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In defense of 'niche modeling'

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There is a growing awareness of problems with the estimation of the ecological tolerances of species through correlative modeling approaches. These problems have led some investigators to argue for abandoning terms such as 'ecological niche model' and 'environmental niche model' in favor of the ostensibly more value-neutral 'species distribution model', as the models are thought to frequently be poor estimators of the niche. Here, I argue that most applications to which these models are put require the assumption that they do estimate the niche, however imperfectly, and that obscuring this inescapable and potentially flawed assumption in the terminology may only serve to hinder the development of the field.

Taking the niche out of niche modeling

Recent years have seen an explosion of interest in building correlative models of the environmental tolerances of species based on presence, absence and abundance data. There has been a concurrent development in the breadth of the questions to which those models are applied, ranging from studies of the effects of climate change on the distribution of suitable habitat to species delimitation and the study of niche evolution [1–3]. Throughout this period of development, there has been a discussion of what, if any, aspect of the biology of a species these models estimate [4–8], including attempts to determine the appropriate interpretation of these models in the context of the existing literature on niche concepts [7,9,10]. As a result of their entirely justified skepticism and uncertainty about these models, many investigators have recently advocated a move away from calling them 'ecological (or environmental) niche models' (ENM) to the ostensibly more value-neutral term 'species distribution models' (SDM), regardless of how the models are constructed or applied. This terminology has been promoted by some of the most respected investigators in the field [11], and the suggestion has already been widely accepted. However, I argue here for the continued use of the term 'niche model', for the simple reason that most applications of ENM/SDM methods require the assumption that such models estimate some subset of the conditions within which a species can survive and reproduce (i.e. the niche). The question of precisely which aspects of the niche are being estimated is a subject of considerable debate and controversy and, rather than attempt to resolve the issue here, I use the preceding broad definition and refer the reader to the copious literature on the topic for further discussion [4–8,12–14]. I am not arguing that the term 'distribution model' be deprecated, or that anybody should necessarily switch from terminology that they are comfortable with; rather, I am demonstrating that the niche assumption is frequently necessary when constructing and applying these models, and that assumption cannot be avoided by simply avoiding the term. Therefore, this is not simply an argument about terminology. It is an argument, or at the very least a reminder, about the assumptions implicit in the construction and use of these models.

Issues with modeling the niche from distributional data

It is clear why many investigators would prefer to think of ENMs/SDMs as pertaining to the distributions of species rather than to their niches. The data used to construct models come only from the distribution of a species, which at best may represent just the subset of its niche that is present in the realized climate space when the data are collected [15] and from which it is not excluded by biotic and mobility factors [4,6,7,16]. Even within this subset, dispersal may lead to species frequently occurring in sink habitat, resulting in distributional data that may be misleading about the suitability of habitat [17]. The climate variables typically used in model construction are, in most cases, not thought to be directly limiting the distribution of the species, in which case the models they produce are at best indirect estimates of the niche. At worst, any explanatory power these variables have may be simply the result of chance interactions between the spatial autocorrelation in the distributions of the species and the spatial autocorrelation in the environmental predictors [18], rendering any biological interpretation of the models meaningless.

Each of the above factors implies that models built from distributional data should be interpreted with substantial caveats even if the distribution and abundance of the species is known perfectly. When one begins to think about the additional limitations imposed by the manner in which real distributional data are collected, the prospect for estimating the niche seems bleak indeed. Real data are often incomplete, spatially biased, subject to errors in species identification and georeferencing, rarely include abundance or reliable absence information, and are frequently collected across several years in areas subject to substantial interannual climatic variation that is not reflected in the environmental predictor data used in modeling [19]. Any of these sources of inaccuracy may serve to limit our ability to model the niche and, unfortunately, most data sets that are available for model construction are subject to many, if not all, of them. Indeed, it often seems that most of the methodological issues that arise in the construction and application of ENMs stem from dealing with problems in the source data rather than in the modeling process itself.

An additional set of problems arises from the fact that there are both technical and conceptual difficulties with model evaluation, so that it is difficult in many cases even

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to measure the relative value of two models (or modeling approaches) [20–25]. More generally, it is difficult to measure model quality using presence-only data when the optimal fit to both training and test data may be obtained by a model that is a poor estimate of the underlying biology (i.e. when the model is strongly affected by processes such as spatial sampling bias, dispersal limitation, or overparameterization), whereas a model that more accurately represents the tolerances of the species does a comparatively poorer job of predicting their occurrence [26,27].

