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Research Article

Extrapolation strategy matters when transferring ecological niche models: new visualization tools for informed decisions

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Ecological niche models (ENMs) are commonly used to predict species' potential distributions across space and time, allowing researchers and practitioners to assess invasion risk, estimate the impacts of future climate change, and reconstruct past distributions. These predictions, however, often require extrapolation into environmental conditions that fall outside the range of values used for model training (i.e. 'non-analog environments'). Two primary strategies exist for extrapolating into new conditions for some modeling algorithms: unconstrained extrapolation (allowing the modeled response curve to maintain its trajectory) and clamping (holding the response constant at the values observed at the limits of the training data). As these can lead to considerable differences in model predictions, it is important to inspect the behavior of modeled responses under different extrapolation strategies, which is rarely done in ENM studies. Such examination can help promote biologically realistic model transfers, for example by avoiding unconstrained extrapolation when the relevant tail of the modeled response has a sharply increasing trend. Here, we present a proposed workflow and new visualization tools to guide researchers in choosing appropriate extrapolation strategies, including plots for marginal response curves and non-analog pixel densities. As an illustration, we used this workflow and tools to compare extrapolation strategies for two hindcast scenarios at the Last Glacial Maximum (~ 21 kya) for the black-eared mouse *Peromyscus melanotis* in Mexico, which currently occurs in montane forests. Making extrapolation choices individually for each tail per variable ('custom clamping') helped avoid unrealistically high suitability predictions for non-analog environments. This study emphasizes the importance of both inspecting response curves and assessing the total area with non-analog conditions. By making these choices by variable and tail – a first for ENMs – this study and associated code empower researchers to understand how individual extrapolation strategies affect results and to make decisions that should lead to more realistic predictions.



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Introduction

Ecological niche models (ENMs) are used to make predictions of species' niches and potential geographical distributions that often necessitate transferring models across space and/or time. Model transfer can involve making predictions for data with values outside the ranges of the training data, or 'non-analog' conditions, via extrapolation in environmental space (Williams et al. 2007, Fitzpatrick and Hargrove 2009, Zurell et al. 2012). Common uses of transfer include predicting establishment risk for invasive species (Jiménez-Valverde et al. 2011, Cordier et al. 2020), forecasting range shifts in response to climate change (Anderson 2013, Peterson et al. 2018), and reconstructing paleodistributions (Varela et al. 2011). Most ENMs are trained using current occurrence records and environmental variables (especially regarding climatic conditions; Fick and Hijmans 2017, Karger et al. 2017, Abatzoglou et al. 2018), so the degree of extrapolation will thus depend on the difference between current conditions and the non-analog ones under transfer. Unfortunately, low accuracy of transfers can be driven by various factors, including increases in environmental novelty or geographic distance, algorithm selection, or non-stationarity in species-environment relationships across space and time (Heikkinen et al. 2012, Yates et al. 2018, Qiao et al. 2019, Rousseau and Betts 2022, Allyn et al. 2025).

Various approaches, including multivariate similarity metrics, have been developed for quantifying differences between training and transfer conditions (Meyer and Pebesma 2021). These metrics can yield maps showing multivariate distance from training to transfer conditions. Other mapping methods (e.g. 'most dissimilar variable'; Elith et al. 2010) can help pinpoint which variables contribute to these dissimilarities. Nevertheless, researchers typically include all variables when calculating these metrics regardless of their individual contribution to the model and their relevance for extrapolation. As particular outlying values for individual variables can have a large effect on the overall output of similarity metrics, including variables with little or no importance to the model can lead to misinterpreting the magnitude of extrapolation. Additionally, these methods usually cannot identify when multiple variables contribute to dissimilarities (except for mobility-oriented parity [MOP] extensions; Cobos et al. 2024) or consider the different strategies available to extrapolate.

A few fundamental strategies exist for dealing with non-analog conditions (Qiao et al. 2019, Valavi et al. 2022). One option is simply to avoid making any prediction beyond the ranges of the training data, a strategy known as 'no extrapolation' (Phillips et al. 2006) or truncation (Owens et al. 2013, Yañez-Arenas et al. 2016; distinct from the concept of 'niche truncation', Guisan et al. 2025). However, this

strategy is limiting as many studies require geographic predictions throughout the entire study region. Two other options involve making extrapolations but do so differently (Fig. 1). The first, which is available for some but not all algorithms, is to use unconstrained or free extrapolation by extending the modeled response (i.e. lines or curves) beyond the environmental limits of the training data (Thuiller et al. 2004). The second, which is commonly available, is to hold non-analog environmental values to the limits of the training data before making predictions (i.e. the minimum for the lower tail and maximum for the upper one), also known as 'clamping' (Phillips et al. 2006, Phillips and Dudík 2008). Once a training limit is reached (also called 'point of truncation'; Anderson 2013), the estimated response beyond that point is restricted to that of the predicted value at the limit. For algorithms that allow unconstrained extrapolation in addition to clamping, this decision can greatly affect transfer predictions (Elith et al. 2010, Owens et al. 2013).

It has been suggested that the decision to use unconstrained extrapolation or clamping should be based on the direction of a marginal response curve at the training limit (Anderson 2013, Guevara et al. 2018; Fig. 1a). Marginal response curves (hereafter, 'response curves') plot a given variable against the species' modeled response (e.g. probability of occurrence or a measure of environmental suitability) while keeping the values of the other variables constant at their means or medians. Response curves that show decreasing suitability past the training limit should be allowed to continue decreasing (as more extreme environmental conditions should be even less suitable for the species), so unconstrained extrapolation is suggested in such situations (Guevara et al. 2018; e.g. the lower tail in Fig. 1a). In contrast, if response curves are increasing as they approach a training limit, clamping offers a more conservative strategy than unconstrained extrapolation because conditions more extreme should not result in ever-higher suitability for the species indefinitely (Anderson 2013; e.g. upper tail in Fig. 1a). Clamping increasing tails assumes a unimodal response per individual variable (Qiao et al. 2019), which follows classical niche theory (Austin 2007). These decisions apply to the subset of algorithms that allow unconstrained extrapolation, such as regression methods with linear or polynomial fits (including generalized additive models [GAM] and Maxent; Hastie and Tibshirani 1990, Phillips et al. 2006). In contrast, some algorithms only clamp predictions for non-analog conditions, which can affect their accuracy when extrapolating (Heikkinen et al. 2012), both for increasing and decreasing tails. These include climatic envelope models like BIOCLIM (Booth et al. 2014) and tree-based algorithms like random forest and boosted regression trees (Hengl et al. 2018, Malistov and Trushin 2019).

