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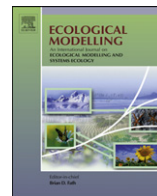
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Short communication

What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods

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ABSTRACT

Species distribution model is the term most frequently used in ecological modelling, but other authors used instead predictive habitat distribution model or species-habitat models. A consensual ecological modelling terminology that avoids misunderstandings and takes into account the ecological niche theory does not exist at present. Moreover, different studies differ in the type of niche that is represented by similar distribution models. I propose to use as standard ecological modelling terminology the terms “ecological niche”, “potential niche”, “realized niche” models (for modelling their respective niches), and “habitat suitability map” (for the output of the niche models). Therefore, the user can understand more easily that models always forecast species’ niche and relate more closely the different types of niche models.

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Ecological niche, species distribution, habitat distribution, or climatic envelope models are different names for similar mechanistic or correlative models, where field observations are related with environmental predictor variables based on statistically or theoretically derived response surfaces (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Peterson, 2006; Pearson, 2007; Kearney and Porter, 2009). Therefore, other modelling methods based only on spatial variables (e.g. interpolation of locations of species’ presences, disregarding any environmental correlation) are not based on ecological niche theory, and thus they cannot be considered ecological niche models. I will consider in this work only those models based on environmental variables.

Species distribution model is the term most frequently used, especially for correlative models (e.g. Austin, 2002; Guisan and Thuiller, 2005; Pearson, 2007; Lobo et al., 2010), but other authors prefer predictive habitat distribution model (Guisan and Zimmermann, 2000) or species-habitat model (Rushton et al., 2004). Notwithstanding their many applications (see for a review Guisan and Thuiller, 2005; Peterson, 2006; Wiens et al., 2009), the procedure always involves the calculation of a model that approximates the species’ distribution niche. However, Soberón and Peterson (2005) and Soberón (2010) made a distinction between species distribution models (for predicting strictly the species’ distribution) and ecological niche models (for forecasting

an approximation to the species’ niche). This distinction illustrates the lack of consensual ecological modelling terminology, necessary to avoid misunderstandings (Kearney, 2006; Hirzel and Le Lay, 2008) and to take into account the ecological niche theory (Peterson, 2006). Hence, I aim to present a proposal for a standard ecological modelling terminology.

The theoretical framework of ecological niche models (hereafter ENM) is based on the ecological niche concept (Guisan and Zimmermann, 2000; Pulliam, 2000; Kearney, 2006; Soberón and Peterson, 2005; Soberón, 2007; Soberón and Nakamura, 2009; Wiens et al., 2009), a central theme in ecology and evolutionary biology (Holt, 2003). Grinnell (1917) understood the niche as a subdivision of the habitat containing the environmental conditions that enable individuals of a species to survive and reproduce, based on broad-scale variables (climate) that are not affected by species density (Hirzel and Le Lay, 2008; Wiens et al., 2009). Elton (1927) emphasized the functional role of a species in a community, especially its position in food webs, based on fine-scale variables (nutrients) that may be consumed or modified by the species. Hutchinson (1957) defined the species’ “fundamental niche” as the n -dimensional volume in the environmental space where a species can maintain a viable population and persist along time. When a species does not occupy its entire fundamental niche due to niche exclusion by competition, Hutchinson used the term “realized niche”. However, the species can be absent from suitable habitats for historical reasons or due to limitations in their ability to disperse to those habitats (Holt, 2003). According to the source-sink theory (Pulliam, 2000), some populations may occupy unsuitable

