

Reflections on the niche

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The niche concept has a long tradition in ecology. This paper discusses the classic concepts by GRINNELL, ELTON and HUTCHINSON and elaborates on an ethological niche concept that tries to incorporate the complex interactions between individuals, populations and species with their environment. Among other things, it stresses the dynamic character of these interactions, which are conceived as mutually influencing systems. The dynamics could be illustrated as trajectories in the corresponding feature spaces. The niche should be used as descriptive term for the environmental part only and not be conflated with competition and evolutionary theories by default. In a critical examination of the scientific value of these concepts, it turns out that they have some heuristic merits, but otherwise are descriptive and do not offer explanations on their own.

WINKLER H., 2020: Reflexionen zur Nische.

Das Konzept der ökologischen Nische hat eine lange Tradition in der Ökologie. Der Aufsatz diskutiert die klassischen Konzepte von GRINNELL, ELTON und HUTCHINSON und arbeitet ein ethologisches Nischenkonzept aus, das die komplexen Interaktionen zwischen Individuen, Populationen und Arten mit ihrer Umwelt einzuschließen versucht. Es betont unter anderem den dynamischen Charakter dieser Interaktionen, die als sich gegenseitig beeinflussende Systeme vorgestellt werden. Ihre Dynamik könnte als Trajektorien in den jeweiligen Merkmalsräumen abgebildet werden, wobei die Nische nur die Seite der Umwelt bezeichnen sollte. Die Nische sollte als Beschreibung nicht von vorneherein mit Konkurrenz und Evolutionstheorien vermengt werden. Bei kritischer Betrachtung des wissenschaftlichen Werts dieser Konzepte stellt sich heraus, dass sie heuristisch einiges beitragen können, sonst aber deskriptiv sind und keine eigenständigen Erklärungen liefern.

Keywords: ecological niche, ethological niche, ecosystem, behavior, competition, explanation.

Prelude

It was about the time when I first met Fritz SCHIEMER, but before any closer interactions, that my friends Karl MAZZUCCO and Bernd LEISLER spent long evenings to discuss various ecologic notions. ‘Niche’ was among them but like many Platonic dialogs, our youthfully enthusiastic discourses ended in aporetic dismay all too often. A bit later, I endeavored to send a paper from the Wilhelminenberg to the Austrian Academy of Sciences that contained a definition of the ecological niche from a behavioral standpoint that was inspired by the Hutchinsonian niche, Jakob VON UEXKÜLL, cybernetics, and in line with my interest in quantitative analyses of behavior (VON UEXKÜLL 1909, VON UEXKÜLL & KRISZAT 1956, HUTCHINSON 1957, SCHLEIDT 1964, DELIUS 1969, WINKLER 1971, 1972). When I joined force with the limnologists at the University of Vienna and the Austrian Academy of Sciences while the International Biological Program of the UNESCO was at its peak (SCHIEMER 2014) that would have been a good chance to work further on this matter particularly because Heinz LÖFFLER had been associated with George Evelyn HUTCHINSON for some time. I did some empirical work on the subject, but kept my hands off the theory although I never lost interest in the matter. FRITZ and colleagues published on the niche recently (PÖRTNER et al. 2010), and that encouraged me to reflect on the problems involved again, quite in the spirit of my earlier conceptions, but with more hindsight, more process-oriented thinking, yet still with enthusiasm.

Introduction: Niche concepts

German and English speaking scientists used the word ‘niche’ for some time before it came to designate certain conceptions in ecology. The interested reader may consult EGERTON (2017); I have, however, to restrain myself to an eclectic treatment of the subject.

After the war, Central European ecological theory, like ecological theory in the New World, reflected the societies in which scientists were embedded. While competition dominated ecological research in the U.S. Despite some controversy (e. g. CODY 1974, SCHÖNER 1982), my teacher professor Wilhelm KÜHNELT took to an Austrian civil service view and coined the term *Planstelle* (established post, KÜHNELT 1965). In Eastern Germany, the forest ecologist Fritz SCHWERDTFEGER with an obvious inclination to produce many terms with a Greek etymology created the term *Monotop* (SCHWERDTFEGER 1963). Both these terms reflected ideas related to the niche concept, but KÜHNELT referred to something that exists in ecosystems independent of whether an organism actually “occupied” that established post while SCHWERDTFEGER referred to the ecological conditions needed by an individual or population (*Demotop*). Neither notion has entered the international discussion perceptibly. The original niche concept of Klaus GÜNTHER (1950) shared a similar fate (SCHMITT 1987).

