

# A retrospective approach for evaluating transference of ecological niche modeling ~~evaluating ecological~~ ~~niche modeling transferences~~ over time: The case of Mexican endemic rodents

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## Abstract

Ecological niche modeling (ENM) is an approach to ~~infer-predict~~ the suitable conditions for species' persistence and their potential geographic distributions. ENM is extensively used to assess the potential effects of climate change on species' distributions, although modeling algorithms are recognized ~~acknowledged~~ as an important source of uncertainty in climate change projections. A problem ~~is~~ that these models cannot be properly assessed in the context of future projections. In this study, we evaluated the performance of seven popular modeling algorithms (Bioclim, Generalized Additive Models (GAM), Generalized Linear Models (GLM), Boosted Regression Trees (BRT), Maxent, Random Forest (RF), and Support Vector Machine (SVM)) for transferring ENM over time for Mexican endemic rodents. To accomplish this, we employed ~~To do so, we followed~~ a retrospective approach by transferring models from the near past (1950-1979) to the present (1980-2009) and vice versa. Our findings yielded three key ~~We~~

**Comentado [IR1]:** Is it the same as number 2, it should be different?

**Comentado [IR2]:** Is it a problem, maybe use a sentence like: The main challenge....

29 ~~found three important~~ results: (1) The quality of input data and the algorithm had a significant  
30 effect on model output and performance; (2) algorithm performance was different for transferring  
31 models to the future than to the past; and (3) the most robust algorithms were RF, BRT and  
32 Maxent, whereas Bioclim was the least consistent. In conclusion, algorithm choice is critical for  
33 transferring ENM over time. Since no algorithm performed consistently better than the rest, we  
34 recommend ~~to testing~~ different algorithms *prior* transferring models to future scenarios under a  
35 retrospective approach.

**Comentado [IR3]:** Choice of algorithm?

**Comentado [IR4]:** More results and conclusions

## 37 Introduction

38 Current climate change is affecting biodiversity in a myriad of ways (Parmesan &  
39 Yohe, 2003; Bellard et al., 2012; MacLean et al., 2018; Widick & Bean, 2019; Cuervo-Robayo et  
40 al., 2020; Habibullah et al., 2022) and biotas are changing due to alterations in the abundance  
41 and distributional shifts of species (Moritz et al., 2008; Kharouba, Algar & Kerr, 2009; Dobrowski  
42 et al., 2011; Pacifici et al., 2015; Peterson et al., 2015b; Jaroszynska et al., 2023). For some  
43 years now, ecological niche modeling (ENM) is a popular tool for analyzing geographic  
44 distributions of species in the context of past and current climatic changes (Araújo et al., 2005;  
45 Beaumont et al., 2009; García-Callejas & Araújo, 2016; Sequeira et al., 2018; Yates et al., 2018;  
46 ~~García-et al., 2023~~). ENM includes a suite of concepts and methodologies based on ecological  
47 niche theory that has taken advantage of other disciplines, such as informatics, geographic  
48 information systems (GIS), and statistics (Austin, 2007; Jiménez-Valverde, Lobo & Hortal, 2008;  
49 Soberón & Nakamura, 2009; Wiens et al., 2009).

**Comentado [IR5]:** Not in the reference list, please check it.

50 ENMs are correlative methods that require georeferenced species' occurrence data  
51 and a set of predictor variables in the form of GIS raster layers to reconstruct the ecological  
52 characteristics that define the conditions where species inhabit (i.e., its ecological niche) and  
53 then project these conditions onto the landscape to produce a geographical expression of the  
54 species' niche, commonly referred to as its potential distribution (Elith et al., 2006; Peterson,

2011; Sillero, 2011). Several methods have been implemented to produce niche models, which can be classified according to the type of input occurrence data as presence-only (e.g., Bioclim, environmental distances), presence-absence (e.g., Generalized Linear Models [GLM], Generalized Additive Models [GAM]), presence-pseudoabsence (e.g., Genetic Algorithm for Rule-set Prediction [GARP]), and presence-background (e.g., Ecological Niche Factor Analysis [ENFA], Maxent) (Phillips, 2008; Barbet-Massin et al., 2012; Warton & Aarts, 2013; Fan et al., 2018; Qiao et al., 2019; Sillero et al., 2023). From these, presence-absence methods are generally more robust when unequivocal absence data exist (Brotons et al., 2004; Golicher et al., 2012; Merow et al., 2014); however, in most cases, reliable absences are lacking. Therefore, presence-only, presence-pseudoabsence and, presence-background algorithms have become popular in the last two decades (Vaz, Cunha & Nabout, 2015).