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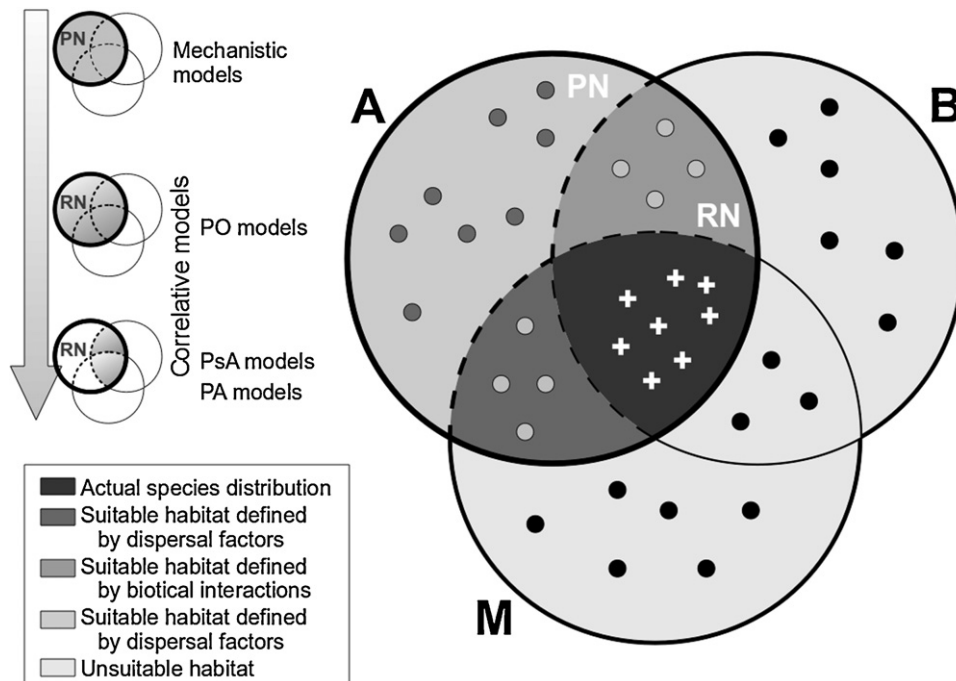


Fig. 1. The BAM (biotic, abiotic, movement) diagram is an abstract representation of geographic space (see Soberón and Peterson, 2005; Soberón, 2007; Soberón and Nakamura, 2009). The diagram is divided in regions where the three main factors limit the distribution of a species (Peterson, 2006; Hirzel and Le Lay, 2008): abiotic (A), biotic (B) and historical or dispersal (M) factors. Outside the space defined by the three factors, the habitat is unsuitable for the species. However, it is also unsuitable outside the area common to the three factors. This area represents regions in space where the species actually occurs. Therefore, the area common to A and B represents regions in space where the realized niche (RN) occurs; and A represents regions in space where the fundamental niche (FN) occurs. The suitable area defined by dispersal factors correspond mainly to sink populations (Pulliam, 2000). Circles are species absences and pluses are species presences. Depending on the location of the species absences (inside A, B or M) the model will calculate the actual species distribution, Grinnellian or Eltonian niches. In reality, this is almost impossible as the factor areas may be not separated. Only mechanistic models can identify the FN. In consequence, ecological niche models are placed in a gradient, from mechanistic models, presence-only (PO) models, pseudo-absence (PsA) models, to presence/absence (PA) models.

habitats (sinks) due to immigration from healthier nearby populations (sources). Although individuals in the sinks may die because of adverse conditions, they are replaced by new immigrants. Here, the realized niche is larger than the fundamental one, as the species occupies habitats that are inadequate and not contained in the fundamental niche (Pulliam, 2000). Jackson and Overpeck (2000) discussed the concept of “potential niche”, which is the intersection between the fundamental niche space and the available environmental space: some portion of the fundamental niche space may lie outside the environmental space at a particular time. Therefore, the realized niche is a subset of the potential niche. Colwell and Rangel (2009) and Soberón and Nakamura (2009) considered that there are three different niches: the fundamental, potential and realized niche. Pearson (2007) introduced the concept of the “occupied niche”, where the species distributions are constrained by geographical and historical factors, as well as biotic interactions (competition, predation, symbiosis and parasitism). Hutchinson (1957) considered that the realized niche was only constrained by species competition, not by other factors such as dispersal limitations. Therefore, the occupied niche is smaller than the realized one. Soberón and Peterson (2005) referred to the “region that has the right set of biotic and abiotic factors and that is accessible to the species, as is equivalent to the geographic distribution of the species” (see Fig. 1 in their article). This region is equivalent to the occupied niche defined by Pearson (2007).

