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SPECIAL ISSUE

Ditch the niche – is the niche a useful concept in ecology or species distribution modelling?

Greg J. McInerny[1,2]* and Rampal S. Etienne[3]

[1]Department of Computer Science, University of Oxford, Oxford, OX1 3QD, UK, [2]Computational Ecology and Environmental Science Group, Computational Science Laboratory, Microsoft Research, Cambridge, CB3 0FB, UK, [3]Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, 9700 CC, Groningen, The Netherlands

*Correspondence: Greg J. McInerny, Department of Computer Science, University of Oxford, Oxford OX1 3QD, UK.
E-mail: gmcinerny@hotmail.com

ABSTRACT

In this first of three papers we examine the use of niche concepts in ecology and especially in species distribution modelling (SDM). This paper deliberately focuses on the lack of clarity found in the term 'niche'. Because its meanings are so diverse, the term niche tends to create confusion and requires constant qualification. The literature houses many idiosyncratic ideas of what the niche is, but few examples where niche is more explanatory than the terminologies of population and community ecology or the statistical methods used to implement SDM analyses. In many cases the original (and inspirational) concepts are not directly applicable to our modern applications (e.g. set theory). There are some conceptual limitations found in individual definitions of niche (e.g. the fundamental niche concept), so it is perhaps understandable why more neutral terminology is becoming popular in SDM. An examination of the literature reveals a wide range of uncritical use of niche terminology. Our findings in this paper do not necessarily support the position of niche as a universally useful concept.

Keywords

Distribution, environment, fundamental niche, model, model selection, niche concept, policy, range, realized niche, species.

WHY DO WE NEED ANOTHER PAPER ABOUT THE NICHE?

This is the first of three papers that examine the utility of the niche concept in ecology and species distribution modelling (SDM) from three different points of view (see also McInerny & Etienne, 2012a,b). Without suggesting any particular definition or usage of the term 'ecological niche', nearly every reader will already have some personal view on what 'niche' means. But these ideas are not necessarily equivalents. Be it an internet search, casual conversation, or communication within published documents, conference or workshop presentation, there is plenty of opportunity for misdirection and/or crosstalk when using the term niche. This confusion can be counterproductive for ecology (e.g. Kulesza, 1975; Peters, 1991).

Whatever the term 'niche' actually means, it is definitely three things. (1) It is old, having a history almost as old as ecology itself, and is old enough for some uncertainty on where it originated (see Johnson, 1910; Chase & Leibold, 2003). (2) It is also pervasive, as arguably no area of ecology is independent of some concept of the niche (Chase & Leibold, 2003), including both pure and applied ecological sciences (Elith & Leathwick, 2009). Many areas of evolutionary biology also have deep roots in niche concepts (e.g. Wiens & Graham, 2005). (3) It is diverse, as a function of its age and influence through the development of ecology (Schoener, 2009). Thus, different individuals and disciplines have different concepts and conventions about what the term niche is for (Peters, 1991; Holt, 2009).

It is precisely because of these three characteristics that constant clarification is required whenever we use the term 'niche', which demands some questioning of its efficacy. We cannot meaningfully write 'the niche' without considerable qualification of which particular definition is being referred to. Thus, unless otherwise indicated, we use 'niche' to refer to that collection of terms and concepts in this paper and the two papers that follow (McInerny & Etienne, 2012a,b). In this first paper we take on a deliberately critical tone as we focus on difficulties and issues with the use of the niche concept. Our investigations focus on the applied activity variously known as ecological and environmental niche modelling, and species distribution modelling (SDM) (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009) but our

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arguments have a broader scope. Throughout these papers we encourage readers to consider whether 'niche' is useful for communicating our science to ourselves and to non-specialists (e.g. for policy purposes).

