoria). Due to certain geological processes, from the very

origin the lakes were reliably isolated from other water bodies, thus they found themselves in a situation similar to that when a new island comes to the surface in the ocean far from the nearest land. Bacteria, protists and invertebrates were probably among the first to inhabit the new lakes. Later, it is believed, individual cichlids were transported from the adjacent water bodies, probably as spawn. It seems that such cases of “seeding” were not numerous throughout the whole course of evolution: it was established by various methods that the origin of cichlids in Lake Tanganyika is oligophyletic, in Lake Malawi monophyletic and in Lake Victoria diphyletic. The “sown” cichlids were small omnivorous fish, the diet of which was dominated by invertebrates. Absence of competitors and predators made the process of diversification of ancestral forms very fast. Several decades ago there were about 250 endemic cichlid species recorded in Lake Tanganyika, about 1000 in Lake Malawi and approximately 500 in Lake Victoria. Although such abundance of cichlids is unprecedented, their niches do not overlap, and trophic niches of the majority of them are extremely narrow. The following trophic guilds are found: herbivores, zooplankton feeders, mollusc crushers, rock scrapers, invertebrate pickers, diggers, pursuit-hunting piscivores, ambush-hunting piscivores, scale-eaters, scavengers and some others. A congeneric group of fish species occupied niches that usually belong to at least several families or even several orders in other water bodies.

This example of adaptive radiation is cited here to demonstrate another fact which is, in my opinion, of exceptional importance. Sets of trophic guilds, with some minor exceptions, are identical in all the three lakes. Convergence is observed at the species level also: almost every species from one lake has its ecological equivalent in another. The morphological resemblance is sometimes astounding, in spite of the fact that the species compared are not closely congeneric. This fact is usually explained in the following way: these species occupied the same niche, structural changes being determined by functional requirements (Fryer, Iles, 1972; Stiassny, Meyer, 1999). This convergence took place despite climatic and hydrological differences among the lakes, various natural cataclysms, numerous accidental mutation cases, gene drift, acts of immigration and emigration, which probably took place over the past millennia. How can one explain such astonishing determinism? Is it possible that at the level of ecological community there are invariant constraints of some kind which determine the similar direction of species evolution everywhere and throughout time? Unfortunately, ETAR (Schluter, 2000; Streelman, Danley, 2003; Dieckmann et al., 2004; Seehausen, 2006) seems not to have provided answers to these questions so far.

Quite a number of studies have been published attempting to explain which form of selection operates when an initial population, continuously colonizing newer and newer niches, gives rise to new species (e. g. Smith, Skulason, 1996; Streelman, Danley, 2003; Dieckmann et al., 2004). Empirical and theoretical data allow presuming the existence of the fol-

lowing succession (Smith, Skulason, 1996): invasion into a vacant niche (1); adaptation and disruptive selection (2); stable polymorphism (3); reproductive isolation of populations (4). The majority of scientists modeling this process maintain that when differences in nutrition and habitats are significant, species may also diverge sympatrically. Diversification may be sometimes greatly impacted by sexual selection, in addition to natural selection (Streelman, Danley, 2003).

In the ninth decade of the last century, the idea of evolution as a process of filling vacant niches seemed to be so empirically grounded that there appeared theoreticians who tried to model this process. For instance, Valentine and Walker's (1986) model predicts that the diversification rate is diversity-dependent. It decreases together with the number of vacant niches. The course of diversification is subject to the logistic curve, thus sooner or later an equilibrium is achieved. However, global equilibrium does not necessarily mean that a community is saturated with species: vacant niches are still available, and they can be occupied on condition that the regional species pool contains pertinent species.

More than one similar model with similar conclusions has been promulgated since then, see e. g. the surveys of Gavrillets (2004) and Chowdhury, Stauffer (2005). Experimental data strongly support these results also. Experiments conducted on bacteria of the genus *Pseudomonas* (Rainey, Travisano, 1998; Brockhurst et al., 2007) have showed that the process of diversification can be very fast, but only on condition that niches are not occupied. The absence of vacant niches, inhibits diversification.

EVOLUTIONARY ASSEMBLY OF NUTRIENT CYCLES AND ECOLOGICAL PYRAMIDS

In my opinion, ETAR is quite a successful synthesis of contemporary ecology and evolutionary biology. However, the synthesis of ecology and evolutionary theory has hardly been completed. There are still some questions waiting for answers. For instance, ETAR does not focus on the idea that organisms that occupy vacant niches through evolution often turn into such niches themselves, thus provoking the appearance and evolution of their enemies. There seem to be no doubts left that, let us say, every flock of piscivorous cichlids originated (at least in Victoria and Malawi) from one common omnivorous ancestor (Danley, Kocher, 2001; Salzburger, Meyer, 2004). One trophic level gave rise to another, higher level, the latter to a still higher. This theory does not deal with assembly of nutrient cycles, either.

