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# **Predicting the expansion of invasive species: how much data do we need?**

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## Abstract

Ecological niche models (ENMs) are a powerful tool to predict the spread of invasive alien species (IAS) and support the implementation of actions aiming to reduce the

25 impact of biological invasions. While calibrating ENMs with distribution data from  
26 species' native ranges can underestimate the invasion potential due to possible niche  
27 shifts, using distribution data combining species' native and invasive ranges may  
28 overestimate the invasion potential due to a reduced fitness and environmental  
29 tolerance of species in invaded ranges. An alternative may be using the increasingly  
30 available distribution data of IAS as they spread their invaded ranges, to iteratively  
31 forecast invasions as they unfold. However, while this approach accounts for possible  
32 niche shifts, it may also underestimate the species' potential range, particularly at the  
33 early stages of the invasion when the most suitable conditions may not yet be  
34 represented in the distribution range data set. Here, we evaluate the capacity of ENMs  
35 to forecast the distribution of IAS based on distribution data on invaded ranges as  
36 these data become available. We further use dispersion models to assess the  
37 expansion process using the predicted potential distributions. Specifically, we used  
38 the common waxbill (*Estrilda astrild*) in the Iberia Peninsula as a model system,  
39 building ENMs with distribution records for each decade from 1960 to 2019 and yearly  
40 bioclimatic variables, to forecast the species potential range in the coming decades.  
41 Then, we analysed the performance of the models for each decade in forecasting the  
42 species observed range expansion in the following decades and evaluated how the  
43 number of distribution records determined the quality of the forecasts. Finally, we  
44 performed dispersal estimates (based on species traits, topography, climate and land  
45 cover) to analyse the prediction capacity of models as their uncertainty may be  
46 reduced when projecting them to the next decades. Our results show that invasion-  
47 only ENMs successfully forecasted the species' range expansion over three decades  
48 after invasion, while dispersion models were not important in forecasting common  
49 waxbill expansion. Our study highlights the importance of constantly monitoring alien

50 species, suggesting that iterative updating of ENMs with observed distribution data  
51 may accurately forecast the range expansion of alien species.

52

## 53 **Keywords**

54 alien species, common waxbill, dispersal analyses, ecological niche models, *Estrilda*  
55 *astrild*, forecasts

56

## 57 **Introduction**

58 Biological invasions are among the most worrisome environmental problems of  
59 modern times (Díaz et al. 2019). The spread of invasive alien species (IAS) across the  
60 globe has been responsible for population declines of native species, changes in  
61 community composition (Bellar et al. 2016, 2021), alterations of ecosystem processes  
62 and functioning (Ehrenfeld 2010), disruptions of socio-economic activities (Diagne et  
63 al. 2021) and public health concerns (e.g. Naeem et al. 2009; Fournier et al. 2019;  
64 Ogden et al. 2019). In a globalised world, the number of IAS is expected to increase  
65 (Seebens et al. 2021) as well as their potential impacts (Fournier et al. 2019; Essl et  
66 al. 2020), promoted by increasing international wildlife trade and global changes  
67 (Scheffers et al. 2019; Naimi et al. 2022). As a response to this urgency, several  
68 international regulations and mechanisms have been implemented in the last decades  
69 aiming at preventing the introduction and spread of IAS. This includes the  
70 establishment of a legal framework with specific legislation, as the EU Regulation  
71 1143/2014 on IAS (Regulation EU 2014). However, the successful implementation of  
72 these mechanisms requires the anticipation of new invasion areas which have been  
73 hampered by the lack of monitoring data on species distributions at adequate spatial  
74 and temporal resolutions. There is thus a need for a continuing effort to develop

75 approaches, which may include ecological modelling tools, to accurately predict IAS  
76 expansion, in order to reduce both ecological and socio-economic impacts of IAS.

77

78 Modelling and projecting the realised niche of IAS in the geographical space allows  
79 for identifying the areas at risk of invasion ([Jiménez-Valverde et al. 2011](#); [Guisan et](#)  
80 [al. 2014](#)). The realised niche is part of the fundamental niche, i.e. the abiotic  
81 environmental space where a species can maintain a viable population and persist  
82 over time without immigration, which is then further limited by biotic interactions,  
83 dispersal capacity, or historical aspects ([Soberón & Peterson 2005](#)). This assessment  
84 is often done through correlative ecological niche modelling (ENM) ([Peterson and](#)  
85 [Vieglais 2001](#); [Jiménez-Valverde et al. 2008](#); [Jeschke and Strayer 2008](#); [Capinha and](#)  
86 [Anastácio 2011](#); [Venette 2015](#); [Sillero et al. 2021](#)), which quantify species-  
87 environment relationships based on observed patterns of species distributions and  
88 environmental predictors ([Franklin 2010](#); [Peterson et al. 2011](#); [Guisan et al. 2019](#);  
89 [Sillero et al 2021](#)). A procedure of key practical importance concerns the geographical  
90 areas used to calibrate the ENMs. For IAS, these models can be calibrated using  
91 distribution data from the species' native range ([Peterson et al. 2003](#)), thus assuming  
92 that the native species distribution represents the entire suite of suitable environments  
93 (i.e., distributional equilibrium; [Guisan and Zimmermann 2000](#); [Araújo and Pearson](#)  
94 [2005](#); [Araújo et al. 2005](#)), or at least, all suitable habitats where the species is able to  
95 disperse (i.e. pseudo-equilibrium; [Anderson and Raza 2010](#); [Sillero et al. 2021](#)).  
96 However, species' realised niches may shift in new areas or time periods (i.e. niche  
97 shift *sensu* [Guisan et al. 2014](#)), which implies that IAS will not be necessarily  
98 circumscribed to areas that are environmental analogues to their native ranges  
99 ([Peterson 2003](#); [Jeschke and Strayer 2008](#); [Elith and Leathwick 2009](#)). This is

100 because, when the environmental conditions change, or the species arrives in a new  
101 area, the drivers limiting the species' realised niche can change (e.g. the new area  
102 lacks a competing species or the species can now disperse to new habitats), enabling  
103 the exploration of new areas inside its fundamental niche (Sillero et al. 2022). Some  
104 IAS have shown marked climatic niche shifts during invasion (i.e., a divergence  
105 between climatic conditions in native and alien ranges; *sensu* Broennimann et al.  
106 2009), likely driven by adaptive changes enabling species to endure conditions that  
107 were previously unsuitable (Blossey and Notzold et al. 1995), i.e., shift in its realised  
108 climatic niche (Sillero et al 2022).

109

110 Considering the potential for realised niche shifts, previous works have recommended  
111 calibrating ENMs using distribution data of IAS in both native and invasive ranges  
112 (Fitzpatrick et al. 2006; Broennimann 2007; Broennimann and Guisan 2007; Urban et  
113 al. 2007; Beaumont et al. 2009; Pili et al. 2020). While this approach potentially  
114 captures niche shifts as they emerge in invaded areas, the combination of native and  
115 invasive distribution data also raises relevant practical and conceptual issues. The  
116 existence of higher quality distribution data for the species in one range versus the  
117 other (Vanette et al. 2010), may require the reduction of the spatial resolution leading  
118 to information loss when merging both dataframes (Jarnevich et al. 2022). Although  
119 spatial downscaling can be employed to enable modeling at a coarse resolution and  
120 projection onto the Schuyler area at a higher resolution, this approach introduces  
121 uncertainty due to assumptions regarding the consistent relationships between coarse  
122 and fine-resolution data within the area, on the employed methods (Key et al. 2012).  
123 On the other hand, and perhaps more importantly, the use of native distribution data  
124 may overestimate invasion ranges, as there are circumstances where invasive species

125 may not be able to colonise similar environmental conditions to their native areas, due  
126 to the presence of novel negative interspecific interactions (e.g., predators, parasites,  
127 competitors) (Sih et al. 2010; Dostal et al. 2013; Carthley and Banks 2018), genetic  
128 bottlenecks and founder effects, driving a reduction in the species environmental  
129 tolerances, and species dispersal capacity, that cannot be included directly in the  
130 native model, which will provide the maximum extent of the species distribution in the  
131 invasive range if the environmental conditions are the same (Jarnevich et al. 2022).