Competition became for some time the central principle in ecology and the notion “that every instance of apparent coexistence must be accounted for” (HARDIN 1960, emphasis by the author) was the guiding theme of countless ecological and evolutionary studies, including Fritz’ study on nematodes (SCHIEMER 1985) and my humble ones on woodpeckers (WINKLER 1973). The question in focus was “why are there so many kinds of animals?” (HUTCHINSON 1959), or rather, how many species can be squeezed into one community? (MACARTHUR & LEVINS 1967). The number of species and diversity were seen as a problem of community theory whose central theme was competition, mirroring more American society rather than ecological reality. If evolution was considered at all, natural selection was the central evolutionary process, the role of speciation and its evolutionary mechanisms were largely neglected. That changed eventually, when it became clear that one could not neglect the question where species come from. Researchers realized that speciation rates and biogeography are at least as important for explaining local species richness as standing diversity and its interaction with resource availability (CRACRAFT 1985, COTGREAVE & HARVEY 1994, QIAN & RICKLEFS 2000, RICKLEFS 2004, MORLON et al. 2010, AGUILÉE et al. 2018). A neutral null model, useful because it helps to formulate testable predictions, posits that random dispersal and stochastic local distinction explain the relative abundance of species in communities. As an explanation, it has not been very successful. Related research has shown that modes of speciation interplay with neutrality, and that ecosystems may undergo competitive (for most researchers associated with ‘niche’) and neutral phases in the course of their history (HUBBELL 1997, 2001, GILBERT & LECHOWICZ 2004, ETIENNE 2007, LEIGH 2007, FISHER & MEHT 2014). Research on niches peaked in the seventies and eighties of the previous century, and declined somewhat thereafter (CHASE & LEIBOLD 2009).

Joseph GRINNELL studied the distribution of Californian birds and mammals, and tried to explain the patterns observed with fundamentally non-interactive, slowly changing variables and environmental conditions on broad scales, relevant to understanding coarse-scale ecological and geographic properties of species (GRINNELL 1917a, SOBERÓN 2007). He used

the term 'niche' in his seminal paper on the Californian Thrasher (Mimidae, *Toxostoma redivivum*), trying to explain its restricted distribution comparing it with the occurrences of other mimid species (GRINNELL 1917b). He identified, among other things, temperature, humidity and vegetation as important. In his view, the species' dependence on these environmental factors is due to its specific morphological and behavioral features.

The niche concept developed by Charles ELTON (1927) focuses on biotic interactions and resource-consumer dynamics that one can measure principally at local scales. At the beginning of the book, he used the word 'niche' in a discussion of succession dynamics without actually defining it. It was, however, already clear from the context that he referred to an organism's position in an ecological community. Equally casually, he refers to an empty niche left by a species that goes extinct upon arrival at a community at a certain succession stage. When another species fills that niche, this may look as though competition had been at work here. Later authors were less cautious about the role of competition, and the niche became almost synonymous with it. Later in his book, ELTON paints vivid pictures about the many ecological interactions taking place on an English hillside. How predator-prey relations link various species, how the activity of one species (e.g. the Green Woodpecker) creates opportunities for other species and so on. ELTON (1927, 63ff.) stipulated, "... the ground plan of every animal community is much the same". Every community has its herbivores, carnivores and scavengers. Every animal has its distinct food habits and corresponding morphological adaptations. Because of the overwhelming diversity of these adaptations, it seemed to be convenient to have a term that describes the status of an animal in its community. This term is the 'niche'. This concept is community centered, holistic (focuses on relations rather than properties and features), and stresses the role of the animal in a community, its relations to food and enemies. Body size and food habits were thought to largely characterize an animal's niche.