Stanley (1973, 1976) may have been the first to explore the problem of the assembly of ecological pyramids. He chose the Precambrian and the early Cambrian for the demonstration of his ideas. In his opinion, the Precambrian was dominated by unicellular algae and cyanobacteria. As there were no biophages, there was no cropping. Finally, in the late Precambrian. “...herbivorous and carnivorous protists arose almost simultaneously (...) These events automatically

triggered the formation of a series of self-propagating feedback systems of diversification between adjacent trophic levels. Comparable systems arose among multicellular groups, which radiated rapidly from the newly diversifying protist taxa. The sudden proliferation of complex food webs formed by taxa invading previously vacant adaptive zones produced an explosive diversification of life over a period of a few tens of millions of years" (Stanley, 1973). He explains: "Thus, the adaptive breakthrough to algal feeding, when it finally came, rapidly led to the addition of successive trophic levels. Not only autotrophs, but also heterotrophs below top carnivore levels were permitted to diversify (...) Thus when one trophic level diversifies, a mutual feedback system is set up with both super- and subadjacent trophic levels. In diverse communities this system is damped".

It seems that those ideas ("the cropping hypothesis") didn't attain a lot of attention by colleagues. By the way, they were exploited by Butterfield at some time (1997, 2001). Meanwhile other authors that are interested in the assembly of ecological pyramids during the Precambrian and Cambrian do not discuss the possible mechanisms of this process.

Walker (1980) also tries to reconstruct ecosystems of the past, applying principles of ecology, i. e. by deduction. Initially he introduces axioms, the 'guiding principles': substances move in cycles (1); nutrient cycles are leaky – as substances constantly leak from the cycles and are conserved (2); satisfied creatures do not change – the author's metaphor implying that organisms are not prone to reclaim new resources unless there is a shortage of substances and energy (3); organisms are greedy – the metaphor implying that organisms are prone to increase their total biomass at any cost (4). Adhering to these principles, Walker (1980) concludes that new forms of life would appear on a regular basis, most often after vitally important resources had been exhausted by the old forms. That happened sooner or later as "organisms are greedy". Then an ecological crisis would arise, and life was made to invent ways to exploit new, until then unused resources. The scenario leading to the formation of nutrient cycles was slightly different: waste produced by some organisms in the course of their metabolism turned into a source of energy, electrons or carbon for other organisms. If such organisms did not exist, nature would necessarily produce them by evolution. In such a way, waste-free although not closed ("substances move in cycles", but "nutrient cycles are leaky") cycles appeared. The first nutrient cycles, in Walker's opinion, could have been formed in the early stages of evolution after the emergence of photosynthesizing sulphur bacteria. Contemporary cycles formed much later, approximately at the same time as aerobic respiration.

Unfortunately, it seems that the methods that Walker applied as well as the results he obtained were not met with widespread approval and did not attract many followers. At least I have not succeeded in tracking the further development of these ideas in works published since 1980, i. e. since the publication of Walker's article reviewed herein. Such a

possibly undeserved lack of acknowledgement could be explained by the population-centered viewpoint entrenched in ecology since the beginning of the ninth decade of the last century (for a more detailed discussion see Lekevičius, 2006). Only in the countries of the former soviet camp did the evolution of nutrient cycles and ecosystem structure receive slightly greater attention. In its essence, the holistic (systemic) approach is still popular in these countries. Some scientists (Zavarzin, 1995) refer to this viewpoint as the Russian paradigm in ecology and evolutionary biology. The formula "only an ecosystem is living" or "life can exist indefinitely only in the form of an ecosystem (= nutrient cycle)" expresses the core of this approach. It follows from this formula that the first nutrient cycles emerged together with the appearance of life (e. g. Kamshilov, 1966; Zavarzin, 1979, 2000; also see Lekevičius, 2006 and references therein). Representatives of the "Russian" paradigm make a wide use of the vacant niche concept while modelling the evolution of ecosystems (e. g. Zavarzin, 2000; Lekevičius, 2002). Incidentally, these evolutionists sometimes replace the term "vacant niche" by "ecological free license", i. e. the term derived from literature in German (Sudhaus, Rehfeld, 1992).

