

## Global Change Biology

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### **Parapatric species and the implications for climate change studies: a case study on hares in Europe**

Running title: **Parapatric species and climate change**

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27 distribution models.

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29 **Primary Research Article**

30

31 **ABSTRACT**

32 Parapatry is a biogeographic term used to refer to organisms whose ranges do not  
33 overlap but are immediately adjacent to each other; they only co-occur – if at all – in a  
34 narrow contact zone. Often there are no environmental barriers in the contact zones,  
35 hence competitive interaction is usually advocated as the factor that modulates species  
36 distribution ranges. Even though the effects of climate change on species distribution  
37 have been widely studied, few studies have explored these effects on the  
38 biogeographical relationships between closely related, parapatric, species. We modelled  
39 environmental favourability for three parapatric hare species in Europe – *Lepus*  
40 *granatensis*, *L. europaeus* and *L. timidus* – using ecogeographical variables and  
41 projected the models into the future according to the IPCC A2 emissions scenario.  
42 Favourabilities for present and future scenarios were combined using fuzzy logic with  
43 the following aims: i) to determine the biogeographical relationships between hare  
44 species in parapatry, that is *L. granatensis/L. europaeus* and *L. europaeus/L. timidus*;  
45 and ii) to assess the effects of climate change on each species as well as on their  
46 interspecific interactions. In their contact area *L. granatensis* achieved higher  
47 favourability values than *L. europaeus*, suggesting that if both species have a similar  
48 population status, the former species may have some advantages over the latter if  
49 competitive relationships are established. Climate change had the most striking effect  
50 on the distribution of *L. timidus*, especially when interspecific interactions with *L.*  
51 *europaeus* were taken into account, which may compromise the co-existence of *L.*  
52 *timidus*. The results of this study are relevant not only for understanding the distribution  
53 patterns of the hares studied and the effects of climate change on these patterns, but also  
54 for improving the general application of species distribution models to the prediction of  
55 the effects of climate change on biodiversity.

56

## 57 INTRODUCTION

58 Parapatry is a biogeographic pattern in which two species have separate but contiguous  
59 distributions without physical barriers between them, and they only co-occur – if at all –  
60 in a narrow contact zone. This is a common distribution pattern in closely related  
61 species and in species with a weak phylogenetic relationship but with a high level of  
62 ecological similarity (Bull 1991). Since parapatry is considered as an opposite state to  
63 coexistence, most explanations of parapatric distributions assume negative interactions  
64 as the cause of interspecific exclusion along geographic gradients; as a result, the  
65 species with the highest persistence potential displaces the other (Bull & Possingham  
66 1995 and references therein).

67 A key step in species distribution modelling (SDM) (Guisan & Thuiler 2005) involves  
68 taking into account the biotic factors (i.e., interactions with other species that modify  
69 the ability for a given species to maintain populations) that contribute to delimiting  
70 species' ranges. The inclusion of biotic interactions improves SDM performance for  
71 both positively-related species, such as specialist species requiring a specific biotic  
72 resource (e.g., Araújo & Luoto 2007; Kissling *et al.* 2010), and for other systems in  
73 which competitive forces modulate species distribution ranges (e.g., Meier *et al.* 2011).  
74 Biotic interactions are especially relevant in the context of studies predicting  
75 distributional shifts under climate change scenarios, since the distribution of a species  
76 may change not only because of altered climatic conditions, but also because interactive  
77 species move in response to climate change (Meier *et al.* 2011). Thus, understanding the  
78 biogeographical relationships between parapatric species and how they vary in response  
79 to climate changes is needed to improve the predictions on shifts in species  
80 distributions.

81 Even though biotic interactions are highly relevant in SDM, studies investigating  
82 procedures to account for them are still scarce. The simple approach of including the  
83 distribution of other species as predictors in a predictive model of a given species (e.g.,  
84 Araújo & Luoto 2007) may not in fact reflect a biotic interaction, but rather the absence  
85 of important environmental predictors in the model (Guisan & Thuiller 2005). In  
86 addition, the inclusion of these predictors in the model may only provide information on  
87 potential interaction between species, but not on the possible role of each species in the  
88 interaction. Biotic interactions, such as those producing parapatry, are usually  
89 asymmetric relationships in which the distribution of one species is strongly mediated  
90 by another, but not always *vice versa* (Bull & Possingham 1995). Thus, the inclusion of  
91 other species' ranges as predictors ideally requires prior knowledge to choose the  
92 correct biotic predictors from among many alternatives; nevertheless, this is not always  
93 possible when, for example, competitive exclusion between species has not been  
94 previously documented.