Here, to illustrate these issues and explain advances in visualization and decision-making, we describe technical aspects

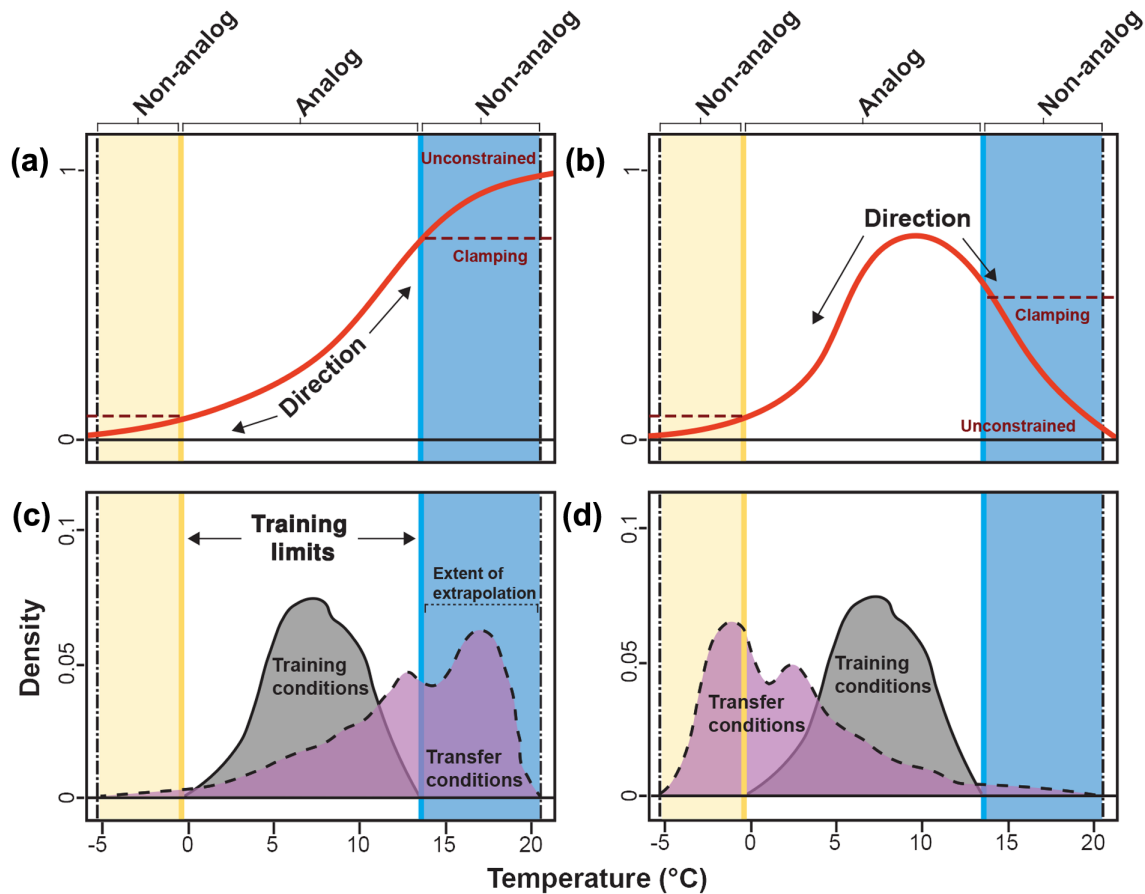


Figure 1. Hypothetical response curve for an ecological niche model including non-analog environments, and kernel density plot of training and transfer conditions, illustrating behavior of different extrapolation strategies. Panels (a) and (b) show the response curve representing the change in model prediction (y-axis) against a single environmental variable (x-axis). Panels (c) and (d) show gray and purple pixel density plots that correspond to the environmental conditions of the training and transfer region, respectively. Solid vertical lines represent the training limits (the environmental bounds of the training data; also termed points of truncation). Dot-dash vertical lines indicate the environmental limits of the transfer environment. Shaded areas correspond to non-analog environments (lower tail in yellow, upper tail in blue). The solid red line represents a response curve under unconstrained extrapolation, while dashed red lines show clamping in non-analog environments.

of extrapolation in the context of the algorithm Maxent. This algorithm provides a flexible set of model fits that includes complex responses (e.g. 'hinge' features) as well as simpler linear and quadratic features (Phillips et al. 2006, 2017). We focus on Maxent because it is one of the most widely used algorithms for ecological niche modeling (Phillips et al. 2017) and it offers both extrapolation options: unconstrained and clamping. Notably, the decision-making process regarding these strategies is also applicable to other algorithms that offer both, such as regression-based methods (e.g. GAM, generalized linear models [GLM]). Current options available both in the Maxent Java software and the R package 'maxnet' (Phillips et al. 2017) restrict researchers to a single analysis-wide decision between unconstrained extrapolation and clamping for all variables (and both upper and lower tails of their response curves). However, the R package 'ENMeval' (ver. 2.0; Kass et al. 2021) that facilitates tuning of complexity for Maxent models provides the option for separate clamping decisions by variable response-curve tail (termed 'custom

clamping'), a general functionality that can be used for any algorithm that allows unconstrained extrapolation. Custom clamping is useful in scenarios when individual extrapolation decisions are desirable for different variables (or tails of the response curves).

Whereas the selection of an extrapolation strategy is typically applied as a single decision during model training, ideally it should be made after model construction and before transfer. First, some variables used during model training may be excluded from the final model (e.g. under L1 regularization for Maxent; Feng et al. 2019), or a variable's importance for the final model may be so low that its effect on overall extrapolation will be minimal. Second, some variables retained in the final model may show no difference between unconstrained extrapolation and clamping for one or both variable tails (e.g. a unimodal curve in which a prediction of 0 is reached before the training limit; lower tail in Fig. 1a). Therefore, decisions regarding extrapolation strategy should focus exclusively on the variables in the final model, primarily

on those with the highest variable importance, and specifically on the particular tails that show differences between extrapolation strategies.

