

THE ENVIRONMENTAL REPRESENTATIVENESS EFFECT IN SPECIES DISTRIBUTION MODEL EVALUATION WITHOUT ABSENCE DATA

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Abstract. In species distribution modeling (SDM), the environmental representativeness effect hinders the comparison and generalization of discrimination statistics, as their values are context-dependent and may vary without reflecting actual differences in model accuracy. To address this issue, a harmonization approach based on the uniform distribution of suitability values has been proposed, demonstrating effectiveness when true absence data are available. However, in most cases, models solely rely on presence records and use background points instead of true absences, posing additional validation challenges. This study simulates habitat suitability and presence-absence data, and evaluates the robustness of several validation indices: background-based AUC (AUC_b), its harmonized version ($uAUC_b$), and two variations of the Boyce index. The results show that the Boyce index remains unaffected by the representativeness effect, whereas AUC_b varies across scenarios, confirming the influence of the representativeness effect on SDM results with background data. Harmonization through $uAUC_b$ successfully makes values comparable, but its reliability depends on sample size, requiring at least 100 presences and 10,000 background points.

Key words: background data, Boyce index, evaluation, ecological niche models, uniform AUC

INTRODUCTION

In species distribution modelling (SDM; Franklin 2009; Peterson et al. 2011), a critical step is model validation, typically assessing how accurately species occurrence data are predicted using discrimination statistics (Fielding and Bell 1997). Jiménez-Valverde et al. (2013) cautioned that discrimination measures estimated on different evaluation datasets may not be directly comparable, because their values depend on the statistical distribution of suitability scores, which in turn is shaped by the distribution of predictor variables. They termed this phenomenon the environmental representativeness effect, which implies that discrimination statistic values are inherently context dependent. Consequently, a model may exhibit high or low performance only due to the statistical distribution of the suitability scores in the evaluation dataset rather than on its intrinsic accuracy. This means that a given species may respond to the environment in the same way as modelled across different territories, yet the evaluation statistic may yield different values in each case. While this behavior is expected from those statistics that measure how well the instances of presence are discriminated against those of absence (i.e., they function as intended), it complicates com-

parisons and significantly influences the conclusions that can be drawn (Jiménez-Valverde 2022).

Harmonizing discrimination statistics, defined as recalculating these metrics after weighing the cases in the evaluation dataset to impose a uniform distribution of suitability values, has been shown to appropriately account for the representativeness effect (Jiménez-Valverde 2022, 2025a). This method has been demonstrated to perform well specifically when true absences are available for evaluation, but in SDM this is rarely the case. Modelers typically have only presence records for the species but lack information on where the species is absent. Even when absence data are available, their reliability is often questionable (Lobo et al. 2010). As a result, researchers often have to select a random set of locations within the study area with no information on the presence or absence of the target species and use these as absences, the so-called background points (Stockwell and Peters 1999; Phillips et al. 2006). How harmonization handles the representativeness effect in scenarios without a gold standard for validation (i.e., presences and true absences) remains unclear (Jiménez-Valverde 2022).

Using discrimination statistics in presence-background data scenarios has been questioned on numerous occa-

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n = 100000                # total dataset size
scenarios = {a, b, c}     # HS distributions (see Fig. 2)
n1 = {15, 100, 1000}   # number of presences
nb = {100, 1000, 10000} # number of background points

FOR each scenario in scenarios
  FOR each combination (n1, nb)
    FOR iterations = 1 to 10000
      1. Generate n habitat suitability values (hsi)
      2. Generate species presence-absence data (spi)
      3. Build the validation dataset (sample n1
         presences + nb background points)
      4. Calculate AUCb, uAUCb, BW and BS
    END FOR
  END FOR
END FOR

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Figure 1. Pseudocode summarizing the simulation procedure used in this study. Habitat suitability values (*HS*) were simulated under three alternative distributions (scenarios a, b, c) representing different environmental representativeness scenarios. Species occurrences were then generated using a Bernoulli process with probability equal to *HS*, resulting in perfectly calibrated predictions. Validation datasets were constructed by sampling presences (n_1) and background points (n_b) with different sample sizes. For each scenario and validation dataset, the procedure was repeated 10000 times and four validation statistics were calculated: AUC_b , uniform AUC_b ($uAUC_b$), and two versions of the Boyce index (BW and BS).