95 Fuzzier approaches have been applied to assess interspecific relationships in a  
96 biogeographical context. For example, Chefaoui *et al.* (2005) explored variation in the  
97 suitability scores for two species along an environmental gradient and showed the  
98 usefulness of this approach to describe potential sympatry between two species (see also  
99 Acevedo *et al.* 2007a, 2007b). Sattler *et al.* (2007) examined biogeographical  
100 relationships between cryptic species by combining Ecological Niche Factor Analysis  
101 (Hirzel *et al.* 2002) and discriminant analysis. The discriminant factor correlates with  
102 the variables that best segregate the species. These authors used the discriminant factor  
103 as an integrative variable to compare the "niches" of the species and estimate their  
104 degree of overlap. Based on the conceptual framework applied in these studies and  
105 using the favourability function (see Real *et al.* 2006), Acevedo *et al.* (2010) developed

106 an approach to explore the biogeographical relationships between related species. Even  
107 though this approach was proposed in a context of native *versus* introduced species, it  
108 can be used to study other types of biotic relationships. This approach can be used to  
109 map species interaction and to create directional hypothesis about the role of each  
110 species in the interaction, although species interactions cannot be conclusively  
111 demonstrated using these kinds of approaches (Anderson *et al.* 2002; Jiménez-Valverde  
112 *et al.* 2007).

113 European hares provide a suitable model by which to study the biogeographical  
114 relationships between parapatric species. At present, taxonomic experts accept five  
115 species of the genus *Lepus* occurring naturally in Europe: *L. europaeus*, *L. timidus*, *L.*  
116 *granatensis*, *L. castroviejo* and *L. corsicanus* (Mitchell-Jones *et al.* 1999; Alves &  
117 Hackländer 2008). The latter two species, although being genetically similar (Alves *et*  
118 *al.* 2008), have restricted allopatric ranges – *L. castroviejo* in the Cantabrian Mountains  
119 of the Iberian Peninsula and *L. corsicanus* in the Apennines and Sicily – and the other  
120 three species have wider distributions (see Figure 1). This complex distribution pattern  
121 certainly reflects specific ecological adaptations, and enhances different putative contact  
122 zones. However, the relationship between each pair of parapatric species is not expected  
123 to be symmetrical as usually one species prevails over the other in the contact zones,  
124 even when competitive exclusion relationships have not been firmly evidenced. On the  
125 one hand, it is known that populations of *L. granatensis* are increasing but those of *L.*  
126 *europaeus* are decreasing in their contact areas in the Iberian Peninsula (Gortázar *et al.*  
127 2007). On the other hand, other studies have identified the expansion of *L. europaeus* as  
128 one of the causes of the generalized decline of *L. timidus* (see Thulin 2003; Jansson &  
129 Pehrson 2007; Patton *et al.* 2010; Reid 2011).

130 Using European hares as a study model and the analytical procedure described in  
131 Acevedo *et al.* (2010), this study has the following aims: i) to determine the  
132 biogeographical relationships between hare species with wider distributions, namely *L.*  
133 *granatensis/L. europaeus* and *L. europaeus/L. timidus*; and ii) to assess the effects of  
134 climate change on each species and their interspecific interactions. The results may  
135 assist in improving the general application of species distribution models for assessing  
136 the effects of climate change on biodiversity.

137

## 138 MATERIAL AND METHODS

### 139 Species data

140 The European distribution of *Lepus* spp. was extracted from The Atlas of European  
141 Mammals (Mitchell-Jones *et al.* 1999; Figure 1). Information refers to UTM 50×50 km  
142 squares as they were the territorial units used for modelling purposes. Due to the fact  
143 that the sampling effort used to create the Atlas was not spatially homogeneous, we  
144 calculated the number of mammal species in each square as a proxy of sampling effort;  
145 for modelling purposes, we only considered the UTM squares in which at least one  
146 species has been reported (n = 2557). This filter excluded most of Eastern Europe which  
147 coincided with the most incomplete area identified by the Atlas authors (A.J. Mitchell-  
148 Jones, personal communication). In the study area, the most frequent hare species was  
149 *L. europaeus* (n = 1119 presences), followed by *L. timidus* (n = 532 presences) and  
150 finally the Iberian endemism *L. granatensis* (n = 118 presences).

