

1  
2  
3 1 ORIGINAL ARTICLE4  
5 26  
7 3 Evidence for niche similarities in the allopatric sister species *Lepus castroviejo* and8  
9 4 *L. corsicanus*10  
11 5 Pelayo Acevedo<sup>1,2,3\*</sup>, José Melo-Ferreira<sup>1</sup>, Raimundo Real<sup>2</sup>, Paulo C. Alves<sup>1,4,5</sup>12  
13 614  
15 7 <sup>1</sup> CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBio16  
17 8 Laboratório Associado. Universidade do Porto, 4485-661 Vairão, Portugal.18  
19 9 <sup>2</sup> Biogeography, Diversity and Conservation Research Team, University of Malaga,20  
21 10 29071 Malaga, Spain.22  
23 11 <sup>3</sup> SaBio-IREC (UCLM- CSIC-JCCM), 13071 Ciudad Real, Spain.24  
25 12 <sup>4</sup> Dpto. de Biologia, Faculdade de Ciências, Universidade do Porto, 4169-007 Porto,26  
27 13 Portugal.28  
29 14 <sup>5</sup> University of Montana, Wildlife Biology Program, College of Forestry and30  
31 15 Conservation, Missoula, MT 59812-0004 Montana, USA.32  
33 1634  
35 17 \* Correspondence: Pelayo Acevedo, CIBIO, Centro de Investigação em Biodiversidade36  
37 18 e Recursos Genéticos, InBio Laboratório Associado. Universidade do Porto, 4485-66138  
39 19 Vairão, Portugal. E-mails: [pacevedo@irec.csic.es](mailto:pacevedo@irec.csic.es), [pelayo.acevedo@gmail.com](mailto:pelayo.acevedo@gmail.com)40  
41 2042  
43 21 **Running title:** Niche similarities in allopatric sister species44  
45 22 **Word count:** 5750 (2 pages for tables and figures)46  
47 2348  
49 2450  
51 2552  
53 2654  
55 2756  
57 2858  
59 2960  
61 30

1  
2  
3 **ABSTRACT**

4 **Aim** *Lepus castroviejo* and *L. corsicanus* are sister species with allopatric distributions  
5  
6  
7 that share extensive phenotypic and genetic variation. Under the framework of niche  
8  
9  
10 conservatism, we assessed whether these species have similar ecological niches, which  
11  
12 could provide insights on their mode of divergence, conservation, and taxonomic status.

13  
14 **Location** The distribution range of *L. castroviejo*, in the Northern Iberian Peninsula,  
15  
16 and of *L. corsicanus* in mainland Italy and Sicily.

17  
18 **Methods** We developed spatially explicit ecological models to characterize the niches  
19  
20 of the species, modelling the individual species separately and together. Individual  
21  
22 models were transferred onto the territory of the sister species to explore their niche  
23  
24 relationships. Predictions were assessed in terms of discrimination and calibration in a  
25  
26 cross-assessment procedure.  
27  
28

29  
30 **Results** The model trained for *L. castroviejo* was not able to predict the range of *L.*  
31  
32 *corsicanus*. The model trained on *L. corsicanus* was able to discriminate the *L.*  
33  
34 *castroviejo* distribution better than chance alone (AUC=0.814) but the reliability of the  
35  
36 predictions was limited. However, the model trained on *L. corsicanus* in Italy's  
37  
38 mainland (excluding range in Sicily), discriminated *L. castroviejo* presences/absences  
39  
40 (AUC=0.788) and accurately predicted its probability of occurrence. Furthermore, a  
41  
42 well-calibrated model, which was able to discriminate the species distributions  
43  
44 (AUC=0.828 and AUC=0.956; for *L. castroviejo* and *L. corsicanus*, respectively), was  
45  
46 obtained when species were considered together.  
47

48  
49 **Main conclusions** Our results suggest that *L. castroviejo* and *L. corsicanus* share  
50  
51 extensive niche properties, which reinforces their possible conspecific status. The  
52  
53 ecological niche of their ancestor may have resembled the present one in mainland Italy  
54  
55 since this model was able to accurately predict the distribution range of both species.  
56  
57  
58  
59  
60

1  
2  
3 48 Finally, ecological evidences suggest that niche conservatism may explain the  
4  
5 49 fragmentation of the distribution range of their ancestor, and thus may have been the  
6  
7 50 driver of the initial stages of divergence.  
8

9 51

10  
11 52 **Keywords:** allopatric speciation, Apennine Hare, Broom Hare, conservation

12  
13 53 biogeography, ecological niche, lagomorphs, macroecology, species distribution

14  
15 54 modelling.  
16

17  
18 55  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

For Peer Review

## 56 INTRODUCTION

57 The general tendency of species to maintain similar ecological requirements over  
58 evolutionary time scales is commonly known as ‘niche conservatism’ (Peterson *et al.*,  
59 1999; see also Wiens & Graham, 2005). However, whether species retain their  
60 ecological niches throughout time is currently being highly debated (see e.g. Peterson,  
61 2011). While some authors argued that speciation is not typically accompanied by  
62 ecological innovation, i.e., niches are conserved (e.g. Peterson *et al.*, 1999), others have  
63 found evidence of the contrary (e.g. Graham *et al.*, 2004; Schluter, 2009). The main  
64 discrepancies among studies may derive from methodological artefacts (Warren *et al.*,  
65 2008) and, to a certain extent, from the evolutionary age of the community (Losos *et al.*,  
66 2003). Aside from the debate of whether niche conservatism exists, which should  
67 probably be addressed in terms of identifying degrees of conservatism/divergence, the  
68 concept of niche conservatism is highly valuable for evolutionary biology and  
69 conservation biogeography; most importantly, it allows for the combination of inference  
70 methods from both disciplines.

71 Among other topics in evolutionary biology and conservation biogeography, the  
72 conceptual framework behind niche conservatism allows for the exploration of the  
73 ecological relationships within and between phylogenetically related taxa (see Wiens &  
74 Graham, 2005). Initial studies on this topic suggested that closely related species have  
75 more similar niches (e.g. Peterson *et al.*, 1999). However, some studies have examined  
76 the degree to which niche similarities among taxa is a direct function of the  
77 phylogenetic similarity, and have concluded that patterns of niche evolution beyond  
78 sister taxa are inconsistent (Losos *et al.*, 2003; Knouft *et al.*, 2006; Kalkvik *et al.*,  
79 2012). While some closely related taxa have widely divergent niches, other distantly  
80 related taxa can maintain similar niches. Knouft *et al.* (2006) suggested that some

1  
2  
3 81 species – the anole *Anolis sagrei* group – in a given territory are segregated by  
4  
5 82 environmental characteristics, and thus phylogenetically related species can be  
6  
7 83 ecologically distant due to disruptive ecological adaptation. In such cases, interspecific  
8  
9 84 interactions are stronger among closely related species, and niches tend to diverge from  
10  
11 85 that of near relatives (Losos *et al.*, 2003). This is the expectation for parapatric species,  
12  
13 86 closely related taxa with separate but contiguous distributions without physical barriers  
14  
15 87 between them, which only co-occur in a narrow contact zone (Bull, 1991). Parapatric  
16  
17 88 species usually display divergent ecological niches, that are forced by asymmetric  
18  
19 89 competitive exclusion (Acevedo *et al.*, 2012a), otherwise the distributions could tend to  
20  
21 90 coalesce (Bull & Possingham, 1995). Niche conservatism along phylogenetic trees  
22  
23 91 cannot therefore be considered a rule in nature, but it depends on whether the  
24  
25 92 divergence is caused by differential ecological adaptation. For example, niche  
26  
27 93 conservatism in allopatric sister species would imply little ecological differentiation  
28  
29 94 despite geographic separation, which can be tested empirically. Thus, integrating  
30  
31 95 phylogenetic and macroecological studies within the niche conservatism conceptual  
32  
33 96 framework allows the testing of different evolutionary hypothesis regarding the onset of  
34  
35 97 species divergence (e.g. Kozak & Wiens, 2006; Kalkvik *et al.*, 2012).  
36  
37 98 The genus *Lepus* (hares) is a promising model for studying questions related to niche  
38  
39 99 conservatism. Hares are distributed worldwide and include over 30 presently recognized  
40  
41 100 species that are thought to have resulted from recent rapid radiation, presumably from  
42  
43 101 North America (Matthee *et al.*, 2004; Melo-Ferreira *et al.*, 2012). Many taxa have  
44  
45 102 parapatric distributions (e.g. Acevedo *et al.*, 2012a), which occupy distinct ecological  
46  
47 103 niches even if they are phylogenetically closely related (Melo-Ferreira *et al.*, 2012). On  
48  
49 104 the contrary, *L. castroviejo* and *L. corsicanus* display high morphological (Palacios,  
50  
51 105 1996) and genetic similarities (Alves *et al.*, 2008a; Melo-Ferreira *et al.*, 2012), but  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 106 currently have allopatric ranges (Figure 1). While *L. castroviejo* is endemic to the  
4  
5 107 Cantabrian Mountains in the Iberian Peninsula (Palomo *et al.*, 2007), *L. corsicanus* is  
6  
7 108 endemic to the Italian Apennines and Sicily (Angelici & Luiselli, 2001; Angelici *et al.*,  
8  
9 109 2008), and it was rediscovered in Corsica (Scalera & Angelici, 2003; see also Pietri *et*  
10  
11 110 *al.*, 2011). Furthermore, Melo-Ferreira *et al.* (2012) suggested that ancient hybridization  
12  
13 111 between the ancestors of *L. castroviejo*-*L. corsicanus* and *L. timidus*, an arctic or boreal  
14  
15 112 taxa currently distributed in the northern Palaearctic, must have occurred. These events  
16  
17 113 led to the complete replacement of the original mitochondrial DNA (mtDNA) variants  
18  
19 114 of *L. castroviejo*-*L. corsicanus* by that of *L. timidus*, and explain the close genetic  
20  
21 115 similarity between the mtDNA haplotypes of *L. timidus*, *L. corsicanus* and *L.*  
22  
23 116 *castroviejo*, which have been previously described (Alves *et al.*, 2003; Wu *et al.*,  
24  
25 117 2005). The data suggest that *L. corsicanus* and *L. castroviejo* are sister species which  
26  
27 118 have shared a very recent common ancestor during the Late Pleistocene.  
28  
29 119 In this work, we assessed whether *L. castroviejo* and *L. corsicanus* conserve similar  
30  
31 120 ecological niches, which could provide key insights on the mode of divergence,  
32  
33 121 ecological requirements, conservation, and taxonomic status of these species. The work  
34  
35 122 specifically tested whether the niche properties of one of these species is capable of  
36  
37 123 predicting the distribution range of the other, and whether the species distribution  
38  
39 124 ranges of both could be accurately predicted by a unique ecological model. Analyses of  
40  
41 125 the niches were fully integrated into an evolutionary context.  
42  
43  
44  
45  
46  
47  
48