Ditch the crosstalk and tautology

What is the niche? It is an imaginary space (Van Horne & Ford, 1982) but we can measure it; at times it is a concept (Hutchinson, 1957), at times it refers to a living object (Elton, 1927), sometimes it is physical environmental factors (Holt, 2009), sometimes the concept is named after a process (Holt, 2009; Ricklefs, 2010), sometimes an author (Soberón, 2007). There can be different forms of niche objects, realized and fundamental (Hutchinson, 1957), or qualitative environmental realized niches (Austin *et al.*, 1990). There are environments and habitats that are niches (see glossary in Pearman *et al.*, 2008), and niches that are found in habitats and environments (Austin, 1985). Different niches use different meanings for 'habitat' and 'environment' (Whittaker *et al.*, 1973), or niches may occur in 'biotopes' and 'ecotopes' (Whittaker *et al.*, 1973; Colwell & Rangel, 2009). Niche can have an auto-ecological meaning, or the term can be used in community and ecosystem ecology (Chase & Leibold, 2003; Schoener, 2009). Niche can be used alternatively in theoretical advancement (Holt, 1996) and applied management (Graham *et al.*, 2004). A niche can be constructed (Odling-Smee *et al.*, 2003), vacant (Begon *et al.*, 1996, p. 777) and colonized (Marín *et al.*, 2001), but it can also evolve (Warren *et al.*, 2008), shift (Broennimann *et al.*, 2007), diverge (McCormack *et al.*, 2010), be conserved (Wiens & Graham, 2005), be unconstrained (Hurlbert, 1981) and be packed (Case, 1981). Then there are alternative vocabularies used in different concepts: bionomic and scenopoetic (Hutchinson, 1978); conditions and resources (Holt, 1996); n-dimensional hypervolumes (Hutchinson, 1957); environmental complexes, niche-, habitat- and ecotope-hyperspaces, and m-dimensional co-ordinate systems (Whittaker *et al.*, 1973); and Euclidean hyperspaces (Hardesty, 1975). In sum, the neologisms require that each meaning and its terminology always carries a qualification. This dilution of the term defies any single true definition of niche and lowers our ability to communicate ideas.

Ditch the author-ian niche

The literature often discusses 'niche' in terms of its history (Chase & Leibold, 2003; Schoener, 2009) a history rich in 'scholarly gems and scholarly trivia' (Colwell & Rangel, 2009). However, a focus on the origin of ideas can distract from our contemporary applications and scientific developments. We could avoid this by ditching 'author-ian' prefixes, for example 'Grinnellian', 'Eltonian' and 'Hutchinsonian' niches (Grinnell, 1917; Elton, 1927; Hutchinson, 1957). It cannot be denied that Grinnell's ideas were highly influential, but maybe we should not take those ideas farther than was intended. Grinnell did not provide quantitative frameworks for 'Grinnellian' niches; no equations, no explicit metrics and no explicit numerical abstractions or model (Grinnell, 1917). Instead, his niche was a verbal exploration and not a quantitative description or algorithm that would be tractable given modern data sets and computational technology. 'Hutchinsonian' niches are a great example in this regard because the original inspirational explanation, described in set theory (Hutchinson, 1957), later lost favour to a more implementable explanation put forward in demographic theory (Hutchinson, 1978).

Really, the enduring contribution of author-ian concepts is in their heuristic value. As distinguished by Peters (1991), this requires differentiation between *scientific aspects* (relating to predictive power of theoretical constructs) and *social aspects* of scientific concepts (relating to the communicability of concepts and their inspirational value):

> For example, the papers of G.E. Hutchinson have their greatest impact by inspiring others to explore new directions in ecology. Since the strength of such contributions does not lie in the predictions they make, the standard criteria of predictive power do not apply. Regrettably, there are few Hutchinsons and appeals to heuristic power set a dangerous precedent for scientific judgement since they can become a defence of last resort for bankrupt theory.
>
> (Peters, 1991, pp. 35–36)

We should not forget history lest we make the same mistakes, but we should not allow social and historical aspects of our science to become confused with, or take over from, scientific aspects (and vice versa). These authors contributed to the contemporary grammar of ecological thinking, but this does not mean that these ideas directly give rise to predictive, operational or tractable concepts given our modern applications. Instead, we should acknowledge how our science has developed since the oldest version of ecological ideas and discard 'author-ian' niches.

