

# A practical framework for a theory-driven ecological niche modeling workflow

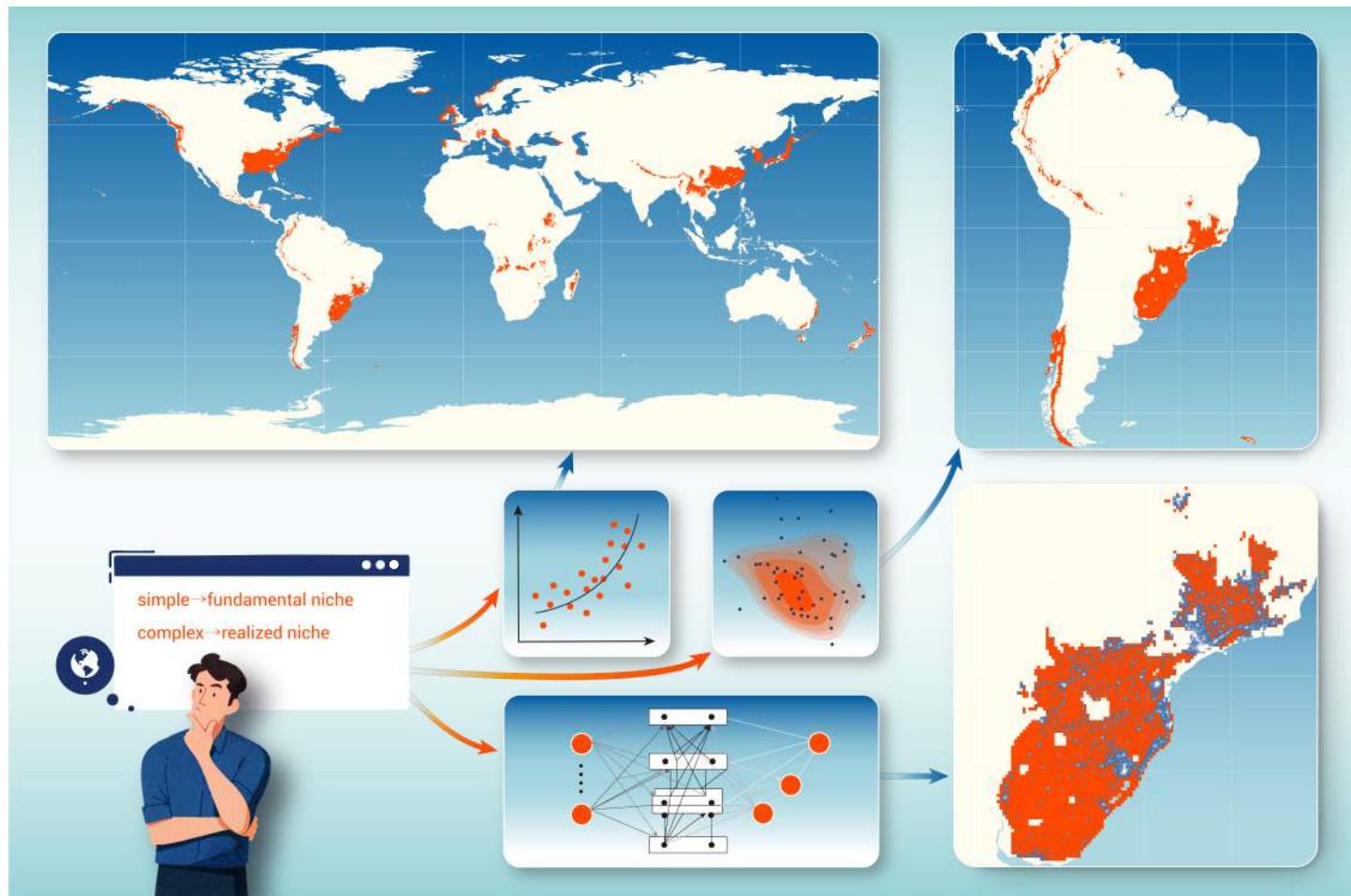
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## GRAPHICAL ABSTRACT



## PUBLIC SUMMARY

- Accurate ecological niche modelling (ENM) requires differentiating between potential and actual habitats.
- Simple models often predict a species' full environmental tolerance better than complex, overfitting ones.
- A framework guides ENM by setting clear research goals and integrating ecological theory for robust outcomes.
- Theory-driven ENM provides accurate predictions, directly improving conservation decisions.

# A practical framework for a theory-driven ecological niche modeling workflow

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Distributional ecology provides a multidimensional understanding of the complex ecological, evolutionary, and biogeographic factors shaping species' distributions. Distributional ecology uses ecological niche modeling (ENM) serving as a quantitative approach to estimate species' ecological niches and their manifestation as likely geographic ranges. Its application is particularly crucial for invasive species, where predicting their potential spread is paramount. An important ongoing debate is how to choose a suitable algorithm and its parameters to perform models well. Nevertheless, a main question should be what ecological niche is being reconstructed, the realized or fundamental? Current protocols and emergent evaluation metrics have only focused on reconstructions of the realized niche, driven by the unbalanced credibility between present and pseudo-absence (or background) occurrences, which often prioritize fitting to the available data while overlooking species' physiological and ecological constraints. Our findings indicate that generalized linear models (GLMs) effectively reconstruct most of the fundamental niche, whereas hypervolume methods, such as kernel density estimation (KDE) and Marble Algorithm (MA), tend to overfit the data and perform poorly. Similarly, Maxent exhibits limitations in characterizing the fundamental niche. We present a conceptual framework to guide assumptions and workflows in ENM applications to facilitate model selection and interpretation.

## INTRODUCTION

Essentially, ecological niche modeling (ENM) is a mathematical process to analyze the relationship between environmental dimensions and field observations of species. After calibration, ecological niche models are projected from environmental dimensions to geographic dimensions to estimate the potential distribution of the species, which has been widely applied to address questions in conservation biology,<sup>1–3</sup> biogeography,<sup>4</sup> evolution,<sup>5,6</sup> climate change,<sup>7</sup> and invasion ecology.<sup>8,9</sup> Recent studies have further expanded its applications, such as investigating niche dynamics and climate change sensitivity, understanding the ecological niche of aquatic, and exploring the role of ENM in biodiversity informatics. Additionally, advancements in ENM software, such as Maxent,<sup>10,11</sup> dismo,<sup>12</sup> and biomod2,<sup>13</sup> have enhanced its utility in predicting species distributions under varying environmental conditions.