Comentado [IR6]: Because.. could you explain why?

ENM has been broadly used to evaluate the potential geographic consequences of climatic changes by projecting the modeled species' niche under current climatic conditions to past or future climatic scenarios, a process also known as model transference (Pearson & Dawson, 2003; Peterson, Martínez-Meyer & González-Salazar, 2004; Thomas et al., 2004; Waltari & Guralnick, 2009; Heikkinen, Marmion & Luoto, 2012; Garcia et al., 2016). At least three main assumptions are behind model transferences over time that may or may not hold true: (1) the ecological niche does not evolve during the timeframe when the transference is performed (Soberón & Nakamura, 2009); (2) during a climatic change, even if the interactions among variables change, the relationship of those variables with the species remains constant (Hijmans & Graham, 2006; Wiens et al., 2009); and (3) the species is in equilibrium with the environment in the calibration time/area, meaning that they occupy the available suitable areas that are accessible to them (Sequeira et al., 2018; Yates et al., 2018).

Comentado [IR7]: Please, rewrite this sentence

Furthermore, a key issue in model transference is the effect of non-analog climates (i.e., the set of environmental conditions that exist in an alternative climatic scenario different from the calibration one) on model performance (Sequeira et al., 2018). Non-analog climates

81 impose a challenge to algorithms because no calibration exists for those climates, thus, when  
82 algorithms face non-analogues in alternative climatic scenarios (past or future), algorithms  
83 respond differently according to the instructions of the program, producing contrasting or even  
84 contradicting results\_ (Pearson, 2006; Araújo & Peterson, 2012; Essl et al., 2023). This is  
85 particularly problematic in future projections because there are no occurrence data that can be  
86 used to evaluate algorithm performance. Thus, one solution to evaluate algorithm performance  
87 in climate change studies is to project models between two time periods for which they have  
88 occurrence data, for example, from the relatively recent past to the present (Rubidge et al.,  
89 2011; Piirainen et al., 2023).

90         Several studies have focused on evaluating the reliability of niche models for a  
91 specific time (Beaumont & Hughes, 2002; Araújo, Thuiller & Pearson, 2006; Maiorano et al.,  
92 2011; Werkowska et al., 2017; Sequeira et al., 2018), but only a few have analyzed the  
93 performance of algorithms for transferring models over time (Prasad, Iverson & Liaw, 2006;  
94 Hijmans & Graham, 2006; Kharouba, Algar & Kerr, 2009; Rubidge et al., 2011; Moreno-Amat et  
95 al., 2015; García-Callejas & Araújo, 2016), with performance results spanning from good to bad  
96 for different species and algorithms, making it difficult to discern the effect of the algorithm  
97 choice in the results. Herein, we evaluate the performance of seven modeling algorithms for  
98 transferring niche models of Mexican endemic rodents from the mid-20th century to the present  
99 and vice versa. We used Mexican endemic rodents as study model because they have  
100 restricted and relatively well- known distributions\_ and because the evolutionary rate of  
101 mammals is not high enough to expect climatic niche evolution over this period of time  
102 (Martínez-Meyer, Peterson & Hargrove, 2004).

103

## 104 **Materials & Methods**

105

106 Occurrence data of species. We ~~gathered~~collected occurrence records for the 117 Mexican  
107 endemic rodent species (Ramírez-Pulido et al., 2014) from natural history collection databases,  
108 journal articles, books, and theses (Supplementary Material, S1 and S2). For each record, we  
109 noted the collecting year and grouped occurrences into two time periods to match the  
110 climatologies available for the 20th century (see below): 1950-1979 and 1980-2009. We  
111 discarded duplicate records to keep only one record per pixel and also discarded those records  
112 with questionable taxonomic or geographic certainty. Finally, we retained only those species for  
113 which we had at least 10 unique localities per period to produce reliable models (Hernandez et  
114 al., 2006). Because some of the algorithms that we analyzed use pseudo-absence data, we  
115 randomly selected the same number of unique localities with no presence records as with  
116 presence records for each species within the modeling area to generate the pseudo-absence  
117 dataset using the *Ecospat* package (Di Cola et al., 2017) in the software R 3.5 (R Core Team,  
118 2017).

