**ORIGINAL ARTICLE**

# Evidence for niche similarities in the allopatric sister species *Lepus castroviejoi* and *Lepus corsicanus*

Pelayo Acevedo[1,2,3]*, José Melo-Ferreira[1], Raimundo Real[2] and Paulo C. Alves[1,4,5]

[1]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBio Laboratório Associado, Universidade do Porto, Vairão 4485-661, Portugal, [2]Biogeography, Diversity and Conservation Research Team, University of Malaga, Málaga 29071, Spain, [3]SaBio IREC (UCLM-CSIC-JCCM), Ciudad Real 13071, Spain, [4]Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto 4169-007, Portugal, [5]Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812-0004, USA

## ABSTRACT

**Aim** *Lepus castroviejoi* and *Lepus corsicanus* are sister species with allopatric distributions that share extensive phenotypic and genetic variation. Under the framework of niche conservatism, we assessed whether these species have similar ecological niches, which could provide insights into their mode of divergence, conservation, and taxonomic status.

**Location** The distribution range of *L. castroviejoi* in the northern Iberian Peninsula, and that of *L. corsicanus* in mainland Italy and Sicily.

**Methods** We developed spatially explicit ecological models to characterize the niches of the two species by modelling them separately and together. Individual models were transferred to the territory of the sister species to explore their niche relationships. Predictions were assessed for discrimination and calibration in a cross-assessment procedure.

**Results** The model trained with *L. castroviejoi* was not able to predict the range of *L. corsicanus*, whereas the model trained with *L. corsicanus* was able to discriminate the *L. castroviejoi* distribution better than by chance alone (AUC = 0.814), although the reliability of the predictions was limited. The model trained with *L. corsicanus* in Italy's mainland (excluding the range in Sicily), however, discriminated *L. castroviejoi* presences/absences (AUC = 0.788) and accurately predicted its probability of occurrence. Furthermore, a well-calibrated model, which was able to discriminate the species distributions (*L. castroviejoi*, AUC = 0.828; *L. corsicanus*, AUC = 0.956), was obtained when the species were considered together.

**Main conclusions** Our results suggest that *L. castroviejoi* and *L. corsicanus* share extensive niche properties, which reinforces their possible conspecific status. The ecological niche of their ancestor may have resembled the present occupied niche of *L. corsicanus* in mainland Italy, given that this model was able to accurately predict the distribution range of both species. Finally, ecological evidence suggests that niche conservatism may explain the fragmentation in the distribution range of their ancestor, which may have been the driver of the initial stages of divergence.

**Keywords**

Allopatric speciation, Apennine hare, broom hare, conservation biogeography, ecological niche, lagomorphs, macroecology, species distribution modelling.

*Correspondence: Pelayo Acevedo, CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBio Laboratório Associado, Universidade do Porto, Vairão 4485-661, Portugal.
E-mail: pacevedo@irec.csic.es; pelayo. acevedo@gmail.com

## INTRODUCTION

The tendency of species to maintain similar ecological requirements over evolutionary time-scales is commonly known as 'niche conservatism' (Peterson *et al.*, 1999; see also Wiens & Graham, 2005), although the generality of this hypothesis is currently under debate (see e.g. Peterson, 2011). While some authors argue that speciation is not typically accompanied by ecological innovation, i.e. niches are conserved (e.g. Peterson *et al.*, 1999), others have found evidence of the contrary

(e.g. Graham *et al.*, 2004; Schluter, 2009). The main discrepancies among studies may derive from methodological artefacts (Warren *et al.*, 2008), and in part from the evolutionary age of the community (Losos *et al.*, 2003). Aside from the debate of whether niche conservatism exists, the concept is of great value for evolutionary biology and conservation biogeography: most importantly, it allows methods of inference to be combined from both disciplines to explore the ecological relationships within and between phylogenetically related taxa (see Wiens & Graham, 2005). Initial studies on this topic suggested that closely related species have more similar niches (e.g. Peterson *et al.*, 1999), but some studies have examined the degree to which niche similarities among taxa is a direct function of the phylogenetic similarity and have concluded that patterns of niche evolution beyond sister taxa are inconsistent (Losos *et al.*, 2003; Knouft *et al.*, 2006; Kalkvik *et al.*, 2012). While some closely related taxa have widely divergent niches, other distantly related taxa can maintain similar niches. Knouft *et al.* (2006) suggested that anole species of the *Anolis sagrei* group in a given territory are segregated by environmental characteristics, and thus phylogenetically related species can be ecologically distant due to disruptive ecological adaptation. In such cases, interspecific interactions are stronger among closely related species, and niches tend to diverge from those of near relatives (Losos *et al.*, 2003). This is the expectation for parapatric species – closely related taxa with separate but contiguous distributions without physical barriers between them, which only co-occur in a narrow contact zone (Bull, 1991). Parapatric species usually display divergent ecological niches that are forced by asymmetrical competitive exclusion (Acevedo *et al.*, 2012a); otherwise the distributions could tend to coalesce (Bull & Possingham, 1995). Niche conservatism along phylogenetic trees cannot therefore be considered a rule in nature, but it depends on whether the divergence is caused by differential ecological adaptation. For example, niche conservatism in allopatric sister species would imply little ecological differentiation despite geographical separation, which can be tested empirically. Thus, integrating phylogenetic and macroecological studies within the niche conservatism conceptual framework allows the testing of different evolutionary hypotheses regarding the onset of species divergence (e.g. Kozak & Wiens, 2006; Kalkvik *et al.*, 2012).