Later, and on the other side of the Atlantic, George Evelyn HUTCHINSON presented his more organism centered niche concept. His approach was, simply put, geometric and he defined the niche as a volume in a multidimensional space in which every point corresponds to a state of the environment that would permit a certain species to exist indefinitely. HUTCHINSON included some simple set-theoretic considerations along with the basic formulation. Most importantly, he created the notions of a fundamental niche, the hypervolume that defines all ecological properties, and a realized niche. The latter being a subset of the former squeezed to a smaller hypervolume due to interspecific competition. He was aware of the limitations of his model, which he had also linked with the competitive niche-exclusion principle developed in the work of VOLTERRA, LOTKA and GAUSE (HARDIN 1960). Interestingly, he mapped his hypervolume rendering of the niche to a Grinnellian one (HUTCHINSON 1957, p. 421, Fig. 1). However, this type of mapping cannot be treated as bijective in the strict mathematical sense.

This short account of some of the classic niche concepts shows that they all considered environmental factors and species-specific features to a varying degree depending on the scientific enterprise in which the concept was formulated. GRINNELL conceived the niche in relation to habitat features relevant for a species at a small scale by comparing distributions at a larger spatial scale. ELTON emphasized trophic relations, and HUTCHINSON paved the way for a mathematical approach that inspired multivariate measurements of environmental variables. Eugene P. ODUM (1971) summarized the first two versions of the

niche in analogies by saying that the habitat is a species' "address" and the (trophic) niche its "profession".

The ethological niche

All these classic conceptions of the niche, as focused they were on different aspects, tried in some way to include some aspects of the other conceptions as well. The role of behavior and its interaction with morphology and the environment remained rather superficial. ELTON and HUTCHINSON also referred to evolution. However, they did not address the fundamental problem that arises from the fact that all these niche concepts pertained to mechanisms at the ecosystem, species, and population level while the most important evolutionary mechanism, selection, operates on the level of individuals and sometimes of social groups (WILSON & WILSON 2008). Ecologists and evolutionary biologists did not have a common language. This was still in the making when I tried to integrate what I had learned from ethology and ecology alike. The niche concepts appeared to be too static in space and time. Behavior, however, is dynamic, and researchers had realized that niche size and exploitation change opportunistically (ROOT 1967). That motivated me to come up with a definition of the niche of my own that I will introduce and expand now unassumingly.

My starting points for an ethological view were the organization of instincts (units of motor actions), motivations, appetitive behavior and information gathering, and how they - together with morphological adaptations - could explain what my colleagues and I were observing on woodpeckers and warblers. Cybernetic concepts played a decisive role in all the considerations (WINKLER 1971, 1972). Therefore, I defined 1971: *The niche is that set of environmental elements, which allows the action system of a species to attain an equilibrium. The requirements of the species determine these elements. The niche can be part of different ecological systems, communities, and is ordered temporally and spatially.* This definition, which I will dub "ethological" for short and will be developed further below, was part of an attempt to formulate a basis for an eco-ethology that considers both, explaining behavior with ecology and grounding ecological phenomena in ethology. The idea was that animals could only act upon something that they can perceive, UEXKÜLL's *Umwelt*, and the system of their motor skills determines resource usage and their impact on the environment. Eco-ethology of this kind never fledged, however. The prime reason was the emergence of Behavioral Ecology, the science of omniscient agents endowed with optimal behavior that because of natural selection had evolved to maximize (or minimize) some currency. If well chosen, this currency would maximize fitness (HOUSTON & McNAMARA 2014). It was agnostic with respect to behavioral and physiological mechanisms and constraints, and ignored the underlying genetics as well. Evolutionary thinking, and with it selectionist and adaptationist stories, although mocked by liberals like LEWONTIN and GOULD, prevailed. The above ethological niche definition of mine is far from satisfying and needs some explanation because of the special context in which it was formulated. I will pick up here where I left then, and address "equilibrium" and "action system" first, and then modify and somewhat flesh out the concept.

The background for using equilibrium as a criterion had several roots. Cybernetics, engineering and even ecosystems research at that time were concerned with equilibria and its sibling stability. In sociobiology, Evolutionary Stable Strategies (ESS), an extension of (eco-

nomic) beautifully minded stability considerations in game theory, still figure prominently. Homeostasis has been and still is an important notion in physiology. Yet, an equilibrium, be it a single state or some sort of a dynamic one, does not say much without characterizing the phase space involved. Like 'existence' in the Hutchinsonian niche it leaves many questions open or may even be misleading. At the level of the individual, one may observe an equilibrium that, however, does not make sense biologically. Take a battery hen that undoubtedly is at an equilibrium to an observer, with a much reduced niche, behavior and cognitive challenges, and possibly higher survival than a free ranging one. To many people this would not appear to be a satisfactory situation. Similar objections could be made at the population level and when considering evolutionary dynamics. Thus, we need to look at what actually is at equilibrium.

