Mammal Review

Mammal Review ISSN 0305-1838

PREDICTIVE REVIEW

Unravelling the historical biogeography of the European rabbit subspecies in the Iberian Peninsula

Francisco DÍAZ-RUIZ* *Biogeography, Diversity and Conservation Research Team, Dpto. Biología Animal, Facultad de Ciencias, Universidad de Málaga, Campus de Teatinos, 29071 Málaga, Spain. Email: pacodi1480@hotmail.com*
Patricia H. VAQUERIZAS *Instituto de Estudios Sociales Avanzados (IESA-CSIC), Campo Santo de los Mártires 7, 14004 Córdoba, Spain. Email: patricia.hidalgo.vaquerizas@gmail.com*
Ana Luz MÁRQUEZ *Biogeography, Diversity and Conservation Research Team, Dpto. Biología Animal, Facultad de Ciencias, Universidad de Málaga, Campus de Teatinos, 29071 Málaga, Spain. Email: analuz@uma.es*
Miguel DELIBES-MATEOS *Instituto de Estudios Sociales Avanzados (IESA-CSIC), Campo Santo de los Mártires 7, 14004 Córdoba, Spain. Email: mdelibes@iesa.csic.es*
Vicente PIORNO *Parque Nacional de las Islas Atlánticas de Galicia. Consellería de Medio Ambiente, Territorio e Vivenda. Xunta de Galicia, Rúa Oliva 3, 36202 Vigo, Pontevedra, Spain. Email: vicente.piorno.gonzalez@xunta.gal*
Francisca CASTRO *Departamento de Didácticas Específicas, Avda. San Alberto Magno, Universidad de Córdoba, "Sociedad, Ecología y Gestión del Medio Ambiente, UCO-IESA", Unidad Asociada al CSIC, 14004 Córdoba, Spain. Email: ba2canof@uco.es*
Esther RAMÍREZ *Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM, Ronda de Toledo n° 12, 13071 Ciudad Real, Spain. Email: esther.ramirez.rodriguez@gmail.com*
Miguel Ángel FARFÁN *Biogeography, Diversity and Conservation Research Team, Dpto. Biología Animal, Facultad de Ciencias, Universidad de Málaga, Campus de Teatinos, 29071 Málaga, Spain. Email: mafarfan@uma.es*
Jesús OLIVERO *Biogeography, Diversity and Conservation Research Team, Dpto. Biología Animal, Facultad de Ciencias, Universidad de Málaga, Campus de Teatinos, 29071 Málaga, Spain, and Instituto IBYDA, Centro de Experimentación Grice-Hutchinson, Loma de San Julián 2, Barriada de San Julián, 29004 Málaga, Spain. Email: jesusolivero@uma.es*
Raimundo REAL *Biogeography, Diversity and Conservation Research Team, Dpto. Biología Animal, Facultad de Ciencias, Universidad de Málaga, Campus de Teatinos, 29071 Málaga, Spain, and Instituto IBYDA, Centro de Experimentación Grice-Hutchinson, Loma de San Julián 2, Barriada de San Julián, 29004 Málaga, Spain. Email: rrgimenez@uma.es*
Rafael VILLAFUERTE *Instituto de Estudios Sociales Avanzados (IESA-CSIC), Campo Santo de los Mártires 7, 14004 Córdoba, Spain. Email: rafael.villafuerte@csic.es*

Keywords
competitive exclusion, European rabbit *Oryctolagus cuniculus*, favourability function, Iberian Peninsula, Lagomorpha, parapatric distributions, trend surface analysis

*Correspondence

ABSTRACT

1. Understanding the biogeography of species in space and time is essential for the development of evidence-based conservation and management plans. In this paper we propose a biogeographical spatial modelling approach based on the favourability function, and developed under a fuzzy logic framework, to unravel the historical biogeography of the two European wild rabbit subspecies, *Oryctolagus cuniculus algirus* (*Oca*) and *Oryctolagus cuniculus cuniculus* (*Occ*), in the Iberian Peninsula (IP).
2. We first reviewed published and unpublished information (PhD theses, scientific papers, technical reports, etc.) on the occurrence of each rabbit

Received: 10 March 2022
Accepted: 8 September 2022
Editor: DR

doi: 10.1111/mam.12306

subspecies throughout the IP. We compiled data from 201 Iberian rabbit populations and from genetic information of 4348 rabbits that was used to identify subspecies. Only populations in which all rabbits surveyed belonged to one subspecies were considered in the modelling procedure.

3. We modelled rabbit subspecies' distribution separately for populations in which nuclear and mitochondrial DNA sequences were available. We employed a trend surface analysis developed by logistic regressions, which applied the favourability function and fuzzy logic operations.
4. Using our approach we indentify the expansion cores from which both rabbit subspecies would have expanded after isolation during the last glaciations. Furthermore, we reveal the possible existence of a competitive exclusion zone between both rabbit subspecies that may have prevented their further expansion. Finally, our study shows that the *Oca* subspecies is distributed in north-western areas previously attributed to *Occ*.
5. This assessment of the actual and historical distribution of each rabbit subspecies may allow more specific conservation interventions, as the two subspecies are not just genetically distinct but also ecologically and behaviourally different. Our methodological approach could be useful in unravelling the historical biogeography of other lesser-known species.

Palabras Clave
análisis de superficies de tendencias, conejo de monte europeo *Oryctolagus cuniculus*, disrtibuciones parapátricas, exclusión competitiva, función de favorabilidad, Lagomorpha

RESUMEN EN ESPAÑOL

1. Entender la biogeografía de las especies en el tiempo y el espacio es fundamental para el desarrollo de planes de gestión y conservación basados en la evidencia científica. En este artículo proponemos una aproximación de modelación biogeográfica espacial basada en la función de favorabilidad, desarrollada bajo un marco teórico de lógica difusa para desentrañar la biogeografía histórica de las dos subespecies de conejo de monte, *Oryctolagus cuniculus algirus* (*Oca*) y *Oryctolagus cuniculus cuniculus* (*Occ*), en la Península Ibérica (PI).
2. En primer lugar revisamos información publicada y no publicada (Tesis doctorales, artículos científicos, informes técnicos, etc.) sobre la presencia de cada subespecie en la PI. Recopilamos información para 201 poblaciones ibéricas de conejo de monte y de la información genética de 4348 conejos que fue utilizada para identificar la subespecie. Para el proceso de modelación, solamente se utilizaron aquellas poblaciones en las que todos los individuos analizados pertenecieron a una subespecie.
3. Modelamos la distribución de ambas subespecies por separado para aquellas poblaciones analizadas con ADN mitocondrial y nuclear. Utilizamos análisis de superficies de tendencias mediante regresiones logísticas, aplicando la función de favorabilidad y diferentes operaciones de lógica difusa.
4. Mediante nuestra aproximación identificamos los núcleos de expansión desde los que ambas subespecies podrían haberse expandido después de haber estado aisladas en las últimas glaciaciones. Además, revelamos la posible existencia de una zona de exclusión competitiva entre ambas subespecies que podría haber impedido un mayor rango de expansión. Finalmente, nuestro estudio indica que la subespecie *Oca* se distribuiría en áreas del noroeste, anteriormente atribuidas a la subespecie *Occ*.
5. Esta evaluación de la distribución real e histórica de cada subespecie de conejo puede permitir intervenciones de conservación más específicas, ya que las dos subespecies no sólo son genéticamente distintas, sino también ecológica y comportamentalmente diferentes. Nuestro enfoque metodológico podría ser útil para desentrañar la biogeografía histórica de otras especies menos conocidas.