119 *Climatic variables.* We used 19 bioclimatic variables generated for Mexico by Cuervo-  
120 Robayo et al. (2020) for mid-20th century (T1: 1950-1979) and late 20th–early 21st centuries  
121 (T2: 1980-2009) (Cuervo-Robayo et al., 2020). These variables were derived from monthly  
122 averages of precipitation, minimum and maximum temperatures drawn from climatic stations  
123 across Mexico, southern USA, ~~and~~ northern Guatemala and Belize, producing surfaces at 30  
124 arc seconds (~1 km) of spatial resolution, following the same methodology of the Worldclim  
125 dataset (Hijmans et al., 2005). The 19 bioclimatic variables summarize the extreme, mean and  
126 seasonal patterns of temperature, ~~the and~~ rainfall across the country and have been widely  
127 used for ecological analyses and species' distribution modeling (Worldclim has been cited more  
128 than 18,000 times, according to Google Scholar). To reduce the number of variables for  
129 analyses, we performed a Pearson's correlation analysis for each species to eliminate highly  
130 correlated variables (> 0.80) thus reducing model complexity and the risk of overfitting  
131 (Radosavljevic & Anderson, 2014; Moreno-Amat et al., 2015; García-Callejas & Araújo, 2016).

**Comentado [IR8]:** Could you please indicate the species, because in Table S2, there is not 117 species. Is explained in the results but maybe it would be better here.

**Comentado [IR9]:** What does this mean T?

**Comentado [IR10]:** idem

**Comentado [IR11]:** Could you please explain the implication?

132 Finally, we delimited the area of analysis for each species (i.e., "M" in the BAM framework;  
133 (Barve et al., ~~2011~~2011) by clipping the raster layers to the ecoregions (Olson et al., 2001) in  
134 which each species has been recorded, assuming that the boundaries of the ecoregions have  
135 represented a barrier to dispersal for the species (Radosavljevic & Anderson, 2014).

136 *Ecological niche modeling.* We evaluated the performance of seven popular algorithms  
137 for transferring niche models over time: Bioclim (Nix, 1986; Booth et al., 2014), which is a  
138 climatic envelope method; two regression-based techniques, namely Generalized Additive  
139 Models (GAM) and Generalized Linear Models (GLM) (Guisan, Edwards & Hastie, 2002); and  
140 four machine learning algorithms: Boosted Regression Trees (BRT; (Elith, Leathwick & Hastie,  
141 2008), Maxent (Phillips, Anderson & Schapire, 2006), Random Forest (RF; (Breiman, 2001),  
142 and Support Vector Machine (SVM; (Drake, Randin & Guisan, 2006). Detailed information  
143 about the functioning of each algorithm can be found elsewhere (Guisan, Edwards & Hastie,  
144 2002; Beaumont, Hughes & Poulsen, 2005; Drake, Randin & Guisan, 2006; Elith et al., 2006;  
145 Phillips, Anderson & Schapire, 2006; Merow, Smith & Silander, 2013; Booth et al., 2014;  
146 Muscarella et al., 2014), but in general, Bioclim describes the niche of a species in terms of an  
147 *n*-dimensional quadrangular envelope defined by the range of values in which the species  
148 occurs at each individual variable (Nix, 1986). GLM is an extension of linear models without  
149 forcing data into unnatural scales and relating the mean of the response variable with the linear  
150 combination of the explanatory variables. GAM is a semi-parametric extension of GLM which  
151 applies a "smoothing" function to the explanatory variables and replacing the linear predictor  
152 with an additive predictor (Guisan, Edwards & Hastie, 2002). BRT is an ensemble method that  
153 combines regression trees with a boosting algorithm (Elith, Leathwick & Hastie, 2008). Maxent  
154 is an algorithm that uses the maximum entropy principle and a Bayesian procedure to produce a  
155 probability surface where entropy is maximized to reflect the environmental suitability of the  
156 geographic area for the species (Phillips, Anderson & Schapire, 2006). RF is a combination of  
157 individual decision trees that converge in their classification outcome (Prasad, Iverson & Liaw,

**Comentado [IR12]:** The term elsewhere should be modified, please rewrite the sentence.

**Comentado [IR13]:** idem

**Comentado [IR14]:** reference

158 2006). SVM uses a functional relationship known as kernel to map data onto a new hyperspace  
159 (Drake, Randin & Guisan, 2006).