132

133 Invasion monitoring efforts are producing high-quality spatiotemporal data of spread  
134 for a large number of IAS in invaded ranges (e.g. Groom et al. 2019, GBIF - the Global  
135 Biodiversity Information Facility, <https://www.gbif.org/>). Hence, given the impossibility  
136 of reconstructing the invasive process over time, an alternative is to use  
137 spatiotemporal invasion data to iteratively forecast invasions as they unfold. By  
138 restricting the calibration of ENMs to the region being invaded, the issues raised by  
139 using native distribution data are overcome. However, any approach relying only on  
140 invasive distribution data for calibrating ENMs must acknowledge the likely  
141 underestimation of species' potential ranges, particularly at early stages of invasion,  
142 when most suitable conditions may not yet be represented in the distribution range  
143 data set. In this context, it is pivotal to clarify the data requirements ensuring accurate  
144 ENM for IAS, and particularly, the extent to which invasion-only distribution data can  
145 be used to accurately predict the expansion of IAS. Modelling the invasive over time  
146 will provide information about the routes used by the species during the expansion  
147 process.

148

149 Here we evaluate the capacity of iterative calibration of ENM models based on  
150 invasion-only distribution data for predicting the invasion potential and analysing the  
151 expansion process of IAS. We specifically address how much data do we need to  
152 predict IAS expansion range (i.e. the length of the time series of the species  
153 distribution data in the invaded range since establishment) required to provide an  
154 informative prediction of the species' invasion potential. We also assessed the  
155 importance of accounting for the dispersal capacity of species to predict its expansion.  
156 For this, we considered one of the most studied alien bird species, established in  
157 different environments and biogeographic regions worldwide: the afro-tropical  
158 common waxbill (*Estrilda astrild*). Using a unique high-quality database on spatial  
159 dispersion of this species through the Iberian Peninsula over six decades ([Reino and](#)  
160 [Silva 1998](#); [Silva et al. 2002](#); [Reino 2005](#); [Sullivan et al. 2012](#)), we applied a  
161 backcasting approach, fitting each ENM using distribution data available until the end  
162 of each decade and using the resulting model to project the distribution for the next  
163 decade. Then, we analysed how the number of observation records used in each ENM  
164 related to the performance of the forecasts of species dispersal over time. Finally,  
165 because ENMs do not account for species' dispersal per se ([Sillero et al. 2021](#); [Sillero](#)  
166 [et al. 2022](#)), we also implemented a species dispersal model over time considering a  
167 comprehensive set of species traits and climatic and landscape variables ([Engler et](#)  
168 [al. 2012](#)). We discuss these results in light of the amount of distribution data (i.e. length  
169 of the time series since establishment) needed for invasion-only ENMs and dispersal  
170 analyses to predict the invasion potential of IAS and iteratively forecast future  
171 invasions.

172

173

## 174 **Material and Methods**

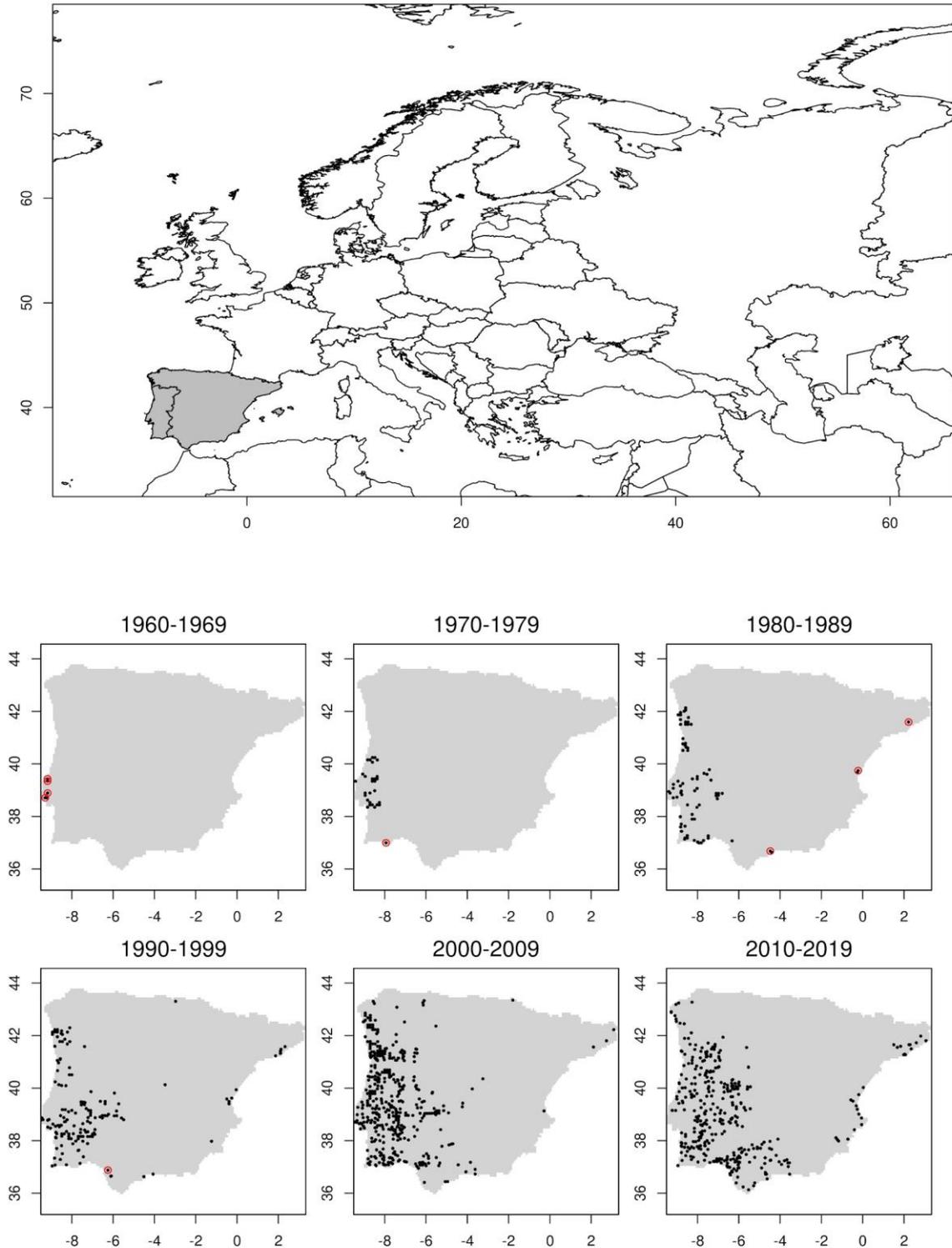
### 175 **Study area**

176 The Iberian Peninsula (southwestern Europe), covers an area of 582,860 km<sup>2</sup> and  
177 mainly includes the continental territories of Spain and Portugal (**Fig. 1**). It is bordered  
178 to the southeast and east by the Mediterranean Sea and to the south, north and west  
179 by the Atlantic Ocean, and is separated from the rest of Europe by the Pyrenees in the  
180 northeast. The Peninsula has a high diversity of climatic conditions, influenced by both  
181 the Atlantic Ocean and the Mediterranean Sea, with a longitudinal gradient of  
182 precipitation and a latitudinal gradient of precipitation and temperature ([Capel 1981](#)).