Ecological niche modeling is based on the conceptualization of the fundamental niche and the realized niche.<sup>14</sup> According to these ecological theories, the fundamental niche would be the set of environmental conditions occupiable by the species (Figure 1). In environmental conditions beyond the fundamental niche populations of a species would be expected to be extinct.<sup>14</sup> Thus, ecological niches are species-specific, with each species having its own particular environmental tolerances expressed as fundamental-niche limits. Theoretically, species could occupy a series of environmental conditions. Those suitable conditions, however, may not necessarily exist in the areas or periods where the species occurs. For example, environmental combinations that are part of the species' fundamental niche could be absent in the areas where the species is unable to disperse and colonize, which occurs for species restricted to islands or restricted due to intraspecific competition. Additionally, species will occupy only parts of the fundamental niche. The portions of the fundamental niche that are actually occupied by the species are termed realized niche (Figure 1). Because not every environment in a fundamental niche may actually exist at a given time and site, the shape of the realized niche may have an irregular shape in environmental space.<sup>15</sup>

It has been shown that variations in resource availability can have significant effects on species fitness,<sup>16</sup> species interactions,<sup>17</sup> and, eventually, community composition,<sup>18</sup> influencing the manifestation of the realized niche in the geography.<sup>19</sup> Similarly, sampling effort could be incomplete, recovering just a portion of the realized niche,<sup>20,21</sup> the portion observed during sampling (Figure 1). Thus, we generally expect that biotic factors be dynamic at local scales.<sup>22</sup> In this manuscript we discuss the strengths and weaknesses of the current ecological niche modeling framework, highlight the areas of disagreement in the research community, and propose potential paths to solve ongoing methodological and theoretical debates.

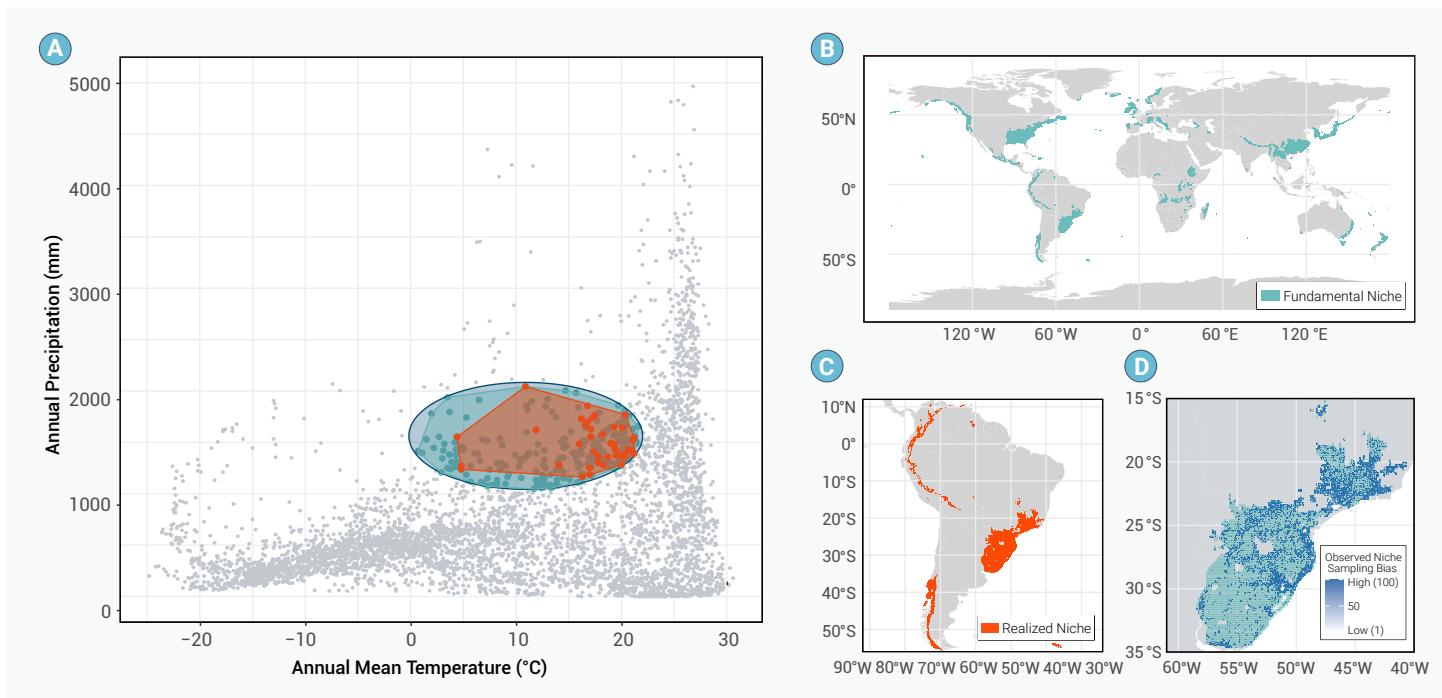
## MATERIALS AND METHODS

### Fundamental vs. realized, what are we modelling?

In niche modeling, are we simulating the fundamental niche of a species or the realized niche? The parsimonious approach is to consider fundamental niches with a simple convex shape manifested in environmental space as observed Gaussian responses of species to environmental variables,<sup>23–27</sup> which could be represented mathematically.<sup>14</sup> However, in the natural world, it is expected that species would not occupy the entire fundamental niche because of the limited climate availability, presence of competitors and predators, and dispersal limitations.<sup>22,28</sup> As a result, attempts to reconstruct the fundamental niche using ecological niche models are limited by data from the realized niche only.<sup>29,30</sup> Furthermore, a biased observation of the realized niche will result in an incomplete representation of both the realized and the fundamental niche (Figure 1).