160 We executed Bioclim in the R package DISMO (Hijmans et al., 2017), where the  
161 resulting map is expressed as a continuous model based on the rescaled calculation of  
162 percentiles assuming that areas near the median are more suitable. We used the SDM package  
163 (Naimi & Araújo, 2016) in R for GLM, GAM, BRT, FR, and SVM. For GLM, we used a binomial  
164 response with logit link, quadratic function and AIC for stepwise selection. We implemented  
165 GAM with a binomial response with logit link function. We parameterized BRT with a learning  
166 rate of 0.005, tree complex of 5 and bag fraction of 0.5. We calibrated RF with 500 trees. We  
167 ran Maxent in ENMeval (Muscarella et al., 2014) under default settings but with the clamping  
168 and extrapolate options disabled and selected the best model per species with the minimum  
169 values of AICc. All output maps were expressed in a continuous scale from 0 to 1.

170 For all algorithms, we used 70% of the occurrence records for model calibration and  
171 the remaining 30% for validation, and we used the same proportion for pseudo-absences in the  
172 algorithms that required so. Then, each resulting model was transformed into a binary map  
173 (presence-absence) by selecting a ten-percentile threshold value; i.e., 10% of all occurrence  
174 records were left out. We decided to use this threshold to avoid over-prediction due to  
175 potentially erroneous occurrences (Radosavljevic & Anderson, 2014). All algorithms were  
176 evaluated for their capacity to produce reliable models within time periods via binomial tests to  
177 compare model results against random expectations (Anderson, Lew & Peterson, 2003).

178 *Model transferences.* The logical procedure to evaluate the capacity of algorithms to  
179 transfer niche models across different temporal scenarios involves calibrating a niche model in  
180 period 1 and transfer it onto the climatic scenario of period 2, then validate the transference with  
181 occurrences from period 2, or calibrate a niche model in period 2 and compare the two maps  
182 (Hijmans & Graham, 2006). A problem with these approaches emerges when the number or  
183 spatial distribution of occurrences in each period is different, because the differences observed

**Comentado [IR15]:** or RF (Random Forest)

**Comentado [IR16]:** All these terms are explained in Table 1, but also should be mentioned at the text.

**Comentado [IR17]:** Meaning...

**Comentado [IR18]:** Can you indicate why these parameters, or include references to the works that they previously used them

**Comentado [IR19]:** AIC is the same as AICc?

184 between the resulting maps of the two time periods may have been due to the disparities of the  
185 occurrences rather than algorithmic performance. To solve this problem, we followed a cross-  
186 temporal approach to identify the species with similar occurrence data structure in the two time  
187 periods. First, we calibrated a model in period 1 with occurrences from that period that we  
188 named *auto1*, then we generated a second model with the climatic layers of period 1 and the  
189 occurrences of period 2, named *cross1*. Second, we calibrated a model using the climatic  
190 surfaces of period 2 with the occurrences from that period (*auto2*) and another model with the  
191 occurrences of period 1 on the climatic surfaces of period 2 (*cross2*). Third, we converted all  
192 resulting maps into binary and geographically compared *auto1* vs. *cross1* and *auto2* vs. *cross2*  
193 (see next section). If the overall similarity between the two pairs of maps was <70%, it meant  
194 that the difference in the number/distribution of occurrences between time periods was large  
195 enough to hinder the response of algorithms to transfer models across temporal scenarios. We  
196 repeated this procedure for all species and the seven algorithms and discarded from further  
197 analyses those species for which their similarity value was <70%. Species with a dataset  
198 suitable for analyses were called *control* and the rest were called *without control*. For *control*  
199 species, we transferred models from period 1 to period 2 (forecast) and vice versa (hindcast),  
200 and evaluated model performance (fig. 1).

201       *Evaluation of algorithm performance.* For each algorithm, every model that was  
202 transferred from period 1 to period 2 was compared against the model that was calibrated in  
203 period 2, and vice versa, in a pixel-by-pixel fashion, as follows. First, we built a confusion matrix  
204 in which the calibration model was the reference; therefore, in the confusion matrix, *a* was the  
205 number of presence pixels correctly predicted by the transferred model (sensitivity), *b* was the  
206 number of absence pixels erroneously classified as presence (commission error or false  
207 positives), *c* was the number of presence pixels erroneously classified as absence (omission  
208 error or false negatives), and *d* is the number of absence pixels correctly predicted (specificity).  
209 Then, we calculated the following indices: True Skill Statistics (TSS; Equation 1), Overlap Index