The genus *Lepus* (hares) is a promising model for studying questions related to niche conservatism. Hares are distributed worldwide and include over 30 presently recognized species that are thought to have resulted from a recent, rapid radiation, presumably from North America (Matthee *et al.*, 2004; Melo-Ferreira *et al.*, 2012). Many taxa have parapatric distributions (e.g. Acevedo *et al.*, 2012a) and occupy distinct ecological niches even if they are phylogenetically closely related (Melo-Ferreira *et al.*, 2012). Conversely, the broom hare, *Lepus castroviejoi* Palacios, 1977, and the Apennine hare, *Lepus corsicanus* de Winton, 1898, display high morphological (Palacios, 1996) and genetic similarities (Alves *et al.*, 2008a; Melo-Ferreira *et al.*, 2012), but currently have allopatric ranges (Fig. 1); *L. castroviejoi* is endemic to the Cantabrian Mountains in the Iberian Peninsula (Palomo *et al.*, 2007),

and *L. corsicanus* is endemic to the Italian Apennines and Sicily (Angelici & Luiselli, 2001; Angelici *et al.*, 2008), and has been rediscovered in Corsica (Scalera & Angelici, 2003; see also Pietri *et al.*, 2011). Furthermore, Melo-Ferreira *et al.* (2012) suggested that an ancient hybridization between the ancestors of *L. castroviejoi*–*L. corsicanus* and of *Lepus timidus*, an arctic or boreal taxon currently distributed in the northern Palaearctic, must have occurred. These events led to the complete replacement of the original mitochondrial DNA (mtDNA) variants of *L. castroviejoi*–*L. corsicanus* with that of *L. timidus*, and explain the close genetic similarity between the mtDNA haplotypes of *L. timidus*, *L. corsicanus* and *L. castroviejoi*, which have been described previously (Alves *et al.*, 2003; Wu *et al.*, 2005). The data suggest that *L. corsicanus* and *L. castroviejoi* are sister species which have shared a very recent common ancestor during the late Pleistocene.

In this work, we assessed whether *L. castroviejoi* and *L. corsicanus* conserve similar ecological niches, which could provide key insights into the mode of divergence, ecological requirements, conservation and taxonomic status of these species. We specifically tested whether the niche properties of one of these species is capable of predicting the distribution range of the other, and whether the species distribution ranges of both could be accurately predicted by a unique ecological model. Analyses of the niches were fully integrated into an evolutionary context.

## MATERIALS AND METHODS

### Study areas and species distribution

As the extent of the geographical background has substantial effects on the outputs of species distribution modelling (see Anderson & Raza, 2010; Barve *et al.*, 2011; Acevedo *et al.*, 2012b), we first delimited the arena of each species model. This was done by modelling the species distribution where the third-degree polynomial of the spatial coordinates were considered as predictors; the geographical background was delimited by localities that had a predicted favourability higher than the minimum value assigned to a presence (for further details, see Acevedo *et al.*, 2012b; Fig. 1). Species distribution data for *L. castroviejoi* in the Iberian Peninsula were obtained on UTM 10 km × 10 km squares (our territorial unit for modelling purposes) from Palomo *et al.* (2007) ($n = 69$ presences); for *L. corsicanus* in mainland Italy and Sicily, the information was provided by Boitani *et al.* (2002) and was adapted to these territorial units ($n = 367$, of which 298 are in Sicily). Although *L. corsicanus* is also present in Corsica, population numbers are low and information on the status of the species in Corsica is unknown (Angelici *et al.*, 2008); hence, information for Corsica was not considered for modelling.

### Ecological variables and spatially explicit modelling

*Lepus castroviejoi* has been described as typically occupying shrublands that frequently form mosaics with pastures and
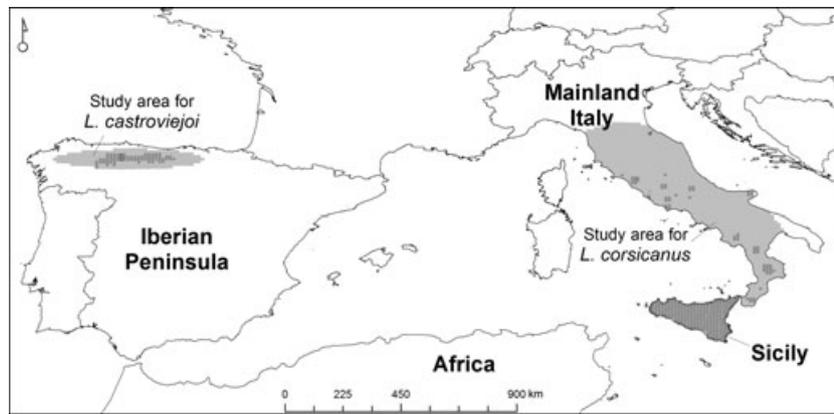
**Figure 1** Location of the study areas in southern Europe. The current distributions of *Lepus castroviejoi* and *L. corsicanus* (excluding the range in Corsica) are represented on a UTM 10 km × 10 km grid (hatching). Species distribution data were obtained from Palomo *et al.* (2007) for the Iberian Peninsula and adapted from Boitani *et al.* (2002) for Italy. Trend surface analyses (see text for details) were used to delimit the arena for modelling purposes (areas in grey).

broad-leaved woods (Acevedo *et al.*, 2007). *Lepus corsicanus* inhabits a broader spectrum of habitats in Mediterranean environments, ranging from coastal dune to high mountain habitats, as well as grassland, pasture and cultivated areas (Angelici & Luiselli, 2007; Angelici *et al.*, 2008). Considering previous knowledge and the availability of environmental predictors for the scale required in this study, a set of 19 environmental predictors were preselected to account for the niches of these species (see Table 1). The predictors were related to two factors: topoclimate (8 predictors) and land use (11 predictors). Bioclimatic variables and altitude (*c.* 1000-m spatial resolution) were obtained from the WorldClim project database (see Hijmans *et al.*, 2005). Land-use data was gather from *Global Land Cover 2005*,

which accurately assigns the land uses for each pixel of *c.* 300 m (see Bicheron *et al.*, 2008).