## 127 **METHODS**

### 128 **Study areas and species distribution**

129 As the extent of the geographical background has substantial effects on the outputs of  
130 species distribution modelling (see Anderson & Raza, 2010; Barve *et al.*, 2011;

1  
2  
3 131 Acevedo *et al.*, 2012b), first we delimited the arena of each species model. This was  
4  
5 132 done by modelling the species distribution where the third-degree polynomial of the  
6  
7 133 spatial coordinates were considered as predictors; the geographical background was  
8  
9 134 delimited by localities which had a predicted favorability higher than the minimum  
10  
11 135 value assigned to a presence (for further details see Acevedo *et al.*, 2012b; Figure 1).  
12  
13 136 Species distribution data were obtained on UTM 10 km × 10 km squares (our territorial  
14  
15 137 unit for modelling purposes) from Palomo *et al.* (2007) for *L. castroviejo* (n=69  
16  
17 138 presences), and for *L. corsicanus* the information was provided by Boitani *et al.* (2002),  
18  
19 139 and was adapted to these territorial units (n=367; of them n=298 are concentrated in  
20  
21 140 Sicily). Although *L. corsicanus* is also present in Corsica, its presence is considered  
22  
23 141 testimonial (Angelici *et al.*, 2008); thus information for Corsica was not considered for  
24  
25 142 modelling.  
26  
27  
28  
29  
30  
31

#### 32 **Ecological variables and spatially explicit modelling**

33  
34 145 Previous studies reported some of the ecological requirements of the studied species. *L.*  
35  
36 146 *castroviejo* has been described as typically occupying shrub lands in which mosaics  
37  
38 147 with pastures and broadleaved woods are frequent (Acevedo *et al.*, 2007). *L. corsicanus*  
39  
40 148 inhabits a broader spectrum of habitats in Mediterranean environments ranging from  
41  
42 149 coastal dune to high mountain habitats, as well as grassland, pastures and/or cultivated  
43  
44 150 areas (Angelici & Luiselli, 2007; Angelici *et al.*, 2008). Based on previous knowledge  
45  
46 151 and the availability of environmental predictors for the scale required in this study, a set  
47  
48 152 of 19 environmental predictors were preselected to account for the niches of these  
49  
50 153 species (see Table 1). The predictors were related to two factors: topoclimate (8  
51  
52 154 predictors) and land uses (11 predictors). Bioclimatic variables and altitude (~1000 m  
53  
54 155 spatial resolution) were obtained from the Worldclim project database (see Hijmans *et*  
55  
56  
57  
58  
59  
60

1  
2  
3 156 *al.*, 2005). Land use data was obtained from Global Land Cover 2005, which accurately  
4  
5 157 assigns the land uses for each pixel of ~300 m (see Bicheron *et al.*, 2008).  
6  
7 158 It is recommended, when conclusions about niche conservatism want to be extracted, to  
8  
9 159 control overfitting by managing the number of predictors (dimensions) in the models  
10  
11 160 (Peterson, 2011). In general, the probability of detecting a conserved niche increases as  
12  
13 161 the number of dimensions in the model decreases (Peterson & Nakazawa, 2008).  
14  
15 162 Following the recommendations provided by Peterson (2011), different strategies were  
16  
17 163 explored to deal with problems deriving from dimensionality (for details Appendix S1  
18  
19 164 of the Supplementary Material). Given that similar interpretations for niche  
20  
21 165 conservatism could be obtained from all the sets of predictors, the results of the most  
22  
23 166 parsimonious models are presented; they were obtained when both topoclimatic and  
24  
25 167 land use predictors were considered together.  
26  
27 168 Using an inductive approach, the macroecological requirements of the studied species –  
28  
29 169 “ecological niche” – based on the locations in which they occurred were determined.  
30  
31 170 Two statistical stages were carried out. To control the increase in type I errors as the  
32  
33 171 number of predictors increased, in a first stage the false discovery rate (FDR) using the  
34  
35 172 procedure proposed by Benjamini & Hochberg (1995) was evaluated. Only predictors  
36  
37 173 that were significantly related to the species distribution under a FDR of  $q < 0.05$  were  
38  
39 174 selected. Predictors selected after controlling the FDR were considered in a multiple  
40  
41 175 logistic regression analysis in a second stage, and the final models were obtained using  
42  
43 176 a forwards-backwards stepwise procedure based on the Akaike Information Criterion  
44  
45 177 (AIC). Statistical analyses were carried out in R 2.15.2 (R Core Team 2012).  
46  
47 178 Four different models were developed: a) an overall model for both sister species, b)  
48  
49 179 one for *L. castroviejoi*, c) one for *L. corsicanus*, and d) one for *L. corsicanus*, which  
50  
51 180 excluded its distribution range in Sicily. To assess the niche similarities between  
52  
53  
54  
55  
56  
57  
58  
59  
60



1  
2  
3 181 species, a model for one species, which was trained on its specific study area, was  
4  
5 182 projected onto the territory of the other species. To project the model developed for one  
6  
7 183 species in another territory (spatial transferability), the similarity in environmental  
8  
9 184 gradients and the correlation structure among independent variables between study  
10  
11 185 areas should be maintained (e.g. Jiménez-Valverde *et al.*, 2011). We successfully  
12  
13 186 checked for model transferability requirements between our study areas (for details see  
14  
15 187 Appendix S2).  
16  
17  
18  
19

### 20 189 **Niche conservatism: a cross-assessment based on discrimination and calibration**

21  
22  
23 190 Warren *et al.* (2008) pointed out the relevance of the null hypotheses in the study of  
24  
25 191 niche conservatism, since both niche similarity and niche identity can be measured, but  
26  
27 192 the results can yield opposite conclusions regarding niche conservatism. Niche  
28  
29 193 similarity tests whether one species' niche model predicts the occurrences of a second  
30  
31 194 species better than expected by chance (e.g. Peterson *et al.*, 1999). The area under the  
32  
33 195 receiver operating characteristic (ROC) curve (AUC), the most popular discrimination  
34  
35 196 capacity measure in species distribution modelling, can be interpreted as the probability  
36  
37 197 that a presence chosen at random will be assigned a higher probability than an absence  
38  
39 198 chosen at random (for details see Krzanowski & Hand, 2009). Therefore, the AUC can  
40  
41 199 be a suitable parameter to quantify niche similarity when the predictions of the model  
42  
43 200 for one species are assessed on the territory of a second species such as it is used in this  
44  
45 201 study. It should be noted that the discrimination performance based only on Sicily  
46  
47 202 cannot be assessed since *L. corsicanus* is present in all territorial units of this island.  
48  
49 203 If we view niche conservatism as a continuum gradient (ranging from niches that are  
50  
51 204 identical to niches that are more similar than random), the AUC can provide  
52  
53 205 information about one extreme. For instance, values significantly higher than 0.5  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 206 indicate niches that are more similar than expected by chance. Yet, the AUC does not  
4  
5 207 provide information on niche identity, since a model can adequately discriminate the  
6  
7 208 distribution of a species even when it is not highly informative of its distribution. This is  
8  
9 209 because the AUC is affected by the distribution of the territory units along the modeled  
10  
11 210 environmental gradient (Lobo *et al.*, 2008; Jiménez-Valverde *et al.*, 2013). Thus  
12  
13 211 calibration, i.e., the degree to which the observed proportion of presences equate to the  
14  
15 212 model estimated probabilities (Pearce & Ferrier, 2000), is useful for informing on niche  
16  
17 213 identity; if the niches of two related species are identical, the niche model for one of  
18  
19 214 them is able to accurately predict the probability of occurrence for the second species.  
20  
21 215 Calibration plots were developed to visually assess the relatedness of the niches. Graphs  
22  
23 216 were constructed with 'ggplot2' R package (Wickham, 2009) by plotting the proportion  
24  
25 217 of occupied evaluation sites of a given species against the predicted probability of  
26  
27 218 presence of the other species (for the ten equal-size probability intervals); points located  
28  
29 219 along the 45° line indicate identical niches. Hosmer–Lemeshow goodness-of-fit statistic  
30  
31 220 (H-L; Lemeshow & Hosmer, 1982) was used for the statistical assessment of the  
32  
33 221 calibration plots. H-L tests assessed whether the observed values matched the expected  
34  
35 222 ones in the calibration plots. Good calibration is obtained when the expected and  
36  
37 223 observed presence rates are not significantly different ( $p > 0.05$ ). Statistical analyses  
38  
39 224 were carried out in R 2.15.2 (R Core Team 2012).  
40  
41  
42  
43  
44  
45  
46

