

# Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas



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## ABSTRACT

Correlational models of species' ecological niches are commonly used to transfer model rules onto other sets of conditions to evaluate species' distributional potential. As with any model fitting exercise, however, interpretation of model predictions outside the range of the independent variables on which models were calibrated is perilous, herein denoted as strict extrapolation to distinguish from extrapolation onto novel combinations of variables. We use novel visualization techniques to characterize model response surfaces for several niche modeling algorithms for a virtual species (wherein the truth is known) and for two transfer-based studies published by one of our group. All modeling algorithms for each species showed strict extrapolation, such that biologically unrealistic response surfaces were reconstructed. We discuss the implications of these results for calibration and interpretation of niche models and analysis of ecological niche evolution. We present Mobility-Oriented Parity (MOP), a modification and extension of the Multivariate Environmental Similarity Surface (MESS) metric currently in use, as a means of both quantifying environmental similarity between calibration and transfer regions and highlighting regions in geographic space where strict extrapolation occurs.

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## 1. Introduction

### 1.1. Transfer and extrapolation

Over the past two decades, methods for characterizing environmental requirements of species have been used to anticipate species' distributional potential in novel regions or under scenarios of environmental change. Despite having diverse objectives, these methods are collectively called 'species distribution modeling' (SDM) or ecological niche modeling (ENM). We make a distinction between SDM and ENM, and advocate use of 'SDM' when focus is on characterizing a species' geographic distribution without transferring the model in time or space. We suggest the use of 'ENM' when emphasis is on estimating environmental preferences of a species, with the objective of looking for similar conditions in different times or spaces. Common applications of ENMs have included characterizing full geographic distributions of species, estimating geographic potential of species' invasions, and

anticipating likely effects of climate change on species' distributions (Peterson et al., 2011).

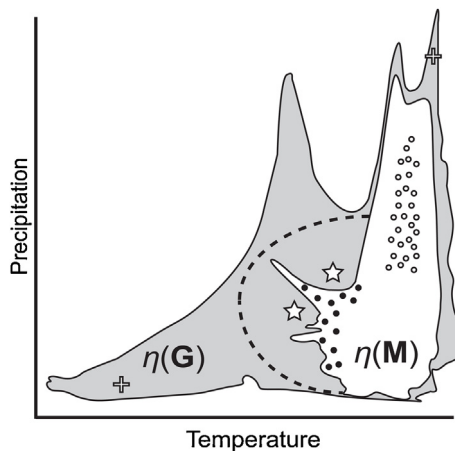
Many of these applications involve transfer of model predictions to novel regions and/or time periods. Model transfer provides some of the most interesting applications of ENM (Pearson et al., 2006); however, when models are calibrated based on conditions in one area or time and transferred to another, assumptions are made regarding how they will perform under conditions outside those used for calibration (Randin et al., 2006; Williams and Jackson, 2007; Williams et al., 2007). These novel conditions can be characterized in two ways: (1) for a given individual variable, values may be outside the range sampled during training (i.e., univariate, strict extrapolation), and (2) portions of environmental space may be within the range of individual variables, but represent new combinations of predictors (i.e., multivariate, combinational extrapolation; Fig. 1) (Zurell et al., 2012).

To interpret model results accurately in transfer situations including novel environments, it is important to understand how models behave when presented with such conditions. Even the simplest and most transparent methods (e.g., BIOCLIM) have subtleties (Beaumont et al., 2005), and advanced regression methods and complex machine-learning algorithms can be quite opaque regarding what the algorithm will do in extrapolative situations of both strict and combinational extrapolation, or when occurrences

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**Fig. 1.** Illustration of situations regarding suitable and accessible areas in environmental space. Environments represented across some area of interest (projection area) are depicted in gray shading; environments associated with **M** are depicted in the white area. Stars indicate areas of combinational extrapolation from **M**, crosses indicate areas of strict extrapolation. Known occurrences for two example species are shown—one as open circles, the other as filled circles. Dashed line indicates possible  $\eta(\mathbf{M})$  designed to avoid extrapolation problems for filled circle species.

are peripheral among environments in the calibration region. Hence, identifying novel environments and characterizing model response surfaces becomes important. Valuable steps have been taken to generate metrics that identify and quantify novel environments (Williams et al., 2007; Platts et al., 2008; Fitzpatrick and Hargrove, 2009; Elith et al., 2010; Zurell et al., 2012); however, model responses under such conditions have not been examined thoroughly. Zurell et al. (2012) analyzed model response curves under combinational extrapolation, but none has examined how models respond under strict extrapolation, or when a species is distributed peripherally to the environments available in their accessible area, **M** (e.g., species represented by filled black circles in Fig. 1).

Hence, the purpose of this contribution is twofold: (1) to explore and characterize response surfaces estimated by diverse ENM algorithms when challenged to extrapolate strictly (including implications for modeling methods and interpretation); and (2) to introduce Mobility-Oriented Parity (MOP), a modification of MESS (Elith et al., 2010), that can be used to identify regions of strict extrapolation and better-characterize degrees of novelty of areas to which model rules are to be transferred. We illustrate these ideas initially using a virtual species; empirical complexities are then explored further via analyses of two real-world species that have been the subject of previously published ENM-based analyses.