INTRODUCTION

The combination of phylogenetic and spatial data, or phylogeography, can be used to assess how species have evolved in space and time (Avise 2000). Phylogeography is considered a part of historical biogeography, which aims to explain the geographic distribution of organisms according to their evolutionary history (Sanmartín 2012). Although different approaches have been used to infer the historical biogeography of species, these approaches can have distinct limitations (Sanmartín 2012, Quintero et al. 2015). For example, the identification of genetic lineages through the analysis of genomic compartments can generate different geographical distributions (Ferrand 2008). Also, there may be limitations associated with the difficulty of attributing a geographic location to a particular taxonomic category (Quintero et al. 2015). Sometimes historical biogeography is inferred without explicit reference to an underlying statistical process model (Sanmartín 2012). In this sense, species' distribution models based exclusively on spatial variables may reflect pure spatial structures derived from historical biogeographical processes that are functionally independent of environmental factors (Rapoport 1975, Legendre 1993, Real et al. 2003). These models may be developed using the favourability function defined by Real et al. (2006). This function allows the integration of biogeographical analytical procedures into a fuzzy logic framework (Zadeh 1965, Bojadziev & Bojadziev 1995), which provides great potential to address different ecological and biogeographical issues (Acevedo & Real 2012). This approach has been successfully used in species' distribution and macroecology studies (e.g. Cheung et al. 2005, Acevedo et al. 2012, Chamorro et al. 2021).

A detailed knowledge of the geographical and historical distribution of a species can be useful to determine its current spatial range and to predict its possible future distribution (Acevedo et al. 2012). Historical biogeography can also be used to assist in the development of evidence-based conservation and management plans for species in need of protection, particularly those facing significant conservation and management challenges (Elith et al. 2006, Muñoz & Real 2006). One such species is the European wild rabbit *Oryctolagus cuniculus*, a native to the Iberian Peninsula (IP), and a multifunctional keystone species in the Iberian Mediterranean ecosystem (Delibes-Mateos et al. 2007). Although the rabbit was historically abundant in the IP, populations declined sharply during the last decades due to habitat loss and the impact of viral diseases. This decline has been so pronounced that the International Union for Conservation of Nature (IUCN) recently classified the European rabbit in its native range as Endangered (Villafuerte & Delibes-Mateos 2019).

In the IP, there are two distinct rabbit genetic lineages that have been linked to two rabbit subspecies: *Oryctolagus cuniculus algirus* (*Oca*) and *Oryctolagus cuniculus cuniculus* (*Occ*; Branco et al. 2000, 2002). These lineages differ according to multiple genetic markers (Branco et al. 2000, Ferrand 2008, Geraldes et al. 2008). Although *Occ* has been introduced throughout the world by humans (Corbet 1994, Ferrand 2008), both rabbit subspecies coexist naturally only in the IP. Molecular studies conducted in the 1990s and 2000s showed that the two rabbit subspecies occur in distinct areas in the IP: *Oca* can be found in the south and west of the peninsula, *Occ* in the north-east; and both subspecies' geographic ranges overlap in the central region that intersects the IP from north-west to south-east, regarded as a natural contact zone (Branco et al. 2000, Geraldes et al. 2008, Fig. 1).

According to some authors, the differences in the distribution of the rabbit subspecies in the IP may have emerged because of isolation during the late Pleistocene glacial and interglacial periods, approximately two million years ago (Branco et al. 2000, 2002). Branco et al. (2002) hypothesised that *Oca* populations expanded from the south of the IP through two main routes: one occurring northward and a second north-eastward. According to these authors, *Occ* became isolated in the east and north-east of the IP from where it spread westward (Branco et al. 2002; Fig. 1).

Although Branco et al. (2002) hypotheses of geographical expansion and competitive interactions are plausible, they have not been tested using robust biogeographical spatial modelling. Moreover, the actual distribution of the two wild rabbit subspecies in the IP has not been mapped accurately. In this paper, we propose a more robust spatial biogeographical modelling approach based on the favourability function and fuzzy logic, to: 1) map the distribution of the two rabbit subspecies in the IP, using a larger sample size and greater spatial coverage than in previous studies; 2) explicitly delimit the transition zone between both historical rabbit subspecies' distributions; 3) identify the historical population core (HPCs) areas from which each rabbit subspecies would have expanded after isolation during the last glacial period; and 4) evaluate the subspecies' potential spatial interactions during the expansion process.

METHODS

Compilation of rabbit subspecies data

We compiled data from a total of 201 rabbit populations throughout the species' native geographic range in the IP (see Appendix S1). Most of these populations (n = 185) have been sampled by our research team (1989–2011) as

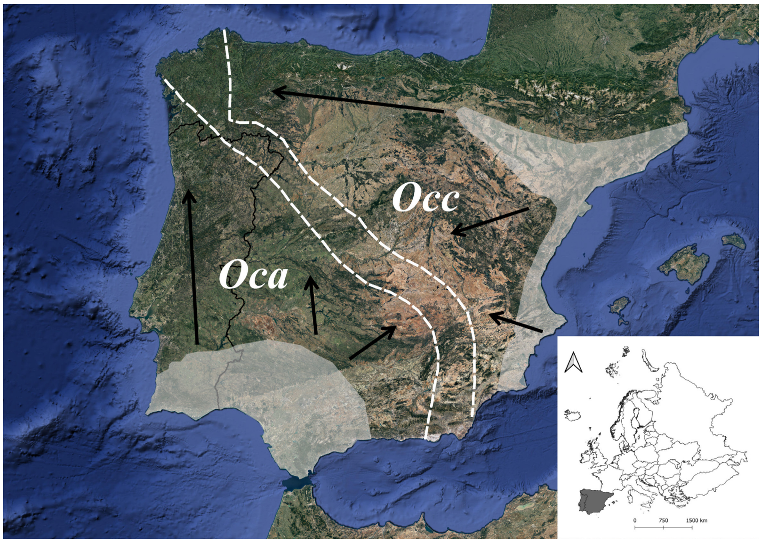

Fig. 1. Natural contact zone between rabbit subspecies between the white dashed lines that delimit the overlapping geographic ranges of *Oryctolagus cuniculus algirus* (*Oca*) and *Oryctolagus cuniculus cuniculus* (*Occ*) in the Iberian Peninsula, as proposed by Geraldes et al. (2008). Pale shaded areas represent putative glacial refugia and arrows represent dispersal routes hypothesised by Branco et al. (2002). The location of the Iberian Peninsula in Europe is highlighted in the bottom-right corner. Satellite image was obtained from 'Google Base Map Satellite' in QGIS.

a part of several ecological and behavioural studies. The rabbit subspecies in each study was identified by the authors of the published scientific articles, unpublished PhD theses, and scientific-technical reports (see Appendix S1). The mean number of animals sampled in each population was 22 (range: 4–102), totalling 4348 individuals (Appendix S1). In each of the afore-mentioned populations, all individuals were assigned to one of the subspecies by means of genetic analyses using at least one of the three diagnostic loci located on cytochrome b (mitochondrial DNA; mtDNA) and/or on the X and Y chromosomes (nuclear DNA; nucDNA). Full descriptions of molecular analyses can be found in Branco et al. (2000) and Geraldes et al. (2006, 2008).

Although the range of the European rabbit within the IP, without the influence of humans, is affected by ecological and historical factors, human-induced translocations of rabbits have resulted in the movement of thousands of rabbits over the past few decades (Carro et al. 2019). The translocations were attempts to recover stocks heavily depleted by viral diseases and habitat loss, and were conducted either to increase hunting opportunities or to feed predators of conservation concern (Delibes-Mateos et al. 2008, Carro et al. 2019). Rabbits of one subspecies have been released often in the distribution area of the other without considering their origin, likely contributing to obscuring the original distribution of both rabbit subspecies in some areas of the IP (Delibes-Mateos et al. 2008). To avoid this effect of translocations on rabbit subspecies' distributions, our modelling procedure was based exclusively on rabbit populations in which all the individuals that were sampled belonged to a single subspecies according to their mtDNA or nucDNA, i.e. 'pure populations' (n = 123; see Appendices S1 and S2). In our modelling exercise we thus assumed that these populations best reflect the original geographic distributions of the two rabbit subspecies, as suggested in previous studies (Branco et al. 2000, Geraldes et al. 2006, 2008). Populations containing concurrent presence of *Occ* and *Oca* rabbits, and that hence may also contain *Occ*Oca* hybrids, (hereafter 'mixed populations'; Appendices S1 and S3), were subsequently used to validate the predictions of the spatial distribution models (see below). For our analyses, we used Universal Transverse Mercator (UTM) 10×10 km grid squares as operational geographic units (OGU, n = 6041 squares in the IP). Each rabbit population (pure or mixed) was assigned to its corresponding UTM square.

