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Habitat, environment and niche: what are we modelling?

M. Kearney, Dept of Zoology, The Univ. of Melbourne, Victoria, Australia 3010 (mrke@unimelb.edu.au).

The terms 'habitat', 'environment' and 'niche' are used inconsistently, and with some confusion, within the ecological literature on species distribution and abundance modelling. Here I suggest interrelated working definitions of these terms whereby the concept of habitat remains associated with descriptive/correlative analyses of the environments of organisms, while the niche concept is reserved for mechanistic analyses. To model the niche mechanistically, it is necessary to understand the way an organism's morphology, physiology, and especially behaviour, determine the kinds of environment it experiences when living in a particular habitat, and it is also necessary to understand how those environmental conditions affect fitness (growth, survival and reproduction). While distributions can potentially be predicted by modelling descriptions or correlations between organisms and habitat components, we must model an organism's niche mechanistically if we are to fully explain distribution limits. A mechanistic understanding of the niche is also critical when we want to predict an organism's distribution under novel circumstances such as a species introduction or climate change.

It has long been recognized that fundamental ecological concepts including 'habitat', 'environment' and 'niche', lack rigorous and consistent definitions (Haskell 1940, Whittaker et al. 1973). The rapidly expanding field of species distribution modelling is plagued by loose and inconsistent application of these concepts in describing different methodological approaches. For instance, statistical models of point distributions of species in relation to spatial data have been variously described as modelling a species' 'habitat', 'fundamental niche', 'realized niche' or 'environmental niche'. This has led to significant confusion about what is actually being modelled and how the models should be applied. Can a 'habitat' model be used to explain a species distribution and abundance (Mitchell 2005)? Does a statistical correlation between distribution points and physical spatial data constitute the 'fundamental niche' or the 'realized niche' (Austin et al. 1990, Kearney and Porter 2004, Soberón and Peterson 2005) or should it be called a niche at all? And can we project these 'niches' onto novel landscapes, past or future, to predict changes in distribution (Thomas et al. 2004)? Perhaps it would help to answer these questions if we are more explicit and consistent about what is meant by 'habitat', 'environment' and 'niche'.

Recently, Mitchell (2005) has called into question the usage of the term 'habitat' in the context of understanding the distribution and abundance of organisms. He argued that our concept of habitat needs to be extended from its current status as a description of an organism's abiotic environment to a more mechanistic concept that includes biotic interactions, and which can be used to make quantitative predictions of distribution and abundance. He also criticized the relatively arbitrary nature of variable selection in analyses of habitat. While Mitchell's article was particularly focused on studies of distribution and abundance at the scale of the home ranges or sub-populations, his arguments equally apply to the modelling of species entire distributions since it is essentially the same process, albeit at a larger spatial and temporal scale.

I propose a solution to these problems, at both small and large scales, by suggesting integrated working definitions of the concepts of 'habitat', 'niche' and 'environment' for the purpose of modelling species distributions and abundances. In particular, I suggest that the concept of habitat remain descriptive, but that we reserve the niche concept for what Mitchell (2005) is calling for; a mechanistic analysis of how different environmental factors in an organism's habitat interact with the organism itself to affect its growth, survival and reproduction, i.e. its fitness. I illustrate the application of these ideas to predicting and explaining the distribution of organisms using the example of a terrestrial nocturnal lizard and its association with climate. I conclude that statistical models of species' distributions and abundances are best considered as 'habitat models' since they describe associations between the distributions and numbers of organisms across a landscape and physical or biotic features, without an explicit mechanism. Models that take into account the mechanistic interactions between organisms and their environments, and their fitness consequences, are best described as 'niche models'.

Integrated definitions of habitat, environment and niche

Habitat: *a description of a physical place, at a particular scale of space and time, where an organism either actually or potentially lives*.

There are many definitions of habitat, with the simplest being 'a place where an animal lives' (Morrison et al. 1998). While habitats are usually described using physical and biotic features that are thought to be of importance to an organism's distribution and abundance, a mechanistic understanding of how these features affect fitness is not necessary, and is typically lacking. Indeed, studies of habitat selection are often the first step in generating hypotheses about the mechanistic links between an organism and its surroundings. Hence I have defined a 'habitat' as simply a description of the physical nature (biotic and abiotic) of a place of interest with respect to an organism, with no direct mechanistic links necessarily occurring between those descriptors and the organism's fitness.

