



To what degree are philosophy and the ecological niche concept necessary in the ecological theory and conservation?

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ABSTRACT

Ecology as a field produces philosophical anxiety, largely because it differs in scientific structure from classical physics. The hypothetical deductive models of classical physics are simple and predictive; general ecological models are predictably limited, as they refer to complex, multi-causal processes. Inattention to the conceptual structure of ecology usually imposes difficulties for the application of ecological models. Imprecise descriptions of ecological niche have obstructed the development of collective definitions, causing confusion in the literature and complicating communication between theoretical ecologists, conservationists and decision and policy-makers. Intense, unprecedented erosion of biodiversity is typical of the Anthropocene, and knowledge of ecology may provide solutions to lessen the intensification of species losses. Concerned philosophers and ecologists have characterised ecological niche theory as less useful in practice; however, some theorists maintain that it has relevant applications for conservation. Species niche modelling, for instance, has gained traction in the literature; however, there are few examples of its successful application. Philosophical analysis of the structure, precision and constraints upon the definition of a 'niche' may minimise the anxiety surrounding ecology, potentially facilitating communication between policy-makers and scientists within the various ecological subcultures. The results may enhance the success of conservation applications at both small and large scales.

KEYWORDS

Niche; Philosophy; Ecology; Conservation

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1. THE 'ANXIETY' SURROUNDING ECOLOGICAL THEORY:

'Much of ecology is confused in its goals, uncertain of its strengths and inconsistent in its terminology.' (Rigler and Peters 1995) (cited in Renner and Lockwood 2010).

The state of philosophical anxiety in ecology is due primarily to one reason: It is not a natural science easily predictable like physics (Reiners & Lockwood 2010). The simplicity of classical physics models (i.e. science models) results from one invariance: except in the realm of quantum physics, an atom always behaves in the same way. There are not best all purposed biological models, particularly in applied ecology almost ever sacrifice generality by precision and realism (Levins 1966). Therefore, Levins (1966) assumed that a general ecological model usually is less precise and realistic. Orzáck (2012) proposed that the three conditions above can occur simultaneously but are arbitrary and lack logical coherence, instead

suggesting that conceptual coherence and empirical adequacy define a good model.

In order for this anxiety to be properly acknowledged and minimised (as it likely cannot be eradicated), one must consider the influence of four biological peculiarities: organisms are genetically variable; they differ qualitatively and quantitatively, as a consequence, they perform different functions; and these factors produce variability in ecological systems and processes (Reiners & Lockwood 2010).

The ecological significance of this variability should be understood in terms of 'ultimate' and 'functional' causes (Mayr 1963). The definitions of the concepts should be clear in order to facilitate communication between ecologists, conservationists and policy-makers. This variability amongst entities and processes form distinct scientific 'subcultures' that 'see' nature differently (Reiners & Lockwood 2010), principally when one subculture integrates theory, concepts, methodologies, materials and instruments from others.

Theoretical ecologists consider populations as variables with continuous or discrete distribution and thus parameterise, ignoring some of the complexity introduced by individual variables. These models use concepts that may seem strange to empirical ecologists. This causes conceptual confusion and isolation because of technical jargon that is only intelligible to those who initiated it.

Species distribution models and species niche models (SNM) (Guisán et al. 2013) have vastly proliferated. The heuristic utility of these models is incontestable, but in conservation practice, they are barely relevant (see Guisán et al. 2013). Soberón (2007) proposed combining set theory and analogies to formalise the definition of the niche. Is it plausible that a conservationist without training in mathematics would understand and use such models operationally? If the goal is to enhance the way ecology is done, then the philosophical suggestions of Reiners and Lockwood (2010) for ecologists are not easily applicable to those who lack basic knowledge in the philosophy of science. Ecologists with interest in philosophical reflections may better elaborate such concepts and theories (Pickett et al. 2007). Model reality (considering the four peculiarities) should be gauged by verifying the degree of integration between the structural components of the theory, so that it behaves as an operating system (Pickett et al. 2007).

Another hindrance is training bias. How can we expect an ecologist, trained to deal with formulas, charts and tables, to read and understand (sometimes tedious) philosophical texts that use unfamiliar jargon? These limitations can lead to conceptual confusion. In addition, ecologists may create new concepts, or several definitions for one concept (Annex), without concern for clarity or coherence.

Reiners and Lockwood (2010) suggest that the ecologist should understand the content of the truth in the context of the theoretical structure of ecology, through aesthetics, ethics and epistemology. This highlights the importance of philosophical reflection within scientific works to 'cure' (or attenuate) anxiety. For example, when assessing the energy cost of predation, the ecologist could propose an elegant foraging model. But how? Is the deduction original? Or fashionable? Does the data fit the scientific structure of ecology? Is it born from comprehensive theory? Ecologists will establish values for natural resources based on accepted criteria in their culture, and it should be accepted that the information presented expresses the truth. In this context, since the pre-Socratics, the concept of 'true knowledge' in the West has been one of the most intriguing and complex questions in the theory of knowledge. The ecologist, in merely seven pages, can have basic clarification about the problem of ensuring veracity of ecological knowledge (Keller & Golley 2000).

In scientific practice, most feel confident if their conclusions are accepted as true by peers, which then become empirical proof of reality. But does this guarantee truth? What if our colleagues are mistaken? It is possible to accept the truth of a theory by means of structural analysis (see Pickett et al. 2007). One good example is Hubbell (2001). Although

Hubbell's (2001) theoretical framework allows predictions at macro ecological and macro evolutionary scales, the assumption of competitive equivalence amongst individuals is not true (Ricklefs 2012). Hubbell's theory is partially based on Connell (1980), Connor and Simberloff (1979) and Strong et al. (1979), who attempted to refute the hypothesis that competition acts as a structuring force in communities (Roughgarden 1963; Schoener 2000). Roughgarden (1963) analysed the philosophical structure of these authors' arguments and found mistaken philosophical assumptions; experimental evidence was subsequently presented firmly demonstrating the importance of competition. Hubbell (2001) disregarded niche as a central concept in community ecology, but without competition, niche and evolutionary ecology as concepts lose their meaning.