It is recommended, when conclusions about niche conservatism are to be extracted, to control overfitting by managing the number of predictors (dimensions) in the models (Peterson, 2011). In general, the probability of detecting a conserved niche increases as the number of dimensions in the model decreases (Peterson & Nakazawa, 2008). Following the recommendations provided by Peterson (2011), different strategies were explored for dealing with problems deriving from dimensionality (for details, see Appendix S1 in Supporting Information). Given that similar interpretations for niche conservatism could be obtained from all the sets of predictors, the results of the most parsimonious models are

**Table 1** Predictors used in the different models to study the distribution of *Lepus castroviejoi* in the northern Iberian Peninsula and *L. corsicanus* in mainland Italy and Sicily.

| Factor | Codes | Description (units) |
|---|---|---|
| Topoclimate | BIO0 | Altitude (m a.s.l.) |
| | BIO2 | Mean diurnal range (mean of monthly [max $T$ − min $T$]) (°C × 10) |
| | BIO3 | Isothermality (BIO2/annual temperature range) (× 100) |
| | BIO4 | Temperature seasonality (standard deviation × 100) |
| | BIO9 | Mean temperature of the driest quarter (°C × 10) |
| | BIO15 | Precipitation seasonality (coefficient of variation) |
| | BIO18 | Precipitation of the warmest quarter (mm) |
| | BIO19 | Precipitation of the coldest quarter (mm) |
| Land uses | T11 | Post-flooding or irrigated croplands (or aquatic) (%) |
| | T14 | Rain-fed croplands (%) |
| | T20 | Mosaic cropland/vegetation (grassland/shrubland/forest) (%) |
| | T30 | Mosaic vegetation/cropland (%) |
| | T70 | Closed needle-leaved evergreen forest (%) |
| | T100 | Closed to open (> 15%) mixed forest (%) |
| | T110 | Mosaic forest-shrubland/grassland (%) |
| | T120 | Mosaic grassland/forest or shrubland (%) |
| | T130 | Closed to open shrubland (%) |
| | T150 | Sparse (< 15%) vegetation (%) |
| | T210 | Water bodies (%) |

presented; they were obtained when topoclimatic and land-use predictors were considered together.

Using an inductive approach, the macroecological requirements of the studied species – 'ecological niche' – were determined based on the locations in which they occurred. Two statistical tests were carried out. To control the increase in type I errors as the number of predictors increased in the first stage, the false discovery rate (FDR) was evaluated using the procedure proposed by Benjamini & Hochberg (1995). Only predictors that were significantly related to the species distribution under an FDR of $q < 0.05$ were selected. Predictors selected after controlling the FDR were considered in a multiple logistic regression analysis in the second test, and the final models were obtained using a forward–backward stepwise procedure based on the Akaike information criterion (AIC). Statistical analyses were carried out in R 2.15.2 (R Core Team, 2012).

Four different models were developed: (1) an overall model for both sister species; (2) one for *L. castroviejoi*; (3) one for *L. corsicanus*; and (4) one for *L. corsicanus*, excluding its distribution range in Sicily. To assess the niche similarities between species, a model for one species, trained for its specific study area, was projected onto the territory of the other species. To project the model developed for one species onto another territory (spatial transferability), the similarity in environmental gradients and the correlation structure among independent variables between study areas should be maintained (e.g. Jiménez-Valverde *et al.*, 2011). We successfully checked for model transferability requirements between our study areas (see Appendix S2).

## Niche conservatism: a cross-assessment based on discrimination and calibration

Warren *et al.* (2008) pointed out the relevance of the null hypotheses in the study of niche conservatism, where both niche similarity and niche identity can be measured, but the results can yield opposing conclusions regarding niche conservatism. Niche similarity tests whether one species' niche model predicts the occurrences of a second species better than expected by chance (e.g. Peterson *et al.*, 1999). The area under the receiver operating characteristic (ROC) curve (AUC), the most popular discrimination capacity measure in species distribution modelling, can be interpreted as the probability that a presence chosen at random will be assigned a higher probability than an absence chosen at random (for details, see Krzanowski & Hand, 2009). Therefore, AUC can be a suitable parameter for quantifying niche similarity when the predictions of the model for one species are assessed on the territory of a second species, as it is used in this study. It should be noted that the discrimination performance based only on Sicily cannot be assessed, because *L. corsicanus* is present in every territorial unit on the island.

If we view niche conservatism as a continuum or gradient (ranging from niches that are identical to niches that are more similar than random), the AUC can provide information

about one extreme. For instance, values significantly higher than 0.5 indicate niches that are more similar than expected by chance. Yet, the AUC does not provide information on niche identity, because a model can adequately discriminate the distribution of a species even when it is not highly informative of its distribution. This is because the AUC is affected by the distribution of the territorial units along the modelled environmental gradient (Lobo *et al.*, 2008; Jiménez-Valverde *et al.*, 2013). Thus, calibration – the degree to which the observed proportion of presences equate to the model-estimated probabilities (Pearce & Ferrier, 2000) – is informative about niche identity; if the niches of two related species are identical, the niche model for one of them is able to accurately predict the probability of occurrence for the second species. Calibration plots were developed to visually assess the relatedness of the niches. Graphs were constructed with the GGPLOT2 package (Wickham, 2009) in R 2.15.2 (R Core Team, 2012) by plotting the proportion of occupied evaluation sites of a given species against the predicted probability of presence of the other species (for the 10 equal-sized probability intervals); points located along the 45° line indicate identical niches. The Hosmer–Lemeshow goodness-of-fit statistic (H–L; Lemeshow & Hosmer, 1982) was used for the statistical assessment of the calibration plots: H–L tests assess whether the observed values matched the expected ones in the calibration plots. Good calibration is obtained when the expected and observed presence rates are not significantly different ($P > 0.05$). Statistical analyses were carried out in R.

## RESULTS

### Spatially explicit ecological models

After controlling the FDR, 14 predictors were considered for an overall model for both species (BIO0, BIO2, BIO4, BIO9, BIO15, BIO19, T11, T20, T30, T70, T110, T120, T130 and T150); 7 predictors were considered for the *L. castroviejoi* model (BIO2, BIO9, BIO15, T14, T30, T120 and T150), 15 for the *L. corsicanus* model (BIO0, BIO2, BIO4, BIO9, BIO15, BIO19, T11, T14, T20, T30, T70, T110, T120, T130 and T150), and 9 for the *L. corsicanus* model that excluded Sicily (BIO0, BIO2, BIO15, BIO19, T14, T20, T70, T100 and T210).

