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

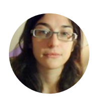
ARTICLE *in* ECOLOGICAL MODELLING · JANUARY 2016

Impact Factor: 2.32 · DOI: 10.1016/j.ecolmodel.2015.10.003

4 AUTHORS, INCLUDING:

Xiaoquan Kong

Anqing Normal University



Sara Varela

University of Alcalá

Ecological Modelling 320 (2016) 197–202

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

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

Minyi Huang[a,1], Xiaoquan Kong[a,1], Sara Varela[b,c], Renyan Duan[a,*]

[a] College of Life Sciences, Anqing Normal University, Anqing 246011, Anhui, PR China
[b] Departamento de Ciencias de la Vida, Edificio de Ciencias, Campus Externo, Universidad de Alcalá, 28805 Alcalá de Henares, Madrid, Spain
[c] Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, 10115 Berlin, Germany

ARTICLE INFO

Article history:
Received 26 May 2015
Received in revised form
14 September 2015
Accepted 7 October 2015

Keywords:
Substitution effect
Habitat suitability index
Niche limitation method
Simulation

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.

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

* Corresponding author. Tel.: +86 556 5500277; fax: +86 556 5500277.
E-mail address: duanrenyan78@163.com (R. Duan).
[1] These authors contributed to this work equally.

http://dx.doi.org/10.1016/j.ecolmodel.2015.10.003
0304-3800/

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 × 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 $H = \left(1/\sum_{i=1}^{n} w_i\right) \sum_{i=1}^{n} W_i H_i + \varepsilon$ 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 ith HSI and W_i is the weight assigned to H_i. Each H_i value is then weighted by a W_i factor and ε 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 ε 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_o (the original threshold of the traditional product method) and T_t (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 × 100 cells

To further illustrate the large differences between the three methods we constructed two grid maps of 100 × 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. Temperature and precipitation have a direct influence on species distribution by changing their ecophysiology,

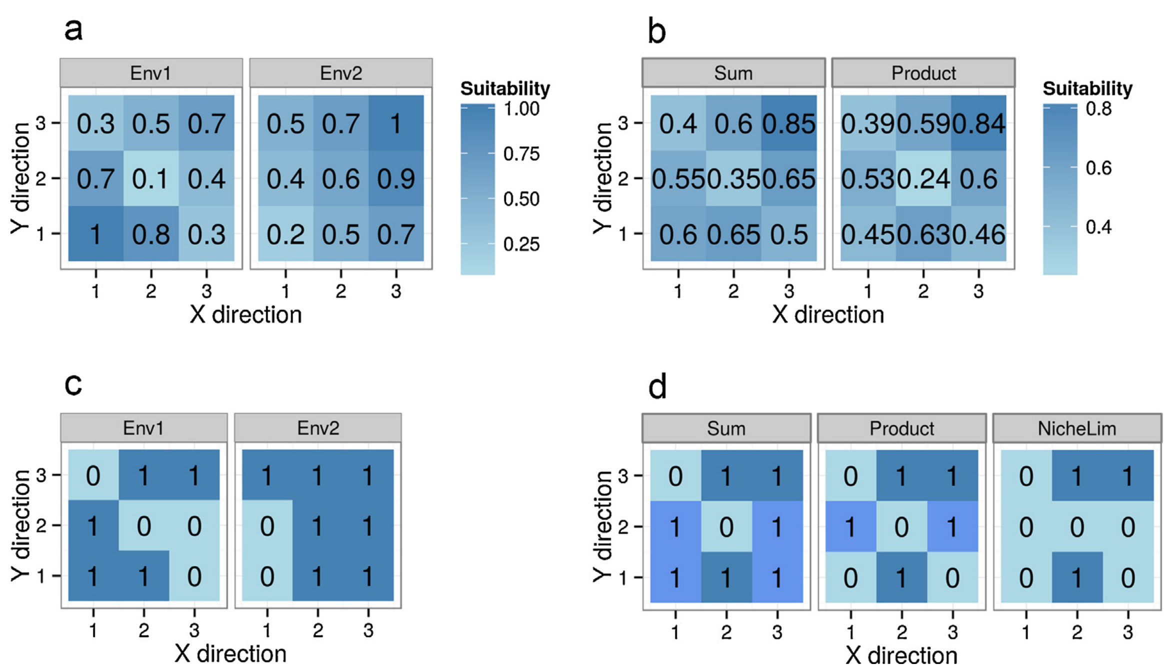


Fig. 1. The difference of virtual species' multivariable suitability calculated by the sum, product and NicheLim methods using nine cells. (a) The suitability of two environmental layers (Env1 and Env2); (b) Virtual species distribution in two environmental layers (Env1 and Env2) in nine cells (1 indicates presence, 0 indicates absence); (c) Virtual species' multivariable suitability calculated by the sum and product methods in nine cells; (d) The distribution map with the three methods (sum, product and NicheLim) generating virtual species (1 indicates presence, 0 indicates absence, 1 in blue indicates the false positives).