Ditch the 'fundamental niche'

Hutchinson conceived the 'fundamental niche' as a description of where a species would exist within an n-dimensional hypervolume of variables in the absence of competition – 'every point in which corresponds to a state in the environment which would permit the species… to exist indefinitely' (Hutchinson, 1957, p. 416). Hutchinson considered this a pre-interactive outcome because competition was absent. The post-interactive realized niche was the portion of that hypervolume occupied after species had interacted (see also 'realized distribution'; Soberón, 2007). Hutchinson's general ideas have been hugely influential (Chase & Leibold, 2003) perhaps because of the mapping between an abstract niche space and a real geography (Colwell & Rangel, 2009; Peterson *et al.*, 2011). However, this mapping is only possible because three key ecological concepts are not included.

First, the n-variables cannot change in the presence of the focal species (see also Leibold, 1995). Thus variables must be conditions (scenopoetic variables) and not resources with which species interact (bionomic variables), i.e. it must be assumed that a tree would not affect the water availability it relies on. This issue is central to the characterization of variables. For instance 'scenopoetic' variables as posed by Hutchinson (1978) are invariant to species but 'bionomic' variables have feedbacks with species. The fundamental niche concept requires that variables and species are independent of each other and that they are at equilibrium and without any dynamic feedbacks.

Second, the *n*-variables cannot have interactions with any other *n*-variables. For example, flowers are essential dimensions of pollinators' fundamental niches but the flowers' fundamental niches will include different types of responses or different variables to those of the pollinators. Similarly to the principle above, it is then difficult to rationalize the fundamental niche because the fundamental niche of one species contains the realized niche of another species, but the fundamental niche of that species contains the realized niche of the first.

Finally, the species cannot affect their own responses to those *n*-variables, e.g. there are no intraspecific interactions such as Allee effects, density-dependent effects, dispersal limitation, or source–sink dynamics (e.g. Begon *et al.*, 1996; Tilman & Kareiva, 1997). Intraspecific effects are the most overlooked issue for the fundamental niche concept but responses to population density (e.g. population regulation and Allee effects) and the spatial geometry of the landscape (e.g. dispersal limitation and source–sink dynamics) are ubiquitous in ecology and make it difficult to map indefinite existence to a single hypervolume as envisaged in Hutchinson's fundamental niche. Again, Hutchinson's (1957) definition implicitly assumes that demography results in equilibrium outcomes and that there is invariance to intraspecific context.

Thus, fundamental niches are only coherent concepts when species are invariant to themselves, variables are invariant to everything else, and where direct mapping from fundamental to realized niche space is possible. Otherwise, the 'chicken or the egg' arguments arise because a fundamental niche cannot be calculated without knowing a realized distribution. Each realization of the realized niche is dependent on a real world context, e.g. defined by resource availability and species' interactions.

The models and numerical languages we use to describe systems are synthetic and are only simplified versions of the systems being modelled. We might statistically model a system and create a look-up table from which we may project any given scenario (Fig. 1), the essence of SDM (Peterson, 2006; Colwell & Rangel, 2009). In contrast, we may attempt a dynamic model that follows representations of real-world steps (e.g. Cabral & Schurr, 2010), and where the properties emerge from systems' history and feedbacks (Fig. 1). The fundamental niche is not necessarily as relevant for 'dynamic' models because of the chicken-and-egg arguments outlined above. Thus, we have to recognize when the fundamental niche concept is a property of only some, rather than all, ecological models. We could always look for some part of any model that is invariant to context (e.g. Holt, 2009; Ricklefs, 2010) but that does mean it is equivalent to the fundamental niche concept. For instance, the look-up table of SDM is widely considered to be of the realized distribution (Guisan & Thuiller, 2005) and not the fundamental niche. Arguably, the fundamental niche concept posed by Hutchinson has not yet been implemented for SDM because SDM does not include direct representations of competitive interactions. Because we cannot reconcile the Hutchinsonian niche concept with a broader sample of contemporary ecology, we should reconsider when it is useful and relevant for SDM and ecology.