sions (Boyce et al. 2002; Lobo et al. 2008; Peterson et al. 2008; Jiménez-Valverde 2012; Smith 2013; Leroy et al. 2018). Essentially, since the background data is a mixture of true absence and presence data, the true negative rate (proportion of correctly predicted absences) and the commission error rate (proportion of absences incorrectly predicted as presences) are unreliable. Thus, for instance, the maximum possible value of the very well-known Area Under the ROC Curve (*AUC*) statistic (Krzanowski and Hand 2009) is no longer 1 and depends on the actual but unknown distribution of the species (Wiley et al. 2003). Yet, one could argue that, despite these limitations and for practical purposes, the *AUC* could still be used to rank models, with a higher *AUC* indicating a better model than a lower one (Phillips et al. 2006), at least when comparing models for the same species to ensure that the range area remains constant. Despite its challenging and nuanced interpretation, the *AUC* remains a common choice among modelers in presence-background scenarios, which are the most frequent in species distribution modeling. It is thus important to understand how its harmonization to account for the representativeness effect -the so-called uniform *AUC* or *uAUC*- works in this type of presence-background

frameworks (Jiménez-Valverde 2022). However, it is important to note that the *uAUC* does not address the absence of a true gold standard when reliable absence data are unavailable.

METHODS

Since the purpose of this study is to analyze the behavior of various validation indices and how they respond to the environmental representativeness effect, I directly simulated habitat suitability (*HS*) values and species occurrences with a known relationship between them, rather than following the traditional approach of first generating virtual species, then sampling them, followed by parameterizing distribution models, and finally validating them. The procedure followed in this study is simpler and eliminates many sources of uncertainty and variation that may arise with the traditional method. Idealized simulations are necessary to understand the theoretical behavior of the method. The overall simulation workflow is summarized in Fig. 1. Following the general procedure of Jiménez-Valverde (2022), I simulated *HS* values bounded between 0 and 1 using the truncnorm package (Mersmann et al. 2018) for R (R Development Core Team 2024), and I con-

sidered three different scenarios, setting the sample size (n) to 100,000: **Scenario a:** cases with low and high HS values were more frequent than cases with medium values (Fig. 2A). To generate hs_i , $n/2$ random numbers were generated from two truncated normal distributions bounded between 0 and 1 and with $\mu_1 = 0, \mu_2 = 1$ and $\sigma_1 = \sigma_2 = 0.15$, and concatenated. **Scenario b:** HS follows a hump-shaped distribution (Fig. 2B). To generate hs_i , n random numbers were generated from a truncated normal distribution bounded between 0 and 1 and with $\mu = 0.5$ and $\sigma = 0.2$. **Scenario c:** cases with high and medium HS values were less frequent than cases with low HS values (Fig. 2C). To generate hs_i , $n/2$ random numbers were generated from a truncated normal (with $\mu = 0$ and $\sigma = 0.05$) and from a uniform distribution, both bounded between 0 and 1, and concatenated.

I also considered three sample size levels for the validation presence set ($n_i = \{15, 100, 1000\}$) and the validation background dataset ($n_b = \{100, 1000, 10,000\}$), resulting in nine different validation datasets.

For each scenario and validation dataset, I ran 10,000 iterations. In each iteration, first, a vector hs_i was simulated. Then, a vector sp_i with the presence-absence data was generated by drawing n values from a Bernoulli distribution, where the probability of presence was determined by the corresponding hs_i value. In this way, the simulated predictions were perfectly calibrated (i.e., the species respond to the environment in the same way). The AUC values calculated from the presence-absence data were approximately 0.930, 0.716, and 0.909 for scenarios a, b, and c, respectively, evidencing the environmental representativeness effect, that is, the response of the species is the same but the AUC values differ simply because the distributions of HS are dissimilar. Next, out of the n cases (each case has two associated values, hs_i and sp_i), n_i were randomly extracted under the condition that they corresponded to a presence; from the remaining $n-n_i$ cases, n_b were randomly sampled. Both subsets were combined to form the validation dataset with which four statistics were finally calculated: the AUC_b (I use the subscript to differentiate this AUC value calculated with background data from the reference AUC value calculated with presence-absence data of each scenario, see above), the uniform AUC_b ($uAUC_b$) as proposed in Jiménez-Valverde (2025a), the Boyce index estimated with the moving window approach (BW) as proposed in Hirzel et al. (2006), and the Boyce index estimated with the smoothing approach (BS) as proposed in Liu et al. (2024). I estimated the Boyce index since it is the recommended measure for background data scenarios (Boyce et al. 2002; Hirzel et al 2006). The AUC_b was estimated non-parametrically by the trapezoidal rule