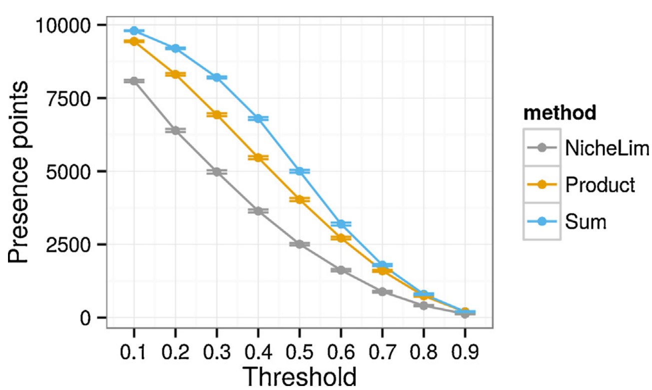


Fig. 2. Presence points with different thresholds with two environmental variables.

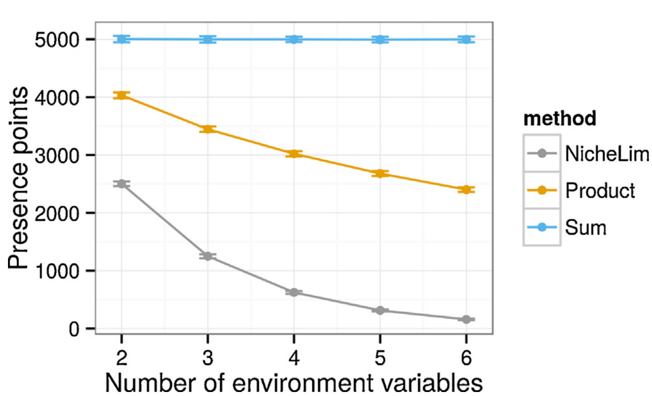


Fig. 3. Presence points with different numbers of environmental variables.

habitat selection and survival (Austin et al., 2006; Meynard and Quinn, 2007).

We used a bell-shaped response to create the partial suitability indexes for the environment variables. The bell-shaped response uses a center point and standard deviation (S.D.) to build a normal curve (Gaussian curve) to translate the environment variable to a suitability index (method parameters are listed in Table 1, suitability is shown in Fig. 4). We respectively used the sum, product and NicheLim methods to combine the partial suitabilities to make the HSI (all details are the same as in the section "A demo using nine cells", multivariable suitability is shown in Fig. 5). The threshold to translate suitability to the distribution map in the sum and the product methods are the same as in the NicheLim method (0.5).

Table 1
Parameters of the artificial bell-shaped response method.

Environmental variable	Symbol name	Mean	S.D.
Max temperature of warmest month (°C)	Bio5	37	8
Min temperature of coldest month (°C)	Bio6	5	10
Precipitation of driest month (mm)	Bio14	50	40

3. Results

3.1. The substitution effect using nine cells

To highlight those cells with substitution effects among the three methods, they are noted in blue (e.g., the coordinates (1, 1), (1, 2), (3, 1) and (3, 2) in the sum method, and the coordinates (1, 2) and (3, 2) in the product method) (Fig. 1d). These are "false" presence points when compared to the NicheLim method. The sum and product methods have more occurrence points primarily because of their substitution effects. For example, in the sum method, the cell with the coordinates (1, 1) is constrained by Env2 (the suitability value under Env2 is 0.2, lower than the species tolerance limit 0.5), but this cell has the highest suitability under Env1 (the suitability value in Env1 is 1) (Fig. 1a). The high suitability in Env1 compensates for the limitation of Env2, such that the sum of the suitabilities falls in favor of virtual species occurrence (the multivariable suitability at this site is 0.6 times higher than the threshold 0.5) (Fig. 1b). However, this cell is in fact not suitable for virtual