In contrast to an environment or a niche (below), a habitat can exist and be described without reference to an organism, even though the potential presence of some kind of organism is always implied. Most broadly, one could refer to a grassland, a savannah or a desert habitat without any specific reference to an organism. We can also describe habitats without imagining the peculiarities of the organisms that might potentially live there. For instance, a habitat on Mars could be described as an arid terrain with sandy soils and loose rock, high temperature fluctuations and a relatively low oxygen concentration (the particular descriptors just used, however, do reflect a bias towards factors known to generally influence life on earth). More often, of course, we do have a particular species in mind when referring to a habitat, but it is not necessary to refer to the traits of that organism when describing habitat. It is necessary to refer to an organism's traits, however, to know how it experiences that habitat, i.e. to understand its environment.

Environment: *the biotic and abiotic phenomena surrounding and potentially interacting with an organism*.

An 'environment' cannot be described without reference to a particular organism (Lewontin 2000), although the organism in question could be real or imagined. This usage is consistent with the etymology of the term environment, since it means 'that which surrounds or encircles'. The particular environment experienced by an organism is the result of the interaction between the characteristics of that organism and the habitat in which it occurs. This means that two organisms inhabiting the same general region on a landscape, i.e. the same habitat, may experience very different environments. Two lizards living in the same desert habitat will experience dramatically different radiation environments if, for example, one is nocturnal and the other is diurnal. They may also experience very different predators, competitors and pathogens.

Organisms can modify and, in a sense, create their environments through their behaviour, morphology and physiological processes (Lewontin 2000, Wright and Jones 2006). For instance, the concentration of nitrogen, oxygen and carbon dioxide surrounding an organism in a burrow is partly a result of its own respiration. The structure of the soil a plant is growing in depends in part on the effects of its root system. The construction of nests by birds, and dams by beavers, are other obvious examples of the way organisms dictate their own environments. Not all components of an organism's environment, however, will necessarily influence its capacity to grow, survive and reproduce.

Niche: *a subset of those environmental conditions which affect a particular organism, where the average absolute fitness of individuals in a population is greater than or equal to one*.

The concept of the niche has had a chequered history in ecological and evolutionary thought, and in recent years there has been a push to revitalize it (Pulliam 2000, Chase and Leibold 2003, Oldling-Smee et al. 2003). Most modern conceptualizations of the niche represent a version of Hutchinson's idea of the niche as a multidimensional space whose axes comprise the conditions and resources that limit an organism's survival and reproduction – the so called 'n-dimensional hypervolume' (Hutchinson 1957). This definition is very useful in the context of understanding a species distribution and abundance, and is the one used here. The niche dimensions are a subset of the environmental dimensions, comprising only those that affect fitness. Thus for many organisms, the strength of the magnetic field they experience would represent an environmental dimension but not necessarily a niche dimension. Crucially, the niche is also defined by the organism, since the specific properties of the organism determine which environmental dimensions are relevant. For example, red and blue wavelengths in sunlight are critical for a plant's photosynthetic capacity, but this quality of light may be largely irrelevant to a lizard basking on one of its branches. In this sense, a niche is a property of an organism and cannot exist without reference to a particular kind of organism. A very useful distinction within the niche concept is idea of a fundamental and a realized niche (Hutchinson 1957). When the effects of biotic interactions (competition and predation) are excluded in calculations of the effects of niche dimensions on fitness, one obtains the fundamental niche. This is the region within a multidimensional environmental hyperspace where the average absolute fitness of individuals in the population is greater than or equal to one, i.e. where the population is replacing itself or growing. When biotic interactions are included in the calculation of the niche, one obtains the realized niche which is typically a smaller volume.