In addition to the difference between extrapolation strategies, another factor that affects model predictions when transferring is the total geographic area (i.e. the number of pixels, or pixel density) with non-analog conditions. If the goal of transferring a model is to predict a small area of the distribution (e.g. the range inside a protected area), the existence of even a few pixels with non-analog conditions could warrant a detailed selection of extrapolation strategy. In contrast, if the goal is predicting a species' potential distribution over a large area, a relatively small number of non-analog pixels will not drastically affect the overall geographic prediction, especially because ENMs using a logit link are constrained to a maximum prediction value of one (Elith et al. 2011, Heit et al. 2024; note that models of abundance based on count data instead can apply a log link that is not similarly limiting). For example, if no or few pixels with non-analog conditions exist for a response tail, regardless of whether the two extrapolation strategies differ, there would be no or limited effect on the area predicted as suitable (e.g. lower tail in Fig. 1c). Similarly, even if the density of non-analog environments is relatively large (e.g. lower tail in Fig. 1d), the two strategies could lead to similar predictions if both result in low suitability. Predictions will only differ markedly if the density of non-analog environments is relatively large and the unconstrained response and clamping differ considerably (e.g. upper tails in Fig. 1a, 1c).

To promote understanding of these issues, better decision-making, and more realistic predictions, here we present new visualization tools and refined guidelines for transferring ENMs to non-analog environments. Specifically, we: 1) develop tools to visualize response curves and the number of pixels with non-analog conditions, facilitating selection of extrapolation strategy per variable response-curve tail; and 2) use these tools to assess and interpret how and when the choice of extrapolation strategy matters, using worked examples for hindcasting the potential distribution of the black-eared mouse *Peromyscus melanotis* in Mexico.

Material and methods

Study species, data, and modeling

The black-eared mouse *Peromyscus melanotis* is a small, omnivorous rodent that typically inhabits coniferous and mesic deciduous forests, patches of perennial bunchgrass, and marshes at elevations ranging between 2100 and 4300 m a.s.l. (Álvarez-Castañeda 2005). This species is confirmed to be distributed in Mexico across the Trans-Mexican Volcanic belt and both the Sierras Madre Oriental and Occidental (Bradley et al. 2014, García-Mendoza et al. 2018, Burgin et al. 2025). Like many montane species, the distribution of *P. melanotis* likely expanded during transition from the prior interglacial into the Last Glacial Maximum as it tracked changes in climate and vegetation, followed subsequently

by an upward movement and constriction post-glaciation (Caballero et al. 2010, Correa-Metrio et al. 2012, Guevara 2020). We selected this species for two reasons: its environmental associations are known (and correspond to intuitive factors associated with climatic changes over the late Pleistocene to the present), and it has an extensive distribution (in a region with an even wider range of environmental conditions). For this example, we used only georeferenced occurrence records with published taxonomic verifications confirmed by specialists, in this case records ($n = 113$) from García-Mendoza et al. (2018), and thus intend these results to be demonstrative for the method and not definitive for the species. The number of localities was reduced using a spatial thinning distance of 5 km to reduce the effects of sampling bias, with the R package 'spThin' (ver 0.2.0; Aiello-Lammens et al. 2015, Boria et al. 2017) in R ver. 4.4 (www.r-project.org). After thinning, 71 occurrences remained for model training and cross-validation. Given the complex topography in montane regions, and especially for species currently inhabiting higher elevations, extrapolation is commonly required when transferring models to glacial conditions, an ideal situation for assessing and illustrating extrapolation decision-making.

Present-day environmental data (1981–2010) were obtained from CHELSA ver. 2.1, a dataset that offers bioclimatic variables at 30 arcsec resolution (Karger et al. 2017). CHELSA implements an orographic correction that improves precipitation estimates in mountainous regions relative to similar climate datasets, thereby enhancing model accuracy in estimations of species' potential distributions (Bobrowski and Schickhoff 2017). We chose four bioclimatic variables to simplify the visualization of response curves and facilitate interpretation of the decision-making process regarding extrapolation strategies. These variables were the maximum temperature of the warmest month (bio05), minimum temperature of the coldest month (bio06), precipitation of the wettest month (bio13), and precipitation of the driest month (bio14). Previous studies have shown the utility of these variables for small montane mammals in Mexico, as they capture the extreme average conditions of temperature and precipitation, which are the main climatic factors limiting their distributions (Guevara et al. 2018, Pinilla-Buitrago 2023, 2025).

The presence-background algorithm Maxent ver. 3.4.4 was used to build models using the R package 'ENMeval' (ver. 2.0.4; Kass et al. 2021), calling the Java implementation (Phillips et al. 2017). The study region for model training was defined by a 0.5 arc-degree buffer around the occurrence localities, and 10 000 background points were randomly sampled within this area. Partial sampling of the study region (0.04% of pixels in this study area) can limit the range of environmental data used for model training and lead to artificial truncation of response curves (Guevara et al. 2018), providing additional opportunities to explore the effects of environmental extrapolation upon transfer. Maxent is a machine-learning algorithm that uses various feature classes to expand the flexibility and possible complexity of model fit but also employs regularization to increase the penalties on complexity (higher values impose greater penalization,

leading to simpler models). ENMeval can build a suite of models with different combinations of these factors so the user can choose the one with optimal complexity settings for the data. Four sets of feature classes (linear, linear/quadratic, hinge, linear/quadratic/hinge) and 50 regularization multipliers (0.1–5, steps of 0.1) were used, resulting in 200 combinations to explore model complexity. The model with the lowest Akaike information criterion corrected for small samples (AICc) was chosen as the model-selection criterion for these examples, as it helps find an optimal balance between prediction ability and model complexity (Warren and Seifert 2011). Occurrences and background points were split spatially with a latitudinal-longitudinal block partition for cross-validation ($k=4$), and the performance of the selected model was further evaluated using average validation values for area under the curve (AUC), the continuous Boyce index (CBI; Hirzel et al. 2006), and omission rate under the 10th percentile training omission threshold (OR10).

New tools for visualizing response curves and non-analog conditions under transfer

To facilitate interpretation of response curves and the decision-making process regarding extrapolation, we developed two new plotting functions using the 'ggplot2' R package (Wickham 2016). The first function plots the response curve for the ranges of non-analog conditions specific to the transfer region (Fig. 1a), and it also includes the option to visualize both unconstrained extrapolation and clamping for easy comparison. The second function makes density plots of the training and the transfer conditions per variable based on kernel density estimates (Fig. 1b). Both functions are available in 'ENMeval' ver. 2.0.6 and future releases (Kass et al. 2021).

These functions were used to explore two key factors that explain differences in model predictions:

- 1) Substantial difference in predicted suitability values between extrapolation strategies, determined by inspecting tails of response curves beyond the training limits. If no substantial difference in suitability exists between strategies for a given tail, this non-analog environment should not lead to major differences in predicted suitability.
- 2) Considerable (relatively large) number of pixels with non-analog conditions, determined by inspecting density plots of each variable beyond the training limits. If non-analog conditions correspond to few pixels for a given tail, choice of extrapolation strategy will have minimal effect on the overall prediction.