Ecological theories and empirical data support the idea of highest population growth and genetic diversity of a species in the core portion of its fundamental niche, with declines of fitness towards the edges.<sup>31,32</sup> Nevertheless, debate still exists on the use of the niche center to explain abundance of species.<sup>33,34</sup> Recent assessment argues that inconsistency of studies to find (or not) associations between the niche centroid and the abundance of species may be due to artifactual methodologies and neglection of the differences between fundamental and realized niches.<sup>34–36</sup> Theoretically, any ecological niche model from complete and representative data could recover the fundamental niche of a species very well. For example, if the sampled areas correspond an evenly representation of the realized niche, and the realized niche captures the entire range of values corresponding to the fundamental niche. Paradoxically, the reality is often the opposite. Some ecological niche models aiming to reconstruct fundamental and realized niches are usually assessed based on their fit to biased and incomplete data without clear assumptions in the modeling approach.<sup>37,38</sup> That is, it is assumed that fundamental niche = realized niche = sampled sites, which may be a strong assumption especially for species with unknown ecological equilibrium such as invasive species or species strongly restricted by biogeographic barriers such as island species.

Understanding the differences between the environmental conditions where the species has been observed and the physiological tolerances of the species including the upper and lower limits of the fundamental niche is critical to develop sound ecological niche modeling interpretations. Ecological niche modeling methods may not always be used to model the fundamental niche of a species. Instead, researchers could be interested on the fine-scale landscape conditions associated with the presence of the species.<sup>39</sup> That is, data employed and assumptions to model fundamental vs realized niches would differ markedly. For example, while fundamental niches are usually reconstructed using stable data covering large period spans (e.g., decades,



**Figure 1. Ecological niches displayed in a bidimensional environmental space** (A) Empirical data supports an elliptical shape of fundamental niches (green ellipsoid). In this example, the environmental conditions available globally (grey points) may not fulfill the entire fundamental niche of the virtual species. Note the lack of points in some areas inside the ellipsoid, denoting absence of environmental combinations even in the edges of the fundamental niche (green arrow). The species could be restricted to occupy only parts of the fundamental niche due to dispersal limitations (e.g., biogeographic barriers such as mountains), biotic interactions (e.g., absence of hosts for a parasite), or absence of specific environmental combinations (e.g., climate not available in present-day conditions). The portion of the fundamental niche actually used by the species is termed realized niche (red polyhedron). Nevertheless, imperfect sampling in ecology may limit the collection of data of the species across the entire realized niche. The portion of the realized niche actually “observed” or sampled by researchers is a biased and incomplete view of the fundamental niche (blue polyhedron). (B) Fundamental niche manifested in the geography. Note the global environmental potential of the species. (C) Realized niche manifested in the geographic space. Note the geographic restriction of the species to South America due to dispersal limitations (e.g., South Atlantic Ocean at the east, Uruguay river at the west, La Plata river at the south, and rivers Yaguaron and Cuareim at the north). (D) Observed occurrences of the species by researchers. Note the sampling bias (oversampling in dark areas) derived from nighttime light as a proxy of human presence. In summary, field data could result in an underestimation of the species' fundamental niche.

centuries) and scenopoetic variables not affected by the species (e.g., temperature, precipitation). Realized niche modeling instead could include data at fine temporal and spatial scales—days and meters, respectively.<sup>40</sup> Environmental variables for realized niche modeling may include binomic variables, which can be affected by the presence and abundance of the focal species, such as satellite-derived landscape information and also information from other species in the community (e.g., preys, hosts of parasites, type of forest).<sup>41</sup> Thus, realized niche modeling requires high accuracy and precision of data, so the reliability of the model depends on the quality of sampling data. Since the realized niche is affected by the environment, population dynamics and ecological interactions, its prediction results are usually highly spatiotemporal dynamic. In contrast, basic niche modeling focuses on the physiological tolerance of species and relies on long-term stable environmental variables, so it is applicable to a wider range of spatial and temporal scales. The applicability of realized niche models is usually limited to a specific time and place, and it is difficult to directly project to different regions or periods. Understanding the difference between basic niche and realized niche is crucial to correctly interpret the results of niche modeling and can improve its application value in ecological research and conservation practice.

#### Model prediction vs. model fit

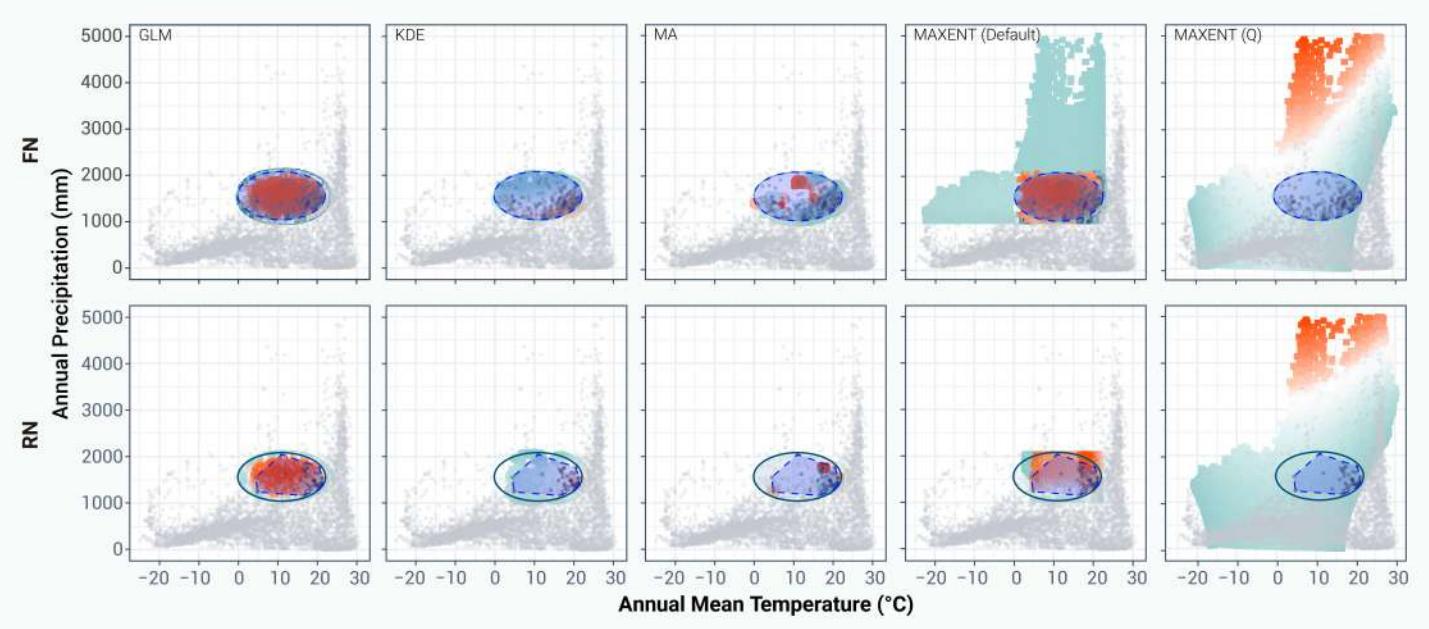
Highly complex models fitting presence-only data are the new paradigm in ecological niche modeling (e.g., hypervolumes,<sup>42,43</sup> Marble<sup>44</sup> and MALPOLON.<sup>45</sup> Nevertheless, available data are usually from the incomplete observation of the species' niche. In this sense, models evaluated only by their capacity to fit to the data observed would underestimate the fundamental niche of the species, and in consequence the estimate of its environmental tolerances and geographic potential. The question of: What is being modeled, the fundamental niche or the realized niche, is critical to determine the assumptions involved, data required, and, in turn, the algorithms to employ.