Animals, like organisms of the other Regna, command competences that allow them to separate themselves from their environment, and at the same time to register changes within themselves and in the environment. They also act upon their environment. Herbert Spencer JENNINGS, who worked with *Paramecium*, defined the 'Action system' of an organism as the characteristic set of movements by which its behavior under all sorts of conditions is brought about (JENNINGS 1915, 107). If we mate this with UEXKÜLL's *Umwelt* then we get a more complete notion of the organisms' side of affairs. Something is still missing. We still need to appreciate what is "moved". Using a very wide notion of "move", all morphological and other features whose change we record as "behavior" have to be included to understand the consequences of behavior and its impacts on the environment (WINKLER 1989). What remains is to combine all these components in a process-oriented concept and to get rid of 'equilibrium'.

Despite the understandable popularity of equilibrium and stability and related aspects of system behavior, focusing on these characteristics hides the fact that life is not maintenance or restoration of some equilibria but living systems follow dynamic trajectories and maintain them as open systems away from equilibria (BERTALANFFY 1968). Individuals, and with them populations and species, continuously change while interacting with their environment, and consequently their niche. Even the interactions of lowly cyanobacteria with their resources are dependent on and different from previous interactions (FALKNER et al. 1989). One does not need to be a Hegelian to appreciate this remarkable fact. Hence, to get a better version of my ethological niche concept introduced above, we have to view the niche as conceptual part of interacting systems that travel in some feature spaces. The 1971 definition stated that the niche is ordered in time and space. In other words, the sequence of behavioral states, the trajectory in the behavioral feature space, and the consecutive locations in physical space are always conditional on the previous ones. The result obtained by mapping of the individual/population/species trajectories in their feature space on the environmental feature space may be called 'niche'. To be clear, 'niche' is supposed to refer only to the environmental trajectory. I should note that this mapping differs from that suggested by HUTCHINSON (1957, 416) who considered only those multidimensional states, which ensure a species to exist indefinitely. It is obvious, that in a specific application of the ethological niche concept, we have to formulate clearly the conditions that define these organismic systems states.

In fall and spring, billions of small passerines migrate between Europe and Africa. Let us look at an individual that is on its way across the Sahara. It maintains a certain height in the atmosphere with a particular temperature, humidity and oxygen regime. Wing beats,

heart rate, and energy consumption are within sustainable ranges, and so is energy flow. This means that the amount of fuel is declining steadily, and with it change the options available for the individual and the relevancy of environmental features. The corresponding niche, not defined by an overall equilibrium criterion but one that considers the individual's actions, would be the set of environmental features that allow for an enactment of behaviors that define "nocturnal migration". These would include suitable wind speeds, humidity conditions, and magnetic field parameters.

As another hypothetical scenario, take again a kind of a battery hen, but this time with a spacious cage equipped with things that make a hen "happy", such as water and litter to dustbathe, and food dispensers that need some more or less complex actions by the hen in order to deliver. While there is no problem to work for food as such (because of contrafreeloading; INGLIS 2017), some or all of the dispensers may not be suited to chicken morphology or a hen's cognitive endowment. Those dispensers that a hen cannot mandibulate successfully can clearly not be part of its niche.

We have to add dynamics to both of these examples. In the previous example, the impoverished cage constrained the possible trajectories the system "hen" could take, in the latter the hen's endowment constrained the set of possible entities that could be part of that subset we might call "niche". With dynamics, niches get even more constrained because a trajectory can be thought of consisting of consecutive states, like for instance modelled with Markov Chains, which imply rules that define possible state transitions. If we restrict the analysis of a niche to a certain period, like in the migration example, it is also necessary to specify the starting conditions of the trajectories as well as the conditions at their end. For example, we may wish that the migrant arrived at an oasis rather than far away from the coast over the Atlantic. In short, we have to specify the finite time period for which our analysis of a niche is supposed to be valid, the phase space for the individual trajectories, populations, species to be studied, the rules that govern these trajectories, the mapping function that maps these trajectories on the environment's phase space, and their influence on the environment, which itself interacts with the organisms at various time scales, especially the evolutionary one (LEWONTIN 1983, WIENS et al. 2010). In all these entangled relations, we could call all the environmental factors that are part of them the "niche". This concept is a framework, viewing point, idealistic program like all the other niche concepts. In any practical application, a subset of the variables or their proxies that may be involved and could form dimensions of a phase space has to be laid down. Similar practical restrictions hold for the mapping functions and physical interactions.