## 47 **RESULTS**

### 48 **Spatially explicit ecological models**

49  
50 228 After controlling the FDR, not all predictors were considered for inclusion in the final  
51  
52 229 models: 14 were considered for an overall model for both species (BIO0, BIO2, BIO4,  
53  
54 230 BIO9, BIO15, BIO19, T11, T20, T30, T70, T110, T120, T130 and T150), 7 for the *L.*  
55  
56  
57  
58  
59  
60

1  
2  
3 231 *castroviejoii* model (BIO2, BIO9, BIO15, T14, T30, T120 and T150), 15 for the *L.*  
4  
5 232 *corsicanus* model (BIO0, BIO2, BIO4, BIO9, BIO15, BIO19, T11, T14, T20, T30, T70,  
6  
7 233 T110, T120, T130 and T150), and 9 for the *L. corsicanus* model excluding Sicily  
8  
9 234 (BIO0, BIO2, BIO15, BIO19, T14, T20, T70, T100 and T210).  
10  
11 235 The forward-backward stepwise procedure allowed one to obtain the final logistic  
12  
13 236 regression models for all species/territories (Table 2, see also Figure 2). In the training  
14  
15 237 territories, models achieved good predictive performance both in terms of  
16  
17 238 discrimination (AUC=0.948, AUC=0.934, AUC=0.954, and AUC=0.813; for the  
18  
19 239 overall model, *L. castroviejoii* model, *L. corsicanus* model, and for the model of *L.*  
20  
21 240 *corsicanus* in mainland Italy, respectively) and calibration (see Figure 3).  
22  
23  
24  
25  
26

241

#### 242 **Niche conservatism**

243 A unique ecological model for both sister species was fitted (Table 2), and it was able to  
244 accurately predict their distribution ranges (Figures 2a). When the discrimination  
245 performance of this model was assessed, a high discrimination capacity was obtained on  
246 *L. castroviejoii* territory (AUC=0.828) and on that of *L. corsicanus* (AUC=0.956).  
247 Calibration plots indicated that the model predicted similarly the probability of presence  
248 for the two species, *L. castroviejoii* and *L. corsicanus* (Figure 3a).  
249 When the model trained on *L. castroviejoii* was transferred to the territory of *L.*  
250 *corsicanus*, it did not discriminate better than chance the distribution of the latter  
251 species (AUC=0.232). On the contrary, the model trained on *L. corsicanus* data was  
252 able to predict the territory of *L. castroviejoii* (AUC=0.814). Furthermore, the model  
253 trained on *L. corsicanus* mainland distribution also discriminated better than chance the  
254 *L. castroviejoii* distribution (AUC=0.789), and *L. corsicanus* overall distribution (AUC=  
255 0.853). Calibration plots for the model trained on *L. castroviejoii*, partially supported the

1  
2  
3 256 interpretations obtained by assessing the AUC (Figure 3b). However, calibration plots  
4  
5 257 showed that the predictions of the model for *L. corsicanus* did not fit accurately the  
6  
7 258 observed frequency of *L. castroviejoii* (Figure 3c), but it did fit the predictions of the  
8  
9 259 model for *L. corsicanus* in mainland Italy (Figure 3d).  
10

11 260

## 12 261 **DISCUSSION**

13  
14  
15 262 Multidisciplinary approaches are fundamental for understanding the past, present and  
16  
17 263 future evolutionary and ecological features of species, and to gather relevant  
18  
19 264 information that can be used to implement adequate conservation measures. Analyses  
20  
21 265 using morphological and genetic data have previously suggested that two allopatric  
22  
23 266 species of hares, *L. castroviejoii* and *L. corsicanus*, are recent descendants of a common  
24  
25 267 species (Palacios, 1996; Alves *et al.*, 2008a; Melo-Ferreira *et al.*, 2012). Here, these  
26  
27 268 taxa were studied from a novel perspective, and extensive similarities were also found  
28  
29 269 in their ecological traits. These results have important implications on the understanding  
30  
31 270 of the evolutionary history of these species and their ecological requirements.  
32  
33 271 Moreover, it contributes to the discussion of the relationship between niche  
34  
35 272 conservatism and evolutionary history.  
36  
37  
38  
39

40 273

### 41 274 **On the methodological approach**

42  
43  
44 275 Various metrics have been proposed to quantify potential niche overlap, and some were  
45  
46 276 comparatively assessed in the context of niche conservatism (e.g. Warren *et al.*, 2008;  
47  
48 277 Rödder & Engler, 2011). Each showed advantages and drawbacks on the desirable  
49  
50 278 characteristics for a metric of potential niche overlap (see Rödder & Engler, 2011).  
51  
52 279 Based on the concept behind the pioneer study on niche conservatism (Peterson *et al.*,  
53  
54 280 1999), a simple and more in-depth exploration of niche similarities between two sister  
55  
56  
57  
58  
59  
60

1  
2  
3 281 species was used here. The approach was based on a cross-assessment focused on the  
4  
5 282 two characteristic of the model's predictive performance, i.e., discrimination and  
6  
7 283 calibration. Assessing the discrimination with the AUC, and according to the model  
8  
9 284 based on the sister species, the probability for a presence chosen at random for one  
10  
11 285 species to be assigned a higher probability than an absence chosen at random was  
12  
13 286 determined. In other words, niche similarity was assessed ( $AUC > 0.5$ ). To determine if  
14  
15 287 two niches are (or are not) identical, the interspecific niche relationships should also be  
16  
17 288 assessed in terms of calibration. In the cross-assessment context, a perfectly calibrated  
18  
19 289 model shows that two niches are identical. The calibration plot informs about the  
20  
21 290 uncertainty of the predictions, and how they are distributed along the gradient of  
22  
23 291 probabilities predicted by the model, which is also needed for a proper understanding of  
24  
25 292 the AUC values (Jiménez-Valverde *et al.*, 2013). Thus, in a cross-assessment context,  
26  
27 293 discrimination and calibration allow for a more in-depth exploration of niche  
28  
29 294 similarities; hence, additional conclusions about niche relationships can be extracted.  
30  
31 295 For instance, a situation in which the model overpredicts species occurrence under a  
32  
33 296 given threshold of probability and underpredicts over that threshold can be identified  
34  
35 297 (see Figure 3a in the *L. corsicanus*'s territory). That situation could be informing about  
36  
37 298 the presence of an unconsidered factor (e.g., a competitor, a resource, human  
38  
39 299 interference, etc.), which is preventing the species from occupying some favorable  
40  
41 300 localities.  
42  
43  
44  
45  
46  
47  
48

49 302 **Ecological similarity of taxa: implications for taxonomy, evolutionary history and**  
50  
51 303 **conservation**

52  
53 304 The spatial resolution of the analysis was suggested as a factor affecting the conclusions  
54  
55 305 about niche conservatism (e.g., Peterson & Nyári, 2007). Therefore, the grain size of the  
56  
57 306 analyses is important to properly understand the interpretations extracted from the  
58  
59  
60

1  
2  
3 307 results. Results obtained in this study – from an ecological perspective and at 10km ×  
4  
5 308 10km spatial resolution – support the close evolutionary relationship between *L.*  
6  
7 309 *castroviejo* and *L. corsicanus*. This similarity adds to the morphological analyses  
8  
9 310 performed by Palacios (1996), and to the molecular inferences made by Alves *et al.*  
10  
11 311 (2008a) and Melo-Ferreira *et al.* (2012), which led these authors to suggest that these  
12  
13 312 taxa could eventually be considered conspecific. If parapatric groups of species (as  
14  
15 313 *Lepus* spp. in Europe) are naturally conceived to be ecologically divergent (Bull &  
16  
17 314 Possingham, 1995), then niche similarities between related species such as *L.*  
18  
19 315 *castroviejo* and *L. corsicanus* (even in allopatry), can be used as arguments to discuss a  
20  
21 316 possible conspecific status. Even if species concepts vary and the classification of *L.*  
22  
23 317 *castroviejo* and *L. corsicanus* as conspecific will depend on the applied criterion, the  
24  
25 318 similarities of these taxa is remarkable and shows how morphology, genes and ecology  
26  
27 319 may be conserved in the initial stages of divergence.  
28  
29 320 According to genetic evidences, *L. castroviejo* and *L. corsicanus* shared a common  
30  
31 321 ancestor possibly at least until the Upper Pleistocene (Alves *et al.*, 2008a; Melo-Ferreira  
32  
33 322 *et al.*, 2012). Similarly, as it has been described for other taxa such as the chamois  
34  
35 323 (*Rupicapra* spp., Masini & Lovari, 1988), it could be hypothesized that their common  
36  
37 324 ancestor occupied a larger range in Europe during the Pleistocene and the subsequent  
38  
39 325 climatic changes split it into two allopatric refugia in the two Southern European  
40  
41 326 peninsulas, Iberia and Italy (Angelici & Luiselli, 2007). Our results suggest that this  
42  
43 327 range of separation was not driven by disruptive adaptation to different ecological  
44  
45 328 settings, but must have resulted from the fragmentation of favorable habitat.  
46  
47 329 Apparently, *L. castroviejo* and *L. corsicanus* did not expand from these refugia, which  
48  
49 330 may have been due to i) competition with other hare species, ii) niche conservatism, or  
50  
51 331 most probably iii) by both factors to certain extent (see below). *L. castroviejo* could  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 332 have initially faced competition by *L. granatensis* and likely by *L. timidus* when this  
4  
5 333 species was present in northern Iberian Peninsula in Late Pleistocene (Altuna, 1970).  
6  
7 334 The presence of *L. timidus* mtDNA type in *L. castroviejo* due to hybridization (Alves *et*  
8  
9 335 *al.*, 2008b; Melo-Ferreira *et al.*, 2012) is congruent with the hypothesis of contact  
10  
11 336 between these species. Also, when the niche expressed by *L. corsicanus* was projected  
12  
13 337 onto Iberia, in general, a high environmental potential for *L. castroviejo* in more  
14  
15 338 southern areas of the Iberian study area was obtained (Figure 2). These areas are not  
16  
17 339 currently occupied by *L. castroviejo* but are highly favourable for *L. granatensis*  
18  
19 340 (Acevedo *et al.*, 2012c). This suggests that competition with *L. granatensis* may have  
20  
21 341 been an important factor impeding colonization of these southern territories by *L.*  
22  
23 342 *castroviejo*. Similarly, in the Italian Peninsula, the northwards expansion of *L.*  
24  
25 343 *corsicanus* could have been prevented by competition with *L. timidus* and *L. europaeus*  
26  
27 344 since the past range of *L. corsicanus* reached more northern latitudes (Angelici &  
28  
29 345 Luiselli, 2007; Angelici *et al.*, 2008).  
30  
31 346 Niche conservatism could have also limited the capacity of these species to colonize  
32  
33 347 new habitats since they are currently occupying “ecological islands” (e.g. Figure 1),  
34  
35 348 separated by intervening landscapes unsuitable for these species, i.e., by an ecological  
36  
37 349 barrier. In this situation, niche conservatism can limit adaptation to suboptimal  
38  
39 350 ecological conditions (see Wiens & Graham, 2005); hence, it restricts the expansion  
40  
41 351 ability of the species. Following this line of thought, niche conservatism may have  
42  
43 352 further implications on the evolution of these sister species. If the species cannot adapt  
44  
45 353 to suboptimal environmental conditions, then the barrier will continue to prevent gene  
46  
47 354 flow between these species, and they will inevitably continue to diverge (Kozak &  
48  
49 355 Wiens, 2006), according to the allopatric speciation model. At this point, it should be  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