Ecological niche modeling algorithm could be categorized as correlative presence-background (General Linear Models; GLM) and presence-only clus-

ter-based (hypervolume kernel density estimation and Marble, KDE and MA, respectively). Theoretically simple models requiring low parameterization (e.g., GLM) would be able to reconstruct the fundamental niche of a species with good data (i.e., data resembling the fundamental niche) and also with some poor data (biased data from the realized niche) if the observed data from the field contain detectable features of fundamental niche (e.g., full range of environments tolerated by the species; Figure 2). Simple models are generally data-driven with limited parameterization required for model fit. Complex models (e.g., hypervolumes), however, would underestimate the fundamental niche of a species independently of the amount of data available, especially due to their abilities to avoid predictions in areas with no data available. Thus, hypervolume methods are able to detect the “edges” and “holes” in data in the environmental space, which may be an important feature to consider when exploring realized niches. Good data would generate models resembling the fundamental niche of both simple and complex models, while incomplete data would be poorly informative on the ecology and geography of species for fundamental niche models (Figure 2). Machine learning methods such as Maxent are highly sensitive to the features selected during model parameterization, so that careful exploration is necessary during model selection and output interpretation.

#### The model evaluation paradox

Different models exhibit varying performance and suitability depending on the characteristics of the available data and the specific research question, possessing distinct capacities to reconstruct features of the species' niche.<sup>46</sup> Nevertheless, ecological niche models are usually assessed based on a single “gold standard” evaluation metric (i.e., area under the curve of the receiver operating characteristic; AUC ROC). AUC ROC, however, fails to robustly differentiate between good and bad models.<sup>47–49</sup> Good models, referred to models that accurately resemble (i.e., fit) the model training set and predict independent test set not used during model calibration, should be defined in the context of fundamental or realized niches.



**Figure 2. Ecological niche modeling visualization in environmental space** Ecological niche modeling based on data from the full fundamental niche (FN) and incomplete data available from the observed portions of the niche derived from field data, where was name as realized niche (RN). Model performance assessed for General Linear Models (GLM), Kernel Density Estimation (KDE), Marble Algorithm (MA), Maxent default, and Maxent with quadratic features. Note that GLM, a simple model, is able to reconstruct most of the fundamental niche, while hypervolume methods (KDE and MA) overfitted the data considerably, resulting in underprediction in conditions where no data were provided to the model. Machine learning methods (Maxent default and with quadratic features) performed poorly when limited field data were used. Importantly, it is expected that in practical applications, researchers will have access to data from an incomplete observation of the fundamental niche. Model results are based on data from Figure 1 and are expressed in continuous values to denote environmental conditions with high (red) mid (white), and low suitability (blue).

Model performance is highly tied to the research question. For example, ecological niche models aiming to reconstruct the fundamental niche should be evaluated differently to the ecological niche models aiming to reconstruct the realized niche. When the interest is to reconstruct the fundamental niche, an important feature of the model should be its predictive performance (extrapolation). That is, because only data from the observable portion of the niche are available, models predicting missing data from biologically sound configurations would be preferred to those models unable to fill "holes" or missing data in the environmental space (Figure 2 GLM vs. KDE).<sup>50</sup> When the goal is to reconstruct the realized niche, for example, model performance should be focused on the descriptive ability of the model and its abilities to faithfully generate a model resembling the data.

Model evaluation can be categorized between predictive and descriptive performance. To assess predictive performance, model prediction should be assessed against an independent test set of data. These test data should be geographically and environmentally independent to the data used during model calibration. Independent data are used to accurately assess a model's ability to extrapolate into unsampled (such as "fill holes" of information) environmental space. When the goal is to assess the descriptive performance of models, evaluations should include the full data available for the species, measuring the amount of information reconstructed by the model. As a result, good predictive models would be those capable to predict independent data better than by chance, while good descriptive models would be those accurately resembling the data available with the minimum of information loss. The fact that the current trend is to solely assess model fit, reduces our gain of knowledge in distributional ecology and our abilities to assess *a priori* hypothesis. Beyond model fit, ecological niche modeling should aim to understand, quantify, and reconstruct ecological patterns of biodiversity. Unfortunately, current ecological niche models are poor attempts to fit the data with limited or none efforts to challenge scientific questions and reject scientific hypothesis, echoing the S. Karlin's concerns that "The purpose of models is not to fit the data but to sharpen the questions.", which was raised from his Fisher memorial lecture, 1983.