When both 1) and 2) are true, choice of extrapolation strategy should lead to a major difference in overall predicted suitability.

Transfers

After selecting the optimal model, we used it in three examples to explore and illustrate differences in model predictions between extrapolation strategies for spatial and temporal transfer. The first example was a spatial transfer to a larger area, which involved transferring the model to a

bounding box around the occurrences with a three-degree buffer. This bounding box includes vast highland areas of the Mexican plateau and the Chihuahuan desert, where *P. melanotis* is not reported to occur (Álvarez-Castañeda 2005). The second and third examples were temporal transfers within the same bounding box, using two different climatic reconstructions of the Last Glacial Maximum (LGM): the Model for Interdisciplinary Research on Climate (MIROC; Watanabe et al. 2011) and the Institut Pierre Simon Laplace IPSL (IPSL; Boucher et al. 2020). For all examples, we used the 10th percentile training omission rule as the threshold to generate binary maps of potential distribution, then overlaid the maps of individual extrapolation strategies to determine differences in predictions. We chose a single threshold to simplify the interpretation of differences among extrapolation strategies. Finally, in cases where different response-curve tails required individual extrapolation strategies, we also overlaid a map of the custom-clamped predictions. We performed custom clamping using the *clamp.vars()* function in 'ENMeval' ver. 2.0.4, which preprocesses the environmental data used for model transfer by reclassifying non-analog values to the minimum or maximum ones observed in the training data, thereby enforcing clamped prediction values (Kass et al. 2021).

Additionally, we quantified the degree of environmental novelty under transfer using two of the most widely used multivariate similarity metrics: multivariate environmental similarity surfaces (MESS; Elith et al. 2010) and MOP (Owens et al. 2013). Both metrics measure how novel transfer environments are by comparing them against reference values used in model training (in this case, the environmental information of the background). For each pixel, MESS shows the similarity of the environment under transfer to the conditions of the training sample, based on the variable that is farthest outside the training range; in contrast, MOP restricts this comparison to the range of the training environment and calculates a multivariate distance to the nearest-neighborhood conditions (Cobos et al. 2024). Here, for calculating the MOP metric we used the full set of values of the training environment. Negative values of MESS highlight areas of non-analog climates, which also correspond to areas flagged as what is termed 'strict extrapolation' by MOP. The 'smop' R package was used to obtain both metrics (Osorio-Olvera et al. 2025).

Results

The selected model showed high ecological realism and quantitative performance. The model with LQ feature classes and regularization multiplier 0.2 was chosen as optimal via AICc. Our expert assessment found that it represented a reasonable present-day potential distribution for *P. melanotis*, as the geographic prediction matched the species' known distribution in mountainous areas of the Sierras Madre Occidental and Oriental and the Trans-Mexican Volcanic belt. The average validation metrics for this model (AUC=0.899,

CBI=0.766, OR10=0.086) also placed it among the candidate models with the highest performance on withheld data (Supporting information).

Example A: spatial transfer in the present (bounding box)

When transferring the model to the bounding box extent in the present, three tails of the response curves (lower tails for bio05 and bio06, and upper tail for bio13) showed substantial differences in predictions between extrapolation strategies, while two extremes of the density plots (upper portions for bio05 and bio06) showed a relatively large number of pixels with non-analog conditions (Fig. 2). However, because neither situation coincided for any individual tail, as expected there was no major difference in geographic predictions between the two extrapolation strategies (and indeed no differences in the areas predicted as suitable after thresholding to produce a binary prediction; Fig. 3a).

Demonstrating ecological realism, the model identified as suitable the mountainous areas of central and northern Mexico (Trans-Mexican Volcanic Belt and the Sierras Madre Oriental and Occidental), aligning with the species' known elevation range. Regarding extrapolation risks, MESS and MOP analyses showed that novel (non-analog) environments were primarily found in arid areas around the Gulf of California, xeric shrublands along the USA–Mexico border (Tamaulipan Mezquital ecoregion), dry forests and shrublands along the Mexican Pacific coast, and dry forests of the Balsas River Basin (Fig. 4a, d). There was minimal spatial overlap between these non-analog areas and the suitable area predicted for the present (Fig. 4g).

Example B: temporal transfer to Last Glacial Maximum (MIROC)

When transferring the model to the LGM using the MIROC reconstruction, the lower tail of bio06 (minimum temperature of the coldest month) and the upper tail of bio13 (precipitation of the wettest month) met both situations expected to lead to a major difference in the overall prediction (substantial difference between extrapolation strategies in response curves and considerable number of pixels with non-analog conditions; Fig. 2). Therefore, as expected, major differences in the geographic predictions indeed existed between strategies (unconstrained extrapolation versus clamping, each employed for all variables). In particular, differences in predicted suitability were greatest mainly in the northern Sierra Madre Occidental and southwestern US, where clamping led to higher suitability predictions (red areas in Fig. 3b). In contrast, unconstrained extrapolation led to larger areas with high suitability predictions in the south (blue areas in Fig. 3b).

Regarding ecological realism at key variable tails, unconstrained extrapolation was more reasonable for a temperature variable and clamping was for one reflecting precipitation (Fig. 2). Unconstrained extrapolation followed a downward direction at the lower training limit for bio06, explaining lower suitability values for extremely cold non-analog temperatures. In contrast, clamping maintained relatively high suitability values

for these extremely cold conditions. The latter is unrealistic for *P. melanotis*, which currently inhabits coniferous and mesic deciduous forests but is absent from extremely cold conditions farther upslope and northward. Moreover, clamping blocked the upward direction of the response curve of bio13, leading to lower values than unconstrained extrapolation for pixels with non-analog (even wetter) values of precipitation of the wettest month. Here, the unconstrained response resulted in highly unrealistic suitability values corresponding to the extremely high precipitation conditions in the MIROC scenario.

Additionally, as different extrapolation strategies were suggested for the two tails most influential under transfer, custom clamping led to a third geographic prediction. Custom clamping applied unconstrained extrapolation to all variable tails except the upper tail of bio13, which was clamped. The suitable area obtained by custom clamping was smaller than that under either of the other two strategies, generally corresponding to the spatial overlap between them (white diagonal pattern in Fig. 3b).