1  
2  
3 356 highlighted that these species offer a fascinating opportunity for a natural experiment in  
4  
5 357 which, for instance, the genetic bases of recent local adaptations can be explored.  
6  
7 358 Finally, but not least, our results suggest that the niche expressed by *L. corsicanus* in  
8  
9 359 mainland Italy retained ecological traits able to accurately predict the global distribution  
10  
11 360 of these sister species. Interestingly, some genetic differences between hares from  
12  
13 361 mainland Italy and Sicily were found using mtDNA (Pierpaoli *et al.*, 1999; Alves *et al.*,  
14  
15 362 2008a; Pietri *et al.*, 2011), which may have originated from a drift during a founding  
16  
17 363 event of the Sicilian *L. corsicanus* population. The ecological divergence can be related  
18  
19 364 to the fact that *L. corsicanus* is the only hare species in Sicily despite the intensive  
20  
21 365 release of *L. europaeus* during the last decades (Angelici *et al.*, 2008). Therefore, the  
22  
23 366 populations in Sicily are evolving in absence of potential competitors, and thus  
24  
25 367 displaying something that could closely resemble the part of its fundamental niche that  
26  
27 368 is present in Sicily. On the contrary, continental populations evolved in contact with  
28  
29 369 competitors species, and the pattern of distribution accounted by the models is closer to  
30  
31 370 the species realized niche (e.g. Soberón & Peterson, 2005; Angelici & Luiselli, 2007).  
32  
33 371 Thus, different parts of the niche could have been occupied in mainland Italy and Sicily  
34  
35 372 which could be related to rather different expressions of the species ecological niche  
36  
37 373 (see Randin *et al.*, 2006). Moreover, the fact that the model trained on *L. corsicanus*  
38  
39 374 mainland population was able to predict the range of *L. castroviejoi* but not vice-versa,  
40  
41 375 suggest that *L. corsicanus* populations in mainland Italy have retained the ecological  
42  
43 376 traits of their ancestor, and thus, these Italian populations have an impressive value for  
44  
45 377 ecological and evolutionary studies. Also, due to the characteristics described above, *L.*  
46  
47 378 *castroviejoi* and *L. corsicanus* are significant evolutionary units that should be  
48  
49 379 preserved.  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60



1  
2  
3 380 Similarly to the seminal studies of Peterson *et al.* (1999) and Wiens & Graham (2005),  
4  
5 381 among others, our study shows that macroecology can be useful to explore diverse  
6  
7 382 topics in evolution. Therefore, the integration of macroecology and phylogeography  
8  
9 383 would contribute decisively in the strengthening of the geographic components of  
10  
11 384 evolutionary biology, which is often omitted (Kidd & Ritchie, 2006).  
12  
13  
14 385

#### 16 386 **ACKNOWLEDGMENTS**

17  
18 387 We are grateful to Miles Silman and three anonymous referees for their useful  
19  
20 388 comments and suggestions on previous versions of the manuscript. Lucía D. Maltez  
21  
22 389 kindly reviewed the English. P. A. had a Jose Castillejo fellowship (2010-2011) in  
23  
24 390 Portugal awarded by the Ministerio de Ciencia e Innovación to conduct this study, and  
25  
26 391 was also partially supported by the CGL2009-11316/BOS Spanish Government and  
27  
28 392 FEDER project. Currently, P. A. and J. M.-F. hold post-doctoral grants from Fundação  
29  
30 393 para a Ciência e a Tecnologia (FCT) funded by Programa Operacional Potencial  
31  
32 394 Humano (POPH) – Quadro de Referência Estratégico Nacional (QREN) from the  
33  
34 395 European Social Fund and by the Portuguese Ministério da Educação e Ciência  
35  
36 396 (SFRH/BPD/90320/2012 and SFRH/ BPD/43264/2008, respectively). Financial support  
37  
38 397 was partially obtained from research project grants PTDC/BIA-EVF/111931/2009 and  
39  
40 398 PTDC/BIA-EVF/115069/2009 funded by FEDER through the COMPETE program and  
41  
42 399 Portuguese national funds through the FCT.  
43  
44  
45  
46  
47  
48