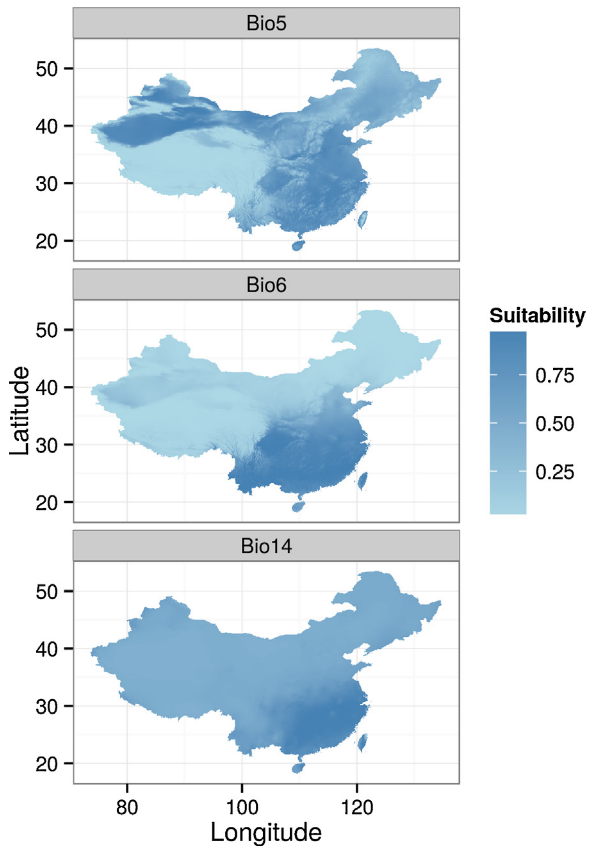


Fig. 4. Suitability of the Bio5, Bio6 and Bio14 environment layers.

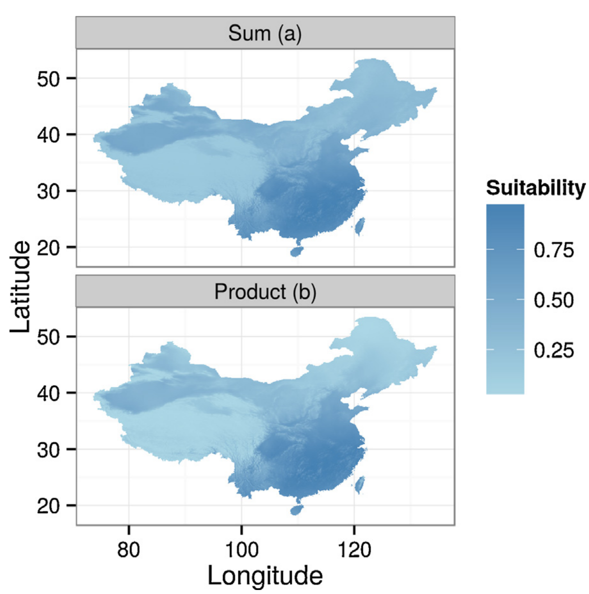


Fig. 5. The multivariable suitability of the sum and product methods.

species occurrence, because Env2 is outside of the tolerance limitation. This substitution effect in the sum method cannot be corrected by tuning the threshold of survival of the species. The cell (2, 3) also has a HSI of 0.6 (Env1 = 0.5, Env2 = 0.7, Sum = 0.6) and in this case, the partial HSIs are both higher than 0.5. Thus, if we set the threshold to 0.65, we will remove both cell (1, 1) and cell (2, 3) for the final distribution of the species.

The product method shows a similar substitution effect, although in general the substitution effect is lower than the sum

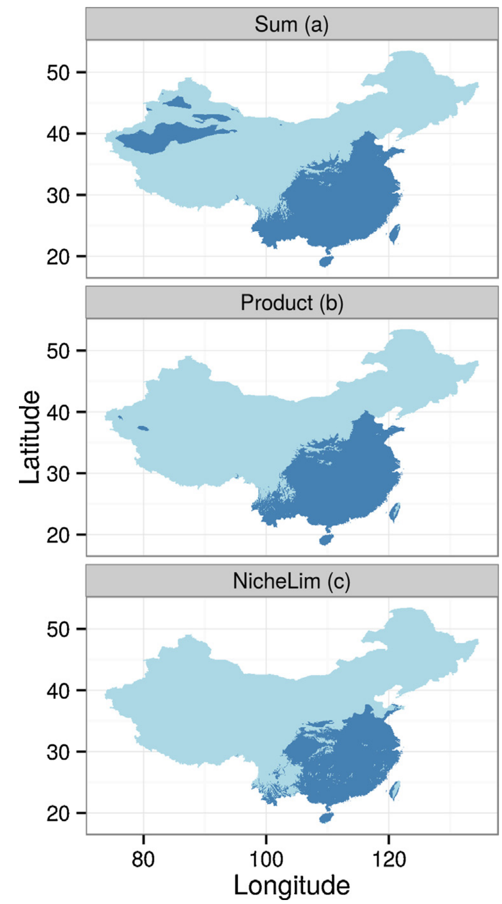


Fig. 6. Final distribution map of the three different methods (sum, product and NicheLim).