Trend surface analysis

Based on purely spatial variables (i.e. latitude and longitude), and their polynomial combinations, the trend surface analysis (TSA) delimits the geographical universe, which reflects the history of ecological interactions affecting a species or, in our case, a subspecies (Legendre 1993, Real et al. 2003). Thus, this spatial pattern can be associated with historical events and population dynamics, reflecting the historical distribution of a subspecies once any ecological-environmental factor has been excluded from analyses. We followed a third-degree TSA approach, a flexible approximation recommended for exploring ecological phenomena occurring at the scale of the study area (Legendre & Legendre 1998). The TSA was based on X and Y average UTM coordinates and their third-order polynomial combinations for each 10 × 10 km square, and was applied independently for each rabbit subspecies. Relationships between rabbit subspecies' presence/absence data and the set of spatial variables were examined through backward stepwise logistic regression models, a commonly used supervised machine learning algorithm; a 0.05 significance threshold was used for the inclusion of the variables and 0.10 for their exclusion (Acevedo et al. 2012).

The geography of the IP overlaps with three UTM zones (29, 30 and 31), which implies different coordinate values and therefore potential biases in TSA results if coordinates from only one UTM zone were used. Accordingly, we fitted a logistic regression model for each UTM zone (i.e. for each population, we obtained the corresponding coordinates values of each UTM zone to develop TSA), DNA type and rabbit subspecies. In other words, we fitted a total of six logistic regression models for each subspecies: three mtDNA models (for UTM zones 29, 30 and 31) and three nucDNA models (for UTM zones 29, 30 and 31). Each of these models provided a value of occurrence probability (P) in each 10 × 10 km square. Finally, for each subspecies-DNA combination, we assembled a single model by choosing, for the squares of a given UTM zone, the P values provided by the model based on coordinates of that UTM zone (Appendix S2).

Spatial favourability

We applied the Favourability Function to turn probabilities into favourability values (F, ranging from 0 to 1), which are independent of sample prevalence (Real et al. 2006, Acevedo & Real 2012):

$$F = \frac{P}{1-P} \Big/ \left(\frac{n_1}{n_0} + \frac{P}{1-P} \right)$$

where n_1 and n_0 are, respectively, the number of presences and absences with regard to populations of the modelled rabbit subspecies, and P is the probability of occurrence.

Favourability values can be regarded as the degree of membership of the localities to the fuzzy set of sites with conditions that are spatially favourable for the species (subspecies in our case). Unlike other biogeographical methods based on probability or suitability values, favourability values are not affected by the prevalence of the subspecies in the study area, and allow direct comparisons and/or combinations between models using fuzzy logic operations (Acevedo & Real 2012). We applied the fuzzy union (i.e. the maximum value between favourabilities; Zadeh 1965) to combine, in a single map for each subspecies (F_{Oca} and F_{Occ}), the spatial favourability models obtained independently for mtDNA and nucDNA (Appendix S3). Final maps for each subspecies (F_{Oca} and F_{Occ}) were used to identify the historical boundaries of their geographic ranges and their cores, utilising different fuzzy logic concepts applied to biogeography, which are detailed below.

Favourability model assessments were based on classification and discrimination capacities. Classification capacity was evaluated by the correct classification rate, sensitivity, specificity (Fielding & Bell 1997), under-prediction rate, overprediction rate (Barbosa et al. 2013) and Cohen's kappa (Cohen 1960), using the favourability value of $F = 0.5$ as classification threshold. Discrimination capacity was evaluated using the area under the curve of the receiver operating characteristic (Lobo et al. 2008), which takes into account all possible favourability thresholds.

To validate the predictions of spatial favourability models conducted for each rabbit subspecies, we used the mixed rabbit populations. We used simple linear regression models to assess whether the percentage of individuals belonging to each subspecies at the population level (hybrid individuals were excluded from these analyses) can be predicted by the spatial favourability value (F_{Oca} and F_{Occ}) estimated for its corresponding UTM square. These relationships were tested at the DNA level for each subspecies.

Transition zone between rabbit subspecies' distributions

We used the concept of fuzzy difference between fuzzy distributions to identify the transition zone between the distributions of both rabbit subspecies (Olivero et al. 2013). In particular, we used an adaptation of the concept 'symmetric difference' (see Alsina & Trillas 2005) to create fuzzy biotic boundaries. This adaptation was developed by Olivero et al. (2013) to identify the biogeographic transition zone (BTZ) between two neighbouring regions. We then calculated the BTZ as follows:

$$\mathrm{BTZ} = 1 - \left| F_{Oca}(\mathrm{OGU_i}) - F_{Occ}(\mathrm{OGU_i}) \right|$$

where BTZ is the degree of membership of each $\mathrm{OGU_i}$ (each 10 × 10 UTM km square in our study) to this transition zone, and $F_{Oca}(\mathrm{OGU_i})$ and $F_{Occ}(\mathrm{OGU_i})$ refer to the values of F_{Oca} and F_{Occ}, respectively, at this $\mathrm{OGU_i}$. We set a threshold value of BTZ ≥ 0.8 as a high degree of membership of the OGUs to the BTZ. This threshold is analogous to the one frequently established to define areas of high favourability ($F \geq 0.8$, whereas $F < 0.2$ defines low-favourability areas; e.g. Muñoz & Real 2006, Chamorro et al. 2021).

Historical population cores

We defined the HPCs as regions without any interference from the distribution of one subspecies over the other. Therefore, we would expect that in these HPCs there was no gene flow between the two rabbit subspecies, which certainly was the case during the Pleistocene isolation in glacial refugia (Branco et al. 2000, 2002). Consequently, our approach could be used as an independent line of evidence to delineate these ancestral distribution areas. Such areas represent the isolation cores from which the expansion of both rabbit subspecies took place once the environmental conditions became favourable for them. To assess HPCs, we defined the spatial favourability difference as the absolute values of the symmetric difference between F_{Oca} and F_{Occ} estimated by the expression:

$$|\,\mathrm{SFD}\,| = |\,F_{\mathrm{Oca}}(\mathrm{OGU_i}) - F_{\mathrm{Occ}}(\mathrm{OGU_i})\,|$$

which measures the degree to which a certain $\mathrm{OGU_i}$ is a member in the spatially favourable area for one subspecies more than in the intersection between both spatially favourable areas (Olivero et al. 2013). Accordingly, higher values for this expression identify regions that are free from interferences from the other subspecies, i.e. this symmetric difference matches our definition of HPCs. We used a threshold value of 0.75 for considering that the |SFD| indicates the existence of an HPC. Above this threshold, the favourability for one subspecies is maximum (at least 0.75), and also at least four times higher than the favourability for the other subspecies. This is mathematically analogous to the 4:1 odds resulting from the threshold value of 0.8 commonly used to define high-favourability areas (see above).