The role of philosophy in ecology is to mediate the dialogue between different modes of knowledge in order to make it more constructive. Reiners and Lockwood (2010) suggested a form of ecological pragmatism called 'constrained perspectivism' as a bridge between different theoretical tendencies. The assumption is that different observers have different needs, desires, capacities and belief systems, whether on a conscious or subconscious level, and that this leads to potential for production of incompatible and irreducible assertions concerning the things of the world. These assertions may indeed contain partial truths, but they limit the ability to empirically verify associated hypotheses.

Ecologists practice a science of synthesis (Keller & Golley 2000). The need to integrate distinct ecological subcultures with other scientific cultures and subjective points of view should be recognised, especially when the focus is conservation. An animal, for example, may be considered as an aesthetic object by the artist, as a moral point of view by the animal rights activist, as food by the farmer, as a mystical being by the Indian, as a vector of diseases by the veterinarian, as an herbivore by the plant ecologist, as a source of carbon by the bio geochemist, as an important influence on the global climate by the climatologist, as a producer of ephemeral resources by the insect ecologist and as a competitor by the community ecologist and reproductive unit by the population ecologist. Reconciling these interests to achieve conservation goals is a task that requires a great deal of skill and sufficient knowledge for interdisciplinary approaches.

Reiner and Lockwood (2010) argue that constrained perspectivism is neither dogma nor does it aim to establish how concepts should be used. The goal is rather to suggest methods or approaches for useful consideration of concepts by ecologists.

The time when the concern of ecologists was the conceptual foundation for scientific development has passed. Although pioneering ecologists have created important concepts, they have not examined their suitability in variable situations such as the ecological niche. Implicitly or explicitly, the work of current ecologists is generally aimed at management and conservation, and 'policy-makers' and 'decision makers'

have to learn that the ecology is a complex task and then, as consequence, try to adapt their agenda to this fact.

Ecologists have known for decades that certain ecological phenomena depend on spatial scale (e.g. Wiens 1989). Species–area relationships based on geographical amplitude and local abundance and the metabolic model are good examples. The predictions of these models may fail at reduced spatial scales because of random factors, as illustrated by the neutral theory of biodiversity. The predictions of the metabolic model (West et al. 1997) refer to biological scales ranging from bacteria to giant sequoias; there are several exceptions to the ratio of 0.75 l of metabolic oxygen consumed per 1 kg of body mass (Ballesteros et al. 2015).

The few examples of successful application of niche theory in conservation are in the grey literature. For example, Guisán et al. (2013) suggest that the effectiveness of niche models for conservation should be further evaluated. Further, they suggest greater interaction between the decision makers and the ecologists who formulate the SNMs. Exceptions to this notion may be models assessing fish stocks applied to conservation and management (e.g. Fluharty 2011). Guisán et al. (2013) show the mismatch between the increasing publication of models and their application to conservation. They suggest that the frequency and effectiveness of such models in conservation practice should be evaluated in numerous countries. Finally, they recommend interaction between modellers and decision makers. Whether the utility of the models can be effectively translated or not remains to be seen.

Caughley and Gunn (1996) suggested actions to diagnose the decline of endangered species: to confirm the decline, study natural history in order to elaborate predictive hypotheses, list potential causal agents, measure the importance of each agent in the decline and experimentally test whether the agent is indeed the cause of decline. These are suggestions that apply to case studies of only one species. The current necessity, however, is containment of biodiversity losses at local and broad scales (Richardson & Whittaker 2010). Such loss leads ecologists to use SNMs for entire clades (e.g. Quintero & Wiens 2013).

The fact that certain authors (e.g. Caughley & Gunn 1996) do not mention the niche in their textbook suggests that they do not deem it necessary for conservation. Other authors defend its importance (e.g. Wiens & Graham 2005; Quintero & Wiens 2013); however, universal application of the niche concept in ecology and conservation is difficult because of the complexity of definitions (McInternly & Etienne 2009a, b, c).

2. THE PERPLEXING CONCEPTUAL NICHE

‘If a habitat has conditions within a species’ niche, a population should persist without immigration from external sources, whereas if conditions are outside the niche, it faces extinction.’ (Holt 2009).

Holt (2009) proposed to refine the ‘Hutchinsonian niche’, defining the ecological niche of a species as an ‘abstract

mapping of population dynamics onto an environmental space, the axes of which are abiotic and biotic factors that influence birth and death rates’. The first statement characterises the niche as a set of conditions. The second refers to abiotic and biotic factors, *sensu* Grinnellian and Eltonian niches (Soberón 2007). It confuses the concept of habitat with niche, whose differences are commonly recognised (Whittaker et al. 1973). If this is how Holt (2009) intends to clarify ‘the abstract mapping of population dynamics onto an environmental space’, this does not seem to be the most appropriate manner; the formalisation of the concept is useless for the decision makers.

