



# The Niche Limitation Method (NicheLim), a new algorithm for generating virtual species to study biogeography



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## ABSTRACT

Virtual species are simplified models of real species that codify the response of those species to the climatic conditions. Virtual species have been used to quantify the response of species to climatic changes, to predict potential shifts in species' geographic ranges and to test the methods used to predict the geographic ranges of species (Ecological Niche Models). Today, there are different methods used to construct virtual species for biogeographic analysis. All of those methods combine partial suitabilities across variables (temperature, precipitation, etc.) to create one multi-variable habitat suitability index. The normal procedure for combining partial suitabilities is to sum or multiply the individual layers. However, this procedure might yield misleading results. In this paper, we run several analyses that indicate that those methods underestimate the role of the limitation factors (factors with unsuitable conditions that should decrease the habitat suitability index to zero). To solve this problem we programmed an algorithm—the Niche Limitation algorithm (NicheLim). NicheLim uses the same philosophy as the BIOCLIM model: species have independent physiological tolerances to the environmental variables. This means that we must first transform each continuous layer into a presence-absence variable, and then combine them. Here, we discuss the current framework for constructing virtual species in biogeography and its main drawbacks. We then explain the improvements of using NicheLim to create our virtual species and test biogeographic hypotheses.

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## 1. Introduction

Modeling Virtual species represent the environmental niche of ideal species and are intended to act as null models to test biological hypotheses (like the expansion-contraction hypothesis, Varela et al., 2015) or methods (e.g., to avoid the inherent errors and biases of real species occurrences, Austin et al., 2006; Hirzel et al., 2001; Zurell et al., 2010; Naimi et al., 2011; Miller, 2014; Varela et al., 2014; Fourcade et al., 2014).

Many virtual species are created by generating a Habitat Suitability Index (HSI) (Austin et al., 2006; Hirzel et al., 2001; Zurell et al., 2010; Naimi et al., 2011; Miller, 2014; Varela et al., 2014). Generally, HSI is generated by: (1) choosing the environmental variables; (2) selecting a suitable method for creating partial HSI for every variable, normally based on basic functions, like a bell-shaped response (Gaussian curve), a linear response (increasing

or decreasing), or a truncated linear (increasing or decreasing) or logistic curve; and (3) combining the partial HSI to generate a multi-variable HSI, normally using either the sum or product method. In the sum method, the multi-variable HSI is the sum of the (weighted) average of partial HSI (with a random error) (Hirzel et al., 2001; Jiménez-Valverde et al., 2009). The product method reflects a multiplicative relationship among the different environmental variables, and the multi-variable HSI in each given cell is calculated by multiplying the partial HSI based on every environmental variable (Barbet-Massin et al., 2012).

At the important step of combining partial HSI to generate a multi-variable HSI, the sum and product methods consider the substitutability and interactions of all environmental factors considered. However, they may cause substitution effects of different environmental variables and weaken the role of the limiting factors. Scarcity of resources limits the growth and distribution of species (Ryabov and Blasius, 2011; Carpenter et al., 2009; Farrior et al., 2013; Ågren et al., 2012; Harpole et al., 2011; Lewis and Wurtsbaugh, 2008). Almost all models of species-essential resource limitation are based on either one or two hypotheses of limiting factors: Liebig's Minimum Hypothesis (LMH) (Liebig, 1847) and

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Multiple Limitation Hypothesis (MLH) (Bloom et al., 1985). LMH states that species should be limited by a single limiting resource (single-resource limitation) and only respond to changes in that resource, while MLH suggests that species are limited by several resources simultaneously (co-limitation by multiple resources). They both emphasize the importance of limiting factors for the distribution of the species essentially governed by one or a few factors at each locality. If any of those key factors are lacking, or are lower than the minimal threshold, the given species cannot survive.

To emphasize the importance of limiting factors and avoid the substitution effect of different environmental variables, we provide a new, simple, and improved method for the generation of virtual species. The niche limitation method (NicheLim) assumes that a virtual species can appear if all environmental variables are suitable (i.e., the HSI values of all environmental variables are higher than the thresholds).

We compared the three different methods for constructing a multivariable HSI to quantify the effects of the different methods in the predicted area (sum, product and NicheLim). To document the substitution effect of the sum and product methods and illustrate the utility of the NicheLim method, we designed three cases: two ideal cases (a demo using nine cells for displaying special cells with substitution effects and an ideal map of  $100 \times 100$  cells for displaying the effect under different threshold values and numbers of environmental variables) and one real case (generating a virtual species distribution using a Chinese map for the substitution effect in the real world). We argue that the NicheLim method presents advantages to the sum and product methods for constructing virtual species because it avoids substitution effects of adding multiple factors and is ecologically meaningful.