The forward–backward stepwise procedure produced the final logistic regression models for all species/territories (Table 2; see also Fig. 2). In the training territories, the models achieved good predictive performance both in terms of discrimination (AUC: 0.948, 0.934, 0.954 and 0.813, for the overall model, *L. castroviejoi* model, *L. corsicanus* model, and for the model of *L. corsicanus* in mainland Italy, respectively), and in terms of calibration (see Fig. 3).

### Niche conservatism

A unique ecological model for both sister species was fitted (Table 2), and it was able to accurately predict their
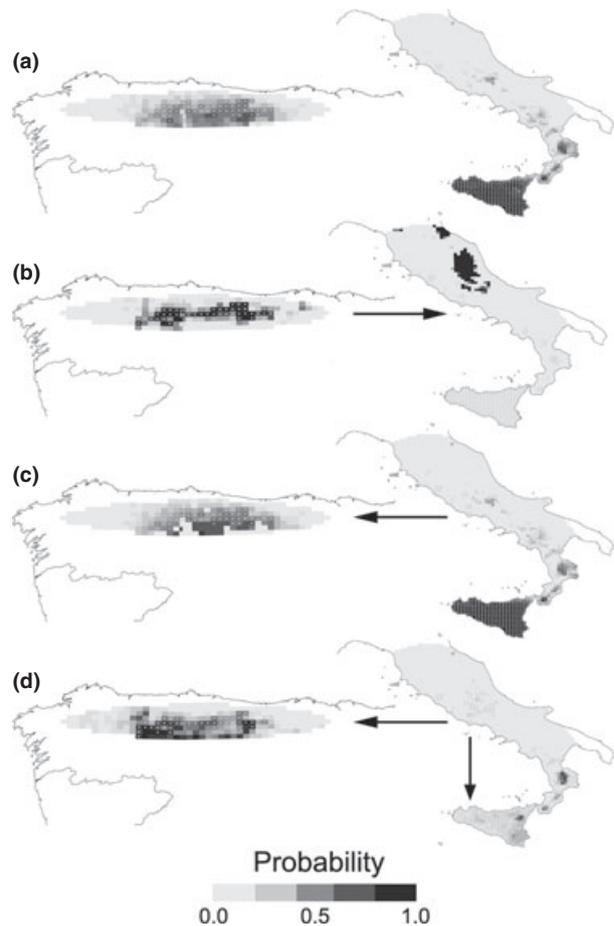
**Table 2** Results of the models developed on the current distribution of *Lepus castroviejoi* in the northern Iberian Peninsula and *L. corsicanus* in mainland Italy and Sicily. Predictors were listed following the order of entrance (the first one in the top) in the stepwise procedure.

| Model | Codes | $B$ (SE) | $z$-value |
|---|---|---|---|
| Overall species distribution | BIO15 | 0.1708 (0.0126) | 13.510*** |
| | BIO0 | 0.0066 (0.0005) | 14.011*** |
| | BIO19 | −0.0209 (0.0018) | −11.822*** |
| | BIO4 | −0.0022 (0.0002) | −10.383*** |
| | BIO9 | 0.0231 (0.0059) | 3.943*** |
| | T11 | −0.3337 (0.1682) | −1.984* |
| | BIO2 | 0.0182 (0.0061) | 2.964** |
| | T30 | −0.0299 (0.0142) | −2.104* |
| | T120 | 0.0959 (0.0455) | 2.106* |
| | T130 | −0.0350 (0.0166) | −2.111* |
| | T150 | 0.0251 (0.0148) | −2.111n.s. |
| | Intercept | −1.1033 (0.5063) | −2.179* |
| *L. castroviejoi* | BIO9 | −0.1622 (0.0217) | −7.475*** |
| | T120 | −3.4344 (1.7825) | −1.927n.s. |
| | T14 | −0.0942 (0.0377) | −2.501* |
| | Intercept | 25.6815 (3.4690) | 7.403*** |
| *L. corsicanus* | BIO15 | 0.1633 (0.0140) | 11.666*** |
| | BIO19 | −0.0251 (0.0023) | −10.863*** |
| | BIO0 | 0.0063 (0.0023) | 9.054*** |
| | BIO4 | −0.0020 (0.0003) | −6.240*** |
| | BIO9 | 0.0253 (0.0076) | 3.341*** |
| | BIO2 | 0.0272 (0.0114) | 2.397* |
| | T30 | −0.0443 (0.0176) | −2.518* |
| | T120 | 0.1180 (0.0493) | 2.397* |
| | T11 | −5.7220 (20.680) | −0.028n.s. |
| | Intercept | −1.4300 (0.5510) | −2.595** |
| *L. corsicanus* in mainland Italy | T70 | 0.0666 (0.0228) | 2.916** |
| | BIO0 | 0.0030 (0.0005) | 5.510*** |
| | BIO15 | 0.0834 (0.0156) | 5.359*** |
| | BIO2 | 0.0444 (0.0157) | 2.828** |
| | T210 | −0.1804 (0.1131) | −1.595n.s. |
| | Intercept | −11.2500 (1.8910) | −5.952*** |