Competitive exclusion between rabbit subspecies

We calculated the fuzzy intersection ($F_{\mathrm{Oca}} \cap F_{\mathrm{Occ}}$) between rabbit subspecies' spatial favourability (Appendix S3; i.e. the minimum favourability value for the two subspecies at any given location; Zadeh 1965), to identify the fuzzy set of areas simultaneously favourable for them (Acevedo et al. 2010). In particular, fuzzy intersection values were grouped into three categories of shared favourability: low shared favourability, i.e. areas that are unfavourable for at least one subspecies ($F_{\mathrm{Oca}} \cap F_{\mathrm{Occ}} < 0.2$); intermediate shared favourability, i.e. areas with favourability values higher than 0.2 for both species but with intermediate favourability for at least one subspecies ($0.2 \geq F_{\mathrm{Oca}} \cap F_{\mathrm{Occ}} < 0.8$); and high shared favourability, i.e. areas that have high favourability for both subspecies ($F_{\mathrm{Oca}} \cap F_{\mathrm{Occ}} \geq 0.8$). We established the following theoretical assumptions so as to identify areas where competitive exclusion would be more likely to occur (Acevedo et al. 2010, Chamorro et al. 2021, Real et al. 2022). We expected no interaction between rabbit subspecies in unfavourable areas for at least one subspecies, where spatial exclusion would occur. Coexistence was expected in areas of high shared favourability. Therefore, competitive exclusion would only occur in areas with intermediate shared favourability values, and the direction of spatial exclusion would be determined by the most favoured subspecies (Acevedo et al. 2010, Chamorro et al. 2021, Real et al. 2022). In those areas, we defined two ranges of exclusion intensity based on the absolute value of spatial favourability difference (|SFD|) between both rabbit subspecies. This means that the competitive exclusion intensity would be higher in intermediate shared favourability areas where $|\mathrm{SFD}| > 0.2$ (i.e. both subspecies have spatial favourability values >0.2, and the dominant subspecies has spatial favourability values at least 0.2 higher than the other subspecies), and lower where $|\mathrm{SFD}| < 0.2$ (i.e. both subspecies have spatial favourability values ≥0.2, and one of the subspecies has slightly higher favourability values than the other).

We used the statistical software SPSS 23 (SPSS Inc., Chicago, IL, USA) to calculate the logistic regression models of the TSA, to conduct simple regressions, and to convert logistic probabilities into spatial favourability. Maps were generated using the open-access software Qgis 3.4.8 (QGIS Development Team 2019; https://www.qgis.org).

RESULTS

Close to 60% of the sampled rabbit populations included individuals belonging to both rabbit subspecies together and, therefore, were not used to build the models but to validate them. This figure was similar for populations in which mtDNA was analysed (56%), and those in which nucDNA was considered (60%; more details in Appendices S1 and S3). Analysis of mtDNA revealed 23 populations with only *Oca* rabbits and 52 populations with only *Occ* rabbits, while nucDNA analysis showed 22 pure populations of *Oca* and 26 of *Occ* (Appendix S1; Fig. 2). *Oca* populations were located in south-western Iberia, while *Occ* occurred in north-eastern areas (Fig. 2).

According to Hosmer and Lemeshow (2000), spatial favourability models for both rabbit subspecies had 'excellent' discrimination values (area under the curve ≥0.8). The classification power of the models was acceptable, as Cohen's kappa values were positive, correct classification rate values were >0.5 and under-prediction rate values were <0.002. Appendix S4 shows the evaluation criteria for the spatial favourability model of each rabbit subspecies. Simple linear regressions showed a significant

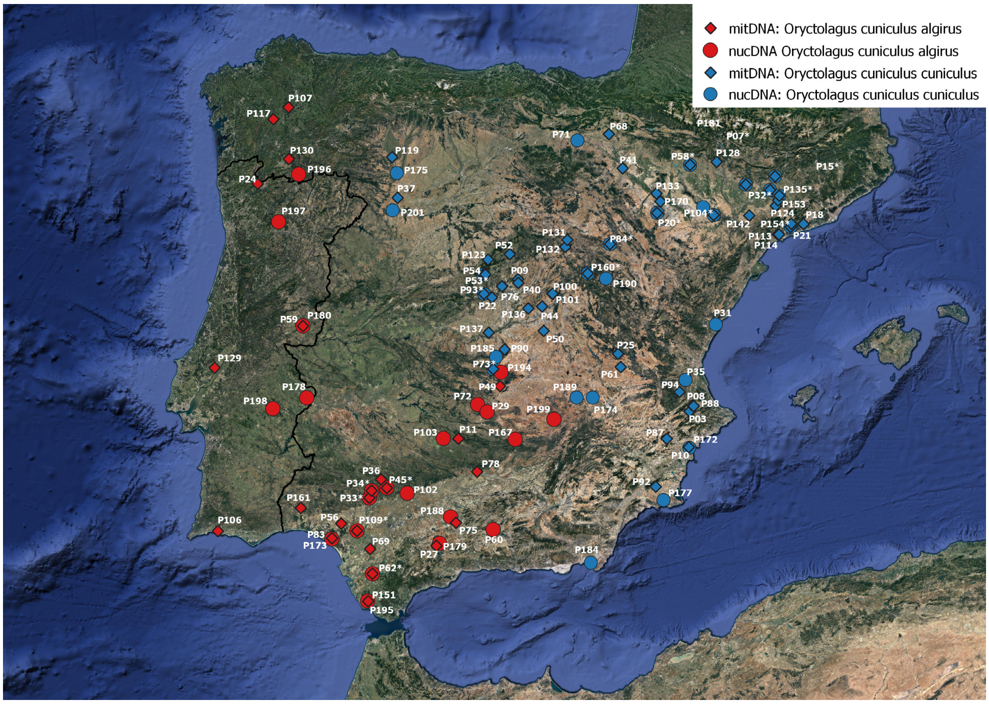

Fig. 2. Geographic distribution of rabbit populations reviewed in this manuscript for which all the individuals belonged exclusively to one of the rabbit subspecies: *Oryctolagus cuniculus algirus* (*Oca*) and *Oryctolagus cuniculus cuniculus* (*Occ*). Diamonds and circles represent populations in which mitochondrial DNA markers and nuclear DNA markers were analysed, respectively. An identification code is shown for each population (see Appendix S1 for details of populations). Populations in which both DNA molecules were analysed are highlighted by * and represented by diamonds overlapping circles. Satellite image was obtained from 'Google Base Map Satellite' in QGIS.

positive relationship between the percentage of individuals belonging to each rabbit subspecies and the spatial favourability for the corresponding subspecies, independently of the type of DNA molecule considered (*Oca*: mtDNA: $R^2 = 0.69$, $P < 0.001$, nucDNA: $R^2 = 0.59$, $P < 0.001$; *Occ*: mtDNA: $R^2 = 0.67$, $P < 0.001$, nucDNA: $R^2 = 0.61$, $P < 0.001$; Fig. 3). This validates the spatial favourability models.

The width of the BTZ ranged between 67 and 144 km and it had a sigmoid shape. It ran obliquely across the IP, from the northernmost central region to the southernmost eastern region (Fig. 4). The BTZ delimits the spatially favourable areas for each rabbit subspecies, which correspond to the potential historical distribution of both subspecies (Fig. 4).

The HPC of each rabbit subspecies was associated with the current lower sections of a great Iberian river and its estuaries, bordering coastal areas (Fig. 4). In particular, the HPC of *Oca* was located at the bottom of the Guadalquivir River valley, southern IP, whereas the HPC of *Occ* was linked to the lower section of the Ebro River valley in northern Spain.

Intermediate shared favourability areas (i.e. $0.2 \geq F_{Oca} \cap F_{Occ} \leq 0.8$) delimited a large area in central-southern IP where gradual competitive exclusion between both rabbit subspecies could have occurred (Fig. 5). The competitive exclusion area included most of the BTZ (only the northernmost region of BTZ was excluded, because it was spatially unfavourable for both subspecies; Fig. 5) where the exclusion intensity would have been lower ($|\text{SFD}| < 0.2$), and two bordering bands where the intensity of exclusion of one subspecies over the other would have been higher ($|\text{SFD}| \geq 0.2$; Fig. 5). The area where *Oca* would have excluded *Occ* was larger than the area where *Occ* would have excluded *Oca* (Fig. 5).