### 151 Environmental data

152 The occurrence of the three hare species in each UTM square was modelled using 35  
153 potential explanatory variables related to the following factors: spatial location (2  
154 variables), topography (1 variable), climatology (15 variables), and land use (17  
155 variables; see Table 1). These variables were chosen on the basis of availability at this  
156 scale and potential predictive power, and were assumed to be correlated with more  
157 explanatory factors.

158 Land use data came from Global Land Cover 2005, which is freely available at  
159 <http://ionial.esrin.esa.int/>. The map (~300 m spatial resolution) covers the entire planet,  
160 and its accuracy has been successfully validated (see Bicheron *et al.* 2008). Bioclimatic  
161 variables (for present and future times) and altitude (~1000 m spatial resolution) were  
162 obtained from the Worldclim project database (see Hijmans *et al.* 2005 for details). The



163 models calibrated for the present period were projected into the future by replacing the  
164 current bioclimatic variables in the models with those expected according to the climate  
165 change scenario for the future period up to 2080 using the A2 emissions scenario  
166 (Nakicenovic *et al.* 2000). This scenario is defined as a world of strengthening regional  
167 cultural identities, with an emphasis on family values and local traditions, high  
168 population growth, and less concern for rapid economic development. We used only  
169 one scenario because our main interest was to assess the changes in interspecific  
170 relationships between parapatric species due to climate, rather than to assess the effect  
171 of different global circulation models or emissions scenarios (see Real *et al.* 2010).

## 172 **Modelling**

173 We used an inductive approach to estimate the macroecological requirements of the  
174 species from the locations in which they occurred (Corsi *et al.* 2000). We modelled the  
175 occurrence of each species assuming that, after correcting for the sampling effort  
176 previously described, if a species was not observed within a UTM square, this was  
177 equivalent to the absence of the species. For each species, the model was calibrated  
178 using a 70% random sample of the data and evaluated against the remaining 30%.  
179 Firstly, to control for the increase in type I errors as the number of independent  
180 variables increased, we evaluated the false discovery rate (FDR; García 2003) using the  
181 procedure proposed by Benjamini & Hochberg (1995), and only accepted variables that  
182 were significantly ( $p < 0.05$ ) related to the species distribution under an FDR of  $q <$   
183 0.05. The selected variables were then used in a multiple logistic regression procedure  
184 (Hosmer & Lemeshow 1989), and the final models were selected following a forwards–  
185 backwards stepwise procedure. Finally, to establish direct comparisons between models  
186 (species), the logistic probabilities were used to obtain favourability values using the  
187 function described by Real *et al.* (2006). The favourability function is a valuable tool to

188 study biogeographical relationships between models whatever the proportion of  
189 presence records (sample prevalence) in the calibration datasets (e.g., see Real *et al.*  
190 2009; Acevedo *et al.* 2010). This is due to the fact that a favourability value of 0.5  
191 always corresponds to the same environmental threshold, thus the independence of  
192 these values in relation to species prevalence enables direct comparisons between  
193 models (species) built with different prevalences.

194 Sensitivity – the percentage of correctly predicted presences to the total number of  
195 presences –, specificity – the percentage of correctly predicted absences to the total  
196 number of absences –, and the area under the ROC curve (AUC) were estimated on the  
197 validation datasets to assess the discriminative capacity of the models (Fielding & Bell  
198 1997; but see Lobo *et al.* 2008). To calculate sensitivity and specificity a threshold of  
199 0.5 was used as a cutoff for favourability values in all the models according to the  
200 favourability concept (Real *et al.* 2006). All statistical analyses were performed using  
201 SPSS 18 (SPSS Inc., Chicago, IL, USA) statistical software.

### 202 **Assessing relationships between parapatric species**

203 An inherent quality of favourability values is that they can be regarded as the degree of  
204 membership in the fuzzy set of sites whose environmental conditions are favourable to  
205 the species (Robertson *et al.* 2004; Real *et al.* 2006). Thus, fuzzy logic operations can  
206 be used to compare different models. This is an advantage of the favourability function  
207 over other SDM techniques when the aim of the study is to combine models for  
208 different species, scenarios, etc. (see Estrada *et al.* 2008; Acevedo *et al.* 2010, 2011).  
209 The biogeographical relationships between two species can be assessed using the fuzzy  
210 overlap index (FOvI; see Acevedo *et al.* 2010), i.e., the ratio between the degree to  
211 which the study area is favourable to the two studied species simultaneously and the  
212 degree to which it is favourable for either species (Dubois & Prade 1980; Kunchenva

213 2001). This index varies from 0 (no overlap in favourability) to 1 (complete overlap in  
 214 favourability). The FOvI can be decomposed into absolute local overlap values (FOvI-  
 215 L) that represent the contribution of each locality (UTM square) to the FOvI. Thus, the  
 216 FOvI-L shows the spatial location of the areas where spatial overlap between species is  
 217 expected to occur (Acevedo *et al.* 2010).