$B$, parameter coefficient and its standard error (SE); $z$-value, test statistics (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$ and n.s. $P > 0.05$). Predictors are coded as in Table 1.
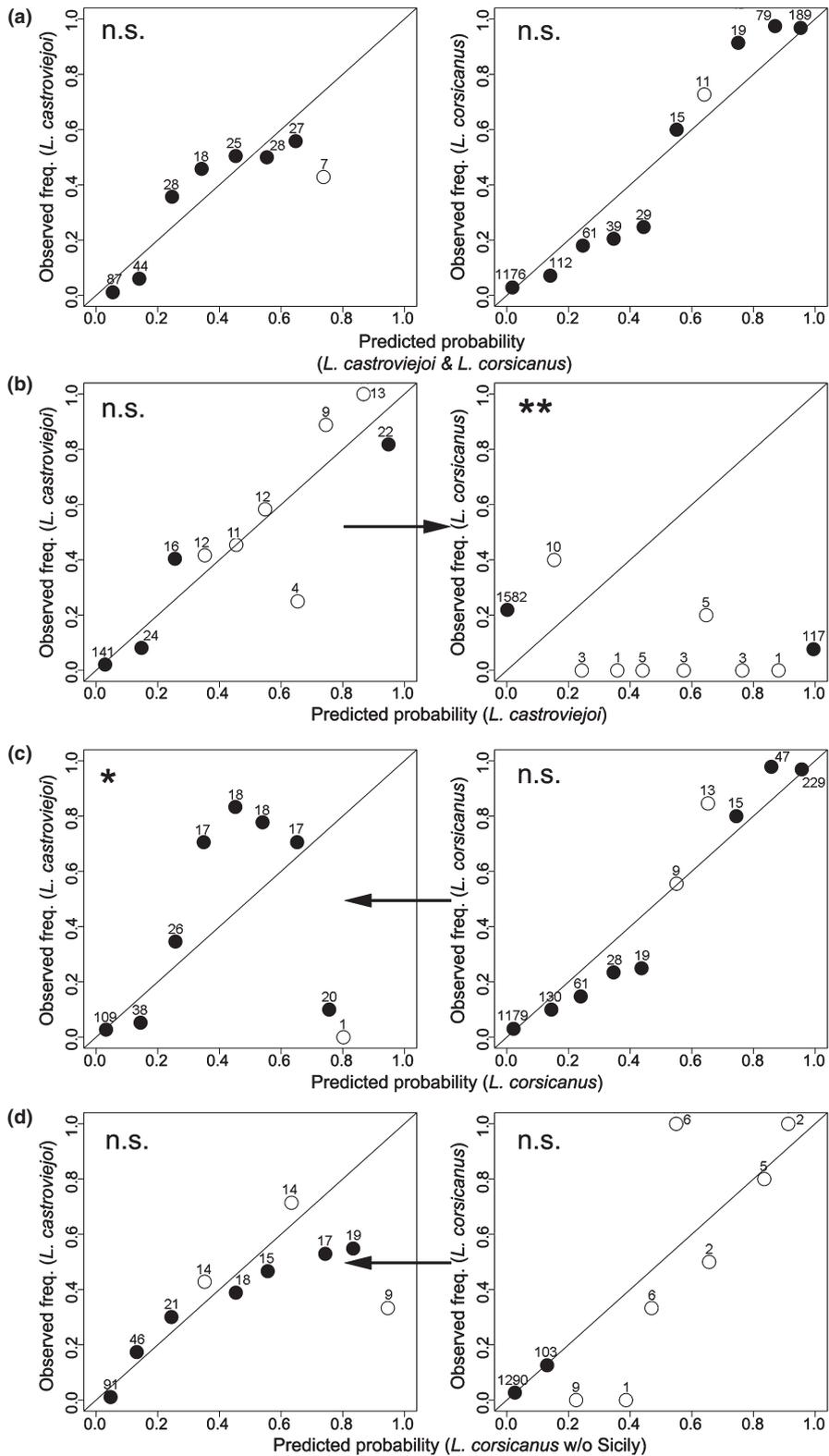


**Figure 2** Probability of occurrence of *Lepus castroviejoi* and *L. corsicanus* in the study areas, from 0 (light grey) to 1 (black), obtained from the different models: (a) overall species distribution; (b) model trained on *L. castroviejoi* and then projected onto Italy; (c) model trained on *L. corsicanus* and projected onto Iberia; (d) model trained on *L. corsicanus*, but excluding its range in Sicily, and projected onto both Sicily and Iberia. Arrows denote the projection of a model from the training area onto the territory of the sister species.

distribution ranges (Fig. 2a). When the discriminatory performance of this model was assessed, a high discrimination capacity was obtained on the range of *L. castroviejoi* (AUC = 0.828) and on that of *L. corsicanus* (AUC = 0.956). Calibration plots indicated that the model predicted similarly the probability of presence for the two species, *L. castroviejoi* and *L. corsicanus* (Fig. 3a).

When the model trained on *L. castroviejoi* was transferred to the territory of *L. corsicanus*, it did not discriminate better than chance the distribution of the latter species (AUC = 0.232). On the contrary, the model trained on *L. corsicanus* data was able to predict the territory of *L. castroviejoi* (AUC = 0.814). Furthermore, the model trained on the mainland distribution of *L. corsicanus* also discriminated better than chance the *L. castroviejoi* distribution (AUC = 0.789) and the *L. corsicanus* overall distribution (AUC = 0.853). Calibration plots for the model trained on

*L. castroviejoi*, partly supported the interpretations obtained by assessing the AUC (Fig. 3b). Calibration plots showed, however, that the predictions of the model for *L. corsicanus* did not accurately fit the observed frequency of *L. castroviejoi* (Fig. 3c), although it did fit the predictions of the model for *L. corsicanus* in mainland Italy (Fig. 3d).

## DISCUSSION

Multidisciplinary approaches are fundamental in order to understand the past, present and future evolutionary and ecological features of species, and to gather relevant information that can be used to implement adequate conservation measures. Analyses using morphological and genetic data have previously suggested that two allopatric species of hare, *L. castroviejoi* and *L. corsicanus*, are recent descendants of a common species (Palacios, 1996; Alves *et al.*, 2008a;

**Figure 3** Calibration plots showing the relationship between the predicted probability of occurrence for a model and the observed proportion of evaluation localities occupied by *Lepus castroviejoi* and *L. corsicanus*: (a) overall species distribution; (b) model trained on *Lepus castroviejoi*; (c) model trained on *L. corsicanus*; (d) model trained on *L. corsicanus* but excluding Sicily. Arrows denote the projection of a model from the training area to the territory of the sister species. Filled and open symbols indicate bins with ≥ 15 or < 15 localities, respectively. In bins with < 15 localities, the observed frequency should be considered with caution (Jovani & Tella, 2006). Significance (***P < 0.001; **P < 0.01; *P < 0.05; n.s., P > 0.05) refers to the Hosmer–Lemeshow goodness-of-fit statistic (Lemeshow & Hosmer, 1982).