183

### 184 **Common waxbill distribution data**

185 We gathered historical data on the common waxbill expansion in the Iberia Peninsula  
186 since its first introduction in the 1960s. For this, we obtained presence data of the  
187 species in the continental territories from [Sullivan et al. \(2012\)](#), including the national  
188 and regional breeding bird atlases from Portugal and Spain, updated with all-year-  
189 round information from the eBird database ([eBird 2019](#)). Following data compilation,  
190 we mapped all records into a 10x10 UTM km grid of Portugal and Spain, keeping only  
191 the oldest record for each cell (**Fig. 1, Suppl. material 1**). We then aggregated the  
192 data by decade, ranging from the first reported record to the present time. Therefore,  
193 we represented the species expansion along six decades: 1960-1969 (8 cells), 1970-  
194 1979 (47 cells), 1980-1989 (97 cells), 1990-1999 (157 cells), 2000-2010 (369 cells)  
195 and 2011-2019 (330 cells) (**Fig. 1**).



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**Figure 1.** Location of the study area in the Iberia Peninsula, southwest Europe (upper panel) and distribution of the common waxbill *Estrilda astrild* from 1960 to 2019 (bottom panel). Black dots: point presences. Circles with dots: points of introduction.

201

## 202 Environmental data

203 We obtained yearly climate data for the temporal period covered by the distribution  
204 data from the EuMedClim Database (<http://gentree.data.inra.fr/climate/>; Fréjaville and  
205 Garzón 2018). EuMedClim provides yearly climate data between 1901–2014 at 1 km  
206 resolution for Europe and the Mediterranean Basin. These data comprise 21 variables:  
207 seven bioclimatic variables available from Worldclim (<https://www.worldclim.org/>; bio1  
208 - annual mean temperature; bio2 - mean diurnal temperature range; bio5 - Maximal  
209 temperature of the warmest month; bio6 - minimal temperature of the coldest month;  
210 bio12 - annual precipitation; bio13 - precipitation of the wettest month; bio14 -  
211 precipitation of the driest month); and 14 variables derived from monthly temperature  
212 and precipitation data from WorldClim: seasonal temperature and precipitation (winter,  
213 spring, summer, and autumn), potential evapotranspiration (PET, annual, minimal  
214 monthly, and maximal monthly) and water balance (precipitation minus PET). From  
215 these variables, to minimize cross-correlation between variables, we kept four  
216 variables that had an absolute value of Pearson correlation coefficient  $< 0.7$  (**Fig. 2**):  
217 mean diurnal temperature range (bio2), minimal temperature of the coldest month  
218 (bio6), precipitation of the wettest month (bio13) and precipitation of the driest month  
219 (bio14).

220

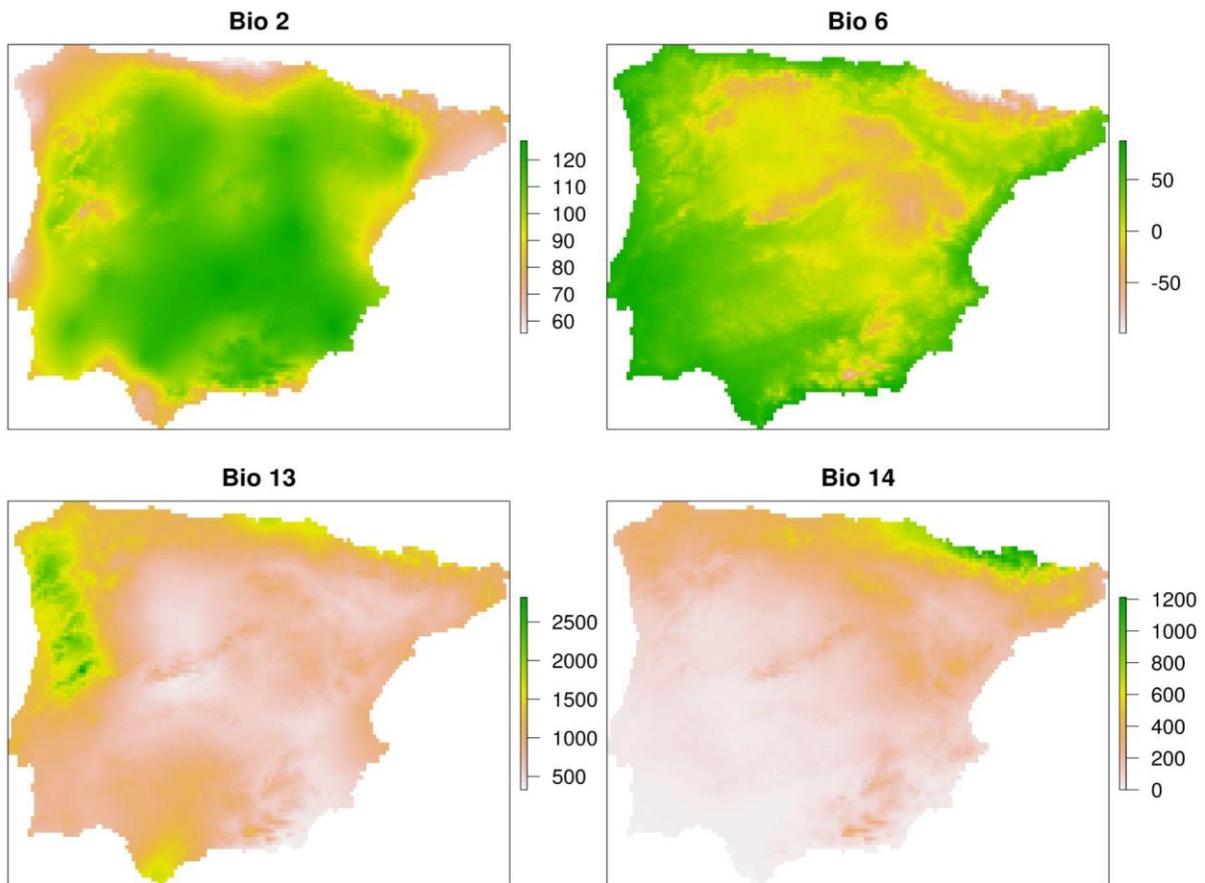
## 221 Statistical analysis

### 222 Ecological Niche Models

223 We estimated the realised niche of the species (*sensu* Sillero 2011) for each decade  
224 represented in our data (1960-1969, 1970-1979, 1980-1989, 1990-1999, 2000-2010  
225 and 2011-2019). For that purpose, we fitted a model using species distribution data  
226 from that specific decade only, i.e., not cumulatively (**Table 1**). Then, we projected the

227 realised niche models for each decade to the following decades (**Table 1**). For  
 228 example, we used the model calibrated with data from the first decade (1960-1969) to  
 229 project the species' potential distribution in each of the next decades, i.e., 1970-1979,  
 230 1980-1989, 1990-1999, 2000-2010 and 2011-2019.