The scientific value of niche concepts

Whether or not one would consider above niche concepts as hypotheses or theories, one could discuss them in terms of their scientific value, which broadly conceived would entail considering their fruitfulness or heuristic value, and explanatory power.

The scientific endeavor starts with a new idea, hypothesis or hunch, which researchers have to operationalize and empirically corroborate. Do our niche concepts provide the incentive to enter the water, have heuristic value, and inspire research? HUTCHINSON's niche concept was arguably the most fruitful one. This abstract view, although not necessarily explicitly stated, stimulated a lot of quantitative work even among young Austrian scientists

(e.g. LEISLER 1981). One reason for its wide acceptance was that it suggested certain mathematical modelling approaches borrowed from set-theory and multidimensional Euclidean spaces. It was the latter that caught on because it recommended how to analyze data with multivariate tools, which started to become accessible with the general availability of computers. Transforming sets of variables to orthogonal ones that satisfy the notion of independent action (1957, 416) is no problem technically (one just needs to apply Principal Component Analyses; the in this context frequently used Discriminant Analysis generates scores that are only approximately orthogonal) but may obscure the direct ecological relationships (see BLONDER 2018 for a recent discussion). Niche as a place in a food chain, or better food web stimulated some research, especially the idea of an empty niche had some appeal. It is remarkable that HUTCHINSON (1959) referred mostly to this conception of the niche rather than to his own. I do not see the heuristic value of the “empty niche”. Stating that the woodpecker niche is empty in Australia is equivalent to saying “there are no woodpeckers” in Australia. If one thinks that a certain organism does fill this niche there, this would end up by noting that, for instance, certain birds eat grubs or ants. The empty woodpecker niche would be fully incomprehensible for an (unlikely) Australian researcher who has never heard of woodpeckers or seen one. It appears that the niche as conceived by GRINNELL has become very popular recently. I am referring to the various studies that refer to “niche modeling”. Methodologically this boils down to finding associations between distributional patterns and some spatially varying variables. GRINNELL’s work hardly inspired these studies directly. They are mainly fostered by the availability of distributional data mostly collected by citizen scientists, the extensive data collected by satellites, and by the easily available software tools that can deal with these large data sets without careful theoretic guidance (SOBERÓN 2007). The ethologically defined niche and the rules sketched above may stimulate further theoretical work and, in a multivariate context, call for treating the niche (and its various mappings) not as an amorphous hypervolume, but as a set of environmental trajectories induced by and interacting with those that describe the fate of individuals, populations, and species in explicitly defined time windows. It may help to reserve more attention to studies that are not restricted to, say, breeding seasons and ask how the organisms in question fare through all parts of their life cycle (for examples see LAUBE et al. 2015 and GÓMEZ et al. 2016).

Does any of those niche concepts explain something? The short answer is no! That needs some elaboration, of course. GRINNELL did try to explain animal distributions via some variables thought to be relevant. In the case of the California Thrasher (GRINNELL 1917b), he conjectured that this bird’s restricted distribution could be explained with its physiological and behavioral adjustments to a narrow range of environmental conditions. What these conditions actually are could be learned by examining the species’ habitat. This approach has obviously some inherent circularity. The niche is just a summarizing shorthand for some environmental conditions and not part of an explanans or theory. The modern offshoots fare not better. There is no stringent *ecological* theory to justify the data analytical tools used. ‘Niche’ serves as a buzzword with little theoretical, and for that matter, empirical content. The methods involve primarily occurrence data that some algorithms, of a statistical, machine-learning or other kind, associate with sets of electronic maps of convenient ecological variables that may or may not important for limiting geographic distributions. The claim is, for example, that “These associations constitute an approximation of species’ fundamental ecological niches (the conjunction of ecological conditions in which a species is able to maintain populations without immigration)” (PETERSON et al. 2002).