The discordance and variety of points of view on the definition of the niche is also reflected in the type of niche represented by ENM, as viewed by different authors. Godsoe (2010) considered that it is not possible to calculate the niche of an organism: it is only possible to infer if a set of variables belong to the species' niche or not. Jiménez-Valverde et al. (2008) considered that ENM

do not derive the realized niche of species, and even less their fundamental niche. They argued that correlative statistical models can project geographical simulations of the species' distributions but cannot provide a description of a species' niche. Hirzel and Le Lay (2008) equated habitat suitability models (HSM) to species distribution models. They considered that HSM can represent the fundamental niche, because in some cases it may be very similar to the realized one, at least at small scales in which abiotic variables can overcome biotic interactions. Therefore, they proposed to distinguish between Grinnellian and Eltonian niche instead of between fundamental and realized niche. However, for Morin and Lechowicz (2008), it is not useful to distinguish between Grinnellian and Eltonian niche as biotic and abiotic factors depend on the geographical scale considered. Soberón and Peterson (2005) defended that most models of ecological niches are not geographic distribution, and thus “ecological niche modelling algorithms generally produce estimates of the FN (or at least something more general than just the distribution)”. However, most authors have regarded correlative models as providing a spatial representation of the realized niche (Guisan and Zimmermann, 2000; Austin, 2002; Pearson and Dawson, 2003; Jeschke and Strayer, 2008; Morin and Lechowicz, 2008; Pearman et al., 2008; Colwell and Rangel, 2009). Biotic and historical factors are included through presence data: the distribution and number of presence records determine directly the result of the model. Moreover, as species are never in equilibrium with their environment due to dispersal limitations or historical factors (e.g. a species can be absent from a suitable place, due to tectonic plate movements), presence data do not reflect the fundamental niche but rather the realized one (Lobo et al., 2010). Thus, the fundamental niche can only be derived by mechanistic models, which are able to establish a causal relationship among the

species distribution and the variables, independently of the species records available (Kearney and Porter, 2004, 2009; Kearney et al., 2008).

ENMs calculated with presence/absence, presence and pseudo-absence, or presence-only data can be therefore considered representations of different realized niches. If we use a well-distributed dataset of true absences (including all absences from suitable habitats), the resulting ENMs approximates to the occupied niche (*sensu* Pearson, 2007; Fig. 1). If instead we use an incomplete distribution of true absences or different sets of pseudo-absences, the model represents the realized niche (Fig. 1). For example, if absences from some suitable and unoccupied habitats are lacking, the model will be located somewhere between the occupied and the realized niche (Fig. 1). Models calculated with pseudo-absences or with absences can be different because of the risk that pseudo-absences do not correspond to true absences. Soberón and Nakamura (2009) provided a probabilistic interpretation of the BAM diagram. If we use presence-only data, the model also represents the realized niche, because correlations among the species distribution and the environmental factors are obtained through the presence data. If the position of species records change, the values of the variables also change (Lobo et al., 2010). Therefore, presence data include biotic and historical information. Depending on the quality and spatial resolution of environmental data, as well as the size of the study area, this realized niche model can be more or less similar to the fundamental one (see Hirzel and Le Lay, 2008). Thus, the different ecological niches are located on a gradient (Jiménez-Valverde et al., 2008), from the fundamental to the occupied niche. The exact position where our model lies on this niche gradient would depend on the species biology, the spatial resolution considered, the variables included in the model, and the modelling method (Soberón, 2010). Establishing the exact thresholds among types of niche may be very difficult; probably, the limits might be identified exclusively by comparing different types of correlative models with mechanistic models. Two main conclusions can be obtained: first, when comparing different ENM calculated by several methods (e.g. Elith et al., 2006), we have to understand that each ENM is a different approximation to the species niche, and therefore, we cannot expect to obtain similar potential species distributions from different ENM; second, following the previous reasoning, when calculating ensemble models (Araújo and New, 2007), we are mixing different species niches.