The conceptual difficulties in ecology are amplified when one of the most important concepts is presented in a confusing manner, as in the works of Grinnell (1917), Elton (1923) and Hutchinson (1959). For some ecologists and evolutionary biologists, the concept does not seem to be considered relevant. For example, Grant and Grant (2008) in a nine-page synthesis on adaptive radiation of Darwin’s finches only mention a generic niche. For these authors, the concept does not need to be explicit, because there is consensus amongst researchers about what it means. This lack of concern for explaining the ‘niche’ is the main cause of conceptual confusion. The importance of the niche concept for ecology and evolution is closely linked to microevolution and macroevolution. The conceptual framework of competition theory for understanding the evolution of adaptation and speciation depends on the concept, and niche diversification is the main result of competition that leads to the diversification of biodiversity. Facilitation can also contribute to such diversification, and in fact, both competition and facilitation are processes of niche evolution. The understanding that a niche can evolve introduces additional complexity to the concept, but it is necessary in order to make it fit for conservation purposes. Ecological niche is dynamic; thus it is important to understand it as a process rather than a static condition (see Rescher 2000). The evolution of conditions and resources influences the evolution of physical and behavioural characteristics of an organism; it is this interaction that interests evolutionary ecologists.

The confusion over the concept of ‘ecological niche’ is one of the symptoms of the previously mentioned, general, philosophical anxiety surrounding ecology. The concept is central to ecology (Wiens 1989; Gibson-Reineme 2015; Pedruski et al. 2016) and integrates the structure of the most prominent theories in science. Some ecologists address the limitations and practical utility; however, with few exceptions, most readily introduce new definitions that they deem enlightening and operational (Annex).

Kingsland (2005) considers the ecological niche as a metaphor that expresses the expectation that organisms perform activities in the community. She argues that niche is not a real entity that occupies a certain physical place in the community. However, the importance of the niche concept was not considered by Kingsland (2005) in his book on the evolution of North American ecology from 1860 to 2000. Only five pages contain mention of the niche, as a metaphor for the role of

researchers and institutions in paving the path for ecology. Further, Kingsland (2005) understands that 'niche' is a Platonic conception that is impossible to measure in practice. But how can one tell a field ecologist that the 'niche' is only an abstraction of heuristic value?

The difficulties in transposing an abstract concept into reality have given rise to a multitude of definitions for niche (Annex). As a result, the niche has become the most ambiguous concept in ecology. This is why philosophers of ecology as well as some ecologists are concerned about the use of the niche concept for theoretical development and application of ecology to conservation and management.

Some authors have chosen to ignore these difficulties (e.g. Wiens & Graham, 2005; Quintero & Wiens 2013). Using phylogenetic methods, Quintero and Wiens determined the width of the climatic niche (using temperature) of 409 species in three clades (salamanders, amphibians and lizards). They discovered that niche breadth within a single locality generally corresponded to overall species climatic niche breadth across the range of distribution and that within-locality (temporal) variation in niche breadth explained most of the total variation in the overall niche breadth of a species. They also found that species with wider climatic niches tend to show greater divergence between localities. Although the researchers did reveal a macroecological pattern, they only list one possible cause. They mention that these data may be important in the context of conservation but fail to indicate the ways in which such data could be used in practice. Making reference to biological conservation in the subtitle of the work and using SNM, Quintero and Wiens point out that 'niche conservatism' can limit the expansion of geographic range; influence allopatric speciation, historical biogeography, patterns of species richness, community structure, the distribution of introduced species and species responses to global climate change; and influence on human history over the past 13,000 years, a task of great breadth, which the subtitle commemorates with the pretension of integrating evolution, ecology and conservation biology. However, they do not demonstrate this integration or its practical consequences.

Chase (2011) recognises the conceptual confusion but uses theory and concept for niche. Chase (2011) and other researchers also consider it as theory (e.g. Cavender-Bares et al. 2009). Niche is an integral concept in the theoretical structure of ecology, an idea that is agreed upon by Gibson-Reineme (2015) and Pedruski et al. (2016). If we apply a structural model of theory (Pickett et al. 2007), we see that the niche fits only as a concept. The structure of the concept is based on definitions (and it is difficult to think of a theory as only a concept with several definitions) (Annex).

Soberón (2007) proposed distinguishing the Grinnellian and Eltonian niche, with the former referring to conditions and the latter to resources. This distinction may have a practical effect on the appropriate application of the concept and perhaps may unify some definitions and simplify their use. For example, researchers may refer to the Grinnellian niche when

addressing questions about thermal amplitude (e.g. see Quintero & Wiens 2013) and the Eltonian niche when addressing question of resource use.

McInternly and Etienne (2012a,b,c) discuss the validity of application of the niche concept in ecology and SNM. The first work, entitled 'Ditch the niche', suggests that the concept has no universal application in ecology and SNM, mainly because of the limitations of some definitions (e.g. the fundamental niche). In the second work, entitled 'Stitch the niche', they propose a practical philosophy for the concept in order to reach the correct level of abstraction. The procedure essentially involves decomposition into effect and response and reconstruction as a general scheme. In the final work ('Pitch the niche'), through balanced argumentation, they established a general definition of niche and accepted that the various definitions are not necessarily essential to ecology. The preference is not to perfect the concept but rather to establish it (pitch) in terms of ecology. They suggest that the niche definitions best aligned with ecology are those used responsibly and by means of explanatory models (in particular SNMs) using other concepts. They argue that despite the difficulties of having a general concept, they trust in their own definition: 'a term to describe abstractions of an organism's relationship to an "ecosystem" as described by both effect and response interactions the organism has, both directly and indirectly, with and on other biotic or abiotic objects that are part of that ecosystem'. They emphasise that the concept is heuristic and that the term 'abstraction' has utility for SNM. However, the decision makers would not understand the utility, perhaps, because of 'abstraction' in the definition. The question is: what is the usefulness of SNM for conservation and management? The concept put forth by McInternly and Etienne (2009c) is not adequate. This is why theory advances exponentially whilst practicing mathematically. In specific situations in which the theory does not work, the best are 'case studies' (Schrader-Frechete & McCoy 1994).