Melo-Ferreira *et al.*, 2012). Here, these taxa were studied from a novel perspective, and extensive similarities were also found in their ecological traits. These results have important implications for our understanding of the evolutionary history of these species and their ecological requirements. Moreover, it contributes to the discussion of the relationship between niche conservatism and evolutionary history.

### On the methodological approach

Various metrics have been proposed to quantify potential niche overlap, and some were assessed comparatively in the context of niche conservatism (e.g. Warren *et al.*, 2008; Rödder & Engler, 2011). Each showed advantages and drawbacks on the desirable characteristics for a metric of potential niche overlap (see Rödder & Engler, 2011). Based on the concept behind the pioneering study on niche conservatism (Peterson *et al.*, 1999), a simple and more in-depth exploration of niche similarities between two sister species was used here. The approach was based on a cross-assessment focused on two characteristics of a model's predictive performance, i.e. discrimination and calibration. Assessing the discrimination with the AUC, and according to the model based on the sister species, the probability for a presence chosen at random for one species to be assigned a higher probability than an absence chosen at random was determined. In other words, niche similarity was assessed (AUC > 0.5). To determine whether two niches are identical, the interspecific niche relationships should also be assessed in terms of calibration. In the cross-assessment context, a perfectly calibrated model shows that two niches are identical. The calibration plot gives information about the uncertainty of the predictions, and how they are distributed along the gradient of probabilities predicted by the model, which is also needed for a proper understanding of the AUC values (Jiménez-Valverde *et al.*, 2013). Thus, in a cross-assessment context, discrimination and calibration allow for a more in-depth exploration of niche similarities; hence, additional conclusions about niche relationships can be extracted. For instance, a situation in which the model overpredicts species occurrence under a given threshold of probability and underpredicts over that threshold can be identified (see Fig. 3a in the territory of *L. corsicanus*). That situation could indicate the presence of an unconsidered factor (e.g. a competitor, a resource or human interference), which prevents the species from occupying some favourable localities.

### Ecological similarity of taxa: implications for taxonomy, evolutionary history and conservation

It has been suggested that the spatial resolution of an analysis may affect conclusions about niche conservatism (e.g., Peterson & Nyári, 2007). Therefore, the grain size of the analyses is important to properly understand the interpretations extracted from the results. The results obtained in this study – from an ecological perspective and at 10 km × 10 km

spatial resolution – support the close evolutionary relationship between *L. castroviejoi* and *L. corsicanus*. This similarity adds to the morphological analyses performed by Palacios (1996), and to the molecular inferences made by Alves *et al.* (2008a) and Melo-Ferreira *et al.* (2012), which led these authors to suggest that these taxa could eventually be considered conspecific. If parapatric groups of species (as *Lepus* spp. in Europe) are naturally conceived to be ecologically divergent (Bull & Possingham, 1995), then niche similarities between related species such as *L. castroviejoi* and *L. corsicanus* (even in allopatry) can be used as an argument to discuss possible conspecific status. Even if species concepts vary, and the classification of *L. castroviejoi* and *L. corsicanus* as conspecific will depend on the applied criterion, the similarities of these taxa are remarkable and show how morphology, genes and ecology may be conserved in the initial stages of divergence.

Genetic evidence suggests that *L. castroviejoi* and *L. corsicanus* may have separated as late as the late Pleistocene (Alves *et al.*, 2008a; Melo-Ferreira *et al.*, 2012). It could be hypothesized that their common ancestor occupied a larger range in Europe during the Pleistocene and that the subsequent climatic changes split it into two allopatric refugia in the two southern European peninsulas, Iberia and Italy (Angelici & Luiselli, 2007), as has been described for other taxa such as the chamois (*Rupicapra* spp.; Masini & Lovari, 1988). Our results suggest that this range of separation was not driven by disruptive adaptation to different ecological settings, but must have resulted from the fragmentation of favourable habitat. Apparently, *L. castroviejoi* and *L. corsicanus* did not expand from these refugia, which may have been (1) due to competition with other hare species, (2) due to niche conservatism, or most probably (3) partly due to both factors (see below). *Lepus castroviejoi* could have initially faced competition from *Lepus granatensis* and probably from *L. timidus* when this species was present in northern Iberian Peninsula in the late Pleistocene (Altuna, 1970). The presence of the mtDNA type of *L. timidus* in *L. castroviejoi* due to hybridization (Alves *et al.*, 2008b; Melo-Ferreira *et al.*, 2012) is congruent with the hypothesis of contact between these species. Also, when the niche expressed by *L. corsicanus* was projected onto Iberia, a high environmental potential for *L. castroviejoi* was generally obtained in more southern areas of the Iberian study area (Fig. 2). These areas are not currently occupied by *L. castroviejoi*, but are suitable for *L. granatensis* (Acevedo *et al.*, 2012c). This suggests that competition with *L. granatensis* may have been an important factor impeding colonization of these southern territories by *L. castroviejoi*. Similarly, in the Italian Peninsula, the northward expansion of *L. corsicanus* could have been prevented by the competition with *L. timidus* and *L. europaeus*, because the past range of *L. corsicanus* reached more northerly latitudes (Angelici & Luiselli, 2007; Angelici *et al.*, 2008).