DISCUSSION

Our study shows that there are distinct core and expansion zones for each rabbit subspecies in the IP. These correspond to the areas that were accessible for each subspecies via dispersal after the last glacial maximum, suggesting that the zones must have been ecologically and evolutionarily relevant for them (Barve et al. 2011, Acevedo et al. 2012). Conservation efforts should be particularly focused on these areas, as there should be an emphasis on the preservation of ecological-evolutionary processes. This is especially important for *Oca* subspecies, which is only found in the IP (and on a few islands), where populations are mostly declining (Vaquerizas et al. 2020). Besides this, our results

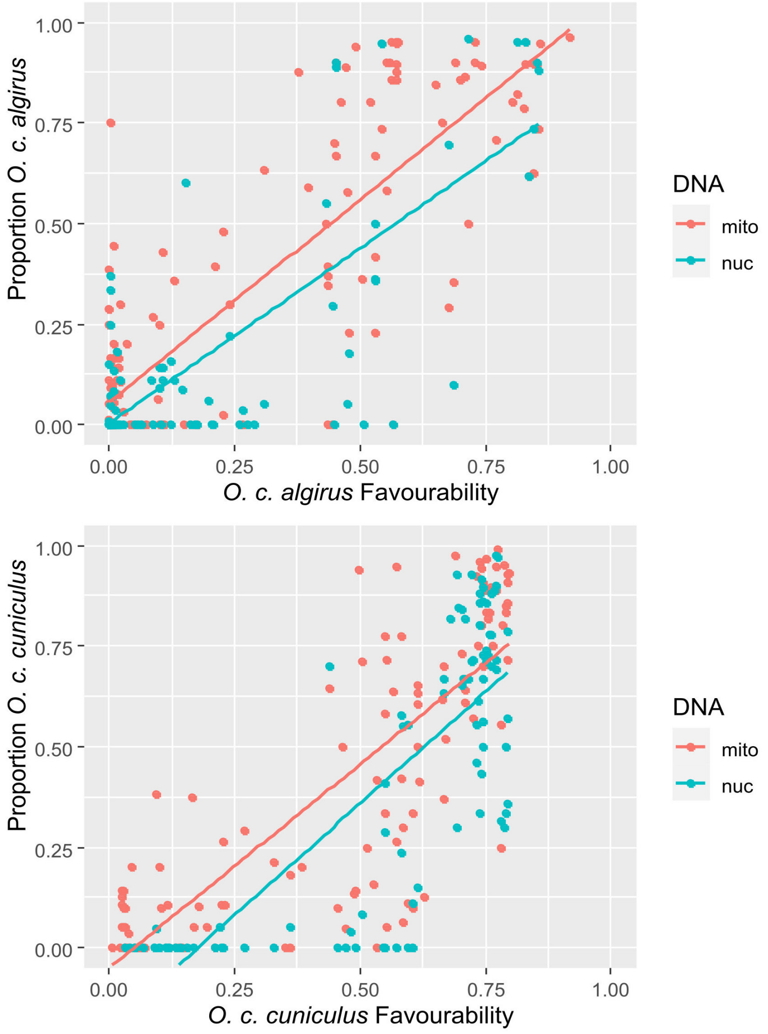

Fig. 3. Linear regressions between the favourability of each rabbit subspecies (*Oryctolagus cuniculus algirus* in the upper panel and *Oryctolagus cuniculus cuniculus* in the lower) and the proportion of rabbits that belonged to each subspecies according to the DNA molecule analysed. Populations in which all rabbits were exclusively from one subspecies (i.e. pure populations) were not included in this analysis, since they were used to build spatial favourability models (see Appendices S1 and S2 for more details about sampled populations).

indicate that the relevant areas for each subspecies can be broken down into core areas, expansion areas, and transition zones. Furthermore, transition zones are made up of areas where competitive exclusion keeps each subspecies separate, as well as other transition areas that are spatially unfavourable for both subspecies.

Branco et al. (2000, 2002), Ferrand (2008) and Geraldes et al. (2006, 2008) already pointed out that the two rabbit subspecies have different distribution areas, which roughly coincide with our spatially favourable areas. Those efforts resulted in independent maps for each genomic compartment. The framework employed here, based on a much larger sample size than previous studies (in terms of both number of populations and number of rabbits sampled), has allowed us to obtain a single distribution map for the two rabbit subspecies by combining the results of the spatial distribution of nucDNA and mtDNA data. Fuzzy logic has been instrumental for this purpose. We have also provided new insights into the location of glacial refugia and transition zones, and into the role of competitive exclusion in shaping the current distributions of the subspecies (see below for a detailed discussion).

Our findings show that the rabbit subspecies' spatial favourability predicts the prevalence of each subspecies at the population level, regardless of the DNA data considered. This means that rabbit populations in which one of the subspecies predominated over the other were located in UTM squares of higher spatial favourability for the predominant subspecies.

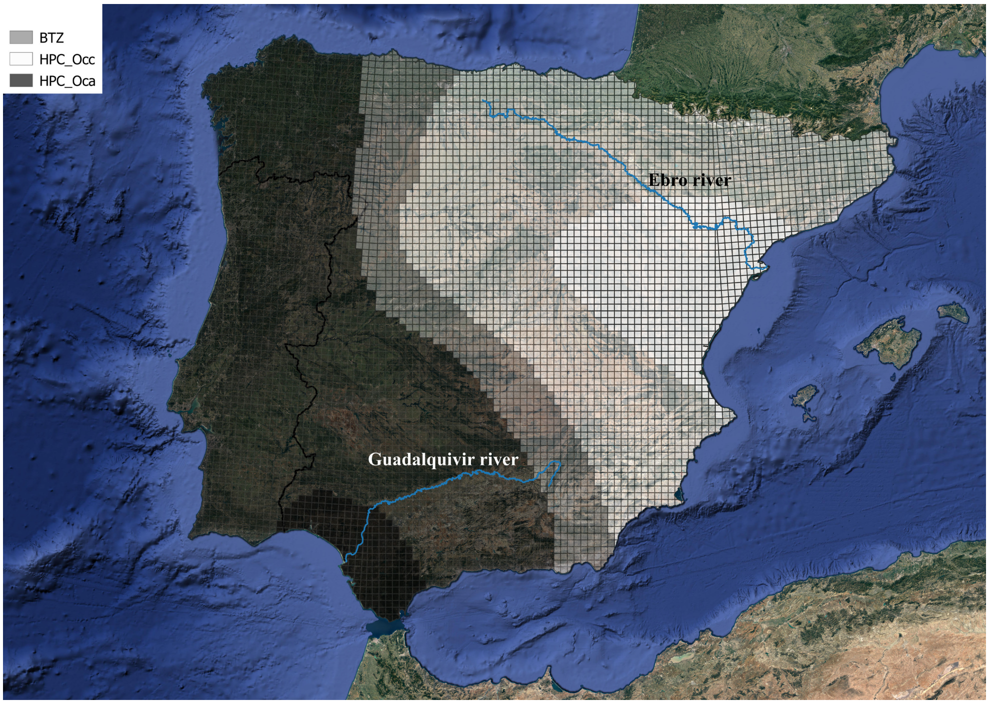

Fig. 4. Historical biogeographical distribution of European rabbit subspecies in the Iberian Peninsula obtained by the symmetric difference of their spatial favourability models (Appendix S2). Mid-grey squares represent the biogeographical transition zone (BTZ) between the historical distributions of *Oryctolagus cuniculus algirus* (dark grey squares) and *Oryctolagus cuniculus cuniculus* (light grey squares). HPC are represented for each subspecies in their respective historical distributions. The current positions of the Guadalquivir and Ebro Rivers are represented. Sampling units are 10 × 10 km UTM squares. Satellite image was obtained from 'Google Base Map Satellite' in QGIS. See Fig. 1 for the scale and position of the Peninsula within Europe.