The conceptual confusion over the niche is far from resolving as long as ecologists do not dispense with use of the terminology in diverse and obscure contexts. Perhaps better understanding the history of the concept can reveal the origin of the confusion and perhaps indicate directions to begin conceptual disentanglement? At least we can hope that some ecologists and others desire to understand the usefulness of history, to which end McInternly and Etienne (2012c) proposed '...we should not allow social and historical aspects of our science to become confused with, or take over from, scientific aspects (and vice versa)'. On the other hand, they do not show that the origin of the confusion began with past researchers who did not bother to establish models and criteria with which to quantify niche. At this time, these authors (Grinnell, Elton, Hutchison) were more concerned with concept itself than with quantification and modelling. They also based their definitions on knowledge of natural history, which is necessary but not sufficient for ecology.

Tansley (1935) discussed the use and abuse of terminology in ecology. His concern was with concepts associated with ecological succession without the mention of niche. Criticising the use of the term 'biotic community', this author assumes that animals do not integrate the plant community: 'The concept of the 'biotic community' is unnatural because animals and plants are too different in nature to be considered as members of the same community. The whole complex of organisms present in an ecological unit may be called the biome". This supposed separation between plants and animals has influenced and still influences some botanists and plant ecologists, who only consider abiotic factors as drivers of plant community structure.

Hullbert (1981) uses the history of the niche concept to show that the origin of the conceptual confusion is caused mainly by the lack of consensus between researchers and authors of ecology textbooks. This author divides the history of the concept into five phases: Grinnelliana–Eltoniana, Hutchinsoniana, Hundred flowers, Despairing and Distillation. In order to characterise each phase, the author has drawn from definitions in the literature and textbooks.

The first two phases focus on natural history perspectives (Grinnell emphasising habitat and Elton diet) and the beginning of the geometric formalisation of the concept by Hutchinson. The conceptual confusion in this first phase was synthesised as follows: 'Confusion has existed as to whether the so-called "Hutchinsonian niche" is a subset of real space or a subset of an abstract space. The fact is that both characterizations are correct, for the term is employed in two ways. Most often it is used as a shorthand for "Hutchinsonian geometric representation of the niche", and that clearly is an abstract space. However, when used in reference to a particular organism, "Hutchinsonian niche" often means *the niche itself* (as opposed to a geometrical representation of it), that is, "the set of all environmental states that permit that species to exist indefinitely"; and that "set" corresponds to a subset of real space, essentially the 'Grinnellian niche'. The third phase was initiated by renewed interest of researchers in the Hutchinsonian geometric conception. Ironically, Hullbert metaphorically refers to this phase as one of different 'flowers', which (despite the pleasant fragrance) has greatly diminished the intelligibility of the literature. The fourth phase is characterised by the discrediting of several researchers regarding the usefulness of the ecological niche concept and the resurgence of the 'niche' as a set of resources that a species uses regardless of its role in the community (Dice 1952). Hullbert (1981) departs from the definition of Dice (1952), which he deems the most consistent and unambiguous of all previous definitions from his survey. From this definition, Hullbert (1981) elaborates what resources are and which resource characteristics should be considered in a complete definition of ecological niche. The author concludes by proposing the use of the following definition at all levels of organisation in ecology: 'If the resource set definition is accepted, no confusion should result from allowing niche such wide applicability. The resources used by any given bio-

logic unit are simply the sum of the resources used by its component subunits. Confusion would be fostered, if a new term for "set of resources utilized" had to be used every time that discussion shifted from one level of organization to another. Use of the single term niche also serves the positive function of spotlighting the centrality of resource use phenomena at all levels of ecological organization'. Whilst Hullbert's (1981) proposal seems attractive by virtue of enabling standardisation of the definition by different ecological subcultures, it is unlikely that ecologists (in general) will adhere to it because of the intrinsic characteristic of each subculture of using definitions that are familiar. Researchers within different subcultures may not consider the definition as universal, and in the current phase of ecology as a basis for conservation, it may be rejected because of the difficulty of practical application by decision makers and policy-makers; the latter issue was not considered by Hullbert. Finally, using Hullbert's (1981) argument about the usefulness of history, for the remainder of this text, we shall extend the historical perspective. What follows is an outline; however, a comprehensive and consistent historiography about the ecological niche concept is still needed.

3. HISTORICAL OUTLINE OF THE ECOLOGICAL NICHE CONCEPT

In the nineteenth century, the niche was a metaphor used to designate the location and function of humans or specific features of human-made structures or buildings (Gibson-Reineme 2015); these two definitions were used in the first three decades of the twentieth century by Grinnell (1917) and Elton (1946), respectively. The first definition used the niche to define the set of physical environmental conditions that influence the presence and abundance of animals in a given location. Elton emphasised the ecological interactions and the functional role of organisms in a community, for example, as predators, competitors or parasites. These definitions lead to naturalists and ecologists interested in understanding animal abundances and distributions to adopt one of the definitions. For example, the Australians Andrewartha and Birch (1954) used the Grinnellian niche concept, whilst Victor Shelford (1913) used the Eltonian concept; however, neither adopted the specific nomenclature.

Although various historical details and circumstances can perhaps shed light on the difficulties in defining and applying the niche concept to realistic situations, Gibson-Reineme (2015) discusses the possible use of the term 'niche' as defined in the first decade of the nineteenth century, which was from the perspective of human communities. However, the concept already carried connotations of location and function.