#### The current framework vs. a new framework

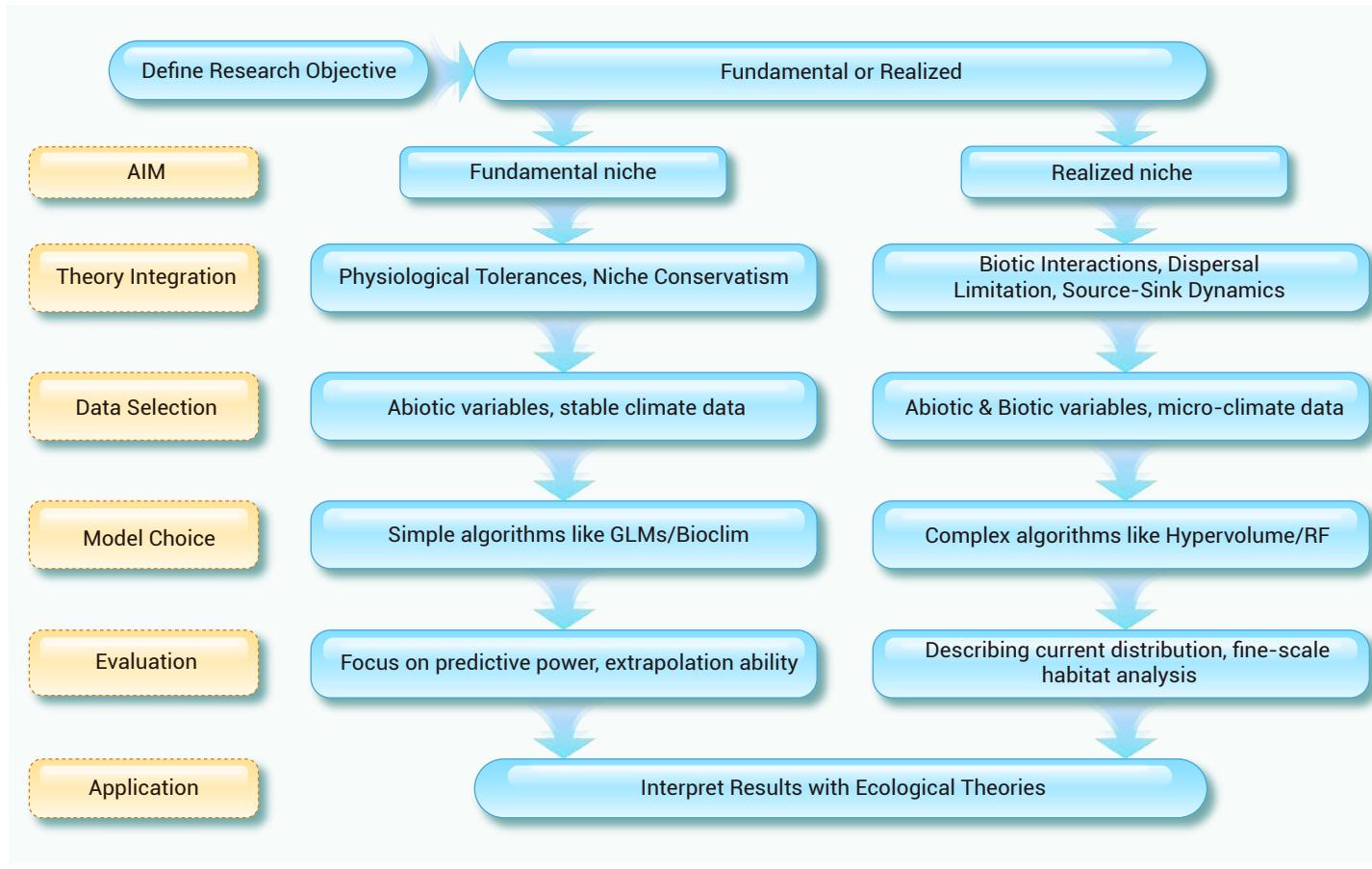
A growing concern in the niche modeling community is the poorly designed and interpreted modeling applications,<sup>51</sup> because the current framework is

often a data-driven process that prioritizes model fit over biological relevance. It focuses on data collection for a focal species, selection of the area of interest, collection of the broadly used bioclimatic variables, model calibration based on default settings, and weak evaluation protocols. This approach, while effective at describing a species' realized distribution based on available occurrence data, frequently overlooks the critical ecological theories that shape a species' true range, which, however, fails to account for the physiology and ecology of the species in the study design. It also avoids testing key hypotheses by failing to compare model results against appropriate baseline expectations, and neglects ecological theories that may guide the selection of the algorithm or the evaluation metric. By focusing on a single-minded goal of maximizing statistical performance, current methods fail to explicitly address the fundamental question: what ecological niche is actually being reconstructed? This over-reliance on a limited set of metrics, coupled with the uncritical use of complex algorithms, often leads to models that are difficult to interpret, have poor predictive power beyond the calibration data, and contribute little to our deeper understanding of a species' ecology and biogeography. It is this set of fundamental shortcomings that necessitates a shift toward a more rigorous and theoretically-grounded approach.

A potential new framework should address these shortcomings by emphasizing a more rigorous and transparent approach. This includes a thorough exploration of the literature to understand the biology and ecology of the focal species, a comprehensive and replicable data collection and curation process, and a study design that aligns with the research objective (e.g., predictive vs. descriptive models). Additionally, the new framework should integrate ecological theories to guide the selection of modeling components and assumptions, ensuring that the models are both biologically meaningful and methodologically robust. By adopting such a structured protocol, the niche modelling community can improve the reproducibility, transparency, and applicability of models in ecological and conservation contexts.

#### A new framework for ecological niche modeling

Our proposed new framework establishes a different paradigm for ENM (Figure 3). It begins by compelling researchers to first distinguish their primary objective: are they seeking to predict a species' potential range by modeling its fundamental niche, or are they aiming to describe its current distribution by modeling its realized niche? This core distinction is crucial



**Figure 3. Conceptual Workflow for the New Ecological Niche Modeling (ENM) Framework** This flowchart outlines our proposed new framework, which guides researchers in selecting appropriate modeling methods based on a clear scientific question. The process begins with defining the research objective (predictive or descriptive), then integrates relevant ecological theories to guide the selection of data and models, and finally, through targeted evaluation, arrives at biologically meaningful conclusions. Detailed explanations of related terms and their application scenarios can be found in Table 1.

because it informs every subsequent decision, from data selection to model choice and final evaluation. For predictive models, which seek to understand a species' potential range, the focus should be on an algorithm's ability to extrapolate reliably into unsampled environmental space. That is to say, simpler, theory-driven models like GLMs or Bioclim are often superior, as they effectively fill data gaps to reconstruct the full physiological potential of a species. Conversely, for descriptive models, which seek to understand the drivers of a species' current distribution, more complex methods (like hypervolume or random forest) that can faithfully capture the patterns and "holes" in the available data may be more appropriate.