These approaches constitute a merger between the Grinnellian and Hutchinsonian niches without any theoretical justification why a particular method, be it some sort of regression or application of other probabilistic criteria (e.g. maximum entropy), would yield that approximation of a niche. The predictions produced by these analyses are hypotheses about past and actual distributions, and because of their theoretical limitations do not offer explanations and no theory-based predictions.

The Hutchinsonian niche seems to be a better candidate for producing explanations and predictions. At least it appears to predict that most observed niches, however operationalized, are smaller than the fundamental ones. However, the actual theory would be competition theory, which leaves this niche as a means to phrase related notions and not an indispensable part of an independent theory. Similar objections would apply to the ethological concept presented here. Still, it could serve as a framework within future theories of interacting ecological systems have to be formulated, with the ‘niche’ once again only a summarizing reference to a certain part of such a model. I restrict the evaluation of the Eltonian niche to a discussion of the notion of an “empty niche”. Assume that we have three nodes “upstream” in a food-web and five “downstream”. Simple combinatorics show that there would be 271 unique intermediary nodes. Of course, if we forsake the competition exclusion principle, there would be even more. In any practical terms, the concept is therefore not able to make reasonable predictions. Take for instance the web depicted in SCHIEMER et al. (1982, Fig. 10): could anyone say whether there are still vacant niches there, or how many? The phrase “empty niche” may help to formulate what happened when Sinhalese engineers created artificial lakes to hold back water for use in the dry season in the 4th century. However, it does not deliver a prescription to predict the cascade of ecological events that ensued and which was even more intriguing when African *Oreochromis mossambicus* was introduced in the 20th century (SCHIEMER 1983). The “empty niche” could only be a more or less useful or even misleading phrase within post hoc descriptions. The concept has been used by the original author and others to analyze biological invasions and phylogeographic dynamics (e.g. PRICE et al. 2014). Niche filling, however, is a descriptive term that needs to be explained or only serves as a summarizing term within a theory that, for instance, pertains to competition, ecology and phylogenetic constraints. I know of no paper that predicts the filling of an empty niche on an ecological or phylogenetic time scale without referring to a known organism.

The ideas behind the ethological niche concept relate closely to other concepts that focus on the interactions between organisms and the environment. For BOCK & VON WAHLERT (1965) ‘niche’ encompassed both the properties of the organism (‘faculties’), and the fitting environmental feature. GÜNTHER (1950) depicted the niche as overlap of the organismic (‘autozoic’) and the environmental (‘oecic’) dimensions (SCHMITT 1987). The ethological niche in contrast refers to the environmental part only. The psychologist James GIBSON (1986) has developed another very interesting notion under the heading ‘affordance’, a term he coined in the late 1970ies. It is somewhat similar to the ideas of UEXKÜLL because its starting point, too, is perception. An affordance is a property of the environment that relates to an organism’s capabilities (BERTOLOTTI & MAGNANI 2017, HERAS-ESCRIBANO & DE PINEDO-GARCÍA 2018). There are notable theoretical consequences of the ethological niche concept and the niche-constructionist affordance theories with respect to the classic ecological concepts. The fundamental niche does not make much sense anymore, because these niches are open. Exploration, phenotypic plasticity, including learning, can add new

parts of the environment to an organism's niche at any time. The morphology and motor skills of a woodpecker determine the physical conditions for climbing and probing. An individual has to find out what is climbable or into what it can stick its bill by means of innate and learned abilities. As I have argued in the case of the empty niche, there is no practical way to predict all the resulting niches. Second, the empty niche makes no sense without appreciating the physiological and cognitive endowment of potential users. Hence, its predictive power is close to zero for these reasons, too.

Final thoughts

I focused my treatment of some versions of the ecological niche on clarifying some basic notions, and with that left out many important aspects of its role in ecological theory and practice. By doing so, I attempted to avoid confounding this core concept with its role in various ecological theories. Most evidently, I did not discuss niche breadth and overlap and left out a detailed consideration of the relationship with competition theory. Although one sometimes gets the impression 'niche' and 'competition' are synonymous, these aspects should be kept separate by all means. Analyses could and should incorporate competitive interactions as environmental factors among the many others, like parasitism, predation, mutualism or commensalism. What one needs to avoid is to conflate niche with other theories such as competition theory and the 'niche-exclusion principle'. To keep the niche concept "clean", one should also not to confound it with evolutionary ideas (as in BOCK & VON WAHLERT 1965). Restraining ourselves from such confluations, we make sure that, for instance, it is competition that explains something and not the niche.