According to this conceptualization of the niche, the same environment can have different fitness consequences for different organisms, depending on their particular behaviour, morphology, physiology and life history. For instance, two organisms identical for all traits except reflectivity to solar radiation may experience dramatically different body temperatures under the same environmental conditions of wind, humidity, air temperature and solar radiation. Similarly, the same food may be eaten by two different species, but the nutritional outcome may vary if they have different digestive systems. The effects of organisms on their own environments result in organisms 'constructing' their own niches (Oldling-Smee et al. 2003). A mechanistic understanding of the interaction between the biotic and abiotic environmental conditions impinging on an organism and its fitness is therefore needed to determine which environmental conditions comprise its niche dimensions, and whether a given environment lies within an organism's niche. This is a key distinction between niche and habitat, as I am using the terms; the niche is a mechanistic concept while habitat is a descriptive concept. Since the environmental variables of relevance are decided by the nature of the mechanistic interaction (for example, calculation of body temperature requires knowledge of the radiation, wind speed, air temperature and relative humidity surrounding the organism), the arbitrary nature of variable choice is removed. When a mechanistically derived niche is mapped to a real landscape, i.e. to a particular habitat, one obtains a projection of fitness, or a fitness component, which in turn allows a prediction of the organism's distribution.

Using the concepts of habitat, environment and niche to predict and explain species distributions

There are two approaches to modelling species distributions (Fig. 1). The most frequent approach is to begin with the known distribution of the organism, often using museum records or survey data, and then to statistically associate the presence, presence/absence, or abundance of the organism with spatial habitat data such as soil type, climate, topography, etc (Fig. 1a). The result is a map of the probability of occurrence of a species across a landscape, or some index of the suitability of the area for occupation. For instance, Kearney et al. (2003) modelled the distribution of different lineages of the nocturnal gecko *Heteronotia binoei* across the Australian landscape using annual averages of climatic variables including temperature, rainfall and humidity (Fig. 1a). This correlative approach to distributional modelling would, according to the definitions above, be described as habitat modelling (although admittedly it was described as environmental niche modelling in that paper!). While the climatic habitat variables used by Kearney et al. (2003) were presumed to be in some way related to the fitness of this organism, no direct mechanism of interaction was modelled and no account was taken of the way this organism actually experienced these climatic conditions as environments. For instance, mean annual temperature was important in predicting the distribution of the most southern form of this species. This may represent a direct effect of temperature on adults or eggs, e.g. death by heat or cold. Alternatively, the association with 'temperature' may reflect a thermally dependent biotic interaction with a predator, competitor or pathogen. In this sense, correlative distribution modelling cannot be used to represent the fundamental niche of an organism, despite claims to the contrary (Peterson et al. 1999, Phillips et al. 2005, Soberón and Peterson 2005). This is because the correlative approach begins with the distribution of the organism, which is the end result of all biotic and abiotic interactions. Thus, it implicitly incorporates any biotic interactions that are dependent on the abiotic variables considered (Kearney and Porter 2004). The same issue would apply to studies conducted at the scale of individuals' home ranges. Even if only abiotic factors are considered in a study of microhabitat use, the actual movement patterns of individual organisms through their habitat is likely to be a result of both biotic and abiotic interactions.

The second approach to modelling distributions is to determine the mechanistic links between an organism's environment and its fitness, and then to map the fitness consequences onto a landscape. In contrast to the correlative approach, one begins with the organism itself rather than its distribution (Fig. 1b). The output variables mapped onto the landscape are not a probability of occurrence or an index of habitat suitability, but instead are fitness components (or ideally, absolute fitness). According to the definitions above, this procedure would be regarded as 'niche modelling'. Energy balance equations have been used in this way to calculate the interaction between an animal and its habitat to predict survival, time/space utilization, and potential for growth and reproduction (Porter and Gates 1969, Roughgarden 1981, Tracy and Christian 1986, Porter et al. 2000, 2002). Kearney and Porter (2004) used this approach to map climatic components of the fundamental niche of *Heteronotia binoei* onto the Australian landscape (Fig. 1b). This was achieved by integrating individual-based mathematical models of how microclimatic conditions affect the lizard's mass and energy balance, and its potential for activity and development.