The quantifications of non-analog climates – negative MESS values and strict extrapolation in MOP – showed that non-analog environments were concentrated in the northern and southern portions of the transfer region. These areas extended substantially into the northern sections of the Sierras Madre Oriental and Occidental, as well as high elevations of the Sierra Madre del Sur (which had strongly negative MESS values; Fig. 4b, 4e). Crucially, the overlap between predicted suitable conditions and these non-analog areas occurred mainly in the northern portions of the Sierra Madre Occidental and the Sierra Madre del Sur (Fig. 4h).

Example C: temporal transfer to Last Glacial Maximum (IPSL)

When transferring the model again to the LGM but using the other reconstruction (IPSL), the same extrapolation situations applied again (Fig. 2). As for MIROC, the IPSL reconstruction led to more high-suitability areas in the north under clamping and more in the south for unconstrained extrapolation (Fig. 3c; Supporting information). The southward prediction for the latter was driven by the upper tail of the bio13 response curve, where unconstrained extrapolation led to an unrealistic rise in suitability following a sigmoidal pattern with higher precipitation. Additionally, both predictions now led to extensive areas of predicted suitability throughout upper elevations of central Mexico. These predictions included two high-elevation volcanoes, Citlaltépetl (Pico de Orizaba) and Nauhcampatépetl (Cofre de Perote), the first of which is the highest peak in the country and retains glaciers today (zoomed-in inset in Fig. 3c). In contrast, the custom-clamping strategy resulted in a geographic prediction that generally matched the areas of overlap between the two other extrapolation strategies (each uniformly employed for all variables). Critically, however, it did not predict suitability in extremely high-elevation environments for either of these two peaks, which are unsuitable for the species even today. As for the MIROC reconstruction, custom clamping again was the most reasonable option, as strategies for the response

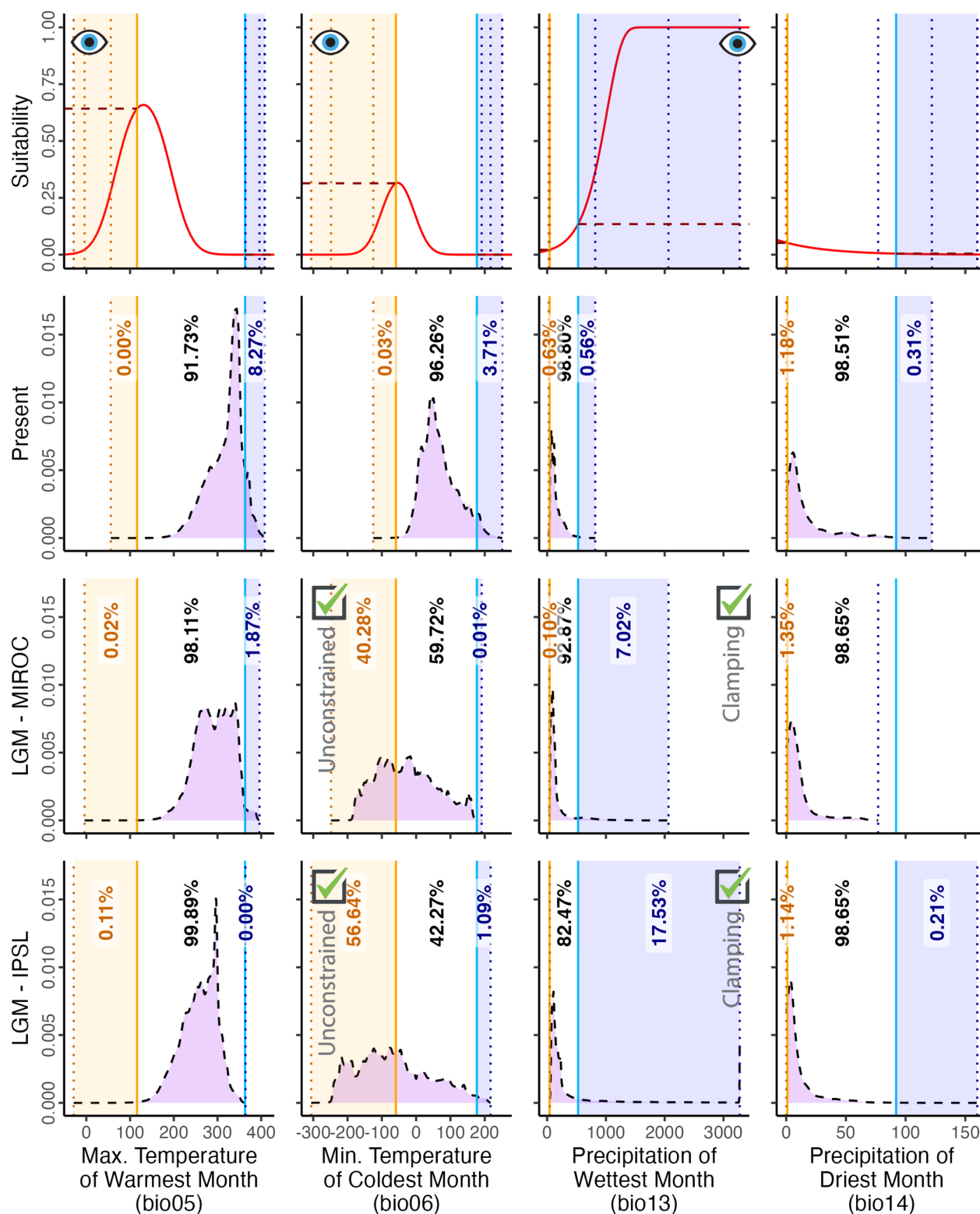


Figure 2. Model suitability response curves and density plots for Maxent models of *Peromyscus melanotis* under three transfer scenarios (spatial transfer in the present, and temporal transfers for two reconstructions of the Last Glacial Maximum; LGM). Line colors and plot styles follow the same conventions as in Fig. 1. In each density plot, the percentages of pixels are given for transfer conditions that correspond to the training region and beyond each of the training limits. Eye symbols for a given tail signify the need to examine the resulting predictions carefully (for response curve tails with extrapolation regions that diverge substantially between strategies). Checkmarks denote cases where individual tails contain both a considerable number of pixels with non-analog conditions and substantial differences between extrapolation strategies.