210 (OI, Equation 2), False Negative Rate (FNR; Equation 3) and False Positive Rate (FPR;  
211 Equation 4) (Fielding & Bell, 1997), as follows:

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218 FPR is a measure of overestimation, whereas FNR indicates overfitting (Rebelo,  
219 Tarroso & Jones, 2010), and both have a scale from 0-1. OI reflects the proportion of overlap  
220 between the two maps. Finally, TSS compares the number of correctly predicted pixels minus  
221 randomly assigned data within a hypothetical set of perfect predictions. TSS score ranges from -  
222 1 to 1, where values between -1 and 0 reflect a model that does not perform better than chance,  
223 while a value of 1 is considered a perfect discrimination. Models with TSS values above 0.7 are  
224 considered reliable (Allouche, Tsoar & Kadmon, 2006). All calculations were made with the  
225 statistical program R 3.5 (R Core Team, 2017).

226 *Statistical Analysis.* We performed a Mann-Whitney-Wilcoxon test to evaluate  
227 differences between forecast and hindcast transferences (Pohlert, 2016). Also, we implemented  
228 a Kruskal-Wallis test to evaluate differences in the transference performance between  
229 algorithms, when a difference was found, we carried out a Nemenyi test, which makes pairwise  
230 multiple comparisons of mean sums of independent samples. ~~These test~~These tests are  
231 implemented in the PMCMR package (Pohlert, 2016). All statistical analyses were performed in  
232 R.3.5 (R Core Team, 2017).

233

## 234 Results

235

236 *Species' occurrences.* We found occurrence data for the 117 rodent species endemic to Mexico  
 237 (Ramírez-Pulido et al., 2014); however, we found sufficient unique records (at least 10) for  
 238 generating models for each time period only for 44 species (Supplementary Material, S2). There  
 239 were no sufficient data for 14 species for one of the two periods, whereas there were 59 species  
 240 for which we did not find 10 unique records for both periods. For the 44 species with sufficient  
 241 data for further analyses, *Peromyscus melanophrys* (n = 504), *Peromyscus difficilis* (n = 440),  
 242 *Chaetodipus arenarius* (n = 248), and *Sigmodon mascotensis* (n=191) held the highest number  
 243 of records.

244 *Temporal consistency of occurrence data.* We evaluated the consistency of occurrence  
 245 data at each period to perform temporal transferences for all 44 species with sufficient data. We  
 246 found that the number of species with high model similarity (>70%) between the two time  
 247 periods was different depending on the algorithm (Table 1). Maxent got the highest number of  
 248 species, whereas GAM the lowest (Table 1).

249 *Niche models and model transferences.* In general, all algorithms produced reliable  
 250 models for calibration in both time periods. Binomial test for models calibrated in the two climatic  
 251 scenarios were significantly different from random expectations for all species, except for GLM  
 252 models for *Callospermophilis madrensis*, *Dasyprocta mexicana* and *Dipodomys phillipsii* for T1  
 253 (1959-1979), and *Dipodomys phillipsii*, *Neotamias durangae*, *Noetoma goldmani* and *Oryzomys*  
 254 *guerrerensis* for T2 (1979-2009); a BRT model for *Pappogeomys bulleri* for T2; and a Maxent  
 255 model for *Dasyprocta mexicana* for T2 (Supplementary Material, S3?).

256 We observed differences in algorithm performance when models were transferred  
 257 across climatic scenarios (fig. 2). Some algorithms performed differently for forecasting and  
 258 hindcasting: our results showed that Bioclim, GAM and Maxent generally produced higher TSS  
 259 values for hindcasting than for forecasting, with significant differences between directions only  
 260 for Maxent ( $w = 139$ ,  $p = 0.04$ ). Similar results were observed for the omission index (OI), with  
 261 significant differences between directions for Maxent ( $w = 140$ ,  $p = 0.043$ ).

**Comentado [IR20]:** I am asking that if you have sufficient records for 44 species maybe it would be better just to work with 44, because if not is confused for the reader.