#### 49 401 **REFERENCES**

50  
51 402 Acevedo, P., Alzaga, V., Cassinello, J. & Gortázar, C. (2007) Habitat suitability  
52  
53 403 modelling reveals a strong niche overlap between two poorly known species, the  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 404 broom hare and the Pyrenean grey partridge, in the north of Spain. *Acta*  
4  
5 405 *Oecologica*, **31**, 174-184.  
6  
7 406 Acevedo, P., Jiménez-Valverde, A., Lobo, J.M. & Real, R. (2012b) Delimiting the  
8  
9 407 geographical background in species distribution modelling. *Journal of*  
10  
11 408 *Biogeography*, **39**, 1383-1390.  
12  
13 409 Acevedo, P., Jiménez-Valverde, A., Melo-Ferreira, J., Real, R. & Alves, P.C. (2012a)  
14  
15 410 Parapatric species and the implications for climate change studies: a case study  
16  
17 411 on hares in Europe. *Global Change Biology*, **18**, 1509-1519.  
18  
19 412 Acevedo, P., Melo-Ferreira, J., Real, R. & Alves, P.C. (2012c) Past, Present and Future  
20  
21 413 Distributions of an Iberian Endemic, *Lepus granatensis*: Ecological and  
22  
23 414 Evolutionary Clues from Species Distribution Models. *PLoS ONE* 7(12):  
24  
25 415 e51529.  
26  
27 416 Altuna, J. (1970) Hallazgo de una liebre ártica (*Lepus timidus*) en el yacimiento  
28  
29 417 prehistorico de Urtiga (Guipuzcoa). *Munibe*, **22**, 165-168.  
30  
31 418 Alves, P.C., Ferrand, N., Suchentrunk, F. & Harris, D.J. (2003) Ancient introgression of  
32  
33 419 *Lepus timidus* mtDNA into *L. granatensis* and *L. europaeus* in the Iberian  
34  
35 420 Peninsula. *Molecular Phylogenetics and Evolution*, **27**, 70-80.  
36  
37 421 Alves, P.C., Melo-Ferreira, J., Branco, M., Suchentrunk, F., Ferrand, N. & Harris, D.J.  
38  
39 422 (2008a) Evidence for genetic similarity of two allopatric European hares (*Lepus*  
40  
41 423 *corsicanus* and *L. castroviejoi*) inferred from nuclear DNA sequences.  
42  
43 424 *Molecular Phylogenetics and Evolution*, **46**, 1191-1197.  
44  
45 425 Alves, P.C., Melo-Ferreira, J., Freitas, H. & Boursot, P. (2008b) The ubiquitous  
46  
47 426 mountain hare mitochondria: multiple introgressive hybridization in hares,  
48  
49 427 genus *Lepus*. *Philosophical Transactions of the Royal Society, Biological*  
50  
51 428 *Sciences*, **363**, 2831-2839.  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 429 Anderson, R.P. & Raza, A. (2010) The effect of the extent of the study region on GIS  
4  
5 430 models of species geographic distributions and estimates of niche evolution:  
6  
7 431 preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela.  
8  
9 432 *Journal of Biogeography*, **37**, 1378–1393.
- 10  
11 433 Angelici, F.M. & Luiselli L. (2001) Distribution and status of the critically endangered  
12  
13 434 Apennine hare *Lepus corsicanus* De Winton 1898, in continental Italy and  
14  
15 435 Sicily. *Oryx*, **35**, 245-249.
- 16  
17 436 Angelici, F.M. & Luiselli, L.(2007) Range, dynamic biogeography and ecological  
18  
19 437 interactions of two species: *Lepus corsicanus* and *Lepus europaeus* in Italy.  
20  
21 438 *Wildlife Biology*, **13**, 251-257.
- 22  
23 439 Angelici, F.M., Randi, E., Riga, F. & Trocchi, V. (2008) *Lepus corsicanus*. In: IUCN  
24  
25 440 2011. IUCN Red List of Threatened Species. Version 2011.2.  
26  
27 441 <[www.iucnredlist.org](http://www.iucnredlist.org)>. Downloaded on 05 June 2012.
- 28  
29 442 Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson,  
30  
31 443 A.T., Soberón, J. & Villalobos, F. (2011) The crucial role of the accessible area  
32  
33 444 in ecological niche modeling and species distribution modeling. *Ecological*  
34  
35 445 *Modelling*, **222**, 1810-1819.
- 36  
37 446 Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical  
38  
39 447 and powerful approach to multiple testing. *Journal of the Royal Statistical*  
40  
41 448 *Society Series B*, **57**, 289-300.
- 42  
43 449 Bicheron, P., Defourny, P., Brockmann, C. *et al.* (2008) *GlobCover 2005 – Products*  
44  
45 450 *description and validation report, Version 2.1, 2008*. Available on the ESA  
46  
47 451 IONIA website (<http://ionial.esrin.esa.int/>).
- 48  
49 452 Boitani, L., Corsi, F., Falcucci, A., Marzetti, I., Masi, M., Montemaggiori, A.,  
50  
51 453 Ottaviani, D., Reggiani, G. & Rondinini, C. (2002) Rete ecologica nazionale: un  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 454           approccio alla conservazione dei vertebrati italiani. Relazione Finale. DCN –  
4  
5 455           Ministero Ambiente, Dep. BAU - University of Rome “La Sapienza”.  
6  
7 456 Bull, C.M. & Possingham, H. (1995) A model to explain ecological paraptry. *The*  
8  
9 457           *American Naturalist*, **145**, 935-947.  
10  
11 458 Bull, C.M. (1991) Ecology of parapatric distributions. *Annual Review of Ecology and*  
12  
13 459           *Systematics*, **22**, 19-36.  
14  
15 460 Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J. & Moritz, C. (2004) Integrating  
16  
17 461           phylogenetics and environmental niche models to explore speciation  
18  
19 462           mechanisms in dendrobatid frogs. *Evolution*, **58**, 1781-1793.  
20  
21 463 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high  
22  
23 464           resolution interpolated climate surfaces for global land areas. *International*  
24  
25 465           *Journal of Climatology*, **25**, 1965-1978.  
26  
27 466 Jiménez-Valverde, A., Acevedo, P., Barbosa, A.M., Lobo, J.M., Real, R. (2013)  
28  
29 467           Discrimination capacity in species distribution models depends on the  
30  
31 468           representativeness of the environmental domain. *Global Ecology and*  
32  
33 469           *Biogeography*, **22**, 508-516.  
34  
35 470 Jiménez-Valverde, A., Decae, A.E. & Arnedo, M.A. (2011) Environmental suitability of  
36  
37 471           new reported localities of the funnelweb spider *Macrothele calpeiana*: an  
38  
39 472           assessment using potential distribution modelling with presence-only  
40  
41 473           techniques. *Journal of Biogeography*, **38**, 1213-1223.  
42  
43 474 Jovani, R. & Tella, J.L. (2006) Parasite prevalence and sample size: misconceptions and  
44  
45 475           solutions. *Trends in Parasitology*, **22**, 214-218.  
46  
47 476 Kalkvik, H.M., Stout, I.J., Doonan, T.J. & Parkinson, C.L. (2012) Investigating niche  
48  
49 477           and lineage diversification in widely distributed taxa: phylogeography and  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 478 ecological niche modeling of the *Peromyscus maniculatus* species group.  
4  
5 479 *Ecography*, **35**, 54-64.  
6  
7 480 Kidd, D.M. & Ritchie, M.G. (2006) Phylogeographic information systems: putting the  
8  
9 481 geography into phylogeography. *Journal of Biogeography*, **33**, 1851-1865.  
10  
11 482 Knouft, J.H., Losos, J.B., Glor, R.E. & Kolbe, J.J. (2006) Phylogenetic analysis of the  
12  
13 483 evolution of the niche in lizards of the *Anolis sagrei* group. *Ecology*, **87**, S29-  
14  
15 484 S38.  
16  
17 485 Kozak, K.H. & Wiens, J.J. (2006) Does niche conservatism promote speciation? A case  
18  
19 486 study in North American salamanders. *Evolution*, **60**, 2604-2621.  
20  
21 487 Krzanowski, W.J. & Hand, D.J. (2009) ROC curves for continuous data. CRC/Chapman  
22  
23 488 and Hall, New York.  
24  
25 489 Lemeshow, S. & Hosmer, D.W. (1982) A review of goodness of fit statistics for use in  
26  
27 490 the development of logistic regression models. *American Journal of*  
28  
29 491 *Epidemiology*, **115**, 92-106.  
30  
31 492 Lobo, J., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the  
32  
33 493 performance of predictive distribution models. *Global Ecology and*  
34  
35 494 *Biogeography*, **17**, 145-151.  
36  
37 495 Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Rodriguez Schettino, L.,  
38  
39 496 Chamizo Lara, A., Jackman, T.D. & Larson, A. (2003) Niche lability in the  
40  
41 497 evolution of a Caribbean lizard community. *Nature*, **424**, 542-545.  
42  
43 498 Masini, F. & Lovari, S. (1988) Systematics, phylogenetic and dispersal of the chamois  
44  
45 499 (*Rupicapra* spp.). *Quaternary Research*, **30**, 339-349.  
46  
47 500 Matthee, C.A, van Vuuren, B.J, Bell, D. & Robinson, T.J (2004) A molecular  
48  
49 501 supermatrix of the rabbits and hares (Leporidae) allows for the identification of  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 502 five intercontinental exchanges during the Miocene. *Systematic Biology*, **53**,  
4  
5 503 433-447.  
6  
7 504 Melo-Ferreira, J., Boursot, P., Carneiro, M., Esteves, P.J., Farello, L. & Alves, P.C.  
8  
9 505 (2012) Recurrent Introgression of Mitochondrial DNA Among Hares (*Lepus*  
10  
11 506 spp.) revealed by Species-tree Inference and Coalescent Simulations.  
12  
13 507 *Systematics Biology*, **61**, 367-381.  
14  
15 508 Palacios, F. (1996) Systematics of the indigenous hares of Italy traditionally identified  
16  
17 509 as *Lepus europaeus* Pallas, 1778 (Mammalia: Leporidae). *Bonner Zoologische*  
18  
19 510 *Beitraege*, **5**, 59-91.  
20  
21 511 Palomo, L.J., Gisbert, J. & Blanco, J.C. (2007) *Atlas y Libro Rojo de los Mamíferos*  
22  
23 512 *Terrestres de España*. Ministerio de Medio Ambiente, Madrid.  
24  
25 513 Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models  
26  
27 514 developed using logistic regression. *Ecological Modelling*, **133**, 225-245.  
28  
29 515 Peterson, A.T. & Nakazawa, Y. (2008) Environmental data sets matter in ecological  
30  
31 516 niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*.  
32  
33 517 *Global Ecology and Biogeography*, **17**, 135-144.  
34  
35 518 Peterson, A.T. & Nyári, A.S. (2007) Ecological niche conservatism and Pleistocene  
36  
37 519 refugia in the thrush-like mourner, *Schiffornis* sp., in the neotropics. *Evolution*,  
38  
39 520 **62-1**, 173-183  
40  
41 521 Peterson, A.T. (2011) Ecological niche conservatism: a time-structured review of  
42  
43 522 evidence. *Journal of Biogeography*, **38**, 817-827.  
44  
45 523 Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological  
46  
47 524 niches in evolutionary time. *Science*, **285**, 1265–1267  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 525 Pierpaoli, M., Riga, F., Trocchi, V. & Randi, E. (1999) Species distinction and  
4  
5 526 evolutionary relationships of the Italian hare (*Lepus corsicanus*) as described by  
6  
7 527 mitochondrial DNA sequencing. *Molecular Ecology*, **8**, 1805-1817.  
8  
9  
10 528 Pietri, C., Alves, P. & Melo-Ferreira, J. (2011) Hares in Corsica: high prevalence of  
11  
12 529 *Lepus corsicanus* and hybridization with introduced *L. europaeus* and *L.*  
13  
14 530 *granatensis*. *European Journal of Wildlife Research*, **57**, 313-321.  
15  
16 531 R Core Team (2012) R: A language and environment for statistical computing. R  
17  
18 532 Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0,  
19  
20 533 URL <http://www.R-project.org/>.  
21  
22  
23 534 Randin, C.F., Dirnbock, T., Dullinger, S., Zimmermann, N., Zappa, M. & Guisan, A.  
24  
25 535 (2006) Are niche-based models transferable in space? *Journal of Biogeography*,  
26  
27 536 **33**, 1689-1703.  
28  
29 537 Rödder, D. & Engler, J.O. (2011) Quantitative metrics of overlaps in Grinnellian niches:  
30  
31 538 advances and possible drawbacks. *Global Ecology and Biogeography*, **20**, 915-  
32  
33 539 927.  
34  
35  
36 540 Scalera, R. & Angelici, F.M. (2003) Rediscovery of the Apennine hare *Lepus*  
37  
38 541 *corsicanus* in Corsica. *Bollettino del Museo Regionale Scienze Naturali Torino*,  
39  
40 542 **20**, 161-166.  
41  
42  
43 543 Schluter, D. (2009) Evidence for Ecological Speciation and Its Alternative. *Science*,  
44  
45 544 **323**, 737-741.  
46  
47 545 Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological  
48  
49 546 niches and species' distribution areas. *Biodiversity Informatics*, **2**, 1-10.  
50  
51 547 Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus  
52  
53 548 conservatism: quantitative approaches to niche evolution. *Evolution*, **62**, 2868-  
54  
55 549 2883.  
56  
57  
58  
59  
60