Pocheville (2015), in a single paragraph, suggested that philosophers and naturalists of Ancient Greece already had the idea of what is now understood as the ecology of organisms. However, he does not clarify whether there was an understanding of the interactions of organisms with the environment in this historical conception. He also suggests that

Carl Von Linné, in his definition of the 'economy of nature', had perceived a linkage between the idea of the 'harmony of nature' from the Book of Genesis with the ideas of contemporary naturalists. This idea of the harmony of nature is fundamental to the 'Arcadian Ecology' concept from White (1901), which essentially means harmony between man and nature. Conversely, 'Imperial' or 'Pastoral Ecology' (Worst 1984) is the idea humans must manage nature to their own ends. Note that both concepts have implications for conservation and for the practical application of niche ecological concepts: 'Arcadian Ecology' addresses the conservation of pristine forest areas (expanded by ecologists to mean any area of natural vegetation), whilst 'Imperial Ecology' explicitly admits the need for management, not directly for conservation purposes, but rather to obtain the necessary means for human survival.

Although these historical facts may have played an important role in advancement of scientific knowledge in their respective ages, the first use of the term 'niche' as the location of an organism in the community can probably be first attributed to Johnson in the first decade of the twentieth century (Pocheville 2015). Perhaps all references to the initial attempts to define the concept retain implications of the 'location' and 'function' of organisms in the community, as is the case in books on the history of ecology (e.g. MacIntosh 1985) and the philosophy of ecology (e.g. Keller & Golley 2000), as well as other influential textbooks (e.g. Odum 1971).

As previously mentioned, Soberón (2007) maintained the original definitions laid out by Grinnell and Elton, specifying in detail the differences between two categories. The first definition was also called the non-interactive niche in reference to the geographical distribution of species (i.e. macroecology); the focus of these studies was to understand the macroclimatic influence on broad-scale species distributions. The Eltonian niche, on the other hand, refers to the limiting or non-limiting role of biotic interactions in species distributions and abundances, particularly at local scales.

In the modern phase of ecology, G.E. Hutchinson, who coined the niche concept as a multidimensional hypervolume determined by ecological variables that affect the 'fitness' of a population, is considered to be the 'father' of modern ecology by virtue of integrating ecology and evolution (Slack 2010). This synthesis resulted in the discipline of evolutionary ecology. Similarly, Niko Tinbergen incorporated behaviour into evolution, emphasising the importance of understanding evolution *via* a naturalistic approach. In this proposal of integration, Tinbergen considered a more comprehensive understanding of behaviour, including functional aspects of behaviour (how it affects fitness), ontogeny (behavioural changes along the development that also influence fitness), phylogeny (the relationship of kinship between species and its impact on the evolution of behaviour) and the evolution of the behaviour itself (as behavioural adaptations evolve under environmental influence). The discipline of Behavioural Ecology, much like Evolutionary Ecology, resulted from taking this original approach. In fact, the distinction between the two disciplines is arbitrary, because

both have the same focus: the influence of interactions on each participant and the influence of environmental variables on the evolution of morphological, physiological or behavioural adaptations. It would be comparatively relevant to jointly discuss the historical evolution of both disciplines, to clarify the origin of the convergence between the conceptual formulations of each, because they have developed under the unifying evolutionary perspective, which must necessarily include the concept of the 'ecological niche', for instance, as in Southerland 1986 (Annex). However, we will only emphasise the evolution (or involution?) of the concept, to attempt to clarify whether such conceptual evolution has provided tangible benefits, not only in terms of communication between peers but also for utility in management and conservation practices.

Some authors criticise the usefulness of this classic niche concept and propose changes in interpretation such that the concept may have utility for conservation (Dias 1996; Wiens & Graham 2005; Quintero & Wiens 2013). Crandal et al. (2000), in their critique of the use of Evolutionary Significant Unity (ESU) for conservation and management, use niche without specification and without fundamental niche when referring to the incorporation of ecology into the evolutionary concept; this causes confusion as to which definition should be considered more appropriate. Further, it suggests a general obviousness of the concept, as if it was well defined and well understood, which is not the case. The operational idea for the ESU concept would include preservation of evolutionary processes; however, these authors ignored that an ecological niche also evolves (Pacala & Roughgarden 1985). Thus, although the study is enlightening in several ways (e.g. the pretension of integrating ecology and genetics and the treatment given to ecology through the unclear use of niche), ignoring that the niche also evolves gives rise to severe limitations on the operational applicability of the concept for management and conservation purposes.

Pedruski et al. (2016) performed an analysis of literature citations from 1900 to 1999 by recording the occurrence of the word 'niche' in the title, 'abstract' or 'keywords' of published works. The purpose was to evaluate the impact of the concept on the development of ecology in the twentieth century and its use amongst the different subdisciplines of ecology. The authors used the results to construct a conceptual network (see Fig. 3, Pedruski et al. 2016) for the purposes of their analyses. The objective was to determine whether the different definitions of niche facilitated its accessibility and if the conceptual integration resulting from its use resulted in integration in the literature and amongst different subdisciplines. As expected, after configuration of the various niche concepts by means of a conceptual network that included 40 subdisciplines, the authors determined that the concept was defined differently amongst subdisciplines according to conceptual convenience. This procedure resulted in a lack of conceptual integration and multiple definitions. Pedruski et al. (2016), despite omitting discussion of published works from 2000 to the present (which would not significantly change the conclusion), cement the

idea that the conceptual entanglement of niche philosophy is far from being simplified and thus operationally useful.