Niche conservatism could have also limited the capacity of these species to colonize new habitats given that they currently occupy ecological islands (e.g. Fig. 1), separated by intervening landscapes that are unsuitable for these species, i.e. by an ecological barrier. In this situation, niche conservatism

can limit adaptation to suboptimal ecological conditions (see Wiens & Graham, 2005); hence, it restricts the expansion ability of the species. Following this line of thought, niche conservatism may have further implications for the evolution of these sister species. If the species cannot adapt to suboptimal environmental conditions, then the barrier will continue to prevent gene flow between these species, and they will inevitably continue to diverge according to the allopatric speciation model (Kozak & Wiens, 2006). At this point, it should be highlighted that these species offer a fascinating opportunity for a natural experiment in which, for instance, the genetic basis of any recent local adaptation can be explored.

Finally, our results suggest that the niche expressed by *L. corsicanus* in mainland Italy retained ecological traits that can accurately predict the global distribution of these sister species. Interestingly, some genetic differences between hares from mainland Italy and Sicily were found using mtDNA (Pierpaoli *et al.*, 1999; Alves *et al.*, 2008a; Pietri *et al.*, 2011), which may have originated from genetic drift during the founding of the Sicilian *L. corsicanus* population. The ecological divergence may be related to the fact that *L. corsicanus* is the only hare species in Sicily despite the intensive release of *L. europaeus* in recent decades (Angelici *et al.*, 2008). The populations in Sicily are therefore evolving in the absence of potential competitors and are thus displaying something that could closely resemble the part of its fundamental niche that is present in Sicily. In contrast, continental populations have evolved in contact with competitor species, and the pattern of distribution explained by the models is closer to the species' realized niche (e.g. Soberón & Peterson, 2005; Angelici & Luiselli, 2007). Thus, different parts of the niche could have been occupied in mainland Italy and Sicily, which could be related to rather different expressions of the species' ecological niche (see Randin *et al.*, 2006). Moreover, the fact that the model trained on the mainland population of *L. corsicanus* was able to predict the range of *L. castroviejoi* but not vice versa, suggests that populations of *L. corsicanus* in mainland Italy have retained the ecological traits of their ancestor. These Italian populations are therefore valuable for ecological and evolutionary studies. Due to the characteristics described above, *L. castroviejoi* and *L. corsicanus* are significant evolutionary units that should be preserved.

As in the seminal studies of Peterson *et al.* (1999) and Wiens & Graham (2005), among others, our study shows that macroecology can be useful for exploring diverse topics in evolution. The integration of macroecology and phylogeography would therefore contribute decisively to the strengthening of the geographical components of evolutionary biology, something that is often omitted (Kidd & Ritchie, 2006).

## ACKNOWLEDGEMENTS

## REFERENCES

Acevedo, P., Alzaga, V., Cassinello, J. & Gortázar, C. (2007) Habitat suitability modelling reveals a strong niche overlap between two poorly known species, the broom hare and the Pyrenean grey partridge, in the north of Spain. *Acta Oecologica*, **31**, 174–184.

Acevedo, P., Jiménez-Valverde, A., Melo-Ferreira, J., Real, R. & Alves, P.C. (2012a) Parapatric species and the implications for climate change studies: a case study on hares in Europe. *Global Change Biology*, **18**, 1509–1519.

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

Acevedo, P., Melo-Ferreira, J., Real, R. & Alves, P.C. (2012c) Past, present and future distributions of an Iberian endemic, *Lepus granatensis*. Ecological and evolutionary clues from species distribution models. *PLoS ONE*, **7**, e51529.

Altuna, J. (1970) Hallazgo de una liebre ártica (*Lepus timidus* L.) en el yacimiento prehistórico de Urtiaga (Guipúzcoa). *Munibe. Sociedad de Ciencias Naturales Aranzadi (San Sebastian)*, **22**, 165–168.

Alves, P.C., Ferrand, N., Suchentrunk, F. & Harris, D.J. (2003) Ancient introgression of *Lepus timidus* mtDNA into *L. granatensis* and *L. europaeus* in the Iberian Peninsula. *Molecular Phylogenetics and Evolution*, **27**, 70–80.

Alves, P.C., Melo-Ferreira, J., Branco, M., Suchentrunk, F., Ferrand, N. & Harris, D.J. (2008a) Evidence for genetic similarity of two allopatric European hares (*Lepus corsicanus* and *L. castroviejoi*) inferred from nuclear DNA sequences. *Molecular Phylogenetics and Evolution*, **46**, 1191–1197.

Alves, P.C., Melo-Ferreira, J., Freitas, H. & Boursot, P. (2008b) The ubiquitous mountain hare mitochondria: multiple introgressive hybridization in hares, genus *Lepus*. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **363**, 2831–2839.

Anderson, R.P. & Raza, A. (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary

tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography*, **37**, 1378–1393.

Angelici, F.M. & Luiselli, L. (2001) Distribution and status of the critically endangered Apennine hare *Lepus corsicanus* de Winton 1898, in continental Italy and Sicily. *Oryx*, **35**, 245–249.

Angelici, F.M. & Luiselli, L. (2007) Range, dynamic biogeography and ecological interactions of two species: *Lepus corsicanus* and *Lepus europaeus* in Italy. *Wildlife Biology*, **13**, 251–257.

Angelici, F.M., Randi, E., Riga, F. & Trocchi, V. (2008) *Lepus corsicanus. IUCN Red List of Threatened Species*. Version 2011.2. Available at: http://www.iucnredlist.org/details/41305 (accessed 5 June 2012).

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., 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.

Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B*, **57**, 289–300.

Bicheron, P., Defourny, P., Brockmann, C. *et al.* (2008) *GlobCover 2005 – Products description and validation report*. Version 2.1, 2008. European Space Agency, Paris, France. Available at: http://ionia1.esrin.esa.int/.

Boitani, L., Corsi, F., Falcucci, A., Maiorano, L., Marzetti, I., Masi, M., Montemaggiori, A., Ottaviani, D., Reggiani, G. & Rondinini, C. (2002) *Rete ecologica nazionale: un approccio alla conservazione dei vertebrati italiani*. Istituto di Ecologia Applicata, Rome.