The niche assumption: it is there whether we want it or not

With all of the methodological issues surrounding the construction and use of niche models, it is easy to understand why many would be willing to use these methods while simultaneously being loath to give the appearance that they interpret them as estimates of the niche of the species. However, I would argue that use of the term 'species distribution modeling' may in many cases serve to obfuscate assumptions that are nonetheless being made. The niche assumption is fairly transparent in most of the evolutionary studies that use niche models. Whether used in species delimitation [1], studies of niche evolution [28–31], or examining the ecological relevance of biogeographic barriers [32,33], the models are usually explicitly used as an estimate of, or proxy for, some aspect of the niche. This approach has enabled the examination of large-scale patterns of niche evolution that would have been intractable via direct observational or experimental approaches. It is not necessary to believe that the models are perfect or complete estimates of the niche to use them in this context: even inaccurate estimates of the niche may still be informative for comparative studies so long as the differences between models are not on average misleading about the true differences among the niches of the species being compared.

The niche assumption made when using these methods in ecological and conservation studies is often less transparent, but is no less fundamental to their use. The assumption is perhaps at its most clear when it comes to the choice of explanatory variables. The typical set of variables used in model construction will include factors such as temperature, precipitation and vegetation. It is difficult to see why these variables would be chosen if the only intent was to model the spatial distribution of the species per se, particularly given the abundance of simple methods that are capable of using strictly spatial data to produce range maps and spatially interpolated density surfaces (Figure 1). In fact, it has been shown that strictly spatial data can, in some cases, model the distributions and abundances of species within the training area as well as, if not better than, the environmental variables that are typically used in the construction of niche models [18].