**Comentado [IR21]:** idem

**Comentado [IR22]:** According to table 1, maxent has 44 but also RF, SVM, BRT, GAM...

**Comentado [IR23]:** In table 1 has also 44

**Comentado [IR24]:** If this paragraph is related with table 1, should be reanalyzed.

**Comentado [IR25]:** You have more than one table in the SP, o please indicate to which one.

**Comentado [IR26]:** Is not explained in the text

We found significant differences between algorithms for transferring models from the present to the past scenario ( $H = 17.71$ ,  $p = 0.006$ ) and from the past to the present ( $H = 21.50$ ,  $p < 0.01$ ), being BRT the algorithm with the highest mean TSS value ( $\bar{x} = 0.84 \pm 0.08$ ) and Bioclim the lowest ( $\bar{x} = 0.46 \pm 0.24$ ) in forecasting. For hindcasting, Maxent obtained the highest mean value ( $\bar{x} = 0.82 \pm 0.11$ ) and Bioclim the lowest ( $\bar{x} = 0.60 \pm 0.15$ ). We observed a similar pattern for OI with significant differences between algorithms for hindcasting ( $H = 27.27$ ,  $p = 0.014$ ) and forecasting ( $H = 15.93$ ,  $p < 0.01$ ). We observed the greatest variation in forecasting for Bioclim ( $\bar{x} = 0.46 \pm 0.24$ ) and GAM ( $\bar{x} = 0.54 \pm 0.40$ ) and, on the contrary, RF showed a very consistent behavior and little variation in both directions (forecasting:  $\bar{x} = 0.81 \pm 0.09$ ; hindcasting:  $\bar{x} = 0.80 \pm 0.075$ ), and GAM for hindcasting ( $\bar{x} = 0.8 \pm 0.07$ ).

The false negative rate (FNR), which indicates model overestimation, showed significant differences between algorithms for hindcasting ( $H = 15.93$ ,  $p = 0.014$ ) and forecasting ( $H = 27.27$ ,  $p < 0.01$ ). Bioclim showed a difference with BRT ( $p < 0.01$ ) and RF ( $p = 0.03$ ) for forecasting and Maxent ( $p < 0.01$ ) for hindcasting. GAM showed the highest FNR for forecasting ( $\bar{x} = 0.29 \pm 0.39$ ) and GLM for hindcasting ( $\bar{x} = 0.10 \pm 0.06$ ), both algorithms with the highest variation in each direction. In turn, the false positive rate (FPR; an indication of overfitting) was not different for hindcasting ( $H = 10.96$ ,  $p = 0.089$ ), but it was so for forecasting ( $H = 13.22$ ,  $p = 0.039$ ). We observed a difference in FPR between directions only for Maxent ( $w = 301$ ,  $df = 6$ ,  $p = 0.04$ ). Conversely, GAM showed the highest FPR values for forecasting.

## Discussion

Transferences of ecological niche models over time have been widely used to assess the response of biodiversity to climatic changes (Allouche, Tsoar & Kadmon, 2006; Araújo, Thuiller & Pearson, 2006; Rebelo, Tarroso & Jones, 2010; Peterson et al., 2015a). Similar to our results, the variation between algorithms in niche model transfers to alternative climatic scenarios seems to be the rule and has been observed in multiple comparative studies

289 (Moreno-Amat et al., 2015; Beaumont et al., 2016; Bell & Schlaepfer, 2016; García-Callejas &  
290 Araújo, 2016; Liang et al., 2018; Qiao et al., 2019). However, to our knowledge, no previous  
291 studies have analyzed the effect of occurrence data structure and direction of transfers in the  
292 performance of algorithms.

293         In this study, we evaluated the performance and consistency of seven popular  
294 algorithms for transferring niche models to past (hindcast) and future (from the past to the  
295 present; forecast) climatic conditions for Mexican endemic rodents as study model. We decided  
296 to use endemic species for two reasons: (1) the ecological niche of the species is better  
297 reconstructed for species with restricted ecological conditions than for those that occupy a great  
298 diversity of environments (Raxworthy et al., 2007); and (2) the climatic databases used in this  
299 analysis were developed specifically for Mexico (Cuervo-Robayo et al., 2020). Our analyses  
300 showed three main results: first, the quality of input data and the algorithm had a significant  
301 effect on model output and performance. Second, algorithms did not perform equally for  
302 hindcasting and forecasting, where we found generally higher performance for the latter. And  
303 third, we found that algorithms performed differently for model transferences, being Random  
304 Forest (RF), Boosted Regression Trees (BTR) and Maxent consistently robust, whereas Bioclim  
305 showed the lowest performance.