Ostensive niche definitions

Whilst the authors who inspired ecology may not have explicitly stated operational or implementable frameworks for their niches (e.g. Grinnell, 1917; Hutchinson, 1957), many researchers have done exactly that in their own studies. These are 'ostensive' niche definitions because they illustrate the meaning of something by giving examples of that thing. For example, a government's policy might be defined by its manifesto (the 'intensional' definition) but alternative ostensive definitions may be revealed by examples of policy implementation. Comparison of these two definitions can reveal where concepts are useful and implementable, but also where real-world complexities require alternatives.

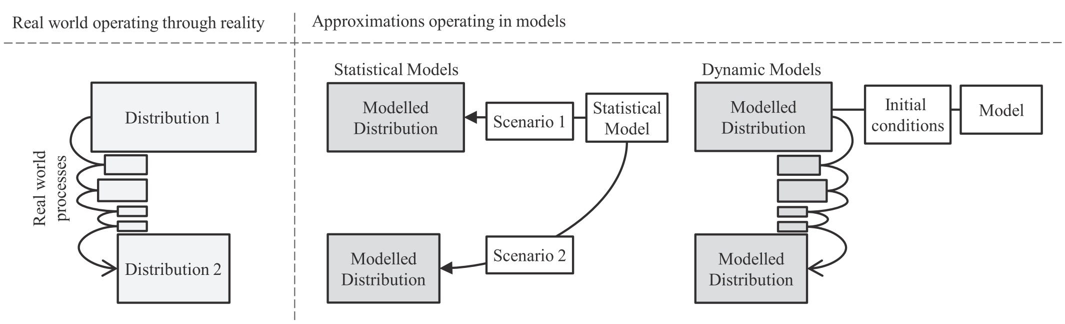

Figure 1 A simple schematic showing the relationship between two observations of a species distribution in the 'real world', 'statistical models' and 'dynamic models'. How we understand the world to work is not always mirrored in our models. Modelling objects by correlation using 'statistical models' allows simple look-up tables. 'Dynamic models' may not rely on equilibrium outcomes and take into account context-dependence that is built up through a system's history.

'Niche' has been modelled in two main ways (see also Holt, 2009). First, 'forward models' that are based on experimental observations of energy balance, survival and growth, or demographic rates of populations, in relation to particular combinations of environmental variables (e.g. Birch, 1953; Davis *et al.*, 1998). Ecophysiological (e.g. see Buckley, 2008) or demographic models (Gause, 1934; Holt, 2009) may be constructed from these measurements. Despite similarities to particular niche definitions, experimental systems more frequently require alternative concepts for their explanation (Benton *et al.*, 2006; Holt, 2009). For instance, alignment with Hutchinsonian concepts, and so the fundamental niche concept, may be paradoxical where density-dependent processes are operating (see above). These ambiguities have inspired sub-definitions such as 'establishment niche' and 'population persistence niche' (Holt, 2009), or the 'individual' and 'population' niche (Ricklefs, 2010) which are explained via the terminology of population ecology (e.g. Allee effects, life histories, maternal effects and source–sink dynamics) and ecophysiology. Because these sub-definitions are heavily reliant on other ecological concepts and terminology for explanation, and those ecological concepts are not reliant on these niche sub-definitions, we should ask whether ecology can be more clearly explained without the term 'niche'.

'Niche' originated from field observations of species' distributions (Grinnell, 1917). The real world is determined by very many more variables but the concepts we use to analyse real distributions are often far simpler. These analyses represent our second ostensive niche definition, 'backward models' such as SDM (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009).