method because of its nonlinearity. The cell at coordinates (3, 2) is limited by Env1 (0.4). However, the product method indicates that its HSI is 0.6, representing a false presence: Env2 (0.9) compensates for the limitation of Env1 (Fig. 1b). Additionally, it cannot be removed by using a higher threshold for the same reasons described for the sum method.

3.2. *The substitution effect under different threshold values and different numbers of environmental variables*

The total area predicted by the different methods varies such that sum > product > NicheLim method (Fig. 2). Sum and product methods generate many “false” presence points (Fig. 2), and thus, their predicted areas are larger. For example, when the threshold is set to 0.5, the map generated by the sum method has 4983 cells, the map generated by the product method has 4044 cells, and the map generated by the NicheLim method has 2509 cells. Thus, the sum and the product methods predict 99% and 61% more cells than the NicheLim method, respectively.

Moreover, our results demonstrate that the sum method does not include information on the new variables when they were added in constructing the distribution maps. Fig. 6 shows that the predictions of the sum method remained similar, in spite of the inclusion of new variables and constraints for the species. The maps obtained using the product method change when including new factors that constrain the distribution of the species (Fig. 3). However, compared to the NicheLim method, the product method still over-predicts the potential range for the species.

3.3. The substitution effect in the real map scenario

Our results show that the distribution of the sum method and product method are larger than the NicheLim method in the real map (Fig. 6). In our study case, the sum method estimates the largest distribution map for the virtual species, and thus has the highest substitution effect (Fig. 6). The NicheLim method generated 29,713 occurrence points while the sum method generated 46,420 and the product method generated 37,276. Thus, 16,707 of the points generated by the sum method are commission errors (36% of total occurrences) and of those generated by the product method, 7563 points are commission errors (20% of total occur points). For example, the sum method predicts that the virtual species is present in northwest China, while the other two methods do not. Compared with the sum method, the product method has fewer substitution effects (Fig. 6). Based on our results, substitution effects have a significant impact on the construction of our virtual species.

4. Discussion

In recent years, virtual species have been used to improve the methods to predict the geographic ranges of species. They have served to control for the quality of presence and/or absence data, helping to better evaluate the prediction accuracy and sensitivity of Ecological Niche Models as well as to better understand ecological problems encountered when studying real species (Liu et al., 2013; Naimi et al., 2011; Jiménez-Valverde et al., 2009; Barbet-Massin et al., 2012; Santika and Hutchinson, 2009). Simulating realistic virtual data should conform to relevant ecological processes but this is limited by our understanding of such processes (Austin et al., 2006).

The generation of a multivariable HSI by combining partial HSIs is particularly important for virtual species (Austin et al., 2006; Hirzel et al., 2001; Zurell et al., 2010; Naimi et al., 2011; Miller, 2014; Varela et al., 2014). Understanding key processes is essential in the assessment of the appropriateness of generating virtual species. By comparing the map predictions of three different methods of virtual species generation—the sum method, product method (the geometric mean of several partial variable suitabilities) and a new method (the niche limitation method-NicheLim), we are able to distinguish differences in their substitution effect (sum > product > NicheLim method). Meynard and Quinn (2007) also demonstrated that the product method was more realistic than the sum method in the generation of virtual species. Our results further indicate that the sum and product methods assume that environmental factors are mutually substitutable, leading to substitution or additive effects, and then over-predicting the potential range, since in the real world, many species are present within a particular environmental gradient lacking substitutable responses (Meynard and Quinn, 2007; Prasad et al., 2006; Termansen et al., 2006). In fact, ecological factors may present substitution effects, but they are poor and/or limited (i.e., not all factors can compensate for each other). Furthermore, the environmental variables in ENMs (Ecological niche models) are independent or uncorrelated to avoid over-fitting and poor prediction performance using Pearson's correlation coefficients (Rs) (Franklin et al., 2006), Principal Component Analysis (PCA) (Barbet-Massin et al., 2012; Jiménez-Valverde and Lobo, 2007) or artificially choosing important independent environmental variables (Hirzel et al., 2001; Rapacciuolo et al., 2014; Thibaud et al., 2014). Our results indicate that the substitution effects still appear, regardless of the threshold or environmental variables chosen. For example, substitution effects increased with the numbers of environmental variables (Fig. 3). Even for only two environmental variables, the substitution effects were still very obvious (Fig. 2). In the real world, understanding which are the limiting factors of the species' distributions may be difficult because (1) our knowledge on ecophysiological and biophysical processes of species is limited; (2) the limiting factors may change with the type of variables (resource/direct/indirect variables) or development stages of species; and (3) some indirect variables may have a linear relationship with direct variables. Further study is required to resolve these challenges in finding the limiting factors for real species, taking into consideration the advantages of the NicheLim method (emphasizing the importance of limiting factors and avoiding the substitution effect of different environmental variables).