4. CONCLUSION

It is surprising that a science can have as many conceptual problems as ecology and the issue has required copious effort from ecologists to consistently define the central concepts of their field. However, a considerable number of theoretical and empirical ecologists have not paid enough attention to the conceptual ambiguities and improprieties regarding the use of concepts. Classical physics is not more robust than ecology; it is only more 'rigid' and 'predictable'. This problem, amongst others, makes it seldom possible to answer the question of 'how much' that is characteristic of ecological studies. Perhaps ecology as a discipline will never be as rigid and predictable as classical physics, but it can be improved if ecologists turn their attention to the

importance of philosophy and modify and improve upon the theoretical structure to reduce the anxiety caused by incoherent and inconsistent use of concepts. As variability of objects and processes is real and the principle focus of ecology, it is important that ecologists pay more attention to use clear concepts, but it is also necessary that decision and policy-makers learn that ecology is a complex science that, many times, can be affected by an excessive reductionism.

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ANNEX: CASUAL SAMPLE OF PUBLISHED PAPERS THAT USE 'NICHE' IN THE TITLE FROM 1975-2015 (24 OUT 35 FROM 2007-2015).

Term	Definition	Comments	Author/Year
Ecological niche	The combination of conditions and resources that influence individual survival and reproduction, and impact population growth	Use should be limited to ecology due to vagueness. More specific terms that facilitate rapid and unambiguous grasping of the study unit should be preferred.	Pocheville, A. (2015) The ecological niche: history and recent controversies. In <i>Handbook of evolutionary thinking in the sciences</i> (pp. 547-586). Springer/Netherlands troversies. In: <i>Handbook of evolutionary thinking in the sciences</i> (pp. 547-586). Springer, Netherlands.
Niche constraint	Can refer to any ecological variable (either condition or resource) that restricts the distribution and abundance of individuals in a given area.	Because it is vague, it is preferable in the title to refer to what type(s) of restrictions the work refers to.	Régis, C.E. Flohr, C.J., Blom, P.B.R. & Hubertus, J.E.B. (2013) Founder niche constrains evolutionary adaptive radiation. <i>Proc. Natl. Acad. Sci. U.S.A.</i> , 110(51): 20663–20668.
Niche expansion	Niche enlargement may have a narrow (local) or broad (regional/geographical) connotation. It may involve phenotypic plasticity or adaptive modifications.	Strong probability of confusing with habitat or home range.	Scott, L.H, Seth D., Newsome, J. & Caselle, E. (2014) Dietary niche expansion of a kelp forest predator recovering from intense commercial exploitation. <i>Ecology</i> , 95(1): 164-172.
Dietary niche	Refers to the diversity of food resources used.	Can be referred to as trophic level, food chain, or food web.	Scott, L.H, Seth D., Newsome, J. & Caselle, E. (2014) Dietary niche expansion of a kelp forest predator recovering from intense commercial exploitation. <i>Ecology</i> , 95(1): 164–172.
Generalized niche	Refers to a species that can occur under a broad spectrum of resources and conditions. The opposite of specialized niche.		Gruber, J. (2012) Generalized Niches: A Tentative Definition. Retrieved from: http://www.lymenet.de/symptoms/cycles/niches.htm
Spatial niche	Locations where a species can be found, either local (e.g., rocky coastlands) or regional. It may involve specialization (specialists that “track” the distribution of a resource on which they are specialized, regardless of environmental conditions).	Can also be confused with habitat or home range.	Tyler, R.L. & Longrich, N.R. (2010) Spatial niche partitioning in dinosaurs from the latest cretaceous (Maastrichtian) of North America. <i>Proceedings of Biological Sciences B</i> , 278(1709): 1158–1164.
Niche space	Synonymous with the previous term, with the same restrictions.	Range of sites in which a species can be found.	Tyler, R.L. & Longrich, N.R. (2010) Spatial niche partitioning in dinosaurs from the latest cretaceous (Maastrichtian) of North America. <i>Proceedings of Biological Sciences B</i> , 278(1709): 1158–1164.
Niche width	Range of conditions and resources under which a population can survive and reproduce.		Craig, A. Layman, J.P.Q., Peyer, C.M, Allgeier, J.E. & Suding, K. (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. <i>Ecological Letters</i> , 10(10): 937–944.
Niche Breadth, Narrow niche	A limitation of conditions and resources in a population that allows the coexistence of interspecific populations in a given area.	Here niche breadth is used as synonymous with phenotypic plasticity.	Michael, C. & Whitlock, M.C. (1996) The Red Queen Beats the Jack-Of-All-Trades: The Limitations on the Evolution of Phenotypic Plasticity and Niche Breadth. <i>The American Naturalist</i> , 148: S65–S77.