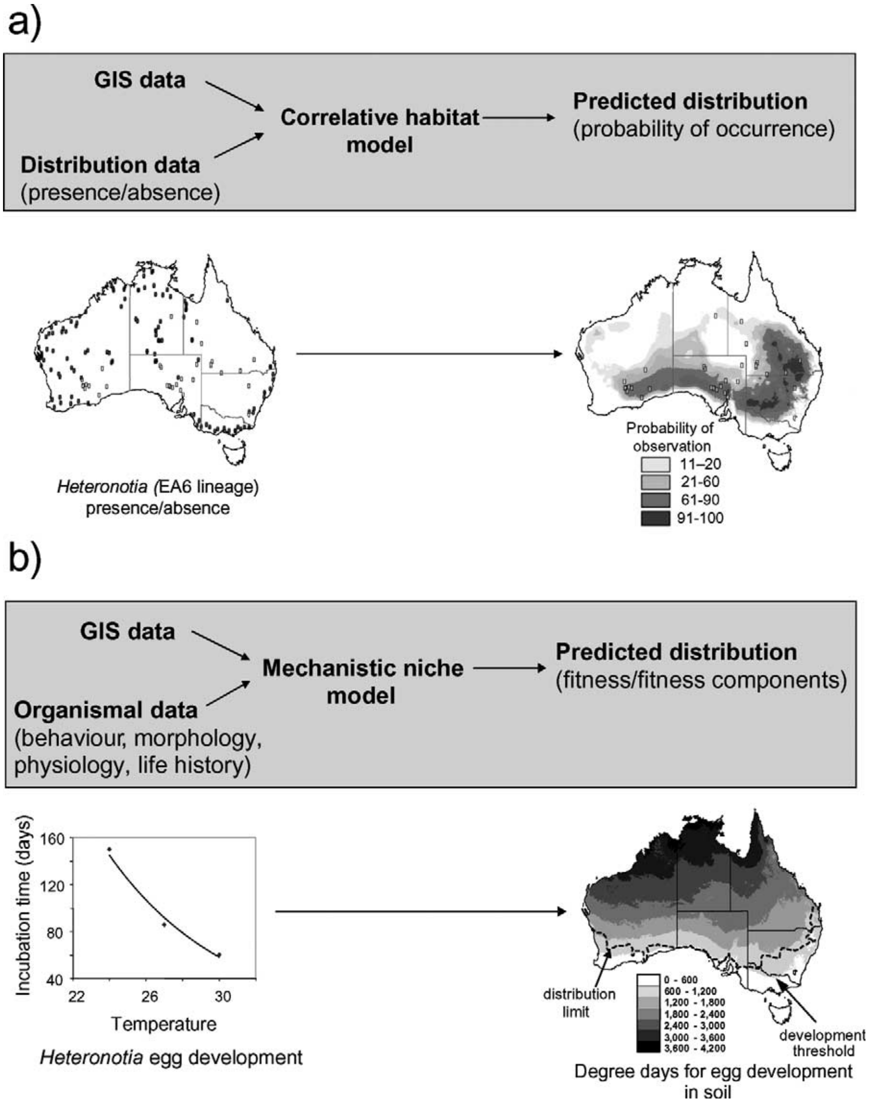

Fig. 1. Two different approaches to modelling species distributions, illustrated using a terrestrial nocturnal lizard (the Bynoe's Gecko *Heteronotia binoei*) from Australia. In the correlative approach (a), distribution data (presence/absence) and GIS habitat data are associated statistically, often in the form of a regression model, and this statistical relationship is interpolated across the all regions for which spatial data is available to predict areas of high probability of occurrence. In the example given, the presence/absence of a particular lineage (EA6) of *H. binoei* in relation to mean annual temperature, rainfall and humidity has been modelled using a logistic regression approach (Kearney et al. 2003). In the mechanistic approach (b), the interaction between the properties of the organism and the environmental conditions surrounding it are mechanistically modelled to determine the fitness consequences, which are then mapped onto the landscape. In the example given, physiological data on rates of egg development at different temperatures have been combined with a microclimate model of soil temperatures to predict the daily accumulation of physiological time (degree days) available above a certain temperature threshold (20°C) for development of *H. binoei* eggs, summed over a year, at 5 km intervals across the Australian continent. The contour of minimum degree days required for hatching (600 degree days) is marked with an arrow, as is the actual distribution limit. For more details see Kearney and Porter (2004).