The NicheLim method is closely linked to the fundamental niche of hypervolume niche theory or a multi-dimensional hypervolume defined by Hutchinson (1957), who described the fundamental niche of species in biotopes. He believed that a species is able to persist indefinitely in the absence of competition with other species. The main foundations of this theory are: (1) It includes different dimensions (environmental variables or limiting factors) that control for the species distribution; (2) Each dimension is independent from other dimensions, and each dimension has a tolerance range; (3) The intersection of each dimension composes the finally hypervolume niche (without a substitution effect); and (4) The boundaries determining the occurrence of virtual species is the value of every limiting factor. If any limiting factor is beyond an environmental critical threshold, the multivariable suitability index drops sharply, and the virtual species cannot appear.

Similarly, some ENMs for real species have been based on sum methods (e.g. multivariate regressions) and/or multiplication (e.g. interaction between variables in multivariate regressions), while others are based on limitation rules (e.g. Bioclim). Bioclim is known to be very simple and, for that reason, researchers intuitively think that it overestimates the species range. However, in this example we can clearly see that multivariate logistic regressions (which add partial suitabilities to obtain a final combined index) might predict a much larger area than "simple" models like Bioclim (see Fig. 6).

There are different ENMs that use the sum method to obtain a final index. For instance, the generalized linear model (GLM) allows the response variables to have a linear correlation with the predicted value by using an iteratively reweighted least squares method for maximum likelihood estimation of the model parameters (McCullagh and Nelder, 1989). Moreover, the generalized additive model (GAM) infers that a linear predictor depends linearly on unknown smooth functions of some predictor variables by blending properties of generalized linear models with additive models (Wood, 2008). If the environmental variable is the key limiting factor, this may be unsuitable as it goes against basic ecological principles (e.g. LMH or MLH). These methods all consider the interaction of environmental variables, but do not consider the key role of limiting factors, which may lead to the expansion of the potential range of species for their substitution effects and reduce their predictive accuracy.

5. Conclusion

Our results suggest that the ecological assumptions made when constructing our virtual species strongly influenced the maps obtained. Virtual species are used to test and improve the accuracy of species distribution model predictions, and thus, generating adequate virtual models of the species is a key step for advancing the field of biogeography and producing better estimations of the real species ranges. We introduce a new algorithm to create virtual species called "NicheLim" that is based on the theory of hypervolume niche. It agrees with basic ecological theory and avoids substitution effects of summing or multiplying individual suitabilities to obtain a multivariate habitat suitability index.

Funding

This work was supported by the National Natural Science Foundation of China (31300342, 31570417). SV is funded by a post-doctoral contract of the Universidad de Alcalá, Spain. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests

The authors have declared that no competing interests exist.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (31300342, 31570417).