Identification of the transition zone to delimit the distribution of both rabbit subspecies

Delimiting the transition zone between the rabbit subspecies' ranges is helpful for explicitly identifying their historical range. Our BTZ roughly coincides with the hybrid zone proposed by Geraldes et al. (2008), which was the most accepted to date of previous studies on rabbit subspecies (e.g. Carneiro et al. 2013, Ferreira et al. 2015, Rafati et al. 2018). Nevertheless, our results place the northernmost extreme of the transition zone between both subspecies ~100 km to the east (Fig. 4) of the previous hybrid zone. This difference is mainly due to the fact that our study included new populations for this area. This suggests that the historical range of *Oca* included a larger area in north-western IP than previously described (Geraldes et al. 2008).

The postglacial dispersion proposed by Branco et al. (2002) for each rabbit subspecies is in agreement with our findings. *Oca* seems to have followed two main expansion routes from the southernmost region of the IP: northward to central IP, and north-westward to the north-western corner of the IP following the western coastal region (Branco et al. 2002). This second route would have allowed *Oca* to colonise the most north-western region of the IP, as there are no strong geographic barriers that would have prevented its expansion. Conversely, it would have been difficult for *Occ* to reach the north-western corner of the IP, because of the presence of Cantabrian Mountains, an inhospitable region for rabbits that could have hindered rabbit genetic exchange between the north-west and the north-east regions (Branco et al. 2002). As mentioned, the location of the transition zone in the Cantabrian Mountains is more displaced to the east than previously suggested (Geraldes et al. 2008). In fact, the northernmost populations identified by Geraldes et al. (2008) as belonging to *Oca* subspecies are on the wrong side of the hybrid zone, but on the right side of our BTZ. Our BTZ is also in agreement with that proposed by Ferrand (2008), particularly with the results based on the Y-chromosome. Nevertheless, the precise location of the contact zone in the north requires further molecular work for confirmation or refutation of our findings.

The information reviewed here also confirms that the recent occurrence of rabbits of one subspecies in the historical range of the other is common, although each subspecies still predominates in its respective historical

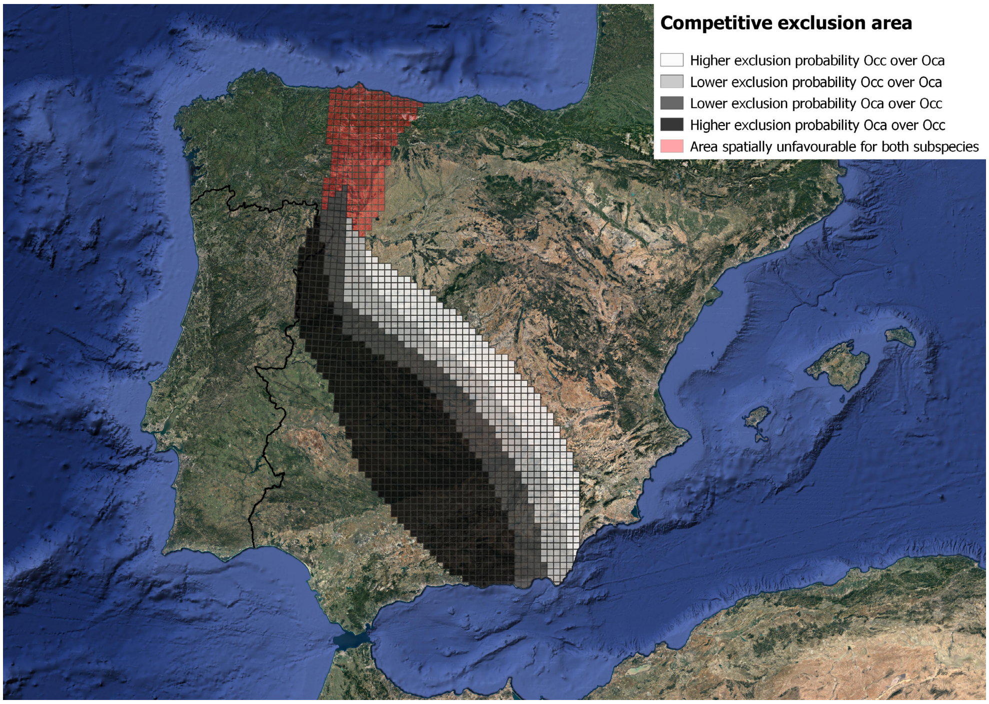

Fig. 5. Competitive exclusion areas between rabbit subspecies obtained using the fuzzy intersection ($F_{Oca} \cap F_{Occ}$) between the two rabbit subspecies' spatial favourability models (Appendix S2) and the absolute value of their difference (|SFD|). Competitive exclusion intensity is higher where $|SFD| > 0.2$ and lower where $|SFD| < 0.2$. Sampling units are 10 × 10 km UTM squares. *Oca* refers to *Oryctolagus cuniculus algirus* and *Occ* to *Oryctolagus cuniculus cuniculus*. The northernmost area of the BTZ is spatially unfavourable for both subspecies. Satellite image was obtained from 'Google Base Map Satellite' in QGIS. See Fig. 1 for the scale and position of the Peninsula within Europe.

geographical range as defined in our study (Fig. 3; Appendix S3). Natural contacts between both rabbit subspecies are more likely in localities close to the BTZ, especially in the central IP where genetic differentiation is lower and follows a genetic cline (Carneiro et al. 2013, Rafati et al. 2018).

The drastic decline in rabbit populations since the mid-20th Century has led to rabbit restocking becoming a common practice in the IP. Restocking is done to increase rabbit numbers, because rabbits are one of the main game species in both Spain and Portugal, and because they are essential for the conservation of some iconic Iberian predators. This common management action has been previously proposed as a plausible explanation for the distribution of mixed populations outside the natural contact zone (Branco et al. 2000, Moreno et al. 2004, Delibes-Mateos et al. 2008, Ferrand 2008). Delibes-Mateos et al. (2008) demonstrated the existence of uncontrolled rabbit translocations in different localities of the IP. More recently, Piorno et al. (2015) demonstrated that the presence of both rabbit subspecies in the north-western corner of Spain, previously considered to be a natural transition zone (Geraldes et al. 2008), is due to human translocations of *Occ* for hunting purposes. Thus, most populations we analysed in this region included both *Oca* and *Occ* rabbits, with a general predominance of the former.

Glacial refugia inferred from HPCs

We identified two HPCs where the symmetric difference between the favourability for each genetic lineage, and thus the genetic isolation between the two rabbit subspecies, was maximum. These HPCs could logically correspond to their glacial refugia. In fact, our HPCs broadly agree with the glacial refugia proposed by Branco et al. (2000, 2002), who located them in large areas in the north-east and the Mediterranean coast of the IP for *Occ*, and in the south-west for *Oca*. This agreement suggests that our approach may be useful to identify glacial refugia of other species for which detailed phylogeographical studies are lacking (Gómez & Lunt 2007). The degree of similarity between the refugia described in this study and those proposed by Branco et al. (2000) is higher for *Oca* than for *Occ* (Figs 1 and 4). Glacial refugia identified in this study share two common features. On the one hand, they were located near coastal areas and associated with low stretches of rivers and estuaries (that is, low-elevation areas), which would have been climatically more stable than other areas, allowing the persistence of temperate taxa during more extreme climatic conditions (O'Regan 2008). On the other hand, both glacial refugia show a remarkable continuity with the continental shelf of the eastern (Mediterranean) and western (Atlantic) coasts (Fig. 4), which emerged during the last glacial maximum, contributing to the persistence of lagomorphs and allowing suitable conditions for dispersal events (Laplana et al. 2015). Known fossils of *Oryctolagus cuniculus* are compatible with our hypothesis, but are not conclusive (López-Martínez 2008).