The seamless integration of ecological theory is a critical component of this framework. Theories on physiological tolerances should guide the selection of abiotic variables, ensuring they reflect the environmental extremes a species can endure. Similarly, an understanding of dispersal limitation should inform the definition of the accessible area ( $M$ ), providing a biological context for why a species might not occupy its entire potential range. Furthermore, theories regarding biotic interactions and source-sink dynamics can justify the inclusion of additional variables or provide a basis for cautiously interpreting predictions in marginal habitats. By intentionally embedding these ecological principles into every step, which are from data curation and variable selection to model calibration and final interpretation, the models we create become not just statistical constructs, but powerful tools for testing and exploring ecological hypotheses.

Moreover, this new framework elevates the practice of ENM from a data-fitting exercise to a hypothesis-driven scientific endeavor. It provides a structured protocol that ensures models are transparent, repeatable, and biologically meaningful. This approach promises to improve the quality of ENM research and will ultimately lead to better-informed decisions in conservation, invasion biology, and biodiversity management.

## CONCLUSIONS

Key ecological theories have been developed thanks to the availability of ecological niche modeling applications (e.g., niche shift, phylogenetic niche conservatism, unfilling niche, ecological equilibrium, among others). User friendly methods have increased the number of ecological niche modeling applications. Current paradigms, however, have neglected hypothesis-driven studies, with data-driven studies dominating the landscape of ecological niche theory and limiting our understanding of biogeographic signals. The necessity for more and better evaluation metrics, the urgency to compare models against baseline hypothesis, and the need for improved ecological niche modeling protocols are the new challenges in the field of distributional ecology.

## Glossary

**Distributional ecology.** the specialization of ecology to quantitatively characterize and predict the distribution of species in geographic space at different spatial and temporal scales by accounting for the environmental conditions limiting or facilitating the distribution of species. Coarse-scale applications of distributional ecology are interpreted using biogeographic approaches.

**Geographic space.** distribution of phenomena, processes, and features in the geography, focused on the dependence of their location with the surface of Earth (e.g., coordinates can be expressed as latitude and longitude).

**Environmental space.** distribution of phenomena, processes, and features in the multidimensional environmental conditions, focused on the dependence of their location with the natural environment (e.g., coordinates can be expressed as precipitation and temperature).

**Fundamental niche.** set of sites in the *environmental space* where a species can in theory maintain populations in the long-term without need of immigration.

Table 1. Ecological Theories Guiding ENM Component and Assumption Selection

Ecological Theory	Relevant ENM Component/Decision Point	Guiding Principle/Assumption	Example Application/Impact
Fundamental Niche	Data selection (species occurrence & environmental data), Algorithm selection, Environmental variable selection, Model evaluation, Result interpretation	Assumes species occupies its full physiological potential; Uses stable, abiotic variables (e.g., temperature, precipitation); Focuses on species' physiological tolerances.	GLMs often better at reconstructing fundamental niche; Use long-term climate data; Evaluate model extrapolation ability.
Realized Niche	Data selection, Algorithm selection, Environmental variable selection, Model evaluation, Result interpretation	Acknowledges influence of biotic interactions (e.g., competition, predation, host) and dispersal limitations; Considers biotic variables (e.g., land use, vegetation type); Focuses on conditions actually occupied by species.	Hypervolume methods (e.g., KDE, MA) may be better for describing realized niche but can overfit; Include land use or biotic interaction data; Evaluate model goodness-of-fit.
Dispersal Limitation	Study area definition (M), Data selection, Model evaluation, Result interpretation	Restricts species distribution in geographic space; Considers biogeographic barriers in models.	Define accessible area (M) to limit model prediction range; Explain discrepancies between model prediction and actual distribution.
Biotic Interactions	Environmental variable selection, Model selection, Result interpretation	Affects species distribution within the realized niche; Can lead to niche contraction or expansion.	Incorporate data on presence of predators, competitors, or hosts; Select algorithms capable of capturing complex interactions.
Physiological Tolerances	Environmental variable selection, Model calibration, Result interpretation	Determines fundamental niche boundaries in environmental space; Sensitive to extreme environmental conditions.	Use environmental variables reflecting physiological thresholds; Ensure model parameterization captures species' response curves.
Niche Conservatism	Model transfer, Paleo-niche reconstruction, Future distribution prediction	Assumes species niche remains relatively stable over evolutionary timescales; Allows model extrapolation across different times or spaces.	Apply current models to future climate scenarios or different geographic regions.
Source-Sink Dynamics	Data selection, Result interpretation	Some areas may not be self-sustaining populations but maintained by immigration; Can lead to occurrence data not fully representing suitable habitat.	Interpret predictions in marginal areas cautiously; May require integration with population dynamics models.
Sampling Bias	Data collection & curation, Model calibration, Model evaluation	Observed data may be incomplete or biased, leading to underestimation of true niche; Affects model fit and prediction accuracy.	Implement bias correction methods; Use spatially independent evaluation data.

**Realized niche.** a subset of the *fundamental niche* in which a species actually maintains populations. The realized niche also occurs in environmental space and account by the interaction of a focal species with other species that limit or facilitate their survival (e.g., pathogens, competitors, predators, preys, or hosts). The realized niche can also be constrained by the availability of the species to occupy the entire fundamental niche due to dispersal limitations in geographic space (e.g., ocean, rivers, mountains).

**Observed niche.** The portion of the realized niche actually sampled by the researcher and from which ecological niche models will be constructed.

**Ecological niche modeling.** The process of using mathematical algorithms to reconstruct the realized or fundamental niches of species and project results to geographic space to estimate the species distribution. Algorithms employed in ecological niche modeling can be categorized as presence-absence data (e.g., classification trees, generalized linear models), presence-only algorithms (e.g., kernel density estimation, Marble, and Bioclim), and presence-background (e.g., Maxent, Genetic Algorithm for Rule Set Production) where the background is represented by a sample of environmental conditions used for model calibration. Species distribution modeling could be used a form of ecological niche modeling for which no ecological theories are considered during model design and interpretation.