231



232

233

234 **Figure 2.** Bioclimatic variables (mean diurnal temperature range, °C [bio2], minimal  
 235 temperature of the coldest month, °C [bio6], precipitation of the wettest month, mm  
 236 [bio13] and precipitation of the driest month, mm [bio14]) considered in Maxent to  
 237 estimate the ecological niche models. Temperature variables are multiplied by 10 to  
 238 avoid decimals.

239

240

241

242

243 **Table 1.** Matrix of realised niche models (blue cells) and respective projections (yellow cells)  
 244 each row includes the model of that decade (M<sub>#</sub>), and all projections for the next  
 245 decades (P<sub>#</sub>).  
 246

	1960-69	1970-79	1980-89	1990-99	2000-01	2010-19
1960-69	M <sub>1960-69</sub>	P <sub>1970-79</sub>	P <sub>1980-89</sub>	P <sub>1990-99</sub>	P <sub>2000-01</sub>	P <sub>2010-19</sub>
1970-79		M <sub>1970-79</sub>	P <sub>1980-89</sub>	P <sub>1990-99</sub>	P <sub>2000-01</sub>	P <sub>2010-19</sub>
1980-89			M <sub>1980-89</sub>	P <sub>1990-99</sub>	P <sub>2000-01</sub>	P <sub>2010-19</sub>
1990-99				M <sub>1990-99</sub>	P <sub>2000-01</sub>	P <sub>2010-19</sub>
2000-01					M <sub>2000-01</sub>	P <sub>2010-19</sub>
2010-19						M <sub>2010-19</sub>

247

248 We calculated realised niche models using Maxent v.3.4.4 (Phillips et al. 2006, 2017)  
 249 following standard procedures (Sillero et al. 2021, Sillero & Barbosa 2021). Maxent  
 250 uses presence/background data as dependent variables, where the background data  
 251 represent the spectrum of environmental conditions available to the species (Phillips  
 252 et al. 2009; Guillera-Arroita et al. 2014). Maxent output represents habitat suitability,  
 253 ranging from 0.0 (not suitable) to 1.0 (suitable), in Cloglog format (Phillips et al. 2017).  
 254 Because Maxent includes stochasticity in the training data random selection, different  
 255 model runs can lead to slightly different outcomes (Phillips et al. 2006, 2017). For that  
 256 reason, we here used the average of 10 distinct modelling events in order to obtain  
 257 final suitability values for each decade, randomly selecting 70% of the occurrence  
 258 records as training data and 30% as test data. We calculated the Maxent models with  
 259 auto features, where different distribution functions are used depending on the sample  
 260 size (Phillips et al. 2006, 2017).

261

262 We measured model discrimination performance with the area under the curve (AUC)  
 263 of the receiver operating characteristics (ROC) plots (Liu et al. 2005). The AUC

264 discriminates a species' model from a random model, with a value equal to or close to  
265 0.5 corresponding to an accuracy similar to that of a random model and a value of 1  
266 corresponding to a perfect discrimination accuracy. Additionally, we calculated a set  
267 of null models following the methodology by [Raes and ter Steege \(2007\)](#). For this, we  
268 generated 100 different datasets with the same number of random points as each  
269 dataset following a Poisson distribution. We calculated a Maxent model for each of  
270 these random datasets and obtained the AUC values of the ROC plots. Then, we  
271 compared the training AUC values of the species models with the ones calculated for  
272 the null models using the non-parametric Wilcoxon test. We calculated the null models  
273 in R 3.4.4 ([R Core Team 2020](#)) with the 'dismo' package ([Hijmans et al. 2017](#)).

274

275 We determined the contribution of each climatic variable in explaining the species'  
276 distribution using a jackknife resampling based on: (1) values of the training and test  
277 gain; and (2) of AUC values. The jackknife resampling comprises two steps: (1) the  
278 generation of a model with all climatic variables except one; and (2) the generation of  
279 univariate models, each using only one climatic variable. In each step, the jackknife  
280 analysis measures the change in training and test gain, and the AUC determines the  
281 importance of each variable. Using the results from each of these procedures, Maxent  
282 calculated an average percentage contribution of each climatic variable. We also  
283 calculated the permutation importance: for each environmental variable in turn, the  
284 values of that variable on training presence and background data are randomly  
285 permuted. The model is re-evaluated on the permuted data, and the resulting drop in  
286 training AUC is calculated, normalised to percentages ([Phillips et al. 2006](#)). When  
287 variables interact, the variable contributions and the permutation importances are not  
288 equally ordered, preventing individual responses for each variable.

## 289 **Ecological Niche Models validation over time**

290 We further validated the ENMs for each decade and their respective projections by  
291 counting the number of presences classified as presences or as absences. We used  
292 the presence records of: 1) each decade; 2) each decade and previous decades, i.e.,  
293 cumulatively; and 3) the last decade (2010-19). In each case, we calculated the  
294 percentage of presences correctly identified as presences reflecting the model's  
295 capacity to produce accurate forecasts. In the last case, we evaluated the capacity of  
296 previous models to predict the final model (2010-19).