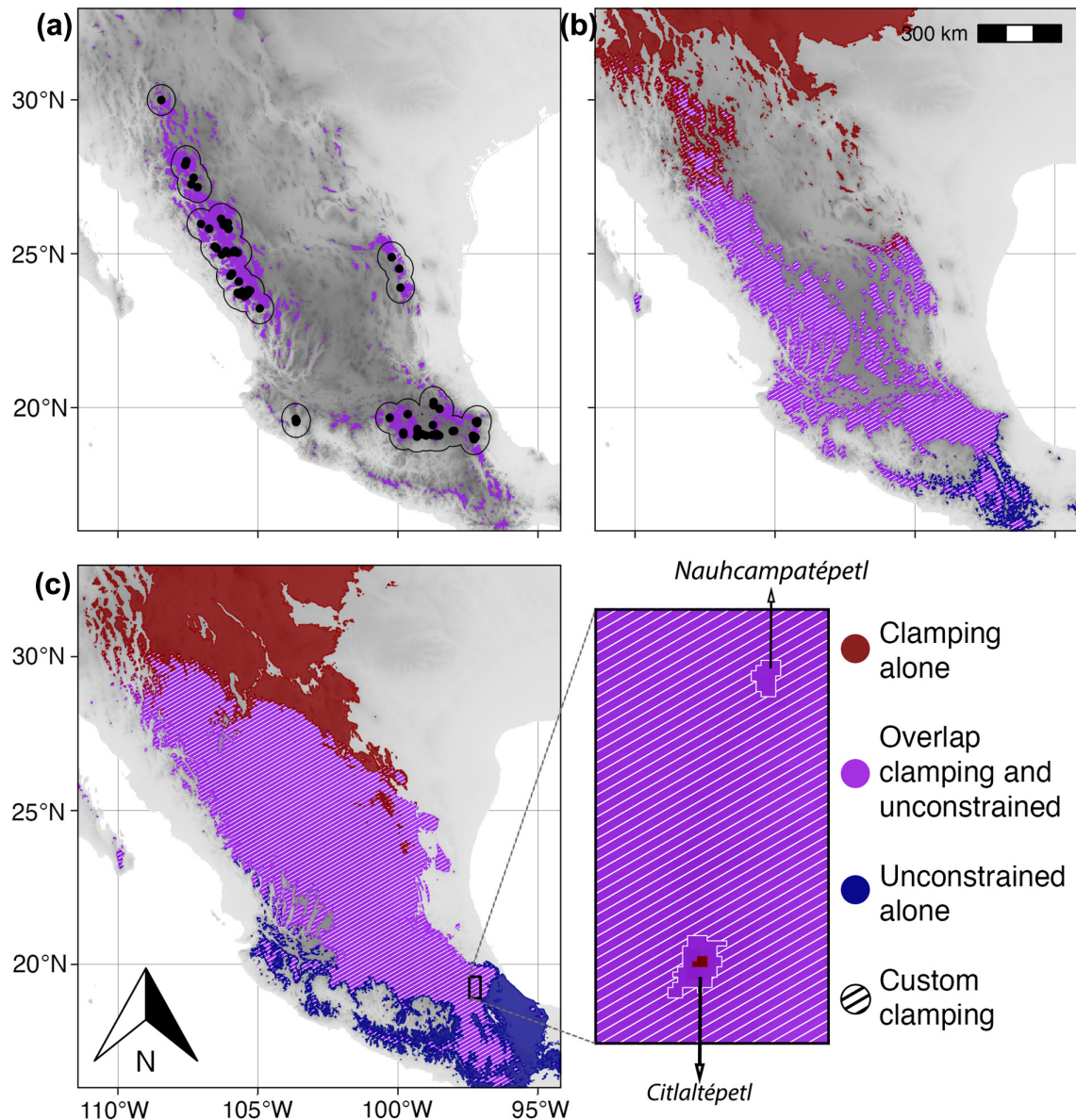


Figure 3. Present and Last Glacial Maximum (LGM) potential distribution maps for *Peromyscus melanotis* made using Maxent. Panel (a) shows the spatial transfer example, displaying species occurrence localities, the training study region (buffered localities), and the binary prediction (purple). The other panels show the temporal transfer examples for MIROC (b) and IPSL (c) paleoclimatic reconstructions at the Last Glacial Maximum, displaying overlap (concordance) between predictions made by clamped and unconstrained extrapolation strategies (purple), areas predicted suitable only by clamping (red), and those predicted suitable only by unconstrained extrapolation (blue). The white diagonal shading indicates areas suitable following custom clamping; in this example, these areas only fall over purple. The zoomed-in inset in panel (c) highlights the region of the Citlaltépetl (Pico de Orizaba) and Nauhcampatépetl (Cofre de Perote) peaks. Elevation is represented with a gray color ramp, where darker colors represent higher elevations.

curve tails were different (unconstrained for lower tail of bio06 and clamping for upper tail of bio13).

Analyses of MESS negative values and MOP strict extrapolation revealed that non-analog environments for IPSL were even more widespread than in the MIROC scenario, extending deep into the highlands of central Mexico (with strongly negative MESS values; Fig. 4c, 4f). Consequently, the overlap between predicted suitability and non-analog areas was extensive, corresponding to lowland regions of

the southwestern USA and northern Mexico, the northern Sierras Madre Oriental and Occidental, the Sierra Madre del Sur, and the Trans-Mexican Volcanic Belt (Fig. 4i).

Discussion

These worked examples emphasize that decision-making regarding available strategies for environmental