## 2. Methods

### 2.1. Sum and product methods

As explained above, the multivariable HSI ( $H$ ) is calculated, respectively, as  $H = (1/\sum_{i=1}^n w_i) \sum_{i=1}^n W_i H_i + \varepsilon$  in the sum method (Hirzel et al., 2001; Jiménez-Valverde et al., 2009) and  $H = \prod_{i=1}^n W_i H_i + \varepsilon$  in the product method (Barbet-Massin et al., 2012). Where  $H_i$  is the value of the  $i$ th HSI and  $W_i$  is the weight assigned to  $H_i$ . Each  $H_i$  value is then weighted by a  $W_i$  factor and  $\varepsilon$  represents a random error (Hirzel et al., 2001; Jiménez-Valverde et al., 2009). Here, to simplify the methods (the sum method and the product method) we assumed that: (1) the value of  $\varepsilon$  is equal to zero to decrease the random error and increase the comparability and stability of results; (2) the weights of all environmental variables ( $W$ ) are the same (the value is 1); and (3) the response of the species to each environmental factor is independent of the others (without interactions).

The product method consists of multiplying the individual HSI to obtain a multivariable HSI. The main disadvantage of this method is that the values of the multivariable HSI will greatly decrease with the number of HSI that are combined. For instance, when multiplying two layers that are 0.5, the result will be 0.25. This means that we would need to set a new arbitrary threshold, different from 0.5 in our example, to construct our binary maps, which is dependent on the number of individual layers that we combined. To avoid these drawbacks, instead of rescaling the multivariable HSI to range from 0 to 1, we rescaled the product using the square root (the so-called geometric mean). This preserves the order of the suitability layer, and threshold  $T_0$  (the original threshold of the traditional product method) and  $T_1$  (the threshold of the new product method) are in the same order in their own layer. The distribution maps, according to corresponding thresholds, are also the same. In other words, a pair of suitability layers and thresholds translated as a

strictly increasing function will not change the final distribution map.

### 2.2. NicheLim method

The niche limitation method (NicheLim) assumes that a virtual species cannot appear if the value of any environmental variable is lower than the threshold. When the values of all variables in the cells are within the threshold value of a given species, the species can appear. Otherwise, the species cannot appear, following the philosophy of the Bioclim Ecological Niche Model (Busby, 1991). NicheLim first uses a threshold for each variable to transform our continuous layers into binomial layers, and then multiplies them. Thus, the main difference between the NicheLim method and the product methods is that we operate after applying the threshold, and not the other way around.

### 2.3. A demo using nine cells

To demonstrate the substitution effect of the sum and product methods we created a micro-environment composed of nine cells. We assumed that our virtual species is limited by two environmental variables (Env1 and Env2), with certain partial habitat suitability indexes (all values in the nine cells for each environmental variable are shown in Fig. 1a). First, we created the potential distribution of the species by only allowing the species to be present when both environmental variables have partial suitabilities greater than or equal to 0.5 (partial distribution maps are shown in Fig. 1c). Second, we used the sum method to generate the final potential distribution (Fig. 1b), and chose 0.5 as a threshold to make the distribution map (Fig. 1d). Third, we used the product method to multiply the two environmental suitabilities, and then calculated the geometric mean (equal to the square root of the product) as the final suitability (Fig. 1b). We also selected 0.5 as the threshold to obtain the distribution map (Fig. 1d). Finally, we obtained the distribution map using the NicheLim method: according to LMH or MLH, we assumed that virtual species cannot appear when the suitability of any one environmental variable is lower than the minimum values (0.5) (Fig. 1d).

### 2.4. An ideal map of $100 \times 100$ cells

To further illustrate the large differences between the three methods we constructed two grid maps of  $100 \times 100$  cells (representing two different environment layers) with random partial habitat suitability indexes. We combined the two partial indexes using the sum, product and NicheLim method, respectively, and used different threshold values (0.1–0.9) to generate the final distribution maps (Fig. 2).

We also tested the effect of the number of environment variables used to calculate the final HSI (Fig. 3). We created six maps with randomly generated partial suitability indexes (0 to 1), and then combined the partial indexes of 2, 3, 4, 5, and 6 variables using the sum, product and NicheLim methods, and repeated this test 100 times to remove potential random effects.

### 2.5. A case study in a real map

To reflect substitution effects in the real world, we used data from three environmental variables in China to generate rule-based virtual species distributions: max temperature of the warmest month (Bio5), min temperature of the coldest month (Bio6), and precipitation of the driest month (Bio14), downloaded from [www.worldclim.org](http://www.worldclim.org). Temperature and precipitation have a direct influence on species distribution by changing their ecophysiology,

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