Backward models have been variously aligned with a number of concepts, from 'environmental' to 'ecological' niches, the ideas of Grinnell (1917) and Hutchinson (1957) (see also Guisan & Thuiller, 2005; Soberón, 2007), and to many other concepts (climate envelope, habitat suitability, resource selection, climate affinity, predictive habitat modelling). But these differences in naming are not necessarily accompanied by significant changes in models or modelling methodologies. What is consistent is the model algorithm, which represents a hard-coded component of our activities, from which our interpretations must be justifiable. Models can be characterized by different data types and dependent variables (e.g. presence, presence–absence, abundance), model structures (e.g. specific model algorithms, model selection and functional forms), statistical algorithms in model fitting (e.g. within likelihood and Bayesian methods), assumptions in that blend of model–data–algorithm (e.g. inclusion of absences and how data constrain parameter estimates), units of parameters (probability distributions and their meaning), and any rules determining model simulation/projection (e.g. stochastic, deterministic, initial conditions). There should be an overall coherence in our definitions which includes our interpretations and our hard-coded models, but when there are so many other interpretations, do niche concepts really enable this backward modelling, or are they one possible set of interpretations amongst many?

Tautology and crosstalk in species distribution modelling

Does SDM model the niche? We look at some anecdotal answers to this question and consider what an intelligent layperson would be confronted by in the literature. For instance, consider someone who is investigating ecological modelling outputs for policy, or simply trying to learn what these activities do. As we shall see, the literature contains some peculiar and confusing messages.

First, publications contain crosstalk within them. For example, the abstract of Veloz (2009, pp. 2290–2291) starts with 'environmental niche models' but switches to 'ecological niche models' without explanation at the start of the introduction (see also Guo & Liu, 2010), but these names imply different types of object. What are we to take from free substitution of abiotic and biotic terms? [This is just the first example we came across and we do not single out Veloz (2009).]

Second, web searches can return important SDM papers that do not mention 'niche' except in their keywords, acknowledgements or references (e.g. Thuiller, 2003; Elith *et al.*, 2006). These papers appear to have already ditched the niche, using it as a link to the literature but not for explanation. For instance, Elith & Leathwick (2009, p. 688) state that 'neutral terminology […] seems preferable' and so use 'species distribution modelling' as opposed to 'ecological niche modelling'. 'Niche' terminology is devalued if it is so interchangeable with 'neutral' terminology.

Our third observation looks at 'software notes' which, in the developer's words, state what methods were developed for. Again, there is considerable crosstalk. For instance, Guo & Liu (2010, p. 637) state that ModEco is for 'ecological niche modelling' but switch to 'environmental niche modelling' later. Guo & Liu (2010, p. 637) also state that there are 'many environmental niche modelling packages… for example, MaxEnt… and GARP' and that 'BIOMOD… implements a range of ecological niche models'. MaxEnt and GARP are not necessarily considered environmental niche models elsewhere, nor is BIOMOD necessarily considered an ecological niche model. Elith *et al.* (2011, p. 43) state that MaxEnt is for 'modelling species distributions', Phillips *et al.* (2006, p. 232) say it is for modelling 'species' environmental requirements', and Phillips *et al.* (2004, p. 655) say it is for 'modelling species geographic distributions' while the software website says 'species habitat modelling' (http://www.cs.princeton.edu/~schapire/maxent/). Stockwell & Peters (1999, p. 143) state that GARP is for 'spatial modelling of the distribution of species', but the website says it creates 'ecological niche models for species' (http://www.nhm.ku.edu/desktopgarp/UsersManual.html). So was BIOMOD an 'ecological niche model'? Not according to the original papers (Thuiller, 2003; Thuiller *et al.*, 2009), where neutral terminology is used. This whole situation becomes very confusing very quickly. Each terminology has different connotations for model selection and interpretation, and associates those models with different literatures.