Bull, C.M. (1991) Ecology of parapatric distributions. *Annual Review of Ecology and Systematics*, **22**, 19–36.

Bull, C.M. & Possingham, H. (1995) A model to explain ecological parapatry. *The American Naturalist*, **145**, 935–947.

Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J. & Moritz, C. (2004) Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution*, **58**, 1781–1793.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Jiménez-Valverde, A., Decae, A.E. & Arnedo, M.A. (2011) Environmental suitability of new reported localities of the funnelweb spider *Macrothele calpeiana*: an assessment using potential distribution modelling with presence-only techniques. *Journal of Biogeography*, **38**, 1213–1223.

Jiménez-Valverde, A., Acevedo, P., Barbosa, A.M., Lobo, J.M. & Real, R. (2013) Discrimination capacity in species distribution models depends on the representativeness of the environmental domain. *Global Ecology and Biogeography*, **22**, 508–516.

Jovani, R. & Tella, J.L. (2006) Parasite prevalence and sample size: misconceptions and solutions. *Trends in Parasitology*, **22**, 214–218.

Kalkvik, H.M., Stout, I.J., Doonan, T.J. & Parkinson, C.L. (2012) Investigating niche and lineage diversification in widely distributed taxa: phylogeography and ecological niche modeling of the *Peromyscus maniculatus* species group. *Ecography*, **35**, 54–64.

Kidd, D.M. & Ritchie, M.G. (2006) Phylogeographic information systems: putting the geography into phylogeography. *Journal of Biogeography*, **33**, 1851–1865.

Knouft, J.H., Losos, J.B., Glor, R.E. & Kolbe, J.J. (2006) Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. *Ecology*, **87**, S29–S38.

Kozak, K.H. & Wiens, J.J. (2006) Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution*, **60**, 2604–2621.

Krzanowski, W.J. & Hand, D.J. (2009) *ROC curves for continuous data*. Chapman & Hall/CRC, New York.

Lemeshow, S. & Hosmer, D.W. (1982) A review of goodness of fit statistics for use in the development of logistic regression models. *American Journal of Epidemiology*, **115**, 92–106.

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

Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Rodríguez Schettino, L., Chamizo Lara, A., Jackman, T.R. & Larson, A. (2003) Niche lability in the evolution of a Caribbean lizard community. *Nature*, **424**, 542–545.

Masini, F. & Lovari, S. (1988) Systematics, phylogenetic and dispersal of the chamois (*Rupicapra* spp.). *Quaternary Research*, **30**, 339–349.

Matthee, C.A., van Vuuren, B.J., Bell, D. & Robinson, T.J. (2004) A molecular supermatrix of the rabbits and hares (Leporidae) allows for the identification of five intercontinental exchanges during the Miocene. *Systematic Biology*, **53**, 433–447.

Melo-Ferreira, J., Boursot, P., Carneiro, M., Esteves, P.J., Farelo, L. & Alves, P.C. (2012) Recurrent introgression of mitochondrial DNA among hares (*Lepus* spp.) revealed by species-tree inference and coalescent simulations. *Systematic Biology*, **61**, 367–381.

Palacios, F. (1996) Systematics of the indigenous hares of Italy traditionally identified as *Lepus europaeus* Pallas, 1778 (Mammalia: Leporidae). *Bonner Zoologische Beiträge*, **46**, 59–91.

Palomo, L.J., Gisbert, J. & Blanco, J.C. (2007) *Atlas y libro rojo de los mamíferos terrestres de España*. Organismo Autónomo de Parques Nacionales, Madrid.

Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.

Peterson, A.T. (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827.

Peterson, A.T. & Nakazawa, Y. (2008) Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. *Global Ecology and Biogeography*, **17**, 135–144.

Peterson, A.T. & Nyári, A.S. (2007) Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, *Schiffornis* sp., in the neotropics. *Evolution*, **62**, 173–183.

Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.

Pierpaoli, M., Riga, F., Trocchi, V. & Randi, E. (1999) Species distinction and evolutionary relationships of the Italian hare (*Lepus corsicanus*) as described by mitochondrial DNA sequencing. *Molecular Ecology*, **8**, 1805–1817.

Pietri, C., Alves, P. & Melo-Ferreira, J. (2011) Hares in Corsica: high prevalence of *Lepus corsicanus* and hybridization with introduced *L. europaeus* and *L. granatensis*. *European Journal of Wildlife Research*, **57**, 313–321.

R Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org/.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689–1703.

Rödder, D. & Engler, J.O. (2011) Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. *Global Ecology and Biogeography*, **20**, 915–927.

Scalera, R. & Angelici, F.M. (2003) Rediscovery of the Apennine hare *Lepus corsicanus* in Corsica. *Bollettino del Museo Regionale Scienze Naturali Torino*, **20**, 161–166.

Schluter, D. (2009) Evidence for ecological speciation and its alternative. *Science*, **323**, 737–741.

Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distribution areas. *Biodiversity Informatics*, **2**, 1–10.

Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*, **62**, 2868–2883.

Wickham, H. (2009) *ggplot2: elegant graphics for data analysis*. Springer, New York.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

Wu, C., Wu, J., Bunch, T.D., Li, Q., Wang, Y. & Zhang, Y.-P. (2005) Molecular phylogenetics and biogeography of *Lepus* in Eastern Asia based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **37**, 45–61.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Controlling dimensionality effects in niche conservatism interpretations.

**Appendix S2** Checking for model transferability between study areas.

## BIOSKETCH

**Pelayo Acevedo** is a researcher at the CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBio Laboratório Associado. His interests include the study of factors affecting the distribution and abundance of pathogens, and their hosts and vectors, through fragmented habitats.

Author contributions: P.A. and P.C.A. conceived the ideas; P.A. analysed the data; P.A., J.M.-F., R.R. and P.C.A. participated in the discussion of the results and wrote the manuscript.

Editor: Miles Silman