- 1  
2  
3 550 Wickham, H. (2009) ggplot2: elegant graphics for data analysis. Springer New York.  
4  
5 551 Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology,  
6  
7 552 and conservation biology. *Annual Review of Ecology, Evolution, and*  
8  
9 553 *Systematics*, **36**, 519-539.  
10  
11 554 Wu, C., Wu, J., Bunch, T.D., Li, Q., Wang, Y. & Zhang, Y. (2005) Molecular  
12  
13 555 phylogenetics and biogeography of *Lepus* in Eastern Asia based on  
14  
15 556 mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **37**, 45-  
16  
17 557 61.  
18  
19  
20  
21 558  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

For Peer Review



1  
2  
3 559 **SUPPORTING INFORMATION**

4  
5 560 Additional Supporting Information may be found in the online version of this article:

6  
7 561 **Appendix S1** Controlling dimensionality effects in niche conservatism interpretations.

8  
9 562 **Appendix S2** Checking for models transferability between study areas.

10  
11 563 As a service to our authors and readers, this journal provides supporting information

12  
13 564 supplied by the authors. Such materials are peer-reviewed and may be re-organized for

14  
15 565 online delivery, but are not copy-edited or typeset. Technical support issues arising

16  
17 566 from supporting information (other than missing files) should be addressed to the

18  
19 567 authors.

20  
21 568

22  
23  
24  
25 569 **BIOSKETCH**

26  
27 570 **Pelayo Acevedo** is a researcher at the CIBIO, Centro de Investigação em

28  
29 571 Biodiversidade e Recursos Genéticos, InBio Laboratório Associado. His interests

30  
31 572 include the study of factors affecting the distribution and abundance of pathogens, and

32  
33 573 their hosts and vectors, through fragmented habitats.

34  
35  
36 574

37  
38 575 **Author contributions:** P.A. and P.C.A. conceived the ideas; P.A. analysed the data;

39  
40 576 P.A., J.M.-F., R.R. and P.C.A. participated in the discussion of the results and wrote the

41  
42 577 manuscript.

43  
44 578

45  
46  
47 579 Editor: Miles Silman

48  
49 580

581 **Table 1.** Predictors used in the different models to study the *Lepus castroviejo* and *L.*  
 582 *corsicanus* distributions. A quarter is a period of three months (1/4 of the year).

Factor	Codes	Description (units)
Topoclimate	BIO0	Altitude (masl)
	BIO2	Mean diurnal range (mean of monthly [max T - min T]) (°C*10)
	BIO3	Isothermality (BIO2/Temperature annual range) (*100)
	BIO4	Temperature seasonality (standard deviation*100)
	BIO9	Mean temperature of driest quarter (°C*10)
	BIO15	Precipitation seasonality (coefficient of variation)
	BIO18	Precipitation of warmest quarter (mm)
	BIO19	Precipitation of coldest quarter (mm)
	Land uses	T11
T14		Rainfed croplands (%)
T20		Mosaic cropland / vegetation (grassland/shrubland/forest) (%)
T30		Mosaic vegetation / cropland (%)
T70		Closed needleleaved 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 (%)

583  
584

585 **Table 2.** Results of the models developed on the current distribution of *Lepus*  
 586 *castroviejoi* and *L. corsicanus* distributions. Predictors were listed following the order  
 587 of entrance (the first one in the top) in the stepwise procedure. B parameter coefficient  
 588 and its standard error (SE), z-value test statistics, Sig. significance (\*\*\*)  $P < 0.001$ , \*\*  $P$   
 589  $< 0.01$ , \*  $P < 0.05$  and ns  $P > 0.05$ ). Predictors coded as in Table 1.

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)	-2.111ns
	<i>Intercept</i>	<i>-1.1033(0.5063)</i>	<i>-2.179*</i>
<i>L. castroviejoi</i>	BIO9	-0.1622(0.0217)	-7.475***
	T120	-3.4344(1.7825)	-1.927ns
	T14	-0.0942(0.0377)	-2.501*
	<i>Intercept</i>	<i>25.6815(3.4690)</i>	<i>7.403***</i>
<i>L. corsicanus</i>	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)	-0.028ns
	<i>Intercept</i>	<i>-1.4300(0.5510)</i>	<i>-2.595**</i>
<i>L. corsicanus</i> 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)	-1.595ns
	<i>Intercept</i>	<i>-11.2500(1.8910)</i>	<i>-5.952***</i>

590

591

592 **FIGURE LEGENDS**

593 **Figure 1.** Location of the study areas. Current distributions of *Lepus castroviejo* and *L.*  
594 *corsicanus* (excluding range in Corsica) represented in UTM 10×10 km (marks).

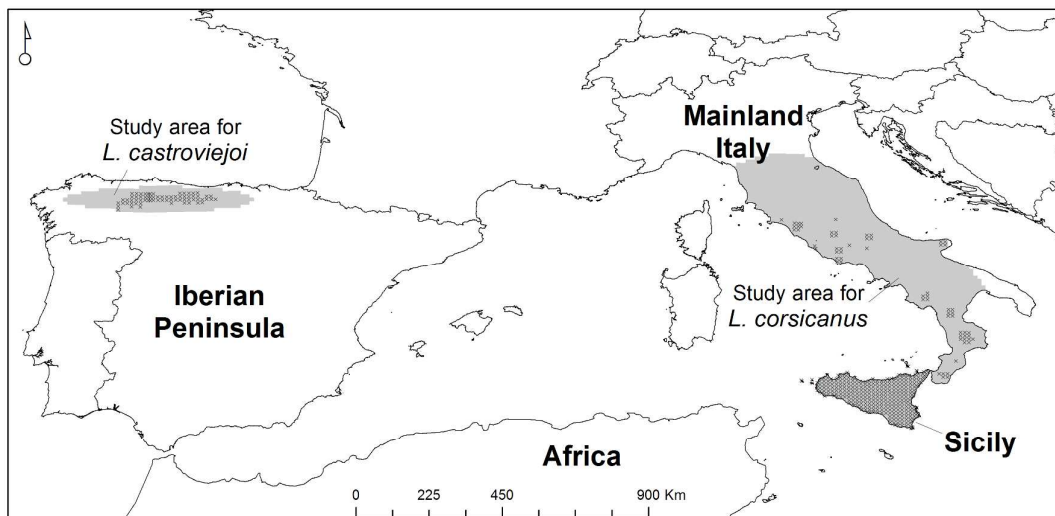
595 Species distribution data were obtained from Palomo *et al.* (2007) for Iberian Peninsula  
596 and adapted from Boitani *et al.* (2002) for Italy. Trend surface analyses (see text for  
597 details) were used to delimit the arena for modelling purposes (areas in grey).

598 **Figure 2.** Probability of species occurrence in the study areas (from dark blue=1 to  
599 yellow=0) obtained from the different models: overall species distribution (a), model  
600 trained on *L. castroviejo* and then projected onto Italy (b), model trained on *L.*  
601 *corsicanus* and projected onto Iberia (c), and finally, model trained on *L. corsicanus*,  
602 but excluding its range in Sicily, and projected onto both Sicily and Iberia (d). Arrows  
603 denote the projection of a model from the training area onto the territory of the sister  
604 species.

605 **Figure 3.** Calibration plots showing the relationship between the predicted probability  
606 of occurrence for a model and the observed proportion of evaluation localities occupied  
607 by the species: overall species distribution (a), model trained on *L. castroviejo* (b),  
608 model trained on *L. corsicanus* (c), and finally, model trained on *L. corsicanus* but  
609 excluding Sicily (d). Arrows denote the projection of a model from the training area to  
610 the territory of the sister species. Full/open symbols indicate bins with  $\geq 15$  or  $< 15$   
611 localities, respectively. In bins with  $< 15$  localities the observed frequency should be  
612 cautiously considered (Jovani & Tella, 2006). Significant codes: \*\*\*  $P < 0.001$ , \*\*  $P$   
613  $< 0.01$ , \*  $P < 0.05$  and ns  $P > 0.05$ , refer to Hosmer-Lemeshow goodness-of-fit statistic  
614 (Lemeshow & Hosmer, 1982).