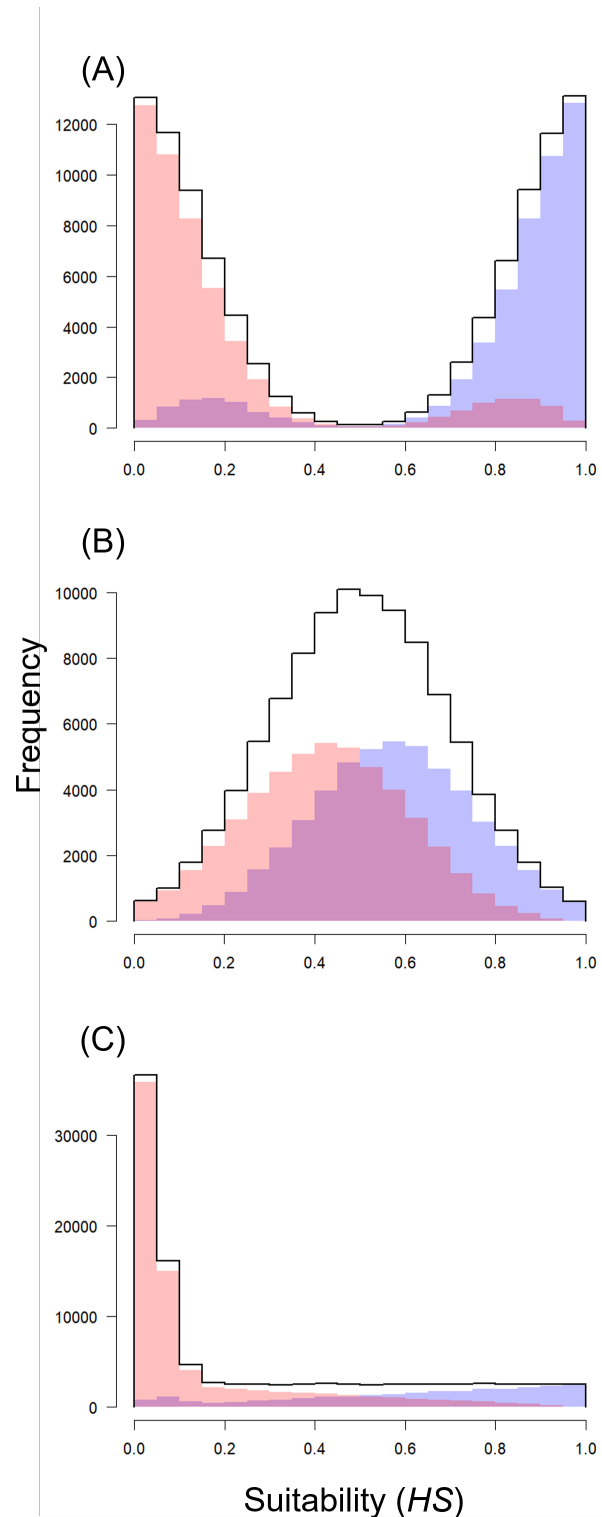


Figure 2. Examples of distributions of suitability values (hs , black line; $hs | sp = 1$, in blue; $hs | sp = 0$, in red). Scenario A represents situations where low and high suitability values are more frequent than cases with medium values. Scenario B represents situations where medium suitability values are more frequent than cases with low and high suitability values. Scenario C represents situations where high and medium suitability values are less frequent than cases with low values.