Proposing a standard terminology for ecological modelling may help to resolve these discrepancies regarding the theoretical framework of ENM. First, I propose to use the term ecological niche model instead of species distribution models, as this latter term is somewhat misleading since it is actually the distribution of suitable habitats that is being predicted by the model, rather than the species' distribution *per se* (Pearson, 2007). Also, the term ENM refers directly to the ecological niche theory (Guisan and Zimmermann, 2000; Pulliam, 2000; Kearney, 2006; Soberón and Peterson, 2005) and should include both mechanistic and correlative models. Second, I propose the terms realized niche model (realized NM; Fig. 1), when predicting the species' realized niche, for those correlative models using presence/true absence species records (PA-realized NM; e.g. Lobo et al., 2010; Soberón, 2007), pseudo-absences and presence species records (PsA-realized NM; e.g. Lobo et al., 2010), or presence-only species records (PO-realized NM; e.g. Hirzel and Le Lay, 2008); and potential niche model (potential NM; Fig. 1), when predicting the species' potential niche (*sensu* Jackson and Overpeck, 2000), for mechanistic models (e.g. Kearney and Porter, 2009). I do not proposed a term for modelling the fundamental niche because mechanistic models only can model the portion of the fundamental niche that exist in the environment. Finally, I propose the term habitat suitability map (HSM) for the final outputs of RN and PN models that result from the transfor-

mation of model probability continuous values in discrete ones through a threshold. An HSM is a subjective interpretation of the ENM. In the case of PA-realized NM and PsA-realized NM, HSM represents potential habitats where the species may be present or absent. In the case of PO-realized NM, HSM represents the suitability of the habitats (in two or more classes). Here, habitat suitability does not imply required presence or absence of the species: the species can be absent from a very suitable habitat (due to historical or biotic factors; Holt, 2003) or can be present in a very unsuitable habitat (due to immigration processes; Pulliam, 2000). In other words, in PA-realized NM and PsA-realized NM, we model the suitability of those habitats strictly occupied by the species; in PO-realized NM, we look for all the habitats suitable for the species. Therefore, with PO-realized NM, we cannot distinguish between occupied and unoccupied habitats, as absence records are not included in the model. The term realized NM substitutes the equivalent one "habitat suitability model" (HSM), traditionally used when modelling fundamental niches or Grinnellian niches (e.g. Hirzel and Le Lay, 2008). HSM may be misleading, as one may conclude that models of realized niches do not predict the species habitats. For instance, Peterson (2006) used the term ecological niche models as equivalent of potential NM, and the term distributional models as equivalent of realized NM. In a similar way, Araújo and Guisan (2006) used "potential habitat models" for potential NM and "potential geographical distribution models" as realized NM. Both studies focus on the fact that only realized NM can predict the species' potential distribution (those places where the species is present or absent) and neglect that both types of models predict habitats. Pearson (2007) and Jiménez-Valverde et al. (2008) obtained the potential distribution when calculating the fundamental niche, and the actual distribution when calculating the realized niche. However, RN models should be considered potential, since any model is just a statistically supported representation of a species' niche: in this sense, the realized NM is not less potential than the potential NM. On the other hand, Kearney (2006) proposed to use the general term "species habitat models" for all ecological niche models, rather than discriminating fundamental and realized niches, suggesting that this may help to reinforce the descriptive nature of correlative analyses and discourage their inappropriate use. Kearney (2006) also proposed to reserve the niche concept for mechanistic models alone. However, authors recognize that correlative models are based on ecological niche theory and are representations of species' niche (Jiménez-Valverde et al., 2008).

In sum, using the terms realized NM and potential NM can provide some advantages. First, the user understands directly that models forecast the species' niche. The theoretical background is implicit in the terms. As recognised by Hirzel and Le Lay (2008), "despite the obvious relationship between niche theory and HSM, they remain weakly linked and there is a strong need for more integration". Second, and as a consequence of the previous advantage, these terms can help to relate more closely the two types of niche models. As explained above, ENMs forecast suitable habitats for species, thus these terms avoid considering them as completely different: they are related types of different niche models. For example, a PsA-realized NM can be very similar to an PA-realized NM if pseudo-absences correspond to true absences, or very different if pseudo-absences are extracted from habitats where the species is actually present. In fact, the several types of niche models can be placed in a gradient (see Fig. 1 in Jiménez-Valverde et al., 2008). The terminology presented here can prevent misunderstandings about which niche is effectively modelled, but more importantly, it can provide congruence between what is modelled in reality and what is believed to be modelled, thus preventing users to model one type of niche and draw conclusions on another type of niche.

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