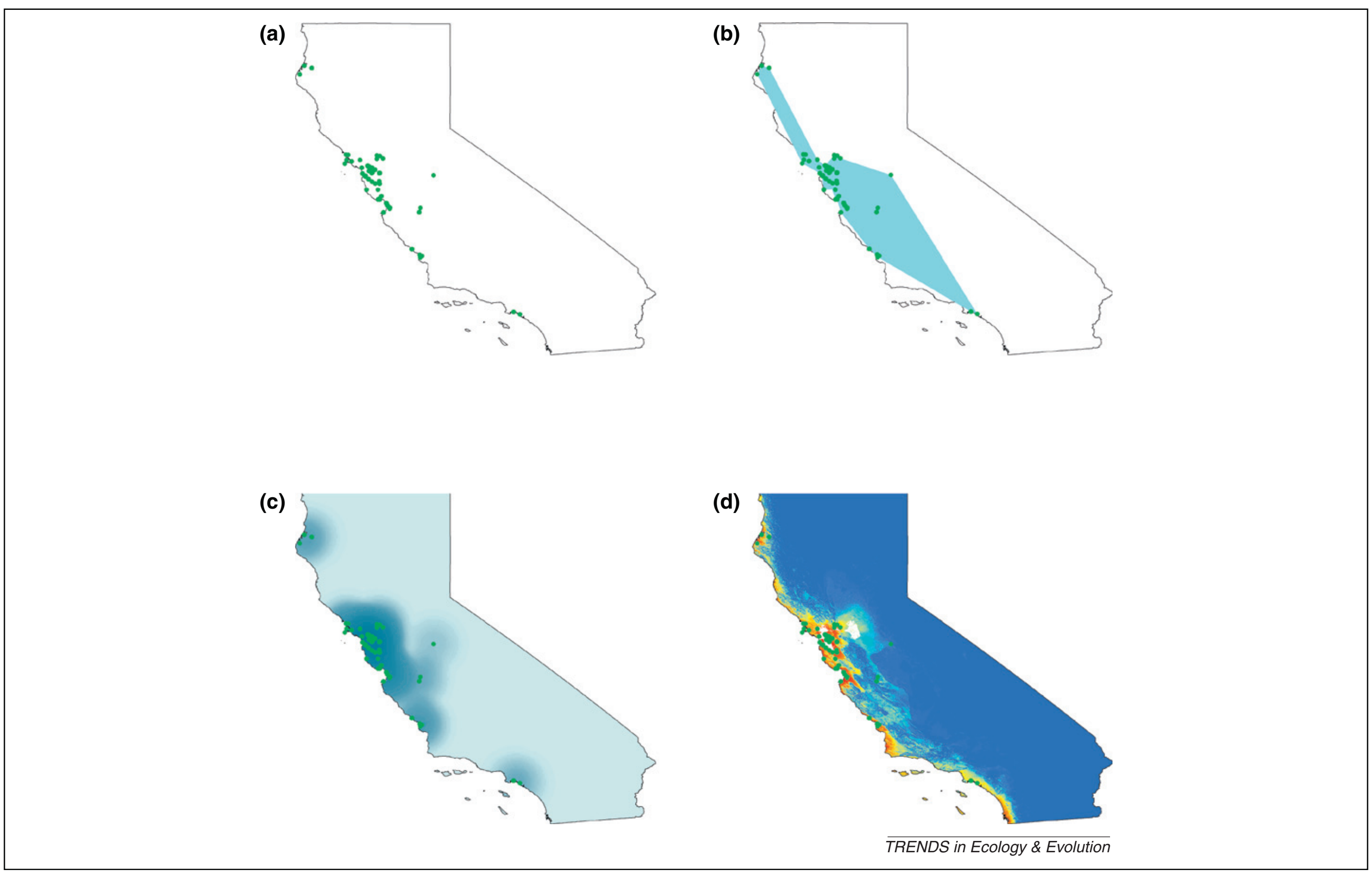

Figure 1. Spatial versus ecological models. For a set of occurrence records in geographic space **(a)**, it is possible to build an entirely spatial model of the distribution of the species. This can either be achieved by producing polygonal range maps based on occurrence points **(b)**, or by creating an interpolated surface based on the local density of observations **(c)**, where intensity of color represents local density. In either case, the intent is not to model the niche, but rather to generalize the spatial distribution of observations By contrast, a niche model attempts to correlate those observations with environmental variables and use those correlations to predict the suitability of habitat **(d)**. Although any of these approaches could be said to model the distribution of the species, it is only the latter approach that can be used to infer the relative importance of environmental variables and to extrapolate to different regions or time periods, as it is the only approach that involves the production of a niche estimate.

There are clear practical reasons why environmental predictor variables are chosen to model the distributions of species. For one thing, strictly spatial models are, by definition, not transferable to other geographic regions. They will inevitably predict that the species is absent (in the case of range maps) or that it appears at very low density (in the case of interpolated density surfaces) in areas that are sufficiently far from the observations used to create them (Figure 1). In a world with a changing environment, they are not usually transferable in time in a useful fashion either; they contain no information about the response of the species to environmental factors, and so cannot estimate range shifts in response to a changing world. However, there is no clear reason to expect better performance from a model based on environmental predictors unless one makes the assumption that the correlations between the distribution of the species and those environmental predictors estimate, however imperfectly, an underlying biological phenomenon that is conserved over time and space. What should that phenomenon be called, if not the niche? Without the niche assumption, there is no clear reason to expect that the present and future distribution of a species should be connected through a set of environmental predictors; if a model built using those predictors is not intended as an estimate of the environmental tolerances of the species, transferring that model to another space or time should be as uninformative as transferring a purely spatial model would be. This is not to suggest that spatial models per se are not useful; there are many applications in evolution and ecology for which a strictly spatial understanding of the distribution of a species is all that is needed. However, strictly spatial models are not useful for many of the purposes to which ENMs are typically applied, and the very reason they are not applicable to those questions is that they refrain from estimating the niche [7].

It is also understandable that some investigators are concerned that the variables typically used in niche modeling may not be directly responsible for limiting the distribution of a species, but may instead only be spatially correlated with some other factor that is more directly relevant to the species. However, this indirectness is not unique to correlative approaches to niche estimation based on distributional data. The history of ecology is one of highly indirect niche estimates, from functional characters [34,35] to isotope ratios [36]. Neither is it unusual for niche estimates to be made on an incomplete subset of the axes that may be relevant to a species. For example, almost the entirety of competition theory (which is historically almost synonymous with 'niche theory') focuses only on the shared niche axes that are limiting for an interacting set of species [9,37–41]. Owing largely to the expense and difficulty of ecological studies, the history of empirical study of the niche is one of indirect, incomplete and almost certainly inaccurate niche estimates. If one was to refrain from using the word 'niche' except in cases where one was certain that the niche was estimated completely, accurately and using variables that were directly relevant to the species, the word would probably not be used in the empirical literature at all.