297

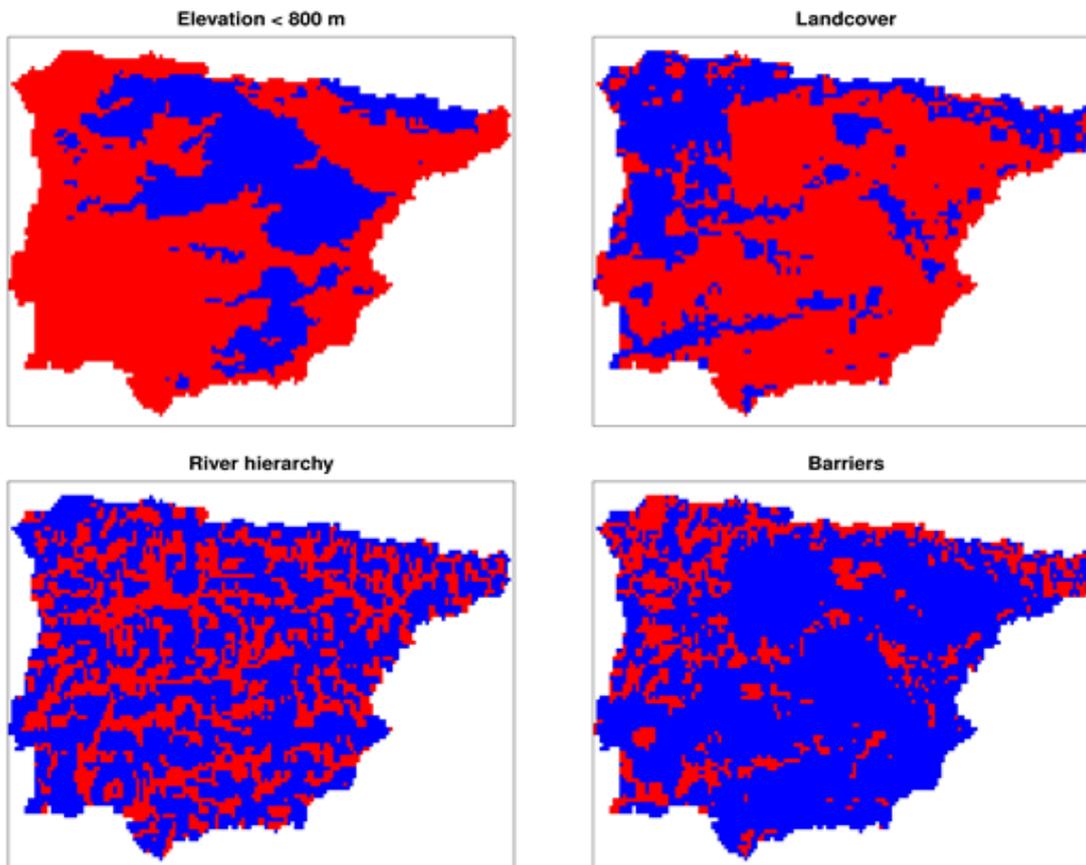
## 298 **Dispersal analyses**

299 Accounting for dispersal barriers/capacity has been pointed out as important to reduce  
300 uncertainty in future projections of species distribution ([Engler et al. 2012](#)). We  
301 estimated dispersal movements over time with R package 'MigClim' ([Engler et al.](#)  
302 [2012](#)), a cellular automaton model that simulates the dispersal of species in the  
303 landscape. MigClim uses ENMs as indicators of landscape permeability: the higher  
304 the habitat suitability index, the higher the permeability. We applied MigClim to each  
305 decadal Maxent model and respective projections (**Table 1**). Therefore, Migclim  
306 modelled how the species dispersed between Maxent models, i.e. from the first model  
307 to the next projections. The MigClim model considers short-distance and long-distance  
308 dispersal events, the type of dispersion through the landscape (using a continuous or  
309 a categorical Maxent model), propagule production probability, initial maturity age, and  
310 the presence of barriers. We considered three possible scenarios: i) no dispersal  
311 barriers; ii) weak barriers (i.e. barriers that can be transposed), and iii) strong barriers  
312 (i.e. barriers that cannot be transposed).

313

314 Dispersal barriers were represented by elevation, hydrological configuration and land  
 315 cover (**Fig. 3**). We obtained elevation data from the Shuttle Radar Topography Mission  
 316 (Farr et al. 2007) at 90 m and aggregated to 10x10km cell resolution. Following the  
 317 results obtained in previous studies in Iberia (e.g. Silva et al. 2002), we considered  
 318 elevations higher than 800 m as barriers to dispersion. We obtained land cover from  
 319 the Global land cover 2000 dataset with 250 m of spatial resolution from the European  
 320 Environmental Agency ([https://www.eea.europa.eu/data-and-maps/data/global-land-](https://www.eea.europa.eu/data-and-maps/data/global-land-cover-250m)  
 321 [cover-250m](https://www.eea.europa.eu/data-and-maps/data/global-land-cover-250m)). We considered the land cover classes including tree cover as barriers  
 322 to the dispersal, as *E. astrild* is mostly associated with open habitats (Payne et al.  
 323 2020, Ribeiro et al. 2020) (**Suppl. material 2: table S1**). We also calculated the  
 324 average hierarchy of watercourses in each grid cell of 10x10 km. River hierarchy  
 325 ranged from 1 to 8, with a value of 8 corresponding to large watercourses such as  
 326 main rivers and 1 to small, often intermittent streams. For this variable, we considered  
 327 as barriers those grid cells with a hierarchy of 1, reflecting the species' association  
 328 with permanent water courses (Ribeiro et al. 2020). The final layer of barriers  
 329 corresponded to the combination (multiplication) of all barrier layers, resulting in a  
 330 layer classified as 0 (without dispersal barriers) and 1 (with barriers) (**Fig. 3**). The  
 331 parameters used in MigClim are shown in **Table 2**.

332



333  
 334 **Figure 3.** Variables (elevation, land cover, and river hierarchy) used to define the  
 335 barriers to dispersal through the landscape, and the barriers used in MigClim to  
 336 measure the dispersion across the landscape. Blue colour means barrier; red colour  
 337 means no barrier.  
 338

## 339 Results

### 340 Common waxbill expansion patterns

341 The geographic distribution of the common waxbill in the Iberia Peninsula spans most  
 342 of the Iberian Atlantic coast, but also through large areas in Southern and Eastern  
 343 Iberia extending to the Mediterranean coast, as far as Catalonia (**Fig. 1**). Although this  
 344 species was initially introduced around the Lisbon region (Central Portugal), it rapidly  
 345 spread in all directions. Its geographic expansion was also enhanced by more recent  
 346 and independent introductions, as in Algarve (southern Portugal), Andalucia (southern  
 347 Spain) and later in other regions in eastern Spain (**Fig. 1**).

348 **Table 2.** Parameters and their values introduced in dispersal models.  
 349

Parameter	Value
Continuous mode	0
Number of environmental change steps to perform	6
Number of dispersal steps to perform within each environmental change step	10
Dispersal kernel: probability of colonising a directly adjacent cell	1
Long-distance dispersal frequency	0.0001
Minimum distance for long-distance dispersal in pixels	2
Maximum distance for long-distance dispersal in pixels	4
Initial maturity age of newly colonized cells	1
Propagule production probability as a function of cell age	1
Number of replicates	100
Barriers	No barriers; Weak; Strong

350

351 The expansion process was faster in the Central and Northern regions of Portugal,  
 352 whereas the spread in the south seemed to have been boosted by an additional  
 353 introduction event (Algarve) that enabled the colonisation of Andalucia (**Fig. 1**). This  
 354 event appears to underlie the colonisation of almost all Iberian southwestern coast,  
 355 unifying the northern population - which had also started to colonise Alentejo  
 356 (Portugal) from the Sado valley - with the southern population (**Fig. 1**). Spread  
 357 eastwards was slower, and several areas remain uncolonized to the present, namely  
 358 the mountainous regions of Northern and Central Spain (**Fig. 1**). Spanish populations  
 359 have arisen from independent introductions and the expansion of Portuguese  
 360 populations through the Tagus and Guadiana valleys in the Southern and Central  
 361 regions, and directly from the extensive area bordered by the river Minho in Galicia  
 362 (**Fig. 1**).

363

364 **Temporal changes in ecological niche projections**

365 ENM for all decades had training and test AUC values higher than 0.8 and significantly  
 366 differed from random (**Table 3**). For the first decade (1960-1969), the variable with  
 367 higher contribution was the mean diurnal temperature range (bio2), while the minimum  
 368 temperature of the coldest month (bio6) was the variable with the higher contribution  
 369 for the following decades (**Table 4**). The permutation importance of variables  
 370 maintained the same order as the variable contributions (**Table 4**). The areas identified  
 371 as suitable widened over time, from the coastal areas towards the interior of the Iberian  
 372 Peninsula (**Fig. 4**). Suitable areas based on data from the first decade (1960-1969)  
 373 were enclosed within the vicinity of the introduction area around Lisbon (Portugal, **Fig.**  
 374 **4**). There was an abrupt change in the extent of suitable areas between the third and  
 375 the fourth decades (1980-1989 and 1990-1999, **Fig. 4, Suppl. material 2: Fig. S1**).  
 376 The increment in suitable areas stabilised in the fourth decade after introduction (1990-  
 377 1999, **Fig. 4, Suppl. material 2: Fig. S1**).

378 **Table 3.** Main Maxent results per decade model: number of training records (Training  
 379 n), number of test records (Test n), mean and standard deviation of training and test  
 380 AUC from empirical models, mean and standard deviation of AUC from null models  
 381 (Null AUC), and Kruskal-Wallis test results for the comparisons of empirical and null  
 382 AUC values ( $\chi^2$ , degrees of freedom - DF, and *p-value*).