(Hanley and McNeil 1982). The $uAUC_b$ was estimated by partitioning the validation dataset into 10 bins according to the values of hs_i . Each case was assigned a weight equal to one divided by the number of observations in the corresponding bin, and the direct weighted trapezoidal estimation procedure was then applied (see Jiménez-Valverde 2025a for details). Both AUC_b and $uAUC_b$ were calculated using the function `AUCuniform.2()` of the `vandalico` package (Jiménez-Valverde 2025b). BW was estimated by using the `ecospat` (Broennimann et al. 2024) package with default values, which in this study implies a width of the moving window equal to 0.1 and a resolution of the moving window equal to 100. BS was estimated with the thin plate regression splines method using the `mgcv` package (Wood 2025); since all the smoothing methods evaluated by Liu et al. (2024) yielded comparable results, I selected one for the analysis and used a simplified version of the R code provided by the authors. Finally, boxplots were generated to interpret the differences between scenarios and validation datasets.

For assessing the results, it is necessary to know the expected value of the AUC_b under a uniformly distributed and perfectly calibrated HS . So, if the HS values in the full dataset are uniformly distributed between 0 and 1, and because the model is perfectly calibrated, the probability that a randomly selected presence case has an HS value higher than a randomly selected background case (i.e., the definition of the AUC) is exactly equal to its HS value. The AUC is therefore the mean HS value among presence cases. When plotting the density of HS values for presence cases against HS , this density has a triangular, increasing shape; the mean HS value among presences corresponds to the horizontal position of the barycenter of this triangle, which is $2/3$ (~ 0.667) (Diccionarios Temáticos Vox 2019). Thus, this is the value we would expect to obtain for the $uAUC_b$ in the three scenarios (in the same way that it is $5/6$ or ~ 0.833 for the $uAUC$; see Diamond 1992 and Jiménez-Valverde et al. 2013).

The R script used to perform the simulations of this study is available in Jiménez-Valverde (2026) for reproducibility.

RESULTS AND DISCUSSION

The environmental representativeness effect is also evident with background data, as reflected in the varying AUC_b values across scenarios (Fig. 3). Interestingly, the effect may differ from that observed with absence data. For instance, scenario c exhibits the highest average AUC_b value, whereas its AUC falls between those of the other two scenarios (see Methods section). This highlights that the AUC_b does not reflect ranking capacity *sensu stricto* (i.e.,

the probability of assigning a higher HS value to a presence than to an absence), but rather a ranking of presences *versus* data that may include suitable locations in an unknown proportion. Scenario c represents a case where unsuitable areas are disproportionately represented in the validation data (Fig. 2C), suggesting that the effect of the spatial extent on the validation of the models (the “there are no elephants in Antarctica” effect, Lobo et al. 2010) might be exacerbated when using background data.

The harmonization procedure successfully makes the values of the discrimination statistics comparable, as evidenced by the $uAUC_b$ values being more similar compared to AUC_b across scenarios (Fig. 3). The precision of the estimated $uAUC_b$ is affected by sample size, especially by n_i ; a value of 15 yields highly imprecise estimations in all scenarios and n_b levels. The lowest level on n_b produces imprecise estimations in all scenarios and n_i levels. Bias, i.e., the departure of the averaged $uAUC_b$ values from $2/3$, shows less clear patterns than precision. For instance, increasing n_i tends to increase bias, which is especially noticeable for $n_b = 100$ and 1000 , although not all scenarios are affected in the same way (compare scenarios a and c). Both presences and background points should be sufficiently numerous so that their distribution across hs_i bins approximates the underlying distributions of occurrences and available conditions; otherwise, the resulting $uAUC_b$ may be biased. This requirement is analogous to the presence-absence situation, in which observations within each hs_i bin must reflect the true prevalence of the species. In both situations, departures from these conditions distort the empirical frequencies used in the bin-based estimation procedure, which in turn biases the estimated $uAUC$. The most accurate estimations, in terms of both precision and bias, occur with $n_b = 10000$ and $n_i = 100$ or 1000 . The fact that the average $uAUC_b$ approaches $2/3$ supports the validity of the harmonization method in the presence-background data scenarios.