Term	Definition	Comments	Author/Year
Niche overlap	For niche overlap to occur, each population must have a narrow niche, i.e., they coexist by surviving and reproducing with only a portion of the resources available.	Food, spatial, and reproductive niche overlap resulting in interspecific coexistence.	Nicholas, J. Gotelli, N.J., Hart, E.M., Aaron, M. & Ellison, A.M. (2015) NicheOverlap. Retrieved from: https://cran.r-project.org/web/packages/EcoSimR/vignettes/nicheOverlapVignette.html
Thermalniche	Refers to temperature.	Co-factors may influence temperature, which can modify the influence of temperature on the distribution and abundance of individuals.	Righton, D.A., Andersen, K.H., Neat, F., Thorsteinsson, V. Steingrund, P. Svedäng, H., Michalsen, K., Hinrichsen, H.H., Bendall, V., Neuenfeldt, S., Wright, P., Patriksson, P., Huse, G., Kooij, J. van der Henrik, Mosegaard, K. & Hüsey, J.M. (2010) Marine Ecology Progress Series, 420: 1–13.
Climaticniche	A very broad and multivariate connotation may refer to the influence of local (microclimate) or regional-geographical (macroclimate) conditions that influence the abundance and distribution of a population.	The breadth of climatic conditions that favor or limit the occurrence of a species.	Blaise Petitpierre, B., Kueffer, C., Broenimann, O., Randin, C., Daehler, C. & Guisan, A. (2012) Climatic niche shifts are rare among terrestrial plant invaders. <i>Science</i> , 335(6074): 1344-1348.
Trophicniche	Can be used in the context of a food pyramid, in this case comparing trophic levels, or in a more specific context, as a synonym of dietary niche.	Synonym of dietary niche.	Ramos, J.A.A., Barletta, M. Dantas, D.V., Lima, A.R.A. & Costa, M.F. (2014) Trophic niche and habitat shifts of sympatric Gerreidae. <i>Journal of Fish Biology</i> Volume 85(5). Version of Record online: 19 AUG 2014
Feeding niche	Refers to the range of food items that may change seasonally, subject to individual or population specialization (either locally or along the geographical distribution of populations).	Feeding niche: set of food items of a consumer.	Snow, B.K. & D.W. Snow. (1972) Feeding Niches of Hummingbirds in a Trinidad Valley. <i>Journal of Animal Ecology</i> , 41: 471-485.
Dietary niche	Can refer to generalists or specialists, or even to individual preferences (individual specialization in diet, for example)	Feeding niche: set of food items of a consumer.	Shipley, L.A., Forbey, J.S., Moore, B.D. (2009) Revisiting the dietary niche: When is a mammalian herbivore a specialist? <i>Integrate Comparative Biology</i> , 49 (3): 274-290.
Reproductive niche	Can refer to the population or individual, in local or regional contexts.	Conditions and resources used by individuals or populations that affect population growth.	Gary, M. & Wessel, G.M. (2013) A special place for a special niche: The reproductive niche. <i>Molecular Reproduction and Development</i> 80 (4). Version of Record online: 12 APR 2013
Fundamental niche	Resources and conditions under which a population can potentially grow exponentially.	Conditions and resources through which a population can grow independent of environmental constraints.	Materna, A. C. (2012) Shape and evolution of the fundamental niche in marine <i>Vibrio</i> . <i>Multi-disciplinary Journal of Microbial Ecology</i> , 6(12): 2168–2177.
Realized niche	Conditions and resources used or tolerated by individuals in a population subject to environmental restrictions.	Conditions and resources that an individual or population effectively uses temporally and spatially.	Lau, J.A., McCall, A.C., Davies, K.F., McKay, J.K. & Wright, J.W. (2008) Herbivores and edaphic factors constrain the realized niche of a native plant. <i>Ecology</i> , 89(3): 754–62.

Term	Definition	Comments	Author/Year
Niche variation	Any variation in the intensity of conditions, or quality and quantity of resources that influence the distribution and abundance of a population.	Can mean the range of conditions and resources used by a species.	Brussow, H., Canchaya, C., & Hardt, W.D. (2004) <i>Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous</i> . Proc. Natl. Acad. Sci. U.S.A., 104: 10075–10079.
Niche partitioning	Also called resource division, when niche overlap occurs and populations of different species can coexist in a given area.	Sharing of resources between two or more species.	Di Bitetti, M.S., De Angelo, C.D., Di Blanco, Y.E. & Paviolo, A. (2010) <i>Niche partitioning and species coexistence in a Neotropical felid assemblage</i> . Acta Oecologica, 36: 403–412.
Niche coexistence	Related to the previous.	When two species use the same type of resource, under the same conditions.	Geervliet, J.B.F. (2000) Coexistence and niche segregation by field populations of the parasitoids <i>Cotesia glomerata</i> and <i>C. rubecula</i> in the Netherlands: Predicting field performance from laboratory data.
Niche division	Related to the previous.		
Niche segregation	The opposite of the previous. Refers to the displacement by means of plasticity or evolution of inter-specific populations that exploit the same type of resource but at different times/periods, minimizing competition or relaxing predation (nocturnal or diurnal temporal niche).e.g., the Island of São Tomé in the Gulf of Guinea has diurnal bats, presumably because there are no predators.		Geervliet, J.B., Verdel, M.S., Snellen, H., Schaub, J., Dicke, M. & Vet, L.E. (2000) Coexistence and niche segregation by field populations of the parasitoids <i>Cotesia glomerata</i> and <i>C. rubecula</i> in the Netherlands: Predicting field performance from laboratory data. Oecologia, 124(1): 55–63.
Niche differentiation	Synonymous with previous, also linked to competition.		Zuppiinger-Dingley, D., Schmid, B., Petermann, J. S., Yadav, V., De Deyn, G.B. & Flynn, D.F. (2014). Selection for niche differentiation in plant communities increases biodiversity effects. Nature, 515: 108–111.
Niche occupancy	Ecological niches being filled, inhibiting subsequent adaptive radiation	Niche occupation is dubious expression, because it is suggestive of habitat as well.	Brockhurst, M.A., Colegrave, N., Hodgson, D.J. & Buckling, A. (2007) Niche Occupation Limits Adaptive Radiation in Experimental Microcosms. Plosone. Retrieved from: https://doi.org/10.1371/journal.pone.0000193
Vacant niche	The same of empty niche	Introduces controversy as to whether niche is a quality of a species or of the environment. Perhaps this discussion is superfluous, because what matters in ecology are interactions: organisms co-evolve with the environment, are part of the environment, and also modify the physical and organic environment.	Gibson-Reinemer, D.K. (2015) A Vacant niche: How a central ecological concept emerged in the 19th century. The Bulletin of the Ecological Society of America, 96(2), 324–335.