383

Decade	Training n	Test n	Training AUC	Test AUC	Null AUC	KW $\chi^2$	DF	<i>p-value</i>
1960-69	4	1	0.99±0.003	0.99±0.008	0.61±0.09	27.43	1	<0.0001
1970-79	21	8	0.99±0.002	0.99±0.005	0.65±0.03	27.03	1	<0.0001
1980-89	51	21	0.95±0.009	0.94±0.006	0.61±0.02	27.03	1	<0.0001
1990-99	102	43	0.91±0.011	0.90±0.018	0.59±0.02	27.03	1	<0.0001
2000-09	269	115	0.87±0.006	0.86±0.014	0.56±0.01	27.03	1	<0.0001
2010-19	229	98	0.86±0.010	0.84±0.014	0.56±0.01	27.03	1	<0.0001

384

385 **Table 4.** Contributions and permutation importance of the bioclimatic variables (mean  
 386 diurnal temperature range [bio2], minimal temperature of the coldest month [bio6],  
 387 precipitation of the wettest month [bio13] and precipitation of the driest month [bio14])  
 388 on the Maxent models per decade. Higher values of variable contribution and  
 389 permutation importance for each decade are highlighted in **bold**.  
 390

Decade	Variable contribution				Permutation importance			
	bio2	bio6	bio13	bio14	bio2	bio6	bio13	bio14
1960-69	<b>50.4</b>	20.9	0.04	28.65	<b>40.39</b>	3.55	0.07	55.99
1970-79	6.62	<b>73.16</b>	6.58	13.64	2.79	<b>89.82</b>	1.89	5.5
1980-89	5.52	<b>79.98</b>	8.3	6.2	5.64	<b>85.13</b>	5.07	4.16
1990-99	8.51	<b>68.19</b>	13.6	9.7	7.85	<b>68.84</b>	17.04	6.26
2000-09	4.53	<b>66.31</b>	20.11	9.05	5.31	<b>59.93</b>	25.16	9.6
2010-19	6.18	<b>66.42</b>	10.46	16.94	5.68	<b>55.01</b>	13.38	25.93

391

### 392 **Ecological Niche Models validation**

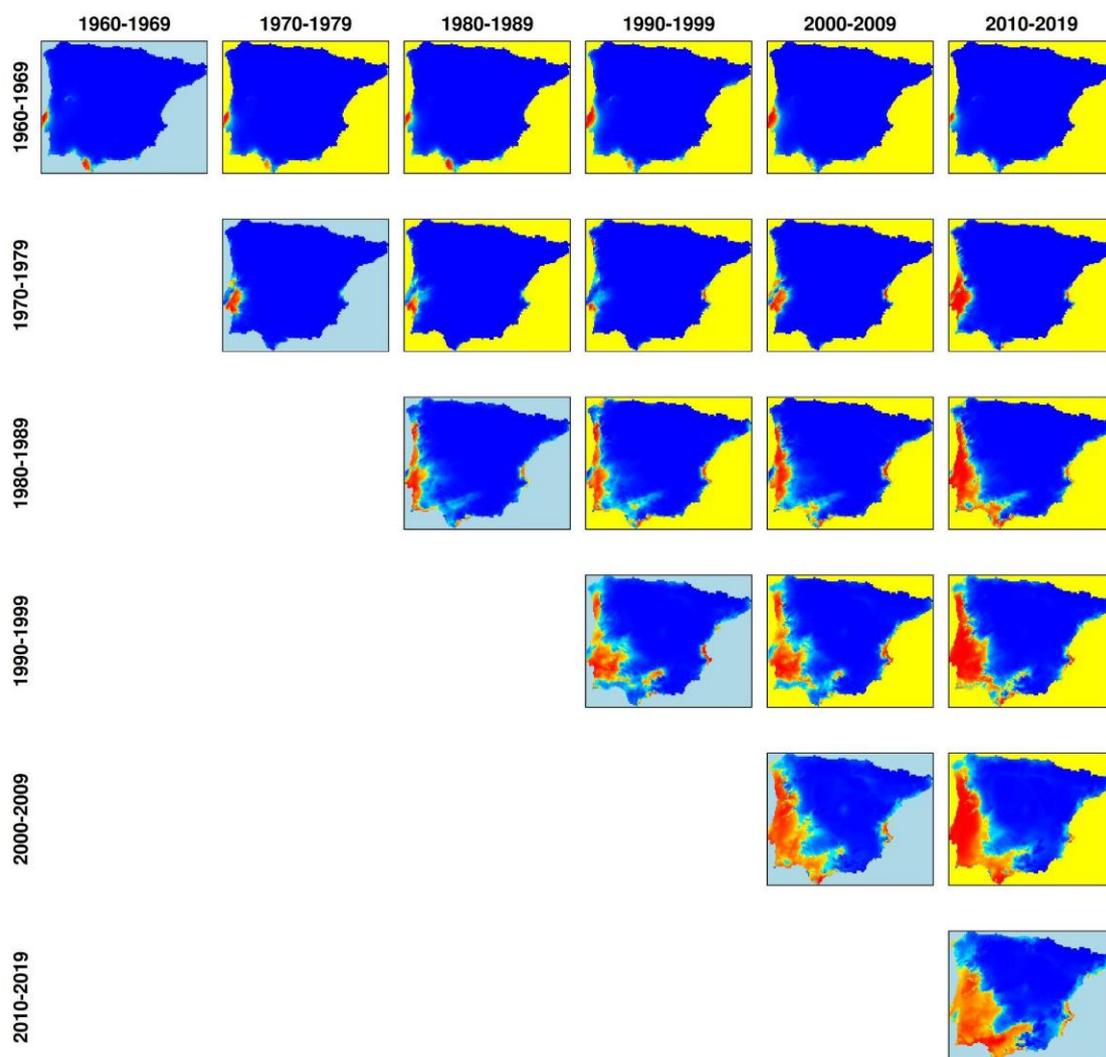
393 Validation of the ENMs of each decade projected to the remaining periods (**Fig. 5a,**  
 394 **Suppl. material 2: table S2**) indicated that the number of presences correctly  
 395 classified decreased over time in each decade, i.e. the model of the first decade  
 396 predicted more incorrectly the models from the furthest decades. On the other hand,  
 397 the number of presences correctly classified increased over time in each decade;  
 398 however, from the fourth decade (1990-99), this number decreased when predicting  
 399 the last decade (2010-19). These patterns were the same when considering the  
 400 number of cumulative presences classified as absences or presences over time (**Fig.**  
 401 **5b, Suppl. material 2: table S3**) or in relation to the last decade (2010-19) (**Fig. 5c,**  
 402 **Suppl. material 2: table S4**; in this case the pattern was opposite).