Another important recent development was the idea of "niche construction" that emphasizes the effects organisms have on their environment, including their social one, and that these modifications feed back to their potential actions and evolutionary fate (LEWONTIN 1983, ODLING-SMEE et al. 1996, FLACK & KRAKAUER 2009, HOLT 2014, BERTOLOTTI & MAGNANI 2017). It too can easily be embedded in the conceptions presented here, especially with the notion of interacting trajectories. However, reifying the niche, treating it as a physical entity, and letting organisms construct this construct, that in turn constitutes as source of selection would potentially mislead us into an epistemological and ontological quagmire.

Blessed with the opportunities open to us by the tourism industry, we are able today to roam not only the temperate forests of Austria, but also those of China, the American Northwest, and the tropical and subtropical forests of Africa and Australia. Even when focused on birds, as thousands of birdwatchers including myself are, one does not fail to see that high bird diversities are associated with tree species diversity and what in the good old times of static niche concepts the MACARTHURS have named foliage height diversity (MACARTHUR & MACARTHUR 1961, MACARTHUR & HORN 1969). A seemingly obvious interpretation would be that more tree species, possibly accompanied by a rich mixture of age classes within species, provide more opportunities or "niches" for various bird species to make a living. This is fine and well as long we do not ask where tree species come from in the first place.

Temperate and boreal forests dominate the northern hemisphere, and there are huge differences in species numbers. Niche theory does not provide a satisfactory answer, neither do resource based speculations. The modern answer to an old problem are historical ex-

planations. The diversity of trees, birds, and other animals reflect a common process rather than niche relations, at least at a regional scale (LATHAM & RICKLEFS 1993, QIAN & RICKLEFS 2000, 2008). Viewed from the vantage point of the ethological niche, the challenge consists of integrating the different time scales represented by individual or cohort life-histories with those of populations and evolving species and ecosystems. The niche, however, will remain a descriptive tool and short hand for conceptual or real entities, a linguistic prop, and not form an essential building block within such integrative theories (cf. POCHEVILLE 2015).

The term 'niche' is used in many ecological papers loosely, often referring to various meanings interchangeably and without clarification. Sometimes it has even a strong spatial connotation in the sense of a cranny or crevice. More interesting, yet, is its use as a concept or analogy in other disciplines. Economy is a prime example grounded in the fact that many, if not most, ecological models have their roots in, and eventually feedback to, economic ones (KANGAS & RICHTER 1979, GALLAGHER 1993, HANNON 1997). People used the term, for instance, when talking about special areas of consumer demands, and linked it like biologists to competition. A remarkable appraisal of GÜNTHERS (1950) niche appeared, for example, in a modern dissertation on market economics (DANNER, 16 f). Even within organisms 'niche' may serve as a useful descriptive reference. It has, for instance, established itself in medical research referring to hiding places for cancer cells or pathogens (e.g. BERNDTSON 2013, JONART et al. 2020). And, people constructing robots worry about the fundamental and realized niches for their creations (DÉNIZ et al. 2007).

The word 'niche' has found a niche of its own in the scientific discourse and is here to stay. We only need to keep it where it belongs to and prevent it from going wild as a concept.

Coda

Our generation has seen an incredible surge of biological research. As we entered our introductory courses, which the University of Vienna offered every other year only, ecology was fascinating and seemed to be perhaps a subject one could master. For me it seemed natural then to enclose ethology into ecology, much to the expressed delight of my supervisor Prof. KÜHNELT. The world of science has changed dramatically since. We were enthralled, motivated and did all to enjoy it and ourselves in due course. We witnessed an enormous diversification of the biological sciences and tried to keep up and contribute. In ecology, and especially behavioral ecology, theory outpaced empirical research in many respects. The program of hypothesis-guided research to me obscures the fact that the fascination that accompanies our astounding tools for collecting and accumulating tons of data and mathematically formulating bold theories has not necessarily led to appropriate synthesis. I hope that Fritz and friends with their decades of scientific engagement will continue to use their wisdom to ensure that such a kind of explanatory gap does not open up any further.

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