Term	Definition	Comments	Author/Year
Empty niche	Synonymous with the previous.	Another term with doubtful meaning. It is an example of absolute connotation, self contained and probably unrealistic. Empty niche simply does not exist, in a manner similar to a vacuum having only heuristic significance.	
Niche shift	Considered an adaptive response in a model with two competitors and two resources. In this case, niche shift evolves by means of character displacement.		Abrams, P.A. (1986) Character displacement and niche shift analyzed using consumer-resource models of competition. <i>Theoretical Population Biology</i> , 29(1): 107–60.
Ecological niche replacement	Same as the previous, and also linked to the idea of evolution through competition. Also used in the context of invasive species with greater competitive potential compared to native equivalent species.		
Niche invasion	Intimately related to the previous.		Peterson, A.T. (2003) Predicting the Geography of Species' Invasions via Ecological Niche Modeling. <i>The Quarterly Review of Biology</i> , 78(4): 419–433.
Niche liability	Tendency of closely related species to be ecologically similar (the opposite is called ecological equivalents in Brazilian and African equatorial tropical forests, meaning species without phylogenetic relationships that are ecologically similar).	Although it appears in the title of the article, liability is only implied in the abstract, when it should be as explicit as it is in the title. (Ecologists are happy to create novel, elegant expressions, although the consequences for understanding are not favorable).	Losos, J.B, Leal, M., Glor, R.E, De Queiroz, K, Hertz, P.E, Rodríguez Schettino, L., Lara, A.C., Jackman, T.R. & Larson, A. (2003) Niche liability in the evolution of a Caribbean lizard community. <i>Nature</i> , 424(6948): 542–545.
Environmental niche	Environmental variable (for instance temperature, prey size) that matters for survival and reproduction of organisms	Clearly redundant.	Warren, D.L., Glor, R.E, & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. <i>Evolution</i> , 62-11: 2868–2883
Ontogenetic niche	Patterns of resource use by an organism that develops from birth until it reaching its maximum lifetime.		Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and interactions in size structured populations. <i>Annual Review of Ecology and Systematics</i> , 15: 396-345.
Behavioral niche partitioning	Behavioral partitioning was revealed both between and within species in Hawaiian albatrosses. Both species were highly active during chick-brooding trips and foraged across day and night;		Conners, M.G., Hazen, E.L., Costa, D.P. & Shaffer, S.A. (2015) Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species. <i>Movement Ecology</i> , 3(1): 28. Retrieved from: https://movementecologyjournal.biomedcentral.com/articles/10.1186/s40462-015-0060-7

Term	Definition	Comments	Author/Year
Nocturnal niche	It refers to temporal niche partitioning.		Gerrish, G.A., Morin, J.G. & Rivers, T.J. (2009) Darkness as an ecological resource: the role of light in partitioning the nocturnal niche. <i>Oecologia</i> , 160: 525.
Temporal and spatial niche	It refers to niche partitioning		Albrecht, N. & Gotelli, N.J (2001) Spatial and temporal niche partitioning in grassland ants. <i>Oecologia</i> , 126: 134–141
Endemic niche	The beetle is able to establish itself in the region and persist, even at very low (endemic) population levels	Can be confusing with endemic populations.	Blaiker, P.K. (2011) Mountain pine beetle range expansion: Assessing the threat to Canada's boreal forest by evaluating the endemic niche. In K.P. Bleiker, A.L. Carroll and G.D. Smith. (Mountain pine beetle working paper ; 2010-02)
Niche construction	Concerns engineering species that modify the habitat, leading certain species to local extinction and favoring colonization by other species.	There is clear overlap with spatial niche.	Kylafis, G. & Loreau, M. (2008) Ecological and evolutionary consequences of niche construction for its agent <i>Ecological Letters</i> , 11(10): 1072-81.
Midwater niche Lithobiontic niche Macroniche Microniche Multidimensional niche		Niche terms easily confused with habitat.	Inman, R.M., Magou, A.J., Persson, J., & Mattisson, J. (2012) The wolverine's niche: linking reproductive chronology, caching, competition, and climate. <i>Journal of Mammalogy</i> , 93(3): 634-644.
The wolverine's niche		Niche terms for particular species or assemblages.	Inman, R.M., Magou, A.J., Persson, J., & Mattisson, J. (2012) The wolverine's niche: linking reproductive chronology, caching, competition, and climate. <i>Journal of Mammalogy</i> , 93(3): 634–644.
Realized niche	From Hutchinson's model, specific conditions in which populations could survive.	Discusses difficulties of measuring niche and overlap with habitat.	Croty, S. M. & Brettness, M.D. (2015) Positive interactions expand habitat use and the realized niches of sympatric species
Niche concept in human ecology	The Hutchinsonian concept of the ecological niche can be made operational for studies in human ecology by defining it in terms of the distinctive ways of using resources for subsistence that set „cultural species“ apart.		Hardesty, D.L. (1975) The niche concept: Suggestions for its use in human ecology. <i>Human Ecology</i> , 3(2): 71–85
Niche geometry	More than temporal or spatial scale, it refers to the organization of the community structure based on models of predator/prey interactions	Although it is organizational, it occurs in space and time, so these scales are implicit in the concept.	Pimm, S.L. (1988) Niche geometry. In <i>Community Ecology</i> (Lecture Notes in Biomathematics, 77), ed. A. Hastings. Springer-Verlag, New York.
Niche evolution	Related to niche conservatism.		Warren, D.L., Gior, R.E., & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. <i>Evolution</i> , 62-11: 2868–2883.
System niche science	Related to systems theory.	Niche is a system science.	Patton, B.C. & Aube, G.T. (1981) System Theory of the Ecological Niche. <i>American Naturalist</i> , 117(3): 893–922.