**Environmental variables.** environmental variables used to estimate the fundamental or realized niche of a species. Variables can vary in the temporal-(months, years, centuries) and spatial- (meters, kilometers) scale, which is usually defined based on the study question and the availability of data of the species for the modeling. Environmental variables can be categorized in two types. *Abiotic (a.k.a scenopoetic) variables*, the set of physical conditions that change very slowly (e.g., temperature, precipitation) and restrict the persistence of populations of a species. *Biotic (a.k.a. binomic) variables*, set of organisms in an ecosystem that limit (e.g., predators, competitors) or facilitate (e.g., preys, hosts) the survival of the focal species; these variables can

change fast and are affected by the presence and abundance of species.

## REFERENCES

1. Nüchel J., Böcher P. K., Xiao W., et al. (2018). Snub-nosed monkeys (*Rhinopithecus*): Potential distribution and its implication for conservation. *Biodivers. Conserv.* **27**:1517–1538. DOI:10.1007/s10531-018-1507-0
2. Escobar L.E., Awan M.N. and Qiao H. (2015). Anthropogenic disturbance and habitat loss for the red-listed Asiatic black bear (*Ursus thibetanus*): Using ecological niche modeling and nighttime light satellite imagery. *Biol. Conserv.* **191**:400–407. DOI:10.1016/j.biocon.2015.06.040
3. Mi C., Song K., Ma L., et al. (2023). Optimizing protected areas to boost the conservation of key protected wildlife in China. *The Innovation* **4**:100424. DOI:10.1016/j.xinn.2023.100424
4. Csergő A. M., Salguero-Gómez R., Broennimann O., et al. (2017). Less favourable climates constrain demographic strategies in plants. *Ecol. Lett.* **20**:969–980. DOI:10.1111/ele.12794
5. Saupe E. E., Barve N., Owens H. L., et al. (2018). Reconstructing ecological niche evolution when niches are incompletely characterized. *Syst. Biol.* **3**:428–438. DOI:10.1093/sysbio/syx084
6. Kirchheimer B., Wessely J., Gatringer A., et al. (2018). Reconstructing geographical parthenogenesis: Effects of niche differentiation and reproductive mode on Holocene range expansion of an alpine plant. *Ecol. Lett.* **21**:392–401. DOI:10.1111/ele.12908
7. Scherrer D., Massy S., Meier S., et al. (2017). Assessing and predicting shifts in mountain forest composition across 25 years of climate change. *Divers. Distrib.* **23**:517–528. DOI:10.1111/ddi.12548
8. Tingley R., Vallinoto M., Sequeira F., et al. (2014). Realized niche shift during a global biological invasion. *PNAS* **111**:10233–10238. DOI:10.1073/pnas.1405766111
9. Ning J., Lu P., Fan J., et al. (2022). American fall webworm in China: A new case of global biological invasions. *The Innovation* **3**:100201. DOI:10.1016/j.xinn.2021.100201
10. Phillips S. J., Anderson R. P. and Schapire R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**:231–259. DOI:10.1016/j.ecolmodel.2005.03.026
11. Elith J., Phillips S. J., Hastie T., et al. (2011). A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **17**:43–57. DOI:10.1111/j.1472-4642.2010.00725.x