403

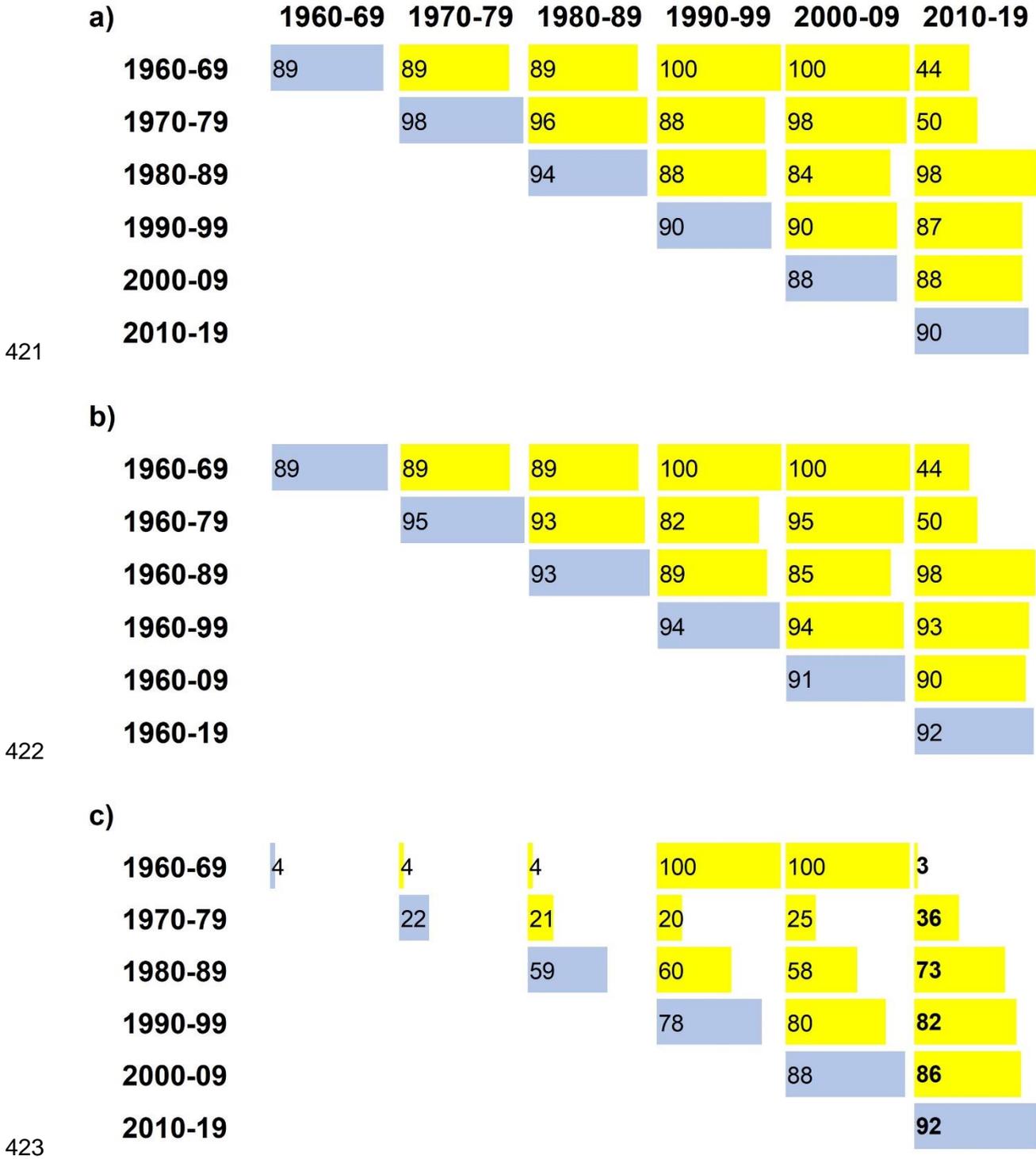
### 404 **Dispersal analyses**

405 The species' potential range accounting for dispersal capacity increased over time  
 406 driven by the results of ENM projections. In the first decade, the range deemed  
 407 susceptible to colonisation is narrow, and almost all of the Iberian Peninsula is beyond

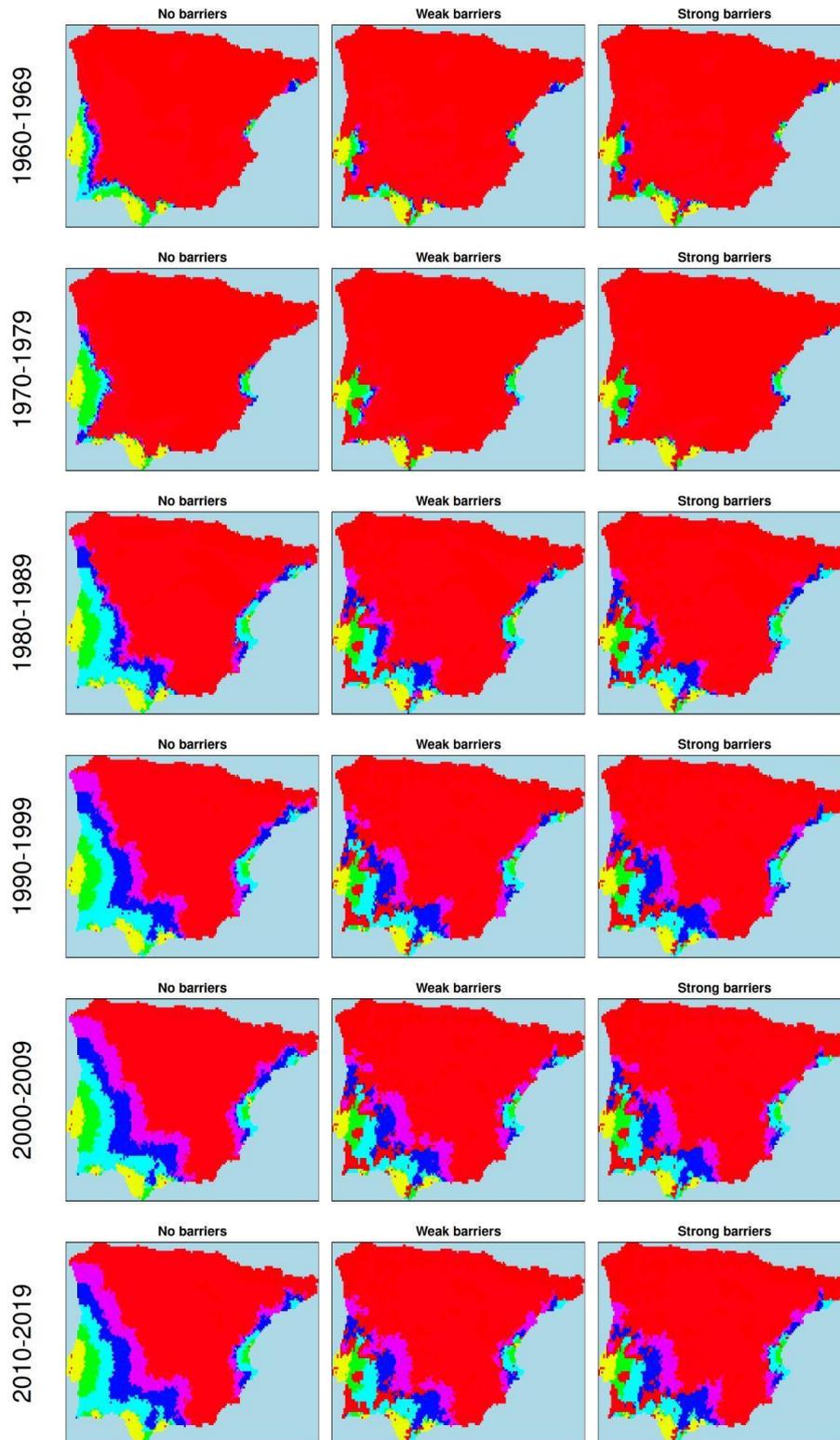
408 reach. On the other hand, for the last decade, these areas are much wider (**Fig. 6**).  
 409 Similarly to what was verified for the ENM, the spatial patterns of the dispersal models  
 410 have remained quite stable since the third decade (1990-1999). There were some  
 411 differences when introducing barriers or not in the dispersal models (**Fig. 6**), but the  
 412 results with weak or strong barriers are very similar. Dispersal models thus confirmed  
 413 that the species was able to disperse over time following suitable areas identified by  
 414 ENM.