One of the newest SDM tools, openModeller is said to be 'a powerful tool for potential distribution modelling' (de Souza Muñoz *et al.*, 2011) with the model website stating an aim for 'fundamental niche modelling' (http://openmodeller.sourceforge.net/), explained as:

> While suitable environmental conditions determine a species' fundamental niche, biological factors such as competition tend to reduce the fundamental niche into the realized niche. The potential distribution of a species can be seen as the geographical expression of its realized niche at a particular time…
>
> (de Souza Muñoz *et al.*, 2011, p. 113)

Thus, openModeller sets itself apart by targeting factors giving rise to species' distributions (hence 'potential distribution') rather than modelling the observed patterns in terms of environmental variables (de Souza Muñoz *et al.*, 2011). A potential distribution is defined by omitting the accessibility of locations to species (through dispersal and landscape characteristics) from the dimensions of the niche (e.g. Peterson, 2006). This is also an example of explaining model outputs by creating another object – potential distribution – which the original concepts do not use (Hutchinson, 1957; Soberón, 2007). This is a key example because openModeller uses some of the same methods [e.g. artificial neural networks (ANN), random forests, and some methods related to BIOCLIM] as BIOMOD, which states different aims (see Thuiller *et al.*, 2009).

Finally, software documentation may state a purpose but it may be used to model something else. Can a species distribution model produce models of niches (e.g. Broennimann *et al.*, 2007)?

Numerous authors have called for clarity about what objects are modelled by SDM (Araújo & Guisan, 2006; Soberón, 2007). Terminology becomes a bigger issue when outputs and projections are compared across different models (Guisan & Thuiller, 2005). Some of this crosstalk represents different schools of thought (Thuiller, 2003; Peterson, 2006; Elith & Leathwick, 2009; de Souza Muñoz *et al.*, 2011). However, this crosstalk builds internal and external barriers to understanding a research domain that may be better defined by methods (see above). Many SDM techniques use very general statistical modelling methods and so we might expect confusion about what niche concept each technique is or is not able to investigate. In summary, while there are supporters of the niche (e.g. Peterson *et al.*, 2011; de Souza Muñoz *et al.*, 2011), there are important components of the literature that do not suggest that SDM methods rely on niche terminology (e.g. Elith & Leathwick, 2009; Thuiller *et al.*, 2009).

SUMMARY

The more we look at the use of niche concepts the less useful they seems. Because of the myriad objects and processes used under the term 'niche', the terminology has become a real barrier to understanding (Kulesza, 1975). Like sets of equations with common symbols for unrelated parameters, or equations with different symbols for the same parameters, 'niche' defies any absolute meaning and requires qualification with a lower-level terminology. Thus it holds a symbolic role in ecology rather than any defining purpose for modern ecological practice in SDM or otherwise.

Aligning method and concept retrospectively may have always meant that the relationship between 'niche' and SDM was destined for confusion and crosstalk. SDM has grappled with niche concepts implicitly and explicitly – explicitly because some authors have tried to resolve the SDM activity through niche concepts (e.g. Araújo & Guisan, 2006; Soberón, 2007; Colwell & Rangel, 2009) and implicitly because key components of niche concepts are touched upon, but 'niche' is ignored (e.g. Thuiller, 2003; Elith & Leathwick, 2009). Reconciling the diversity in methods and concepts perhaps becomes even harder as the SDM literature becomes ever larger. At least this growth offers a chance to examine the failures of the niche concept. Our examination here is deliberately one-sided and sceptical of the importance of 'niche' because a robust concept should pass some basic tests of this kind. The evidence has not proved to be very positive. As it stands, even expert researchers in the field, let alone the public and polity, will struggle to understand the products of niche research. This demands that we develop a more critical usage, or use alternative conceptual grammar; otherwise our communications are easily undermined and our approach to science becomes cloudy. There is no one 'niche' that pervades through ecology or even the sub-discipline of SDM. Let us ditch the niche.

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BIOSKETCHES

Greg J. McInerny is a Senior Research Fellow in Information Visualisation, working on new approaches to both spatial and visual analytics. Alongside his research in species distribution modelling, Greg is interested in the feedbacks between the structure, generation and regulation of biodiversity, and the role of software in modern scientific practice.

Rampal S. Etienne is an evolutionary community ecologist at the University of Groningen, The Netherlands. His research focuses on eco-evolutionary explanations of macroevolutionary and macroecological patterns. In particular, he constructs parsimonious stochastic models and derives likelihood formulae that can be used to fit the models to data. He also has an interest in the philosophy of ecology and evolutionary biology.

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