12. Hijmans R. J., Phillips S., Leathwick J., & Elith J. (2024). Dismo: Species distribution modeling. *R package version 7.3-16*. DOI:10.32614/CRAN.package.dismo
13. Thuiller W., Lafourcade B., Engler R., et al. (2009). BIOMOD - A platform for ensemble forecasting of species distributions. *Ecography* **32**:369–373. DOI:10.1111/j.1600-0587.2008.05742.x
14. Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., & Araújo, M.B. (2011). In Ecological niches and geographic distributions. Levin S.A. and Horn H.S. (eds). Ecological niches and geographic distributions (Princeton University Press), pp. 9–21. DOI:10.1515/9781400840670
15. Jackson S. T. and Overpeck J. T. (2000). Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* **26**:194–220. DOI:10.1666/0094-8373(2000)26[194:roppac]2.0.co;2
16. Dmitriev C. M. (2011). The evolution of growth trajectories: What limits growth rate. *Biol. Rev.* **86**:97–116. DOI:10.1111/j.1469-185X.2010.00136.x
17. Dirzo R., Young H. S., Galetti M., et al. (2014). Defaunation in the Anthropocene. *Science* **345**:401–406. DOI:10.1126/science.1251817
18. Scheffers B. R., De Meester L., Bridge T. C. L., et al. (2016). The broad footprint of climate change from genes to biomes to people. *Science* **354**:aaft671. DOI:10.1126/science.aaft671.
19. Cencı S., Montero-Castaño A. and Saavedra S. (2018). Estimating the effect of the reorganization of interactions on the adaptability of species to changing environments. *J. Theor. Biol.* **437**:115–125. DOI:10.1016/j.jtbi.2017.10.016
20. Warren D. L., Cardillo M., Rosauer D. F., et al. (2014). Mistaking geography for biology: Inferring processes from species distributions. *Trends Ecol. Evol.* **29**:572–580. DOI:10.1016/j.tree.2014.08.003
21. Hughes A. C., Orr M. C., Ma K., et al. (2021). Sampling biases shape our view of the natural world. *Ecography* **44**:1259–1269. DOI:10.1111/ecog.05926
22. Soberón J. and Nakamura M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *PNAS* **106**:19644–19650. DOI:10.1073/pnas.0901637106
23. Chen Z., Snow M., Lawrence C. S., et al. (2015). Selection for upper thermal tolerance in rainbow trout (*Oncorhynchus mykiss* Walbaum). *J. Exp. Biol.* **218**:803–812. DOI:10.1242/jeb.113993
24. Jamil T., Kruk C. and ter Braak C. J. F. (2014). A unimodal species response model relating traits to environment with application to phytoplankton communities. *PLOS ONE* **9**:e97583. DOI:10.1371/journal.pone.0097583
25. Tribouillois H., Dürre C., Demilly D., et al. (2016). Determination of germination response to temperature and water potential for a wide range of cover crop species and related functional groups. *PLOS ONE* **11**:e0161185. DOI:10.1371/journal.pone.0161185
26. Edwards K. F., Thomas M. K., Klausmeier C. A., et al. (2016). Phytoplankton growth and the interaction of light and temperature: A synthesis at the species and community level. *Limnol. Oceanogr.* **61**:1232–1244. DOI:10.1002/lo.10282
27. Canham C. D. and Murphy L. (2017). The demography of tree species response to climate: Sapling and canopy tree survival. *Ecosphere* **8**:e01701. DOI:10.1002/ecs2.1701
28. Qiao H., Feng X., Escobar L. E., et al. (2019). An evaluation of transferability of ecological niche models. *Ecography* **42**:521–534. DOI:10.1111/ecog.03986
29. Goicolea T., Adde A., Broennimann O., et al. (2025). Spatially-nested hierarchical species distribution models to overcome niche truncation in national-scale studies. *Ecography* **2025**:e07328. DOI:10.1111/ecog.07328
30. Feng X., Park D. S., Walker C., et al. (2019). A checklist for maximizing reproducibility of ecological niche models. *Nat. Ecol. Evol.* **3**:1382–1395. DOI:10.1038/s41559-019-0972-5
31. Lira-Noriega A. and Manthey J. D. (2014). Relationship of genetic diversity and niche centrality: A survey and analysis. *Evol.* **68**:1082–1093. DOI:10.1111/evo.12343
32. Martínez-Gutiérrez P. G., Martínez-Meyer E., Palomares F., et al. (2018). Niche centrality and human influence predict rangewide variation in population abundance of a widespread mammal: The collared peccary (*Pecari tajacu*). *Divers. Distrib.* **24**:103–115. DOI:10.1111/ddi.12662
33. Dallas T., Decker R. R. and Hastings A. (2017). Species are not most abundant in the centre of their geographic range or climatic niche. *Ecol. Lett.* **20**:1526–1533. DOI:10.1111/ele.12860
34. Feng X. and Qiao H. (2022). Accounting for dispersal using simulated data improves understanding of species abundance patterns. *Glob. Ecol. Biogeogr.* **31**:200–214. DOI:10.1111/geb.13412
35. Soberón J., Peterson A. T. and Osorio-Olvera L. (2018). A comment on "Species are not most abundant in the center of their geographic range or climatic niche". *bioRxiv*:266510. DOI:10.1101/266510.
36. Ascanio A., Bracken J. T., Stevens M. H. H., et al. (2024). New theoretical and analytical framework for quantifying and classifying ecological niche differentiation. *Ecol. Monogr.* **94**:e1622. DOI:10.1002/ecm.1622
37. Muscarella R., Galante P. J., Soley-Guardia M., et al. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods Ecol. Evol.* **5**:1198–1205. DOI:10.1111/2041-210X.12261
38. Radosavljevic A. and Anderson R. P. (2014). Making better Maxent models of species distributions: Complexity, overfitting and evaluation. *J. Biogeogr.* **41**:629–643. DOI:10.1111/jbi.12227
39. Guisan A., Thuiller W. and Zimmermann N. E. (2017). Ecological scales: Issues of resolution and extent. Habitat suitability and distribution models: With applications in R (Cambridge University Press), pp:135–151. DOI:10.1017/9781139028271
40. Briscoe D. K., Fossette S., Scales K. L., et al. (2018) Characterizing habitat suitability for a central-place forager in a dynamic marine environment. *Ecol. Evol.* **8**: 2788–2801. DOI:10.1002/ee.3382
41. Anderson R. P. (2017). When and how should biotic interactions be considered in models of species niches and distributions. *J. Biogeogr.* **44**:8–17. DOI:10.1111/jbi.12825
42. Blonder B. (2018). Hypervolume concepts in niche- and trait-based ecology. *Ecography* **41**:1441–1455. DOI:10.1111/ecog.03187
43. Blonder B., Lamanna C., Viole C., et al. (2014). The n-dimensional hypervolume. *Glob. Ecol. Biogeogr.* **23**:595–609. DOI:10.1111/geb.12146
44. Qiao H., Lin C., Jiang Z., et al. (2015). Marble algorithm: A solution to estimating ecological niches from presence-only records. *Sci. Rep.* **5**:14232. DOI:10.1038/srep14232
45. Larcher T., Picek L., Deneu B., et al. (2024). MALPOLON: A framework for deep species distribution modeling. *ArXiv e-prints* **2409.18102**. DOI:10.48550/arXiv.2409.18102
46. Qiao H., Soberón J. and Peterson T. A. (2015). No silver bullets in correlative ecological niche modeling: insights from testing among many potential algorithms for niche estimation. *Methods Ecol. Evol.* **6**:1126–1136. DOI:10.1111/2041-210x.12397
47. Fourcade Y., Besnard A. G. and Secondi J. (2018) Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Glob. Ecol. Biogeogr.* **27**: 245–256. DOI:10.1111/geb.12684
48. Lobo J. M., Jiménez-Valverde A. and Real R. (2008). AUC: A misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* **17**:145–151. DOI:10.1111/j.1466-8238.2007.00358.x
49. Peterson A. T., Papeş M. and Soberón J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Model.* **213**:63–72. DOI:10.1016/j.ecolmodel.2007.11.008
50. Qiao H., Escobar L. E., Saupe E. E., et al. (2017). A cautionary note on the use of hypervolume kernel density estimators in ecological niche modelling. *Glob. Ecol. Biogeogr.* **26**:1066–1070. DOI:10.1111/geb.12492
51. Peterson A. T. (2014). Mapping disease transmission risk: Enriching models using biogeography and ecology (Johns Hopkins University Press), pp:75–83. DOI:10.1353/book.36167

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## AUTHOR CONTRIBUTIONS

Both Huijie Qiao and Luis E. Escobar conceived the study and wrote, reviewed and approved the manuscript. Huijie Qiao performed the data analysis and visualization.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

## ETHICAL STATEMENT AND PATIENT CONSENT

Not applicable.

## DATA AND CODE AVAILABILITY

All the data generated or analyzed in this article can be visited via <https://doi.org/10.5776/sciedb.28986>