Competitive exclusion as a biological barrier for expansion

Our study differentiated two areas in the BTZ in which the expansion process would have been halted due to different reasons. Our results suggest that the level of interaction between both rabbit subspecies would have been low in the northernmost region of the BTZ, where exclusion could have occurred due to the great distance to the expansion cores together with the strong geographical barriers existing in that area (see above). In contrast, contact between rabbit subspecies is most likely to have occurred in the transition zone towards central and south-eastern IP, supporting the idea that the major patterns of dispersal were towards central Iberia (Branco et al. 2002). This large area partially includes two parallel bands (Fig. 5), where the intensity of competitive exclusion between rabbit subspecies increases with the distance from the central line of the BTZ. Additionally, our results on the spatial interaction between both rabbit subspecies show a potential distribution broader than observed if competitive exclusion had not occurred (Fig. 4), being greater for *Occ* than for *Oca* (Fig. 5). This is compatible with the previously described asymmetric genetic introgression between rabbit subspecies: the introgression of *Occ* on *Oca* is greater than *vice versa* (Branco et al. 2000, Carneiro et al. 2013, Alda & Doadrio 2014). This asymmetric introgression could be attributed to multiple episodes of isolation and contact tracking the climatic changes throughout the Pleistocene, prior to the current contact between the subspecies (Branco et al. 2002, Rafati et al. 2018). Accordingly, each rabbit subspecies would have acted as a biological barrier that hindered the expansion of the other in this area where both interacted. Several studies have evidenced a selection against hybridisation between both rabbit subspecies throughout their evolutionary history (Geraldes et al. 2008, Carneiro et al. 2010, 2013, Rafati et al. 2018). The BTZ would be maintained by a balance between dispersal and natural selection against hybrids (Carneiro et al. 2013), and this would mainly occur in the competitive exclusion areas identified in our study. Together, these lines of evidence explain why one rabbit subspecies did not displace the other and why hybrids did not spread throughout the IP. Recently, lower viability of hybrid populations has been suggested due to a decrease in the reproductive potential and survival probability of hybrid individuals that increases over generations (Blanco-Aguiar et al. 2010, Rafati et al. 2018). This could be due to a combination of genetic, behavioural and ecological factors acting synergistically as barriers between both rabbit subspecies that would be immersed in an advanced speciation process (Rafati et al. 2018).

Conclusions and management implications

Historical biogeography is a field in continuous development, in which new methodological approaches are being incorporated in order to deal with some limitations (Ebach et al. 2017). In this sense, our methodological approach allows: 1) the combination of information from different genomic compartments typically used to differentiate between subspecies; 2) the study of their historical distributions in a uniform and synthetic way; and 3) the reconstruction of historical distributions that have been artificially altered by human activities. In the particular case of European rabbits, our study is highly relevant for the management and conservation of rabbit subspecies (Delibes-Mateos et al. 2008, Piorno et al. 2020, Vaquerizas et al. 2020). The IUCN has recently classed the European wild rabbit as Endangered, mostly based on the situation within the *Oryctolagus cuniculus algirus* range (Villafuerte & Delibes-Mateos 2019). Indeed, a recent study has revealed stronger negative population trends in the range of this subspecies than in the Iberian range of *Oryctolagus cuniculus cuniculus* (Vaquerizas et al. 2020). Our study contributes to the identification of the historical range of *Oca*, where further efforts should be made to conserve this subspecies. More specifically, a management model that includes stricter control of rabbit restocking activities is needed in the range of *Oca*, particularly in its HPC. Effective regulation is clearly dependent on a good understanding of the distribution of the two subspecies, and our study contributes to that. It is remarkable that endemic Iberian predator species of conservation concern, such as the Iberian lynx *Lynx pardinus* and the Spanish imperial eagle *Aquila adalberti*, occur mostly in the range of this *Oca* and feed mostly on this subspecies (Palomo et al. 2007). Setting management models separately for each subspecies is particularly important because of the increasing evidence for their genetic, biometrical, behavioural and ecological differences (Ferrand 2008, Ferreira et al. 2015, Rafati et al. 2018), which even have led some researchers to raise the question of whether they should be considered as two well-separated species (e.g. Delibes-Mateos et al. 2018).

More broadly, our study highlights the usefulness of the combination of genetic analyses (i.e. subspecies identification) and spatial biogeographic models based on fuzzy logic for the study of the historical biogeography of subspecies. The consistency of our results with previous findings for this well-studied species, the European wild rabbit, makes us confident that our approach can be applied to other case studies. The application of these methods to unravel the historical biogeography of other taxa would help to increase knowledge of their evolutionary history, which is particularly critical for those species and territories that face strong conservation and management challenges.

ACKNOWLEDGEMENTS

Special thanks to all colleagues, hunters and gamekeepers involved in the collection of rabbit samples for our projects.

FUNDING

This research was funded by the project PID2020-114724RB-I00 supported by the Spanish Ministry of Science and Innovation. Francisco Díaz-Ruiz enjoyed these postdoctoral research contracts: “Juan de la Cierva” (ref: FJCI-2015-24949), from the Spanish Ministry of Economy, Industry and Competitiveness, and “Researcher’s incorporation grant-2020 Call” funded by the University of Málaga. P.H. Vaquerizas was supported by a grant (FPU17/04821) from the Spanish Ministry of Science, Innovation and Universities. Funding for open access charge: Universidad de Málaga/CBUA.

REFERENCES

Acevedo P, Jiménez-Valverde A, Lobo JM, Real R (2012) Delimiting the geographical background in species distribution modelling. *Journal of Biogeography* 39: 1383–1390.

Acevedo P, Melo-Ferreira J, R Real, PC Alves (2012) Past, present and future distributions of an Iberian endemic, *Lepus granatensis*: ecological and evolutionary clues from species distribution models. *PLoS One* 7: e51529.

Acevedo P, Real R (2012) Favourability: concept, distinctive characteristics and potential usefulness. *Naturwissenschaften* 99: 515–522.

Acevedo P, Ward AI, Real R, Smith GC (2010) Assessing biogeographical relationships of ecologically related species using favourability functions: a case study on British deer. *Diversity and Distributions* 16: 515–528.

Alda F, Doadrio I (2014) Spatial genetic structure across a hybrid zone between European rabbit subspecies. *PeerJ* 2: e582

Alsina C, Trillas E (2005) On the symmetric difference of fuzzy sets. *Fuzzy Sets and Systems* 153: 181–194.

Avise JC (2000) *Phylogeography: the History and Formation of Species*. Harvard University Press, Cambridge, Massachusetts, USA.

Barbosa AM, Real R, Muñoz AR, Brown JA (2013) New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Diversity and Distributions* 19: 1333–1338.

Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Soberón J, Villalobos F (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling* 222: 1810–1819.

Blanco-Aguiar JA, Carneiro M, Villafuerte R, Rios-Saldaña CA, Ferreira C, Ferrand N (2010) Preliminary results assessing pre and postzygotic isolation between two subspecies, *Oryctogalus cuniculus algirus* and *O. c. cuniculus*, of the European rabbit. In: *Trends in Biodiversity and Evolution (TiBE 2010)*. Vairao: Research Centre in Biodiversity and Genetic Resources, University of Porto, Porto, Portugal.

Bojadziev G, Bojadziev M (1995) *Fuzzy Sets, Fuzzy Logic. Applications*. World Scientific Publishing, Singapore.

Branco M, Ferrand N, Monnerot M (2000) Phylogeography of the European rabbit (*Oryctolagus cuniculus*) in the Iberian Peninsula inferred from RFLP analysis of the cytochrome b gene. *Heredity* 85: 307–317.

Branco M, Monnerot M, Ferrand N, Templeton AR (2002) Postglacial dispersal of the European rabbit (*Oryctolagus cuniculus*) from nested clade and mismatch analysis of mitochondrial DNA genetic variation. *Evolution* 56: 792–803.

Carneiro M, Baird SJE, Afonso S, Ramirez E, Tarroso P, Teotõnio H, Villafuerte R, Nachman MW, Ferrand N (2013) Steep clines within a highly permeable genome across a hybrid zone between two subspecies of the European rabbit. *Molecular Ecology* 22: 2511–2525.