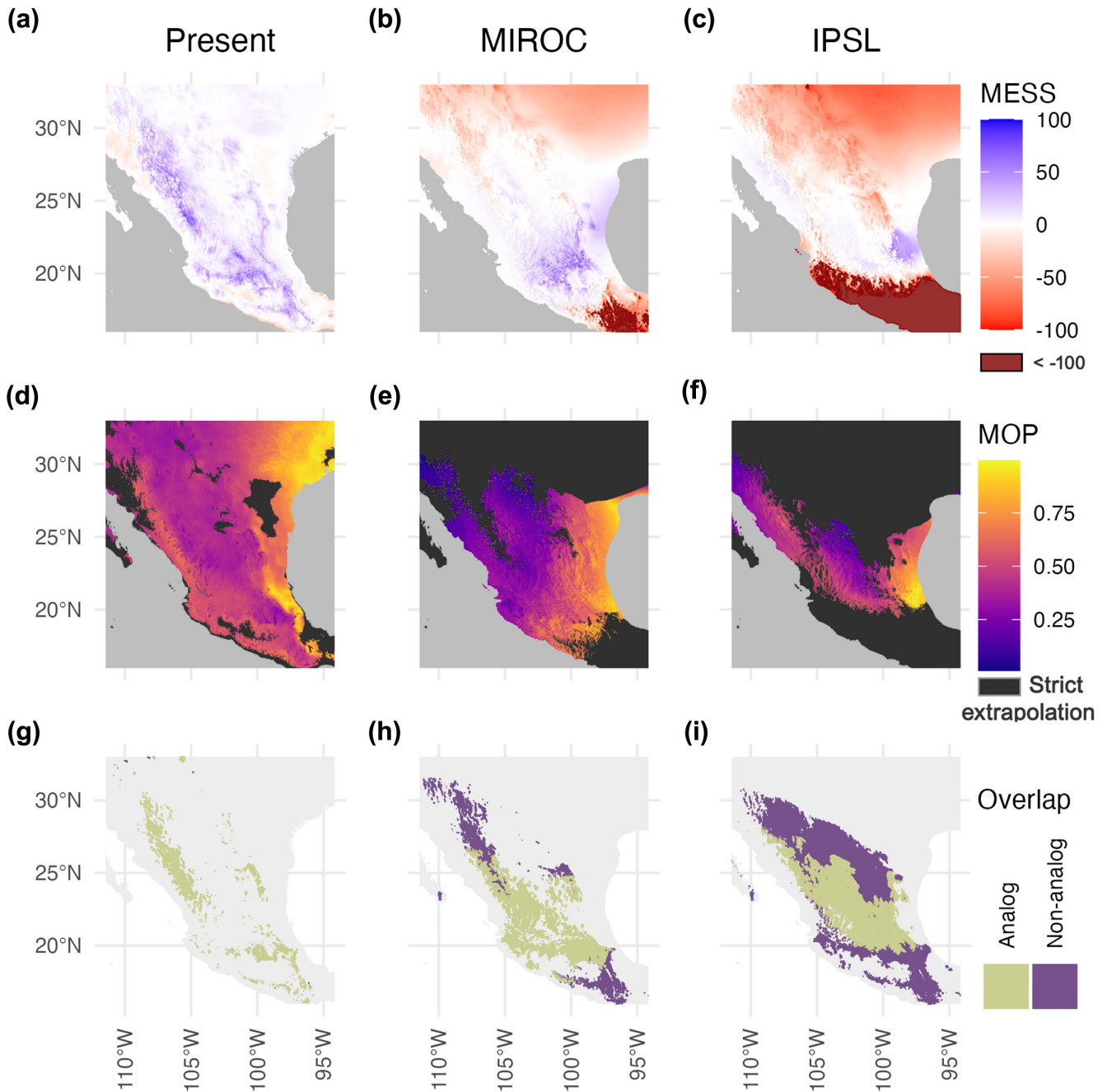


Figure 4. Environmental novelty with respect to the training data when transferring a Maxent model of *Peromyscus melanotis*. Upper and middle panels correspond to the present day (a, d) and the Last Glacial Maximum scenarios based on the MIROC (b, e) and the IPSL (c, f) paleoclimatic reconstructions. Top panels (a–c) show the multivariate environmental similarity surface (MESS), where blue and red represent analogous and novel environments, respectively, with extreme values (< -100) in dark red. Center panels (d–f) map the mobility-oriented parity (MOP) with warmer colors indicating higher similarity and black representing areas termed ‘strict extrapolation’ (non-analog conditions). Bottom panels (g–i) display the overlap between binary model predictions and environmental novelty, indicating predicted presence in analog conditions (olive) versus non-analog ones (purple).

extrapolation can lead to major differences in predictions of ecological niche models transferred to non-analog conditions. This is important, as many studies make predictions of species’ potential distributions for other places and times (e.g. future and deep past) yet do not consider how choices

regarding extrapolation behavior can affect the results. A nuanced approach to making these decisions can be effectively guided by plots of response curves and kernel densities of pixels with non-analog conditions, which together show differences among strategies. To help researchers choose the

most appropriate extrapolation strategy, we propose a four-step workflow (Fig. 5):

- 1) Examine the individual tails of the response curves for variables used in the final model, to identify any with substantial differences in extrapolation behavior between strategies for non-analog conditions (discarding from further consideration any lacking substantial differences).
- 2) Check the number of pixels with non-analog conditions for each tail still under consideration. If the research goal is to predict the overall extent of the species' distribution (and not make interpretations for smaller areas), discard any tails lacking a considerable number of non-analog pixels.
- 3) Consider the direction of the response curve at the training limit to make an informed decision between extrapolation strategies for each tail still under consideration (e.g. clamping if increasing, unconstrained if decreasing).
- 4) Transfer the model under the selected extrapolation strategy or combination of strategies. If all the relevant tails share the same recommendation for extrapolation, apply that single strategy uniformly when transferring the model; if the considered tails include different recommendations, apply custom clamping by processing environmental variables to enforce clamped values for those specific tails before transferring the model.

Although the examples provided here use presence-background data with Maxent, the resulting insights should also be relevant when using other data types and algorithms that can implement both clamping and unconstrained extrapolation. Although it is the default setting for Maxent (and for the predict function in the 'maxnet' R package; Phillips et al. 2017), clamping is not always the most reasonable strategy when transferring a model. For instance, in these examples for transfer to the LGM, clamping resulted in a much larger area predicted as suitable for the species than did unconstrained extrapolation, the latter of which led to more ecologically realistic responses. Similar conclusions were made by Guevara and León-Paniagua (2019), who reported unrealistic predictions when using clamping to estimate the paleo-distribution of the American pika *Ochotona princeps* during the LGM. However, it is important to note that unconstrained extrapolation can also result in unrealistically high suitability predictions when the response curve is increasing at the training limit (e.g. in these examples driven by the upper tail in bio13 for the IPSL reconstruction; Fig. 2, 3c). These scenarios likely represent situations where an optimum lies outside the training range, or where the selected model features (e.g. linear) failed to capture it. This implies that no simple extrapolation strategy, including custom clamping, will always be ideal. Consequently, alternative strategies that