415  
 416 **Figure 4.** Ecological niche models by decade and their projections to the next  
 417 decades. The maps are organised in a matrix as in **Table 1**: each decade is a row;  
 418 models (light blue background) and projections (yellow background) are placed in  
 419 columns. Habitat suitability ranges from blue colours (low suitability) to red colours  
 420 (high suitability), following the rainbow palette.



424 **Figure 5.** Percentage number of presences correctly classified as presences in each model (blue) and projection (yellow) by decade. a) Each decade only includes data  
 425 from that period; b) Each decade includes the number of cumulative presences of the  
 426 previous decade(s); c) In relation to the last decade (2010-19, in **bold**). Our  
 427 backcasting approach showed a high forecast capacity of EMNs models since the third  
 428 decade after the common waxbill establishment (high % of correctly classified  
 429 presences).  
 430  
 431



432

433 **Figure 6.** Dispersal models per decade and type of barriers (no barriers, weak barriers,  
 434 and strong barriers). The colour sequence Orange -> Yellow -> Light green -> Light  
 435 blue indicates the dispersal of species over time in each decade. Blue indicates areas  
 436 where the species did not have time to arrive. Red indicates zones where the species  
 437 cannot occur.

438

## 439 Discussion

440 This study evaluates the use of increasingly available spatiotemporal data of IAS  
441 spread to iteratively forecast invasions as they unfold. The backbone of these  
442 forecasts were ENMs using detailed distribution data of the common waxbill expansion  
443 through the Iberia Peninsula over six decades. Our projections based on invasion-  
444 range data were successful to forecast the species' current distribution after three  
445 decades following its establishment. These results support the idea that ENMs can  
446 successfully forecast the species' range expansion, though they may have limited  
447 utility in the early stages of invasion, supporting the use of an iterative approach  
448 ([Dietze et al. 2018](#)), where models are recurrently updated with the species' most  
449 recent distribution data. This implies the need to constantly monitor IAS, which despite  
450 receiving long-standing support in invasion science and policy ([Genovesi and Shine](#)  
451 [2004](#); [Büyüktaktın and Haight 2018](#)), depends strongly on the availability of  
452 resources ([Groomet al. 2019](#)).

453  
454 Our results are in line with previous studies arguing ENMs may underestimate the  
455 species' potential ranges ([Liu et al. 2020](#)), particularly at the early stages of the  
456 invasion when the most suitable conditions may not yet be represented in the  
457 distribution range data set. Our projections based on invasion-only data failed to  
458 forecast the species distribution in the first two decades after species introduction,  
459 likely because the species range was still not representative of the species' suitable  
460 environmental conditions ([Araújo & Pearson 2005](#)). Models disregarding the species'  
461 global distribution provide worse results than full distribution models ([Barbet-Massin](#)  
462 [et al. 2010](#); [Jarnevich et al. 2022](#)). This is because, ENM algorithms assume that the  
463 species distribution data used is a good representation of the species' environmental

464 requirements (Sillero et al. 2021). In other words, the algorithm assumes that the data  
465 used represents a species in equilibrium with the environment, i.e. the species  
466 occupies all available suitable habitats where it can disperse (Guisan and Thuiller  
467 2005; Anderson & Raza 2010; Sillero et al. 2021). Distributional data representing only  
468 a portion of a species' global range may fail to capture all the suitable conditions where  
469 the species can thrive, potentially leading to an underestimation of its potential range.  
470 Therefore, modeling the realized niche of an expanding alien species presents  
471 significant challenges (Ficetola et al. 2005). It is expected that the ENM of a particular  
472 period will fail to forecast imminent range expansion stages, although this does not  
473 mean that the ENM is wrong (Barbet-Massin et al. 2018). The ENM for that particular  
474 period can be correct, but the ENM does not have enough information to predict the  
475 upcoming dispersion process. This is our case: the increment of new suitable areas in  
476 ENM predictions stabilised from the third decade after introduction (1990-1999), i.e.,  
477 only after three decades of dispersion, the species' occurrence data were  
478 representative of the species' environmental requirements. These results thus suggest  
479 that modelling expansion based on the early stages of introduction may provide limited  
480 results, demanding the interactive recalibration of models as new distribution data  
481 becomes available.

482

483 Contrary to expectations, our results suggest that barriers to dispersion were not  
484 insuperable by the common waxbill, although they might be important for other species  
485 with lower dispersal capacity. The few differences found in the projections using the  
486 ENM-only and dispersion models (with strong and weak barriers) indicate that the  
487 species was able to disperse over time following the suitable areas predicted by ENMs.  
488 Previous studies have suggested that the dispersion capacity of the common waxbill

489 across Iberia was very low in the first decades after the first introduction (e.g., [Silva et](#)  
490 [al. 2002](#); [Reino 2005](#)). Justifications for this relied on the absence of favourable habitat  
491 conditions (i.e. agricultural fields near water bodies, [Ribeiro et al. 2020](#)) out of the  
492 areas where the species was first introduced. This was based on the slower  
493 colonisation process in the southern regions of Portugal, where initial populations were  
494 very small and limited to the Tagus valley around Lisbon and the westernmost region  
495 of Iberia (Portugal) and an acceleration after the 80s. According to these studies, the  
496 additional introductions across Iberia might have jointly fostered higher dispersion  
497 rates to new areas, suggesting that the dispersal capacity of the common waxbill in  
498 Iberia is a combination of both habitat suitability and propagule pressure. However,  
499 our results suggest that this is likely to be a consequence of insufficient data to capture  
500 the species' environmental requirements during the first decades, as they projected a  
501 potential of expansion lower than the real one.

502

## 503 **Conclusions**

504 Accurately anticipating the expansion of IAS is key to ensuring the successful  
505 implementation of preventive and mitigative actions. Forecasting invasions by means  
506 of different quantitative methods and modelling strategies have been used in the last  
507 three decades, and new approaches are constantly emerging ([Peterson 2003](#); [Reino](#)  
508 [et al. 2009](#); [Jiménez-Valverde et al. 2011](#)). However, predictions may be severely  
509 compromised by different methodological options and their specific limitations. ENMs  
510 are powerful tools to predict the spread of IAS and guide management. Although ENM  
511 enables predicting and evaluating biological invasions, it is often compromised by the  
512 amount (time-series length), quality (spatial and temporal resolution) and availability  
513 (data access) of distribution data in both native and invaded ranges. In this study, we

514 demonstrate that invaded range-only data may be used to accurately project the  
515 expansion of alien species in novel regions if enough time (at least three decades) is  
516 given to allow the species to expand and occupy the most suitable conditions. Our  
517 study evaluates the capacity of ENMs based on spatiotemporal data of invaded  
518 ranges-only to forecast the potential distribution of IAS, while it clarifies the amount of  
519 data required in terms of length of the time series of the species distribution data since  
520 establishment, contributing to a better understanding of climatic niche changes during  
521 the expansion process of alien species, and offering a solution to managers and  
522 scientists dealing with the scarcity and asymmetry of distribution data available for  
523 alien species worldwide, in their native and invaded ranges. This helps solve a much-  
524 discussed conundrum, and offers a practical solution to better guide management  
525 actions and significantly improve stakeholders' ability to halt biological invasions.

526

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541

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