Carneiro M, Blanco-Aguiar JA, Villafuerte R, Ferrand N, Nachman MW (2010) The X-chromosome and speciation: patterns of differentiation at multiple loci on the X-chromosome and autosomes of the European rabbit (*Oryctolagus cuniculus*). *Evolution* 64: 3443–3460.

Carro F, Ortega M, Soriguer RC (2019) Is restocking a useful tool for increasing rabbit densities? *Global Ecology and Conservation* 17: e00560

Chamorro D, Martínez-Freiría F, Real R, Muñoz AR (2021) Understanding parapatry: how do environment and competitive interactions shape Iberian vipers’ distributions? *Journal of Biogeography* 48: 1322–1335.

Cheung VWL, Pitcher T, Pauly D (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation* 124: 97–111.

Cohen J (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurement* 41: 687–699.

Corbet GB (1994) Taxonomy and origins. In: Thompson HV, King CM (eds) *The European Rabbit, the History and Biology of a Successful Colonizer*, 1–6. Oxford University Press, Oxford, UK.

Delibes-Mateos M, Ramirez E, Ferreras P, Villafuerte R (2008) Translocations as a risk for the conservation of European rabbit lineages. *Oryx* 42: 259–264.

Delibes-Mateos M, Redpath SM, Angulo E, Ferreras P, Villafuerte R (2007) Rabbits as a keystone species in southern Europe. *Biological Conservation* 137: 149–156.

Delibes-Mateos M, Villafuerte R, Cooke B, Alves PC (2018) *Oryctolagus cuniculus*. In: Smith AT, Johnston CH, Alves PC, Hackländer K (eds) *Lagomorphs of the World*, 99–104. John Hopkins University Press, Baltimore, Maryland, USA.

Ebach MC, Morrone JJ, Sanmartín I, Escalante T (2017) Further progress in historical biogeography. *Australian Systematic Botany* 30: i

Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.

Ferrand N (2008) Inferring the evolutionary history of the European rabbit (*Oryctolagus cuniculus*) from molecular markers. In: Alves PC, Ferrand N, Hackländer K (eds) *Lagomorph Biology: Evolution, Ecology, and Conservation*, 47–63. Springer, Berlin, Heidelberg, Germany.

Ferreira CC, Castro F, Piorno V, Barrio IC, Delibes-Mateos M, Rouco C et al. (2015) Biometrical analysis reveals major differences between the two subspecies of the European rabbit. *Biological Journal of the Linnean Society* 116: 106–116.

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49.

Geraldes A, Carneiro M, Delibes-Mateos M, Villafuerte R, Nachman MW, Ferrand N (2008) Reduced introgression of the Y chromosome between subspecies of the European rabbit (*Oryctolagus cuniculus*) in the Iberian Peninsula. *Molecular Ecology* 17: 4489–4499.

Geraldes A, Ferrand N, Nachman MW (2006) Contrasting patterns of introgression at X-linked loci across the hybrid zone between subspecies of the European rabbit (*Oryctolagus cuniculus*). *Genetics* 173: 919–933.

Gómez A, Lunt DH (2007) Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula. In: Weiss S, Ferrand N (eds) *Phylogeography of Southern European Refugia*, 155–188. Springer, Dordrecht, The Netherlands.

Hosmer DW, Lemeshow S (2000) *Applied Logistic Regression*. 2nd ed. Wiley, Hoboken, New Jersey, USA.

Laplana C, Sevilla P, Arsuaga JL, Arriaza MC, Baquedano E, Pérez-González A, López-Martínez N (2015) How far into Europe did pikas (Lagomorpha: Ochotonidae) go during the Pleistocene? New evidence from Central Iberia. *PLoS One* 10: 1–17.

Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659–1673.

Legendre P, Legendre L (1998) *Numerical Ecology*. 2nd ed. Elsevier Science, Amsterdam, The Netherlands.

Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17: 145–151.

López-Martínez N (2008) The lagomorph fossil record and the origin of the European rabbit. In: Alves PC, Ferrand N, Hackländer K (eds) *Lagomorph Biology: Evolution, Ecology, and Conservation*, 27–46. Springer, Berlin, Heidelberg, Germany.

Moreno S, Villafuerte R, Cabezas S, Lombardi L (2004) Wild rabbit restocking for predator conservation in Spain. *Biological Conservation* 118: 183–193.

Muñoz AR, Real R (2006) Assessing the potential range expansion of the exotic monk parakeet in Spain. *Diversity and Distributions* 12: 656–665.

Olivero J, Márquez AL, Real R (2013) Integrating fuzzy logic and statistics to improve the reliable delimitation of biogeographic regions and transition zones. *Systematic Biology* 62: 1–21.

O'Regan HJ (2008) The Iberian Peninsula – corridor or cul-de-sac? Mammalian faunal change and possible routes of dispersal in the last 2 million years. *Quaternary Science Reviews* 27: 2136–2144.

Palomo LJ, Gisbert J, Blanco JC (2007) *Atlas y Libro Rojo de los Mamíferos Terrestres de España*. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid, Spain.

Piorno V, Arroyo B, Delibes-Mateos M, Castro F, Villafuerte R (2020) European rabbit hunting: management changes and inertia in the governance system in a period of population fluctuations. *Journal for Nature Conservation* 56: 125832

Piorno V, Villafuerte R, Branco M, Carneiro M, Ferrand N, Alves PC (2015) Low persistence in nature of captive reared rabbits after restocking operations. *European Journal of Wildlife Research* 61: 591–599.

QGIS Development Team (2019) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Quintero I, Keil P, Jetz W, Crawford FW (2015) Historical biogeography using species geographical ranges. *Systematic Biology* 64: 1059–1073.

Rafati N, Blanco-Aguiar JA, Rubin CJ, Sayyab S, Sabatino SJ, Afonso S et al. (2018) A genomic map of clinal variation across the European rabbit hybrid zone. *Molecular Ecology* 27: 1457–1478.

Rapoport EH (1975) *Aerografía. Estrategias Geográficas de las Especies*. Fondo de Cultura Económica, México.

Real R, Báez JC, Fa JE, Olivero J, Acevedo P (2022) Making the competitive exclusion principle operational at the biogeographical scale using fuzzy logic. *Frontiers in Ecology and Evolution* 10: 99134.

Real R, Barbosa AM, Porras D, Kin MS, Márquez AL, Guerrero JC, Palomo LJ, Justo ER, Vargas JM (2003) Relative importance of environment, human activity and spatial situation in determining the distribution of terrestrial mammal diversity in Argentina. *Journal of Biogeography* 30: 939–947.

Real R, Barbosa AM, Vargas JM (2006) Obtaining environmental favourability functions from logistic regression. *Environmental and Ecological Statistics* 13: 237–245.

Sanmartín I (2012) Historical biogeography: evolution in time and space. *Evolution: Education and Outreach* 5: 555–568.

Vaquerizas PH, Delibes-Mateos M, Piorno V, Arroyo B, Castro F, Villafuerte R (2020) The paradox of endangered European rabbits regarded as pests in the Iberian Peninsula: subspecies differences in trends matter. *Endangered Species Research* 43: 99–102.

Villafuerte R, Delibes-Mateos M (2019) *Oryctolagus cuniculus*. The IUCN Red List of Threatened Species 2019: e.T41291A45189779. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T41291A45189779.en (accessed 1 August 2020).

Zadeh LA (1965) Fuzzy sets. *Information and Control* 8: 338–353.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. European rabbit populations surveyed in this study.

Appendix S2. Spatial favourability models and fuzzy unions.

Appendix S3. Geographical locations of rabbit populations in which individuals of both *Oryctolagus cuniculus algirus* and *Oryctolagus cuniculus cuniculus* were detected.

Appendix S4. Spatial favourability models assessment based on classification, discrimination and goodness of fit.