306         Algorithm performance for model transferences has been analyzed under different  
307 approaches, including the use of virtual species (García-Callejas & Araújo, 2016) and real  
308 species of different biological groups (Heikkinen, Marmion & Luoto, 2012; Beaumont et al.,  
309 2016; Fan et al., 2018), as well as testing different sets of variables (Barbet-Massin & Jetz,  
310 2014; Warren et al., 2014) and climate change projections to the past and future (Dobrowski et  
311 al., 2011; Veloz et al., 2012). In this study, we assessed algorithm performance for a single  
312 taxonomic group under a retrospective approach and found that occurrence data structure  
313 between time periods plays a critical role. We know that an adequate sampling is necessary to  
314 make a good characterization of the species' ecological niche in the calibration scenario before

**Comentado [IR27]:** You should discuss your results

315 transferring a model to different scenarios (Araújo, Pearson & Rahbek, 2005), but this is the first  
316 time that disparities in the occurrence data between time periods are evaluated in the context of  
317 climate change analyses.

318           One important issue when using correlative modeling under a retrospective  
319 approach to evaluate the geographic responses of species to climate change is to decouple the  
320 effect of data bias or incompleteness from the signal of geographic change. A logical way to  
321 proceed when you have two temporally distinct sets of occurrence data and climatic scenarios  
322 (i.e., T1 and T2) is to calibrate a model in T1 with the occurrences and climatic scenario from  
323 that time period, transfer the resulting model to T2, and use the occurrences of T2 to validate  
324 the transfer, and vice versa. However, this approach may have a problem of inconsistency of  
325 the occurrences between the two time periods, ergo, if the quantity or quality of occurrence data  
326 from the two periods are different, then the two niche models will result somewhat different and  
327 transferences will be affected in an unknown manner. In such case, the geographic shift  
328 observed under these conditions is mostly due to the occurrence differences, rather than to the  
329 responses of species to climatic changes. To avoid this pitfall, our initial step was to test for data  
330 consistency between the two time periods by carrying out a cross-modeling procedure. To do so  
331 for the 44 species with sufficient data in the two time periods, we first calibrated a model with  
332 the climatic scenario and occurrences from T1, and then, we calibrated a second model with  
333 occurrences from T2 under the climatic scenario of T1 and compared the two resulting maps,  
334 and vice versa. If the data from the two time periods were consistent, the two maps should  
335 result highly similar, otherwise they would be significantly different. Interestingly, we found that  
336 the number of species with consistent data was different depending on the algorithm, being  
337 Maxent the most robust ( $n = 21$ ), whereas the General Additive Model (GAM) obtained the  
338 lowest number ( $n = 3$ ) (Table 1). This result corroborates the fact that algorithms have different  
339 sensitivity to data bias or incompleteness (Moreno-Amat et al., 2015); therefore, if the user

**Comentado [IR28]:** Please indicate the benefits of this method

340 knows or suspects about this problem in the dataset, a safer decision is to use a low data-  
341 demanding algorithm (e.g., Maxent, Bioclim).

342         There are at least three assumptions when transferring niche models over time: (1)  
343 the species is in equilibrium with the environment (Araújo, Pearson & Rahbek, 2005), (2) the  
344 species maintains the same response to environmental conditions between time periods  
345 (Anderson 2011), and (3) the ecological niche remains conserved along time periods (Soberón  
346 & Nakamura, 2009; Wiens et al., 2009; Sequeira et al., 2018). However, other factors have a  
347 strong effect on the capacity of niche models to transfer over time, the most critical one being  
348 the variability produced by at least three sources: (1) data completeness and structure (i.e.,  
349 quality and quantity) (García-Callejas & Araújo, 2016; García- et al., 2023); (2) algorithm  
350 performance (Heikkinen, Marmion & Luoto, 2012; Beaumont et al., 2016; Liang et al., 2018;  
351 Qiao et al., 2019); and (3) taxonomic idiosyncrasies (Sequeira et al., 2018; Regos et al., 2019).  
352 Of the seven algorithms that we tested, Random Forest (RF) showed the greatest predictive  
353 capacity and lowest overprediction. This algorithm has proved robust for transferences using  
354 virtual species (García-Callejas & Araújo, 2016), good performance for interpolations (Liang et  
355 al., 2018), relatively low overprediction (Mi et al., 2017), and high performance (Bell &  
356 Schlaepfer, 2016). Our results are consistent with other studies that found BRT having a good  
357 performance (García-Callejas & Araújo, 2016; Liang et al., 2018; Sequeira et al., 2018) and high  
358 variability (Bell & Schlaepfer, 2016). Maxent was also an algorithm that showed a high  
359 performance, particularly for hindcasting. Maxent is the most widely used algorithm  
360 (Radosavljevic & Anderson, 2014; Moreno-Amat et al., 2015) in part because it is robust to data  
361 biases (Heikkinen, Marmion & Luoto, 2012; Liang et al., 2018; Sequeira et al., 2018). In turn,  
362 Bioclim presented the lowest performance, with low overfitting but high overprediction and  
363 variability between projections. Bioclim is sensitive to outliers or insufficient sampling, which  
364 might be the reason for its poor performance (Dobrowski et al., 2011; Beaumont et al., 2016).