615

616 **Figure 1**

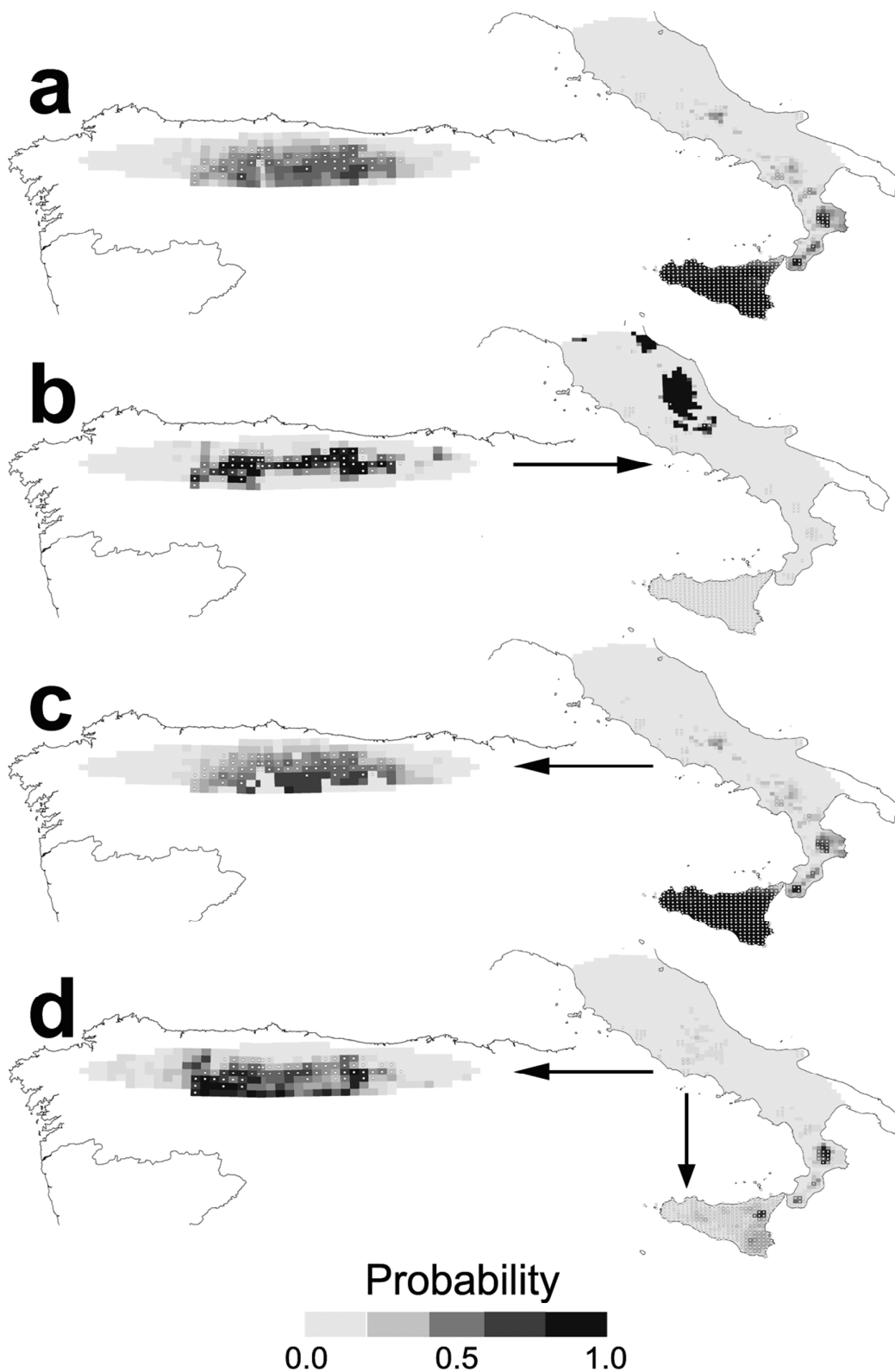


617

Peer Review

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

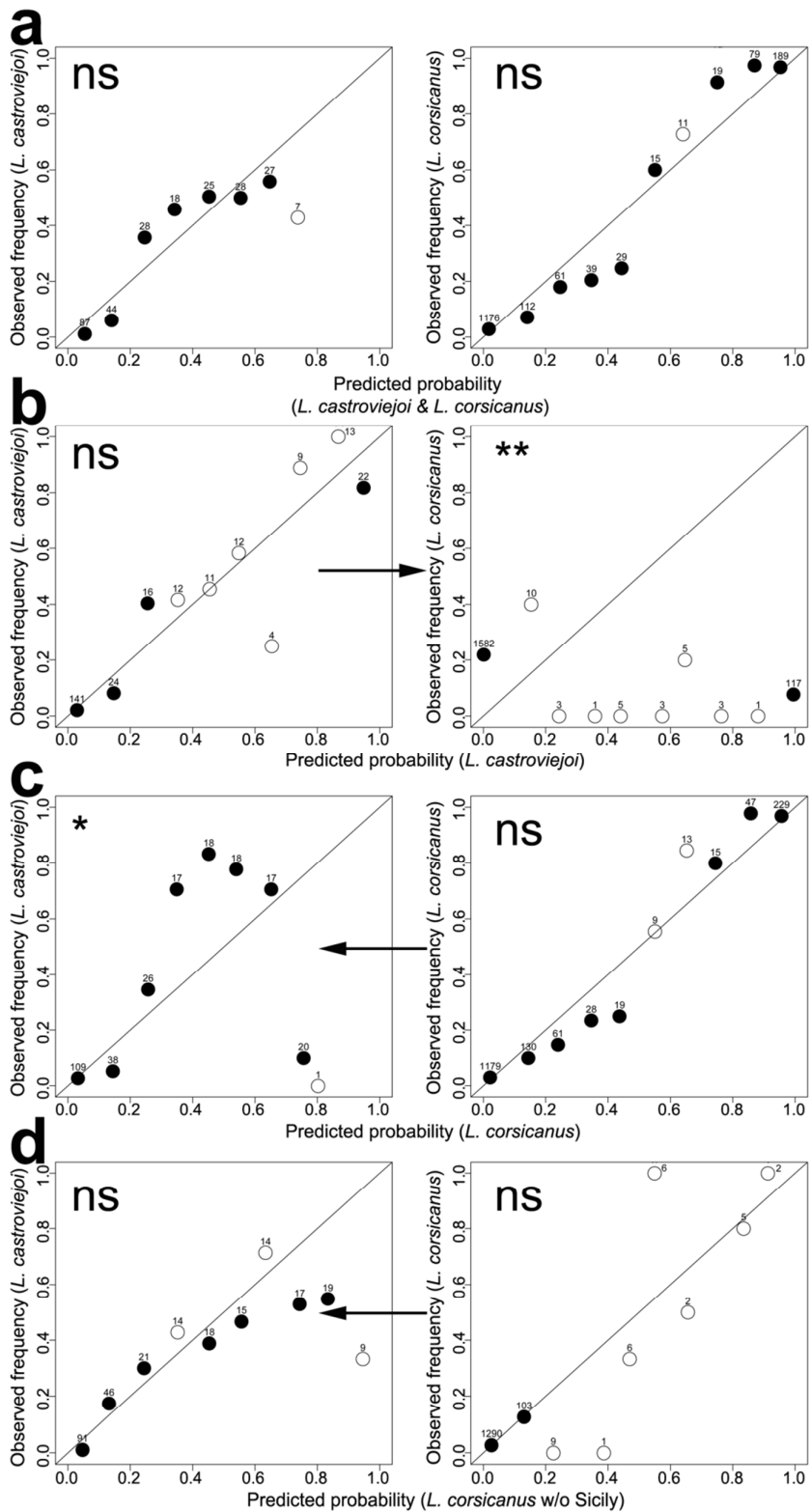
618 **Figure 2**



619

620

621 Figure 3



622

## 1 Supplementary material – Journal of Biogeography

### 2 Evidence for niche similarities in the allopatric sister species *Lepus castroviejo* and

3 *L. corsicanus* - - P. Acevedo, J. Melo-Ferreira, R. Real, P.C. Alves

#### 4 Appendix S1. Controlling dimensionality effects in niche conservatism

##### 5 *interpretations.*

6 We carried out parallel analyses to be sure that the number of parameters in the models

7 – model's dimensionality (see Peterson, 2011) – is not affecting our interpretations on

8 niche conservatism. We run models following three different approaches: i) considering

9 all available climate and land uses predictors (n=19; approach 1), ii) only climatic

10 predictors (n=8) were considered, as they usually yield higher predictive capacity than

11 land uses (approach 2), and iii) models were fitted with the orthogonal factors (n=6)

12 resulting from a principal component analysis (approach 3). For each approach, final

13 models were selected following a forwards-backwards stepwise procedure based on

14 Akaike Information Criterion (AIC; Akaike, 1974). Results are summarized in Table S1

15 and Figure S1.

16

17 **Table S1.** Summary of the models carried out under approaches differing in the set of

18 predictors. Akaike Information Criterion is provided as a measure of model parsimony. The

19 number of predictors included in each final model is reported in brackets.

