



## Predicting fundamental and realized distributions based on thermal niche: A case study of a freshwater turtle



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### ABSTRACT

Species distribution models (SDM) have been broadly used in ecology to address theoretical and practical problems. Currently, there are two main approaches to generate SDMs: (i) correlative, which is based on species occurrences and environmental predictor layers and (ii) process-based models, which are constructed based on species' functional traits and physiological tolerances. The distributions estimated by each approach are based on different components of species niche. Predictions of correlative models approach species realized niches, while predictions of process-based are more akin to species fundamental niche. Here, we integrated the predictions of fundamental and realized distributions of the freshwater turtle *Trachemys dorbigni*. Fundamental distribution was estimated using data of *T. dorbigni*'s egg incubation temperature, and realized distribution was estimated using species occurrence records. Both types of distributions were estimated using the same regression approaches (logistic regression and support vector machines), both considering macroclimatic and microclimatic temperatures. The realized distribution of *T. dorbigni* was generally nested in its fundamental distribution reinforcing theoretical assumptions that the species' realized niche is a subset of its fundamental niche. Both modelling algorithms produced similar results but microtemperature generated better results than macrotemperature for the incubation model. Finally, our results reinforce the conclusion that species realized distributions are constrained by other factors other than just thermal tolerances.

### 1. Introduction

In the last two decades, Species Distribution Models (SDMs) have become one of the most important tools for ecological and biogeographical inferences regarding species' geographic distributions (Guisan and Thuiller, 2005). SDMs have been broadly used to forecast biological invasions, manage threatened species, understand phylogeographic patterns, and evaluate the impacts of climate change on species distribution (reviewed by Guillera-Arroita et al., 2015). Due to the rising concern regarding the reliability of correlative models, process-based SDMs have been proposed (Kearney and Porter, 2009). Despite showing conceptual and methodological differences, correlative and process-based models can be compared to increase confidence in their predictions if they concur, or generate interesting insights if they do not (Buckley et al., 2010; Hijmans and Graham, 2006; Kearney et al., 2010). Both model types are associated with the duality between geographical space and niche space (Colwell and Rangel, 2009), but when correlative models are projected over space they are more prone to represent the species' realized distribution, whether process-based models are more prone to represent the species' fundamental

distribution (Buckley et al., 2010; Kearney et al., 2010).

Correlative SDMs are one of the most used modelling techniques due, in part, to their simple data requirements (Elith and Leathwick, 2009). The shared logic of correlative SDMs is the use of a statistical function linking species' occurrence records and spatial environmental data. The model assumes that apart from environmental variables, additional processes limiting species distribution are captured implicitly by the correlative analyses (Guillera-Arroita et al., 2015). Moreover, it assumes that processes limiting species' ranges are fixed in space and time (Dormann, 2007). Given the expected changes in biotic and abiotic variables that limit species distribution over time (Buckley et al., 2010), correlative models have been criticized, especially when they are used to model species' distribution under climatic changes (Buckley and Kingsolver, 2012).

As an alternative to correlative models, mechanistic or process-based SDMs explicitly assume that species' physiological performance is limited by the environment. Thus, unlike correlative SDMs, these models specify the imposed physiological restrictions of species' fundamental niche (Kearney and Porter, 2009). Although process-based models could overcome the limitations of correlative models, their

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increased complexity is tempered by their loss in generality and simplicity (Levins, 1966). Given the high cost of physiological studies both in budget and time (Buckley et al., 2010), few species present physiological information related to their limitations in physiological performance caused by environmental variables (Schindler and Hilborn, 2015). Moreover, which physiological response of species (e.g. mortality, reproduction, etc) should be included in the model has proved to be a conceptual challenge, because species differ in responses under the same environmental changes (Cahill et al., 2012). Thus, process-based SDMs are specific for each study case and may be impractical for many species.

A crucial issue when predicting the distribution of ectothermic species in general, and the distribution of reptiles specifically, is to understand how temperature determines species survival and distribution (Sinervo et al., 2010; Sunday et al., 2012). Process-based models estimate species' fundamental thermal niche, i.e., the range of temperature conditions in which a species can survive, develop and successfully reproduce in the absence of competitors or predators (Hutchinson, 1957). In contrast, correlative models are associated to species' realized thermal niche, i.e. the range of temperatures defined by species' observed distribution (Peterson et al., 2011). Therefore, comparative studies of species' fundamental and realized niche are fundamental and could shed light into the relative importance of temperature in shaping species' distributions (Allen-Ankins and Stoffels, 2017; Gaston et al., 2009).