## 1.2. Conceptual framework

The question of extrapolation of ENM rule sets requires a coherent and consistent vocabulary to avoid confusion and misinterpretation (Peterson et al., 2011). We use the Biotic–Abiotic–Mobility (BAM) framework (Soberón and Peterson, 2005), which has proven a valuable heuristic for conceptualizing factors limiting geographic distributions of species (see Table 1 and Peterson et al., 2011). The framework states that a species' occupied geographic distribution ( $\mathbf{G}_o$ ) is the conjunction of areas appropriate in terms of abiotic conditions (i.e., **A**, the set of areas meeting conditions of the fundamental niche  $\mathbf{N}_F$  of the species), appropriate in terms of biotic conditions (**B**), and areas accessible via dispersal over relevant time periods (i.e., **M**); this latter set of areas has been discussed in detail in a previous contribution (Barve et al., 2011). To be able to discuss relationships between distributions in geographic space (**G**) and distributions in environmental space (**E**), we note that species

**Table 1**  
Symbol key.

Notation	Definition <i>sensu</i> Peterson et al. (2011)
<b>A</b>	Abiotic conditions suitable for a species ( $\eta^{-1}(\mathbf{N}_F) = \mathbf{A}$ )
<b>B</b>	Biotic factors influencing the distribution of a species
<b>E</b>	Environmental space
<b>G</b>	Geographic space
$\mathbf{G}_+$	Known occurrences of a species
$\mathbf{G}_o$	A species' occupied geographic distribution ( $\mathbf{A} \cap \mathbf{B} \cap \mathbf{C}$ )
<b>M</b>	Calibration region for a model, which is defined as the region accessible via dispersal over relevant time periods
$\mathbf{M} \cap \mathbf{S}$	Area sampled within the accessible area for a species
$\mathbf{N}_F$	Fundamental niche of a species
$\eta(x)$	Environments associated with some geographic region $x$
$\eta^{-1}(y)$	Geographic points associate with some set of environments $y$
<b>S</b>	Area sampled by researchers

are distributed simultaneously in both spaces (i.e., corresponding to geographic range and ecological niche, respectively; Colwell and Rangel, 2009), and that these two spaces correspond to one another in complex ways. We use the notation  $\eta(\mathbf{G}')$  to indicate “environments associated with the geographic set of points  $\mathbf{G}'$ ” and  $\eta^{-1}(\mathbf{E}')$  to refer to “geographic points associated with the environment  $\mathbf{E}'$ ”; sets of known occurrences of species are denoted using  $\mathbf{G}_+$ .

Barve et al. (2011) emphasized the importance of **M** as the appropriate region across which models should be calibrated (see also Elith et al., 2011). **M** should represent the areas to which a species has had access over relevant time periods and has therefore ‘tested’ the associated environmental conditions for suitability; where conditions are suitable for the species within **M**, the species should be present. That is, within **M**, an unoccupied site is posited to be unsuitable for the species, although some suitable sites within **M** may be unoccupied owing to metapopulation dynamics, anthropogenic activity, local extirpation, or non-detection of existing populations (Phillips et al., 2009). Generally, such biases result in omission error in relation to the environmental parameters. In other words, a model may predict unsuitable habitat in an area that is, in fact, suitable but is under-sampled by the species or the researcher for any of the previously mentioned reasons. Indeed, these biases illustrate the importance of an explicit **M** hypothesis when applying ENM/SDM methods, such that potential inaccuracies in model output can be identified and tested a posteriori.

The first part of our study focuses on the behavior of ecological niche modeling algorithms under conditions *outside* ranges of conditions represented within **M** (i.e., how algorithms behave when potentially forced to extrapolate strictly). In symbols, a model should be calibrated with respect to conditions represented within a known or hypothesized **M**, termed  $\eta(\mathbf{M})$ .  $\mathbf{G}'$  is used to denote transfer of a prediction to some region outside of **M**; the environments associated with that new region  $\eta(\mathbf{G}')$  should be assessed against  $\eta(\mathbf{M})$  to detect areas presenting conditions outside of the calibration range for particular environmental variables, which are potentially areas of strict extrapolation (see, e.g., Thuiller et al., 2009; Elith et al., 2010).

In theory, models applied to species with occurrences located centrally within the environments of **M** should not encounter problems with extrapolation, even given the presence of novel conditions within a transfer region. That is, for the situation illustrated by open circles in Fig. 1, where  $\eta(\mathbf{G}_+)$  is buffered on all sides by non-occurrence environments within  $\eta(\mathbf{M})$ , modeling algorithms are likely to have sufficient information to recognize that conditions for each variable beyond those used in the calibration region are unsuitable (Williams and Jackson, 2007; Zurell et al., 2012). However, strict extrapolation becomes an issue when a species' occupation of suitable habitat is dispersal-, or **M**-limited. That is, if  $\eta(\mathbf{G}_+)$  is peripheral within  $\eta(\mathbf{M})$ , the fundamental niche

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