Approach	Model		
	<i>L. castroviejo</i>	<i>L. corsicanus</i>	<i>L. corsicanus</i> in mainland Italy
<i>Approach 1</i>	157.16 (3)	626.94 (9)	410.97 (5)
<i>Approach 2</i>	161.69 (2)	630.29 (7)	413.56 (4)
<i>Approach 3</i>	161.79 (6)	862.35 (6)	426.73 (5)

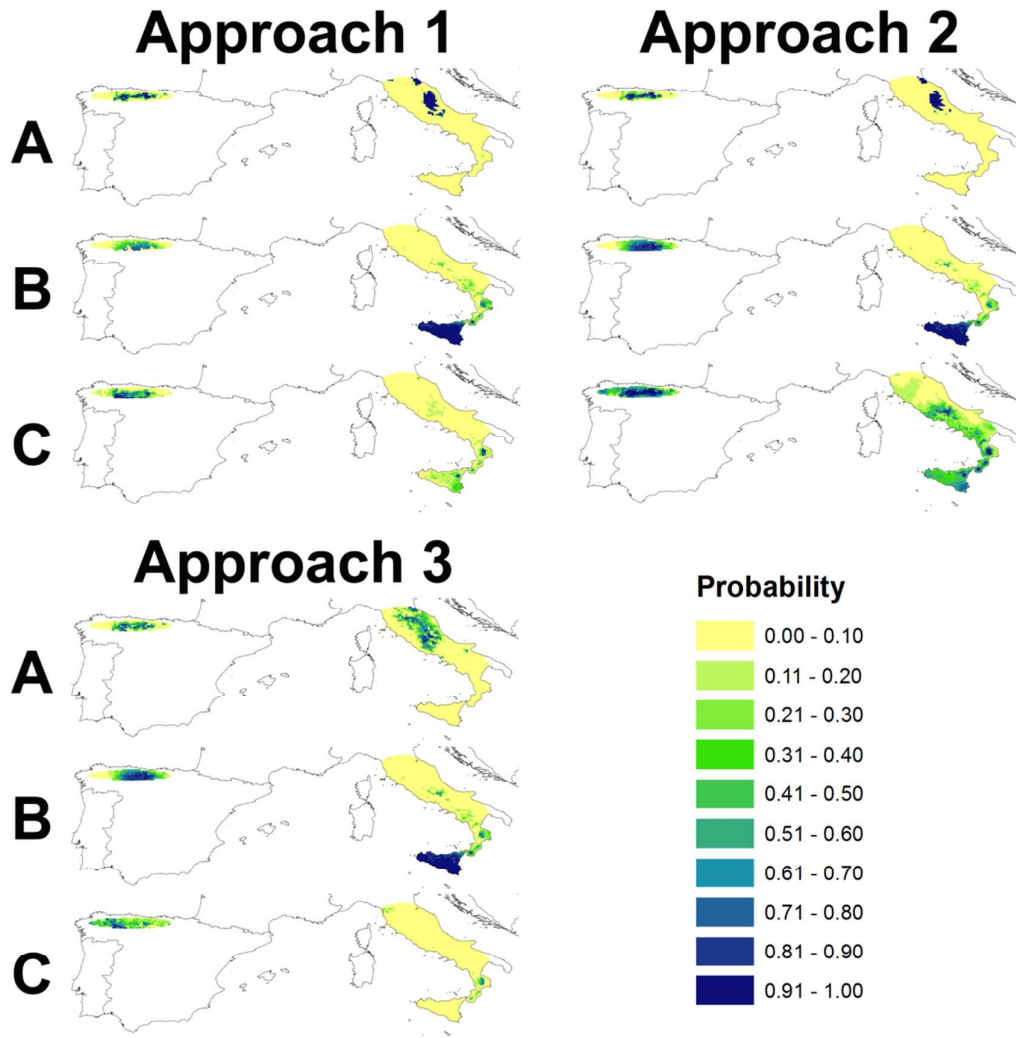
20

21 Independently of the approach, similar interpretations could be obtained when models

22 predictions were mapped (Table S1, Figure S1): only models trained on data for *L.*



1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23 *corsicanus* predicted potentiality in areas occupied by both species. Thus, no effects  
24 derived of the number of predictors are expected to affect our interpretations, and only  
25 results from approach 1 are shown in the main text since it consistently yielded the most  
26 parsimonious models (Table S1).



27  
28 **Figure S1.** Probability of species occurrence in the study areas (from dark-blue=1 to yellow=0)  
29 obtained from the different approaches (see above for details) and models: model trained on *L.*  
30 *castroviejo* and then projected to Italy [A], model trained on *L. corsicanus* and transferred to  
31 Iberia [B], and finally, model trained on *L. corsicanus*, but excluding its range in Sicily, and  
32 projected to both Sicily and Iberia [C]).

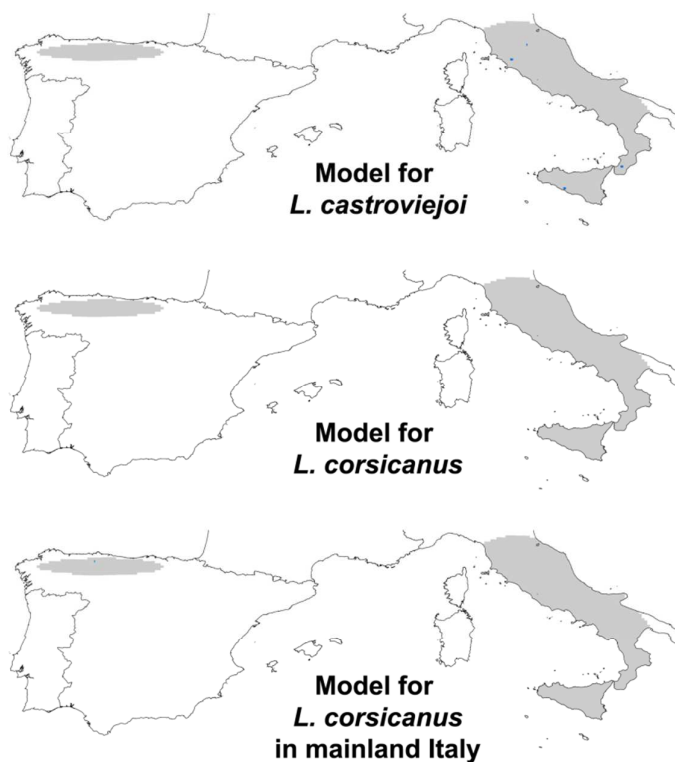
1  
2  
3 **33 Appendix S2. Checking for models transferability between study areas.**  
4

5 34 Three pivotal requirements should be checked when models are transferred outside their  
6  
7 35 training area. First, for each model, Mahalanobis distances were computed to represent  
8  
9 36 the ecological dissimilarity of the transferring area to the training area, i.e. the degree of  
10  
11 37 extrapolation. Second, multicollinearity among predictors in a model can bias the  
12  
13 38 predictions when this model is transferred outside the range where it was trained. The  
14  
15 39 collinearity was quantified using the variance inflation factor (VIF). Given that  
16  
17 40 collinearity can be a problem with VIFs higher than 3 (see Zuur *et al.*, 2010), VIFs were  
18  
19 41 calculated for each predictor and study area as the inverse of the coefficient of non-  
20  
21 42 determination of the regression of each predictor against all others. Finally, Mantel tests  
22  
23 43 were run to assess the maintenance of the correlation structure of the predictors between  
24  
25 44 the training and the transferring areas (see Jiménez-Valverde *et al.*, 2011). Pearson's  
26  
27 45 correlation coefficient between the elements of the matrices was used as the statistical  
28  
29 46 test, and its significance was assessed by permuting the row labels of one matrix relative  
30  
31 47 to the other 9999 times.  
32  
33

34  
35  
36 48 Statistical analyses were carried out in R 2.15.2 (R Core Team 2012). The 'HH' package  
37  
38 49 was used for the variance inflation factor analyses (Heiberger, 2012) and 'ade4' for the  
39  
40 50 Mantel tests (Chessel *et al.*, 2004).  
41  
42

43 51 Results suggest that only in very few localities were the models extrapolated; thus, a  
44  
45 52 certain degree of uncertainty in the predictions can be expected in these localities  
46  
47 53 (Figure S2). According to the obtained VIF values, no effects of multicollinearity are  
48  
49 54 expected when models were spatially transferred (mean VIF value / range: 1.72 / 1.37-  
50  
51 55 2.82; 1.81 / 1.02-2.99; 1.80 / 1.25-2.91 for the areas of Iberia, Italy and mainland Italy  
52  
53 56 (excluding Sicily), respectively). Similarly, the correlation structures of the predictors  
54  
55 57 between training and transferring areas were maintained in all study cases, precisely  
56  
57  
58  
59  
60

1  
2  
3 58 between Italian and Iberian areas ( $r=0.27$ ,  $p<0.05$ ), mainland Italy and Iberia ( $r=0.28$ ,  
4  
5 59  $p<0.05$ ), and mainland Italy and Sicily ( $r=0.51$ ,  $p<0.01$ ). That is, the correlation  
6  
7 60 structures of the predictors between training and transferring areas were maintained in  
8  
9 61 all study cases.  
10  
11  
12 62



63  
64 **Figure S2.** Maps showing the degree of environmental dissimilarity – in terms of the predictors  
65 retained in the models (see Table 2) – between the transferring area and the training ones.  
66 Localities with values in the predictors that were outside their range in the training areas are  
67 depicted in blue.  
68

#### 69 **References for the supplementary material**

70 Akaike, H. (1974) New look at statistical-model identification. *Transactions on*  
71 *Automatic Control*, **19**, 716-723.  
72 Chessel, D., Dufour, A.B. & Thioulouse, J. (2004) The ade4 package-I- One-table  
73 methods. *R News* **4**, 5-10.

- 1  
2  
3 74 Heiberger, R.M. (2012) HH: Statistical Analysis and Data Display: Heiberger and  
4  
5 75 Holland. R package version 2.3-27. <http://CRAN.R-project.org/package=HH>  
6  
7 76 Jiménez-Valverde, A., Decae, A.E. & Arnedo, M.A. (2011) Environmental suitability of  
8  
9 77 new reported localities of the funnelweb spider *Macrothele calpeiana*: an  
10  
11 78 assessment using potential distribution modelling with presence-only  
12  
13 79 techniques. *Journal of Biogeography*, **38**, 1213-1223.  
14  
15  
16 80 Peterson, A.T. (2011) Ecological niche conservatism: a time-structured review of  
17  
18 81 evidence. *Journal of Biogeography*, **38**, 817-827.  
19  
20  
21 82 R Core Team (2012) R: A language and environment for statistical computing. R  
22  
23 83 Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0,  
24  
25 84 URL <http://www.R-project.org/>.  
26  
27 85 Zuur, A.F., Ieno, E.N., Elphick, C.S. (2010) A protocol for data exploration to avoid  
28  
29 86 common statistical problems. *Methods in Ecology and Evolution*, **1**, 3-14.  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60