Adhering to the formula "only an ecosystem is living" and the vacant niche concept as guidelines, representatives of the "Russian" paradigm attempted to reconstruct ecosystems of the past and the mechanisms of their evolution. Ecosystem "assembly rules" are formulated in the following way (Lekevičius, 2002, p. 78): "... it is quite possible that since the very moment of the appearance of life there should have been quite a simple mechanism by which ecosystems and nutrient cycles were formed – metabolism end products of some organisms became waste, i.e. resources potentially usable though used by nobody. Such vacant niches provoked the evolution of organisms able to exploit those resources. The final result was that metabolism end products of detritivores became primary materials for producers. Similarly ecological pyramids should have been formed: producers provoked the evolution of herbivores, the latter that of primary predators, and so on and so forth until eventually the evolution produced common to us pyramids with large predators at the top".

So, vacant niches not only stimulate diversification, but also determine its direction. And this fact, most probably, witnesses causality. This idea can be viewed as a keystone of evolutionary theory because it is not so difficult to explain and at least partly predicts the results of diversification on the basis of data on vacant niches.

In order to clarify the vacant niche concept and its usage by a representative of the "Russian" paradigm, I have constructed a Table demonstrating some steps in ecosystem evolution.

Nutrient cycles assumed the present-day form approximately two billion years ago (Lekevičius, 2002). The block of biophages had been fully formed in marine ecosystems by the end of the Ordovician, approximately 435 million years

Table. Some of the vacant niches / adaptive zones that existed in the Archean and Proterozoic, and their occupants. Attempts are made to list events in chronological order, from the appearance of protobionts to that of secondary predators. Take note of the fact that some vacant niches / adaptive zones existed prior to the emergence of organisms while others presumably were created by organisms themselves (compiled from Lekevičius, 2002)

Description of vacant niches / adaptive zones	Hypothetic occupants
Organic substances as donors of energy, electrons and carbon. Organic substances as final electron acceptors	Protobionts
Light as an energy donor, H ₂ S / H ₂ O as an electron donor and CO ₂ as a donor of carbon	Green and purple sulphur bacteria, cyanobacteria
Detritus as an energy, electron and carbon donor. S ⁰ and SO ₄ ²⁻ as final electron acceptors	Sulphur- and sulphate-reducing bacteria
Fe ²⁺ , Mn ²⁺ , H ₂ S, CO, H ₂ , CH ₄ , NH ₄ ⁺ as energy and electron donors, CO ₂ as a carbon donor. O ₂ as a final electron acceptor	Aerobic chemolithoautotrophs
Detritus as an energy, electron and carbon donor. NO ₃ ⁻ as a final electron acceptor	Denitrifying bacteria
Detritus as an energy, electron and carbon donor. O ₂ as a final electron acceptor	Aerobic decomposers
Biomass as an energy, electron and carbon donor. O ₂ as a final electron acceptor	Protists as "herbivores" and decomposer-eaters
Biomass ("herbivorous" and decomposer-eating protists)	Protists as primary predators
"Herbivores" and primary predators	Multicellular organisms as secondary predators

ago. Stages of terrestrial ecosystem development did not differ much from those of marine ecosystems: producers (1), vegetative detritus (2), emergence of detritivores and local cycles (3), herbivores and organisms feeding on detritivores (4), primary predators (5), and so on up to the top-level predators. The latter came into existence in the late Carboniferous, approximately 300 million years ago. When biophage block formation finished in the seas and 135 million years later on land, there were almost no vacant niches left in ecosystems. Therefore, cases of competitive exclusion, preconditioned by migration and the emergence of new forms, became more frequent. However, species diversification continued: life was penetrating into new territories, and what is more, the process of niche splitting was going on (ibidem).

The topic of evolutionary assembly of ecosystems is related, I think, to another theme already discussed by Odum (1969). He put forward a hypothesis according to which ecological succession and evolution are characterized by the same trends of variation in ecosystem parameters (species diversity, primary production, total biomass, production to biomass ratio, efficiency of nutrient cycle). Although later this hypothesis was used as a target by many critically disposed opponents, it seems to be enjoying popularity among some ecologists and evolutionists (e. g. Loreau, 1998; Solé et al., 2002; Lekevičius, 2002; Lekevichyus, 2003) to date. In the opinion of these authors, forces directing the evolution of ecosystems are in fact the same as those controlling their routine action. Consequently, in both cases trends cannot differ much.

As a matter of fact, there are some similarities. Primary succession as a rule starts with the settlement of herbaceous plants (sometimes lichen). Then vegetative detritus is formed, niches suitable for the settlement of herbivores and detritivores (bacteria, protists, fungi and invertebrates) ap-

pear. As a result, necessary conditions for the appearance of soil are created (Olson, 1958). In its own turn, the formation of soil stimulates the emergence of niches for new plants, woody plants among them. The latter change their surroundings, thus facilitating the settlement of still other plants and animals (facilitation theory – Connel, Slatyer, 1977). The sequence of events is presumed to have been similar in the Palaeozoic when life occupied land (Lekevičius, 2002). However, then occupants came into existence mainly as a result of evolution *in situ*. So, some specialists maintain that ecological succession may be interpreted as a process of niche filling as well, and it should not differ much in its course and final result (having in mind the functional properties of ecosystems) from what is observed in cases of adaptive radiation and evolutionary recovery after extinction. Unfortunately, these ideas lack empirical corroboration. Despite this, the idea that "ontogeny" of ecosystems may recapitulate their "phylogeny", I think, is quite attractive.