The Boyce index quantifies the monotonic increment with HS of the ratio between the frequency of species observations in predicted HS classes and the expected frequency under a random distribution (P/E; Boyce et al. 2002), thus assessing the model’s ability to discriminate between areas of higher and lower suitability. This index is unaffected by the environmental representativeness effect, as evidenced by its constant value of 1 (Fig. 3), which is the expected value given that all the scenarios correspond to well-calibrated HS values. For the same reason, Liu et al. (2024) explained that the Boyce index is insensitive to the extent of the unsuitable area, a key issue in SDM (Lobo et al. 2008; Anderson and Raza 2010; Barve et al. 2011). Note that the extent problem is a special case of the environmental representativeness effect (Jiménez-Valverde et al. 2013;

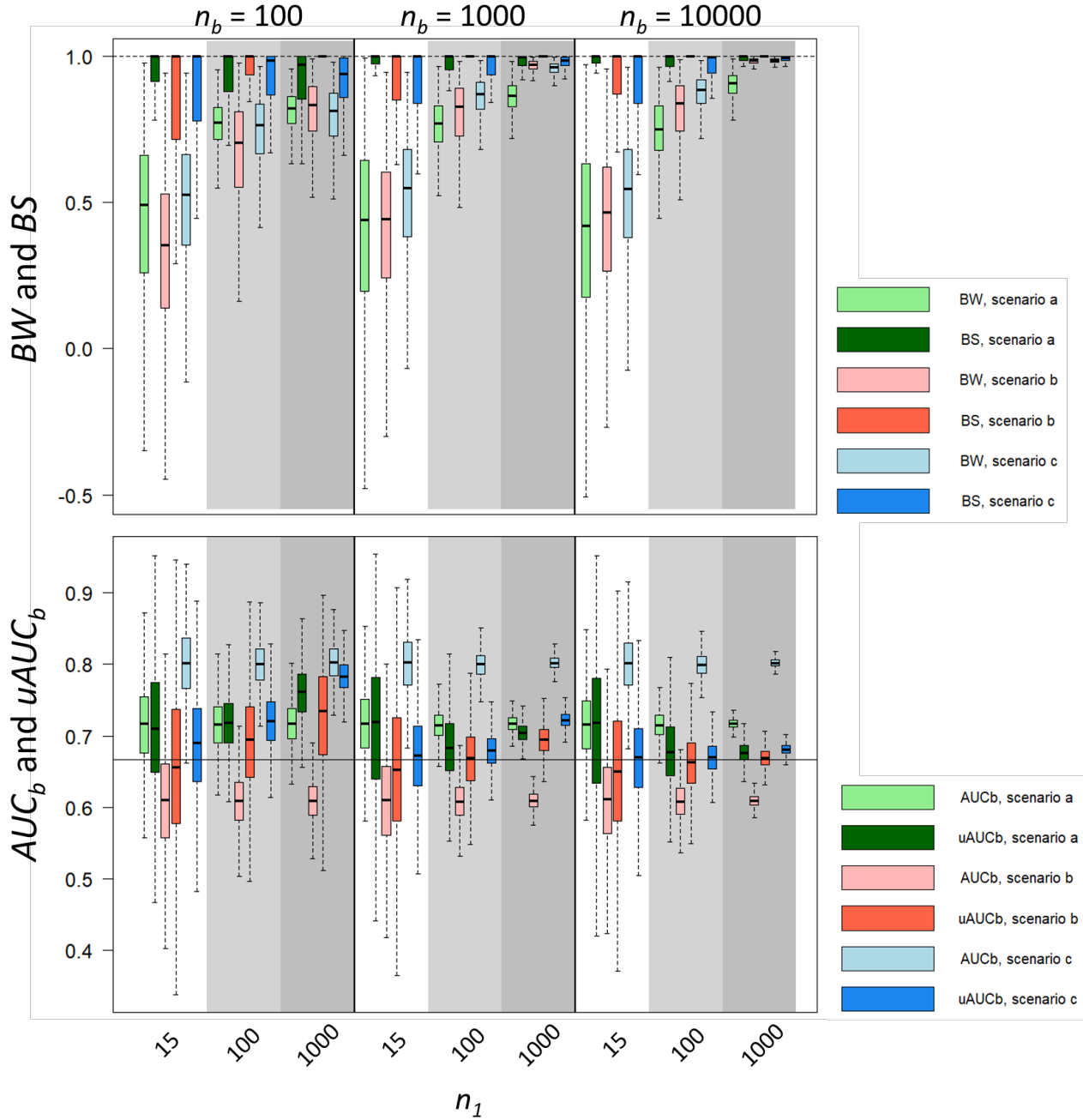


Figure 3. Top: median (horizontal marks), interquartile range (boxes), and $1.5 \times$ spread (whiskers) of the Boyce index calculated with a moving window (*BW*, light colors) and the smoothing method (*BS*, dark colors) for the three different scenarios (scenario a in green, scenario b in red, scenario c in blue; see Fig. 2) and different sample sizes (n_1 , number of presence data; n_b , number of background data). Bottom: same for the background-based *AUC* (AUC_b ; light colors) and the uniform (harmonized) *AUC* ($uAUC_b$). Horizontal line marks the expected value of $2/3$ (see text for details).

Jiménez-Valverde 2022).

Two additional results regarding the Boyce index are worth noting, both aligning with previous findings (Liu et al. 2024). First, *BS* is noticeably more accurate than *BW* (Fig. 3). Second, while both indices are influenced by sample size, *BS* is affected to a much lesser extent and primarily by n_b , whereas *BW* is more strongly impacted and

mainly depends on n_1 (Fig. 3). This is because *BW* relies on data within each moving window to estimate P/E, whereas *BS* is calculated using the entire dataset (Liu et al. 2024).

CONCLUSIONS

The environmental representativeness effect hampers the comparison and generalization of discrimination sta-

tistic values. It affects presence-absence as well as presence-background statistics. Harmonizing the calculation of the $uAUC_b$ successfully improves the comparability of results, although sample sizes of $n_i \geq 100$ and $n_b = 10,000$ are needed for reliability. While background data can be easily generated, obtaining sufficient presence data is challenging for rare species, making their model validation inherently difficult. Note, however, that while the $uAUC_b$ statistic accounts for the environmental representativeness effect, other issues associated with using the AUC without a gold standard (Jiménez-Valverde 2012) may still be relevant.