Certainly the conceptual framework for interpreting ENMs in the context of the ecology of species and more traditional niche concepts is not yet complete, but it is an active area of research and discussion [4–8]. Many of the issues that cause difficulty for modeling also serve to confuse the ecological interpretation of the models, but their effects on model interpretation can often be outlined in concept even if they frequently cannot be estimated empirically. I am not aware of any comparably developed conceptual framework that justifies the use of an ENM for many of the applications for which they are typically used that does not require the assumption that they estimate the niche. In the absence of such a framework, I feel that it is essential that we as ecologists acknowledge the presumptive conceptual framework that is actually being using in our research, with all of the flaws and inaccuracies that accompany it. By acknowledging that we are at least attempting to estimate the niche, we can use that conceptual framework to determine when and how our methods are likely to fail.

Concluding remarks

Given these methodological and conceptual issues, it might seem that there is an impending existential crisis in the niche modeling community. Nothing could be further from the truth. It might be argued that basic evolutionary and ecological studies could wait for more reliable methods and data sources to be developed, although given the current proliferation of such studies, such a hiatus seems unlikely in the near future. However, one of the primary drivers of the use and development of niche modeling methods is the estimation of the biological effects of climate change, habitat loss and invasive species. Here, it is hard to argue for a cessation of modeling while issues of methodology and data quality are ironed out. Although the above problems may limit the reliability of niche models, in many cases they are still the best niche estimates available to us. For many conservation issues, time is a critical constraint. A flawed estimate of the environmental tolerances of a species today is more valuable than a perfect estimate at some unspecified time in the future if that flawed estimate allows timely action that has a positive effect on conservation outcomes. The primary virtue of niche modeling methods is that they are tractable when nothing else is, and that they appear to contain some useful information for many applications where any information whatsoever is desperately needed. They may be deeply flawed as niche estimates, but they are nonetheless extremely useful. Therefore, niche models are here to stay for the foreseeable future.

So what of the terminology? Ultimately, it is of little consequence if it does not change how the models are constructed or applied, and I am not arguing that the term 'species distribution modeling' itself is problematic. Neither would I argue that the proposed distinctions between ENMs and SDMs based on methodology or data sources [7,42] should be abandoned; to whatever extent those distinctions are useful, they should be maintained. However, many applications that are termed SDM by these criteria still rely on environmental data and interpolation or extrapolation from a mathematical model of the environmental tolerances or preferences of the species, and I fear that some may think that retreating from the term 'niche model' allows them to forego the assumption that those models represent some aspect of the niche. This is not the case for most applications, and the history of biology contains many examples where a failure to explicitly state assumptions and definitions has led researchers astray for years at a time and sometimes caused unnecessary confusion and acrimonious debate [43–47]. The fact that one might be justifiably skeptical about the niche assumption is not a sufficient justification for refusing to use the term 'niche', when estimating the niche is the intended purpose of a model. It is precisely when assumptions are at their most questionable that it is most important that they are made explicit; progress in science begins with acknowledging the shortcomings of the current state of the art. Although I sympathize with the motivations for referring to these models as 'species distribution models', I will continue to call them 'niche models' when I am applying them as such. By doing so, I acknowledge that I am of necessity making an assumption that I myself find suspect, and remind myself of the consequences should that assumption fail to be met. The assumptions made are implicit in the ways that models are built and used. One cannot escape making those assumptions, or the consequences of having made them, simply by refusing to speak their names.

Acknowledgments

The author is indebted to Will Godsoe, Amber Wright, Camille Parmesan, Sahotra Sarkar, Stavana Strutz, Ben Labay, Kumar Mainali, Teresa Iglesias and Nichole Bennett for many stimulating conversations on this topic, and NSF grants DBI-0905701 and SES-1049208 for financial support. The author would also like to acknowledge the efforts of four anonymous referees who contributed significantly to this manuscript.

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