CONCLUDING REMARKS

It is hardly possible to claim that the concept of vacant niche and that of community saturated with species are widely applied in the present-day ecological theory. One of the reasons behind this fact is that both of them are difficult to define precisely. However, in evolutionary biology these concepts are used more and more widely despite their indeterminacy. According to some evolutionists, as it has been demonstrated above, niches can be not only occupied but also created by occupants themselves, thus assembly of ecosystems can proceed with acceleration.

Are these ideas in agreement with traditional Darwinism? As a matter of fact, Darwin's theory on natural selection consists of two constituent parts: the ecological and the

genetic ones. The first of them (“struggle for existence”) deals with a surplus in offspring and unfavourable environmental factors which cause mortality of the former. Part on genetics focuses on undirected variability and inheritance of selected traits. Geneticists of the 20th century specified and elaborated the latter part of the theory. Meanwhile, the first part of the theory fell into the hands of ecologists and also underwent elaboration. However, ecologists did not restrict themselves to “struggle for existence” and created something that was new in principle, i. e. the ecosystem conception. Many of its statements are valuable to date. Strange as it is, until recently evolutionists have hardly made any use of this part of ecology, and it lingered where it was created. It is strange because when referring to any hypothetico-deductive theory (Darwinism is undoubtedly such a theory), it is advisable from time to time to revert to its original postulates to verify whether they are in agreement with new data (Popper, 1959). The ecological part of the natural selection theory deals with the way organisms react to the environment. If these relations are not restricted just to “struggle for existence”, it is not only possible but advisable to supplement the premises of the theory with the new ones. In turn, conclusions following from the original statements will change.

From this viewpoint, works by evolutionists reviewed herein could be treated as attempts to supplement the ecological part of Darwinism with new statements, deduction of novel predictions and explanations being their ultimate goal. From this standpoint, it is not so much definite explanations and models presented by evolutionists of the new generation, but the methodological attitude that is significant: if we want to have a more profound evolutionary theory which better corresponds to the present-day achievements, we must revert to Darwin’s original premises and reassess them not only from the viewpoint of genetics, but also from that of ecology. These evolutionists seem to be convinced that it is only with the help of ecological theory that it is possible to give an answer to many fundamental questions which traditional biology did not even raise. For instance: Why did particular species appear on the evolutionary stage at that particular time and not another and in that particular location and not another? Why was the functional structure of ecosystems prone to convergence despite a multitude of stochastic factors? The material presented in this survey raises hope that answers, tentative as they are, to these and similar questions may be perceived in the near future. Such “ecologizing” of Darwinism is likely to benefit not only this theory but also ecology itself.

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LAISVOS NIŠOS GAMTOJE, EKOLOGIJOJE IR EVOLIUCIJOS TEORIJOJE: TRUMPA APŽVALGA

S a n t r a u k a

Pastaraisiais metais ekologinėje literatūroje vis dažniau galima aptikti laisvų nišų sąvoką. Jos suprantamos kaip niekieno nepanaudojami, nors potencialiai panaudotini išteklių. Pasirodžiusiuose darbuose įrodinėjama, jog gamtoje laisvų nišų esama gana daug, ypač žmogaus pažeistose ekosistemose. Tačiau laisvos nišos sąvoka vis dar laikoma kontraversiška jau vien todėl, kad nepavyksta susitarti, kaip apibrėžti situaciją, kai ekosistemoje tokių nišų nėra. Kitaip nei ekologijoje, evoliucinėje biologijoje ši sąvoka sukelia mažiau nesutarimų, ji čia pravertė kuriant ekologinę adaptyvios radiacijos teoriją. Dar kiti evoliucionistai ją panaudojo aprašydami ekosistemų (medžiagų ciklų ir ekologinių piramidžių) evoliucinio kompleksavimo eigą bei mechanizmus. Šie evoliucionistai bando įrodyti, kad diversifikacijos metu laisvos nišos yra ne tik okupuojamos, bet ir sukuriamos naujai evoliucionavusių organizmų.

Raktažodžiai: prisotintos bendrijos, ekosistemų evoliucija, bendrijų kaita, kompleksavimas