365 Another important and novel result derived from our analyses is that most algorithms  
366 performed differently for transferring models to future scenarios than to the past. Bioclim and  
367 GAM performed better for hindcasting than for forecasting, whereas RF, Support Vector  
368 Machine (SVM) and BRT behaved the opposite. Maxent and the Generalized Linear Model  
369 (GLM) were consistent for the two time periods. These differences may reflect the capacity of  
370 models to deal with non-analog climates (Pearson et al., 2006). For instance, Bioclim is  
371 sensitive to extreme values, so it may be more affected by larger differences between climatic  
372 scenarios, as compared to Maxent that has the capacity to clamp and extrapolate into non-  
373 analog values (Phillips & Dudík, 2008). More importantly, these results ~~suggests~~suggest that the  
374 choice of an algorithm has implications beyond its simple capacity to produce adequate models  
375 in the calibration scenario.

376 Finally, a potential limitation of this study is that the taxonomy of Mexican rodents is  
377 continuously updated. While our research relied on the latest revision of Mexican mammals  
378 (Ramírez-Pulido et al. 2014), ~~recent~~, recent proposals suggest species separation for  
379 *Peromyscus melanophrys*, *P. furvus*, *P. levipes*, *P. zarhynchus*, and *Osgoogomys banderanus*  
380 (Lorenzo et al., 2016; Almendra et al., 2018; Cruz-Gómez et al., 2021; Bradley et al., 2022). As  
381 a result, the quantity and spatial structure of occurrences for these species may undergo some  
382 modifications. Nonetheless, based on our calibration tests, we believe that the generality of our  
383 findings remains unaffected by these taxonomic changes

384 Finally, when the aim of a study is to explore the potential distributional responses of  
385 species to climate change under a niche modeling approach, we recommend the following:  
386 First, perform a thorough screening and cleaning of occurrence data and identify the most  
387 important variables to characterize the ecological niche of the focal species. Then, perform a  
388 cross-modeling procedure between time periods in a retrospective fashion (past to present and  
389 vice versa) using different algorithms to identify the effect of sampling bias or incompleteness on  
390 model transferances, and decide whether the target species is suitable for the analysis. Split the

**Comentado [IR29]:** As you are in the discussion your results should be compared with the previous ones. If not you can merge results and discussion sections to minimize redundancy.

391 occurrence data into two time periods (e.g. present-near, past) and model between times with  
392 different algorithms or perform a consensus to identify the model with the highest transferability  
393 over time according to the specific data structure. Finally, identify FNR and FPR to ~~make a~~  
394 ~~decision~~decide on the error that best fits the question to be answered by the transfer.

395

## 396 **Conclusions**

397 We found that both the quantity and quality of data, along with the choice of the  
398 modeling algorithm significantly influence model transferability. Furthermore, we observed that  
399 algorithms exhibit unequal performance when transferring models from the past to the present  
400 compared to the reverse process. Consequently, we assert that not all species are suitable  
401 candidates for transferring models to alternative climatic scenarios; only those species with  
402 sufficient occurrence records to produce robust niche models, should be considered for  
403 projections time periods.

404 Additionally, not all algorithms perform uniformly across different occurrence data  
405 structure and levels of completeness. Some algorithms are more sensitive to small sample sizes  
406 and non-analog climates. Therefore, we recommend conducting preliminary tests on algorithmic  
407 performance to specific occurrence datasets in a retrospective manner before proceeding with  
408 model transferances to future climatic scenarios.

409

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**Comentado [IR30]:** Please, indicate more conclusions of the work.

**Comentado [IR31]:** Which data is needed?



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418

419

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**Comentado [IR32]:** Check the references

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