A microclimate model took coarse climatic spatial data (interpolated from weather stations), as well topographical data, and constructed hourly estimates of spatial variation in temperature, wind, humidity and radiation above and below ground. An animal model then took the output of the microclimate model and determined how these environmental conditions interacted with the behavioural, morphological and physiological properties of different life stages of the lizard to affect important components of its fitness. The outputs could then be projected on a map to visualise regions that were within the fundamental niche of the organism. This approach suggested that temperature was limiting the distribution in southern parts of the range by restricting the potential for above-ground activity, and by limiting the development of eggs below ground.

Ultimately one would extend this process to determine the average absolute fitness of organisms in the population through modelling the total energy and mass balance and obtaining the potential for reproduction.

Recent advances in metabolic (van der Meer 2006) and nutritional (Raubenheimer and Simpson 2004) theories in ecology will undoubtedly enhance the potential for such energetics-based niche modelling in the future. This will bring us closer to generating a complete depiction of the fundamental niches of organisms mapped onto real landscapes. Despite suggestions otherwise (Soberón and Peterson 2005), biotic interactions between key species can also be analysed in this manner by concurrent analyses of competing species, or between predator and prey, and determining, for example, potential overlap in activity times or in the use of space (Roughgarden 1981, Porter et al. 2002). This allows visualisation of the distributional consequences of a constriction of the fundamental niche to a smaller 'realized niche'. Nutritional and metabolic niche models must also be integrated with other individual-based models of processes such as dispersal and adaptation (DeAngelis and Mooij 1995, Pulliam 2000). This will allow mechanistic analyses of the ecological and evolutionary consequences of range expansions and contractions, and other non-equilibrium situations, as well as the consequences of individual variation in morphology, physiology and behaviour.

Implications and conclusion

I have presented an integrated way of using the terms 'habitat', 'environment' and 'niche' in the context of modelling species distributions and abundances. According to these definitions, the concept of 'habitat' can be applied in *describing* the association between organisms and features of a landscape. The concepts of 'environment' and 'niche', however, imply knowledge of the behavioural, morphological and physiological properties of an organism. The niche concept in particular implies and understanding of how an organism's properties interact with its surroundings to influence its fitness.

If correlative analyses of distribution are to be described as niche analyses at all, they are best considered as a multivariate statistical description of the realized Hutchinsonian niche (Austin et al. 1990, but see Whittaker et al. 1973). In a sense this is consistent with Hutchinson's original derivation of the concept since he did not explicitly require a mechanistic link between niche dimension and organism when proposing his concept. More recent treatments of the niche, however, have opted for a more mechanistic framework (Leibold 1995, Pulliam 2000, Chase and Leibold 2003), and perhaps it is time to extend this conceptualization of the niche to distribution modelling (Pulliam 2000, McGill et al. 2006). Describing correlative distribution analyses as modelling species habitats, rather than fundamental or realized niches, may help to reinforce the descriptive nature of correlative analyses, and discourage their inappropriate use. For instance, it is well established that extending a regression beyond the limits of the data from which it is derived is extremely risky as there is no way of knowing if the described relationship will continue in the same fashion. Yet this is routinely done when correlative models of species distributions are extrapolated to novel circumstances such as climate change or species introductions.

Species distribution modelling approaches that are based on knowledge of the mechanistic interactions between an organism and its environment can more confidently be extended to novel situations. While such mechanistic niche approaches are undoubtedly more difficult to undertake, and will often be of reduced predictive power in comparison to correlative habitat analyses, they provide considerably more explanatory power (Kearney and Porter 2004, Chamaillé-Jammes et al. 2006). Presently, the ease with which GIS data can be integrated with species distribution data means that most approaches to modelling species distributions and abundances are descriptive exercises of habitat modelling. Considerably more effort needs to be applied to the problem of using GIS data to mechanistically model species' niches.

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