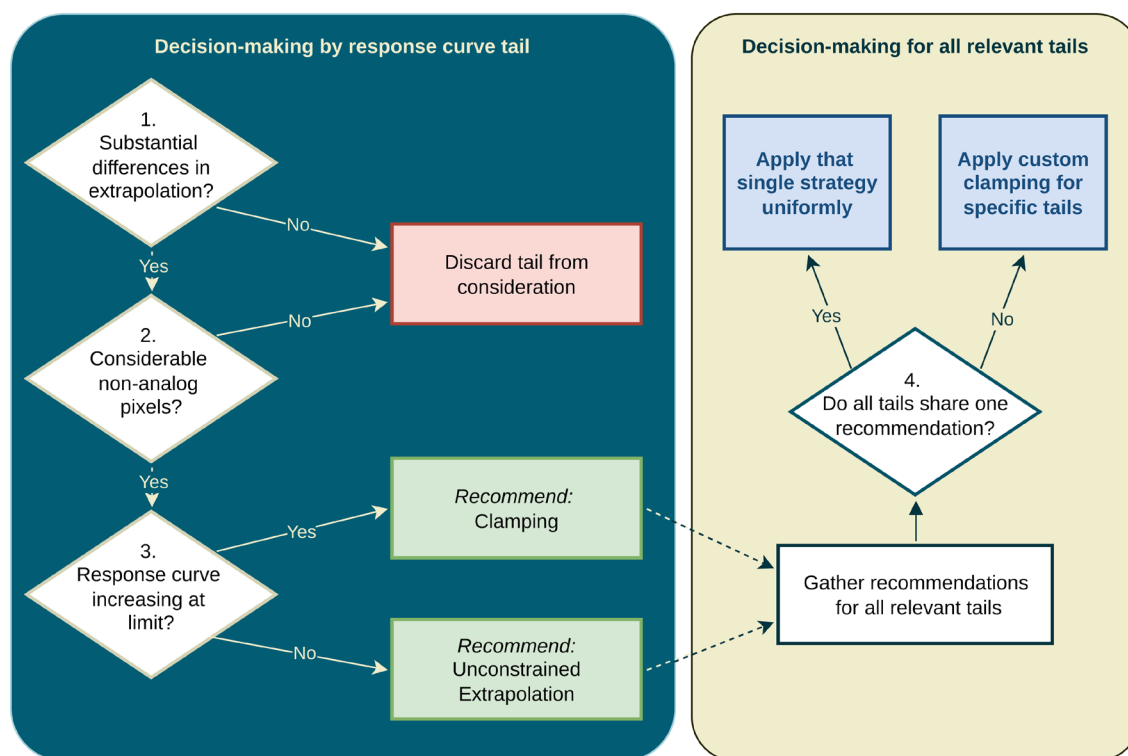


Figure 5. Flowchart illustrating the suggested steps for choosing an extrapolation strategy for non-analog conditions to obtain more reliable geographic predictions. The process involves four main steps: examining response curve tails for substantial differences between extrapolation strategies (Step 1), checking the non-analog conditions available (Step 2), considering the direction of the response curve at the training limit (Step 3), and applying the recommended extrapolation strategy or strategies (Step 4).

limit the extent of extrapolation may be more prudent (as discussed in Future directions).

This study also highlights the utility of checking the number of pixels with non-analog conditions. Considering both this and whether or not the variable even contributes to the final model can help researchers identify and focus on the subset of variables (and tails of them) that will contribute most to differences in prediction when extrapolating into non-analog areas. Current implementations of environmental novelty metrics such as MESS and MOP by default use all the variables for quantifying non-analog environments (even if some variables do not contribute to the final model), but a researcher can subset variables to exclude unimportant ones. These metrics generally recommend caution in areas where extrapolation and highly predicted suitability coincide (Elith et al. 2010, Owens et al. 2013, Cobos et al. 2024). For example, the areas in this analysis predicted as suitable in the northern and southern parts of the study region for both LGM scenarios were assigned high uncertainty due to non-analog environments (negative MESS values or MOP strict extrapolation in Fig. 4). However, exploring and comparing model behaviors by using different extrapolation strategies as in this study can improve predictions in challenging areas such as these. This strengthens an ongoing key research objective of ENMs and machine learning more broadly: to make robust predictions under novel conditions (Yates et al. 2018, Qiao et al. 2019, Pili et al. 2025).

Future directions

Although visual inspection of response curves and density plots can assist in decision-making between extrapolation strategies, such considerations do not directly account for the magnitude of extrapolation. This issue is important as well, because the accuracy of model transfer decreases with environmental conditions more distant from those of model training (Qiao et al. 2019, Brodie et al. 2022, Rousseau and Betts 2022). Although ‘custom clamping’ can be used to limit unrealistic extrapolation, other strategies may be more sophisticated and helpful. For example, alternative strategies could gradually reduce the suitability values to zero as the distance from the training limit increases (decay function; Thuiller et al. 2004) or restrict the extent of extrapolation based on percentiles of the range of analog conditions (Dormann 2007, Sequeira et al. 2018). These possibilities point toward future improvements for algorithms that allow unconstrained extrapolation (including Maxent).

The examples in this study also offer insights into additional ways that researchers can employ the response curves and plots of the density of non-analog conditions to aid in model selection itself. Considering both the model’s extrapolation behavior and the spatial distribution of the non-analog areas allows researchers to consider factors other than the performance metrics typically relied on when tuning model settings for optimal complexity (Kass et al. 2021). For example, based on performance metrics alone, two very different models could appear quite similar in quality (be co-optimal in that regard; Boria et al. 2017) yet correspond to vastly

different situations for extrapolation (e.g. with Maxent, a linear-quadratic model versus. one with only hinge features). If a researcher identified that one of the co-optimal models used fewer variables whose tails were not increasing at the training limit, it could be desirable over another one with similar performance scores. For example, this could be especially useful for model transfers that involve comparing forecasts under different general circulation models (Guevara et al. 2019) or estimating invasion risk (Zurápit et al. 2025).

Additionally, future efforts could develop functions that automate recommended decisions regarding extrapolation strategies. Decisions for clamping versus unconstrained extrapolation could be coded based on both the direction of modeled suitability at training limits and either the absolute or relative number of pixels with non-analog conditions (Fig. 5). Such functions could improve predictions in cases where hundreds or thousands of species are modeled, as the visual inspection of individual tails becomes laborious (Soley-Guardia et al. 2024). Ultimately, the increasing demand for ENMs in both academic studies and biological conservation and management calls for further advances to enhance their reliability in non-analog conditions, building on the advances presented here.

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Author contributions

Gonzalo E. Pinilla-Buitrago: Conceptualization (equal); Formal analysis (lead); Methodology (lead); Software (lead); Writing – original draft (lead); Writing – review and editing (equal). **Jamie M. Kass:** Conceptualization (supporting); Methodology (supporting); Software (supporting); Writing – review and editing (equal). **Robert P. Anderson:** Conceptualization (equal); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data and code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ksn02v7m0> (Pinilla-Buitrago et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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