In this study, we compared the distribution of the freshwater turtle *Trachemys dorbigni* (Duméril and Bibron, 1835) estimated according to its fundamental and realized thermal niche. To estimate *T. dorbigni* distribution according to its fundamental thermal niche (hereafter fundamental distribution), we used data on the relationship between incubation temperature and hatching success, because reproduction is an obvious requirement to ensure species persistence over space and time. Although freshwater turtles may disperse to areas where they are not able to reproduce, the species will not be able to properly establish and develop viable populations there. To estimate *T. dorbigni* distribution according to its realized thermal niche (hereafter realized distribution), we used correlative SDMs, which account for abiotic and biotic processes that can potentially limit species distribution (Peterson et al., 2011). The combination of fundamental and realized species' distribution could provide sound and practical predictions of species ranges.

## 2. Materials and methods

### 2.1. Model species

*Trachemys dorbigni* is a freshwater turtle commonly distributed in southeastern Brazil, Uruguay and northern Argentina (Alcalde et al., 2012). The reproduction of this species has been widely studied in captivity and in natural conditions, providing enough data to generate reliable SDMs. This species lays eggs in natural conditions from October to January (Bager et al., 2007; Fagundes et al., 2010; Gonçalves et al., 2007) and in captive conditions incubation temperature has been shown to be an underlying process influencing species reproductive success (Molina and Gomes, 1998).

### 2.2. Data

#### 2.2.1. Incubation temperature data

We obtained data for incubation success of eggs of *T. dorbigni* from Molina and Gomes (1998), who recorded the number of eggs that successfully hatched under different incubation temperatures in laboratory conditions. Eggs were buried in 2 cm depth vermiculite substrate and kept at almost constant temperature (temperature variation was less than 1 °C). They also reported the number of eggs used in each trial, allowing us to calculate the percentage of eggs that successfully

hatched (see Molina and Gomes, 1998 for more details regarding how these values were obtained).

#### 2.2.2. Occurrence data

We used 49 occurrence records of *T. dorbigni* compiled and used in a previous publication (Rodrigues et al., 2016). These occurrence data were obtained from literature and different digital species occurrence repositories such as GBIF (Global Biodiversity Information Facilitation; [www.gbif.org](http://www.gbif.org)) and SpeciesLink ([splink.cria.org.br](http://splink.cria.org.br)). This data is the most complete database for *T. dorbigni*.

#### 2.2.3. Climatic data

To represent the macroclimatic temperature, we downloaded data of monthly mean temperature (hereafter "macroclimatic temperature") from WorldClim for ~1960–1990 (version 1.4; [www.worldclim.org](http://www.worldclim.org)) (Hijmans et al., 2005). For the microclimatic temperature, we used data of the mean temperature (1961–1990) of sandy substrate at 10 cm depth from microclim database (Kearney et al., 2014) (hereafter "microclimatic temperature"). Both environmental layers were obtained for 10-arc minutes resolution because it was the finest resolution available for the microclimatic variable.

We used mean temperatures instead of maximum temperatures to predict species distribution because incubation process is more related to temperature exposure ranging around a central value during a long time than to extreme occasional values (Feng and Papeş, 2017). We worked only with the mean temperature of the months in which *T. dorbigni* is known to lay eggs (October–January) (Bager et al., 2007; Fagundes et al., 2010; Gonçalves et al., 2007). We used microclimatic temperatures at soil depth of 10 cm and sandy substrate because these nesting characteristics are common for *T. dorbigni* (Bager et al., 2007; Fagundes et al., 2010).

Finally, it is important to highlight that we could have used a broader range of environmental variables to develop SDMs for *T. dorbigni*, but we chose to use only one measure of temperature (and its quadratic term in logistic regression) to provide a direct comparison to models generated using the process-based approach. The inclusion of a wider range of environmental variables in our correlative models would probably improve their performance when compared to process-based models which were based in a single variable, making a comparison between them totally biased.

## 2.3. Modelling procedure

### 2.3.1. Fundamental distribution

The fundamental distribution was estimated using the incubation data. Estimating fundamental distribution requires some estimate of species' fundamental niche, which requires experiments evaluating the direct influence of environmental variables on basic aspects of species such as survival and reproduction (Colwell and Rangel, 2009; Feng and Papeş, 2017; Soberón, 2007). It is widely known that temperature strongly influences egg incubation and reproduction in turtles (Molina and Gomes, 1998; Packard et al., 1987). Then, since reproduction is a basic requirement for the establishment of source populations of an organism, we assumed that only areas with temperature conditions allowing hatching success would compose the fundamental distribution of *T. dorbigni*. Although other environmental factors may also influence egg incubation success (e.g. moisture), there are no experimental data available for these other variables.

We created models associating the percentage of eggs that successfully hatched and temperature using two algorithms: 1) a logistic regression including temperature and its quadratic term (temperature<sup>2</sup>) as explanatory variables; and 2) support vector machines (SVM) including temperature. SVM is a machine learning method for pattern recognition considered highly efficient for modelling species niche and distribution (Drake et al., 2006). Once the models were calibrated, we projected them in the background area of *T. dorbigni* corresponding to

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