The Boyce index might be the preferred statistic when absence data are unavailable, as it avoids the theoretical issues associated with the AUC (Lobo et al. 2008; Peterson et al. 2008; Jiménez-Valverde 2012) and is insensitive to the representativeness effect. Its implementation through statistical smoothing, recently proposed by Liu et al. (2024), appears to be the recommended approach, as it exhibits less bias and greater precision than the traditional Boyce index, especially at low sample sizes. Under these circumstances, the Boyce index may be preferable to AUC_b (see also Liu et al. 2024), especially for rare species, for which the harmonization of AUC_b may yield unreliable results. However, contradictory results reported by Jiménez and Soberón (2020) suggest that the performance of the Boyce index may depend on specific data characteristics, and therefore a definitive recommendation cannot yet be made.

The simulations represent an idealized scenario intended to isolate the environmental representativeness effect and evaluate the theoretical behavior of the statistics. Additional complexities present in empirical datasets (e.g., detection error, spatial autocorrelation, or sampling bias) were not included, as they would introduce additional sources of variation unrelated to the mechanism examined here. Overall, the results highlight the importance of accounting for the environmental representativeness effect when interpreting discrimination statistics, either through harmonization or by using an index intrinsically insensitive to this effect, and provide practical guidance on the appropriate use of $uAUC_b$ and the Boyce index in species distribution model evaluation. Finally, It should be noted that harmonization facilitates the comparison of discrimination metrics across different contexts, but it does not by itself ensure greater ecological validity of the models.

ACKNOWLEDGMENTS

This study was funded by the CliMod project (PID2023-147672NB-I00) financed by MCIU/

AEI/10.13039/501100011033/FEDER, UE, and by the grant 2024ICT253 supported by CSIC. Lucia Maltez reviewed the English.

COMPETING INTERESTS

The author has declared no competing interests.

DATA AVAILABILITY

No new data were used or generated. The code used for the simulations is available at Figshare (Jiménez-Valverde 2026).

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