References

Ågren, G.I., Wetterstedt, J.Å.M., Billberger, M.F.K., 2012. Nutrient limitation on terrestrial plant growth–modeling the interaction between nitrogen and phosphorus. New Phytol. 194, 953–960.
Austin, M.P., Belbin, L., Meyers, J.A., Doherty, M.D., Luoto, M., 2006. Evaluation of statistical models used for predicting plant species distributions: role of artificial data and theory. Ecol. Model. 199, 197–216.
Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338.
Bloom, A.J., Chapin, F.S., Mooney, H.A., 1985. Resource limitation in plants-an economic analogy. Annu. Rev Ecol. Syst. 16, 363–392.
Busby, J.R., 1991. BIOCLIM-A bioclimatic analysis and prediction system. In: Margules, C.R., Austin, M.P. (Eds.), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. , pp. 64–68.
Carpenter, S.R., Brock, W.A., Cole, J.J., Pace, M.L., 2009. Leading indicators of phytoplankton transitions caused by resource competition. Theor. Ecol. 2, 139–148.
Farrior, C.E., Tilman, D., Dybzinski, R., Reich, P.B., Levin, S.A., Pacala, S.W., 2013. Resource limitation in a competitive context determines complex plant responses to experimental resource additions. Ecology 94, 2505–2517.
Fourcade, Y., Engler, J.O., Rödder, D., Secondi, J., 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS ONE 9, e97122.
Franklin, J., Wiser, S.K., Drake, D.R., Burrows, L.E., Sykes, W.R., 2006. Environment, disturbance history and rain forest composition across the islands of Tonga, Western Polynesia. J. Veg. Sci. 17, 233–244.
Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S., Elser, J.J., Gruner, D.S., Hillebrand, H., Shurin, J.B., Smith, J.E., 2011. Nutrient co-limitation of primary producer communities. Ecol. Lett. 14, 852–862.
Hirzel, A., Helfer, V., Metral, F., 2001. Assessing habitat-suitability models with a virtual species. Ecol. Model. 145, 111–121.
Hutchinson, G.E., 1957. Cold spring harbor symposium on quantitative biology. Concluding Remarks 22, 415–427.
Jiménez-Valverde, A., Lobo, J., Hortal, J., 2009. The effect of prevalence and its interaction with sample size on the reliability of species distribution models. Community Ecol. 10, 196–205.
Jiménez-Valverde, A., Lobo, J.M., 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. Acta Oecol. 31, 361–369.
Lewis, W.M., Wurtsbaugh, W.A., 2008. Control of lacustrine phytoplankton by nutrients: erosion of the phosphorus paradigm. Int. Rev. Hydrobiol. 93, 446–465.
Liebig, J., 1847. In: Playfair, L., Peterson, T.B. (Eds.), Chemistry in its Application to Agriculture and Physiology. , Fourth edition. Taylor and Walton, London.
Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. J. Biogeogr. 40, 778–789.
McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models. Chapman and Halls, London.
Meynard, C.N., Quinn, J.F., 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. J. Biogeogr. 34, 1455–1469.
Miller, J.A., 2014. Virtual species distribution models Using simulated data to evaluate aspects of model performance. Prog. Phys. Geog. 38, 117–128.
Naimi, B., Skidmore, A.K., Groen, T.A., Hamm, N.A., 2011. Spatial autocorrelation in predictors reduces the impact of positional uncertainty in occurrence data on species distribution modelling. J. Biogeogr. 38, 1497–1509.
Prasad, A.M., Iverson, L.R., Liaw, A., 2006. Newer classification and regression tree techniques: bagging and random forests for ecological prediction. Ecosystems 9, 181–199.
Rapacciuolo, G., Roy, D.B., Gillings, S., Purvis, A., 2014. Temporal validation plots: quantifying how well correlative species distribution models predict species' range changes over time. Methods Ecol. Evol. 5, 407–420.
Ryabov, A.B., Blasius, B., 2011. A graphical theory of competition on spatial resource gradients. Ecol. Lett. 14, 220–228.
Santika, T., Hutchinson, M.F., 2009. The effect of species response form on species distribution model prediction and inference. Ecol. Model. 220, 2365–2379.
Termansen, M., McClean, C.J., Preston, C.D., 2006. The use of genetic algorithms and Bayesian classification to model species distributions. Ecol. Model. 192, 410–424.
Thibaud, E., Petitpierre, B., Broennimann, O., Davison, A.C., Guisan, A., 2014. Measuring the relative effect of factors affecting species distribution model predictions. Methods Ecol. Evol. 5, 947–955.
Varela, S., Lima-Ribeiro, M.S., Diniz-Filho, J.A.F., Storch, D., 2015. Differential effects of temperature change and human impact on European Late Quaternary mammalian extinctions. Global Change Biol. 21, 1475–1481.
Varela, S., Anderson, R.P., García-Valdés, R., Fernández-González, F., 2014. Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37, 1084–1091.
Wood, S.N., 2008. Fast stable direct fitting and smoothness selection for generalized additive models. J. Roy. Stat. Soc. Ser. B—Stat. Met. 70, 495–518.
Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B., Grimm, V., 2010. The virtual ecologist approach: simulating data and observers. Oikos 119, 622–635.