218 Trends on species favourability were assessed across the range of FOvI-L values for  
 219 each pair of parapatric species (*L. granatensis*/*L. europaeus* and *L. europaeus*/*L.*  
 220 *timidus*) using the procedure described by Acevedo *et al.* (2010). Briefly, FOvI-L values  
 221 were divided into 10 intervals (0.1 width), and mean favourability values at each  
 222 interval were calculated for each pair of species. Throughout the gradient defined by  
 223 FOvI-L, and consistent with the favourableness-severity hypothesis (Richerson & Lum  
 224 1980), it can be assumed that competition between species increases and competitive  
 225 exclusion decreases as FOvI-L increases. Subsequently, we divided the curve into fixed  
 226 intervals: FOvI-L < 0.2 (areas that were unfavourable for at least one species) and  
 227 FOvI-L > 0.8 (areas simultaneously highly favourable to the two species). According to  
 228 the favourableness-severity hypothesis, the area with 0.2 < FOvI-L < 0.8 is where biotic  
 229 interactions could limit species occurrence (Acevedo *et al.* 2010).

### 230 **Assessing changes in distribution patterns between climatic scenarios**

231 We used the fuzzy logic indices described in Real *et al.* (2010) to calculate the increases  
 232 in favourability (*I*), the favourability overlap (*O*), favourability maintenance (*M*) and the  
 233 predicted shift in favourability (*S*) between present-future climate scenarios (date<sub>1</sub>-  
 234 date<sub>2</sub>, respectively) for each hare species and between-parapatric species interaction:

$$235 \quad I = \frac{cF_{date2} - cF_{date1}}{cF_{date1}} \quad O = \frac{c(F_{date2} \cap F_{date1})}{c(F_{date2} \cup F_{date1})} \quad M = \frac{c(F_{date2} \cap F_{date1})}{cF_{date1}}$$

$$S = \frac{\text{Min}[cF_{date1} - c(F_{date2} \cap F_{date1}), cF_{date2} - c(F_{date2} \cap F_{date1})]}{cF_{date1}}$$

237 Where  $cX$  is the cardinality of the  $X$  fuzzy set, i.e., the sum of all squares' favourability  
 238 and  $Min$  is the minimum value. The fuzzy intersection is the minimum value between  
 239 the favourability of two scenarios and the fuzzy union the maximum value between  
 240 them (Zadeh 1965). These indices are useful tools to describe the magnitude and  
 241 direction of the changes in distribution patterns between two scenarios such as those  
 242 driven by climate (Real *et al.* 2010) or land use changes (Acevedo *et al.* 2011). FOVI-L  
 243 can be also included in fuzzy logic operations due to its conceptual characteristics, and  
 244 thus variations can be also assessed in the distribution pattern of the FOVI-L when  
 245 models are projected into a future climate change scenario.

246

247 **RESULTS**

248 Logistic regression procedure selected variables related to spatial situation, climate,  
249 topography and land uses to explain the European distribution of *L. granatensis*, *L.*  
250 *europaeus* and *L. timidus* at 50×50 km spatial resolution (Table 2). By applying the  
251 favourability function, maps were obtained for the studied species (Figure 2) which  
252 determine the localities with ecogeographical characteristics that favour or constrain the  
253 presence of the species ( $F > 0.5$  or  $F < 0.5$ , respectively). The models showed a high  
254 discrimination capacity ( $Se$ ,  $Sp$  and AUC were 1, 0.950 and 0.987 for *L. granatensis*;  
255 0.821, 0.787 and 0.877 for *L. europaeus*; 0.908, 0.935 and 0.970, for *L. timidus*).

256 When the favourability functions were projected into the future (2080), different  
257 situations for each species were observed (Figure 2). Our results suggest that whereas  
258 the *L. granatensis* and *L. europaeus* ranges will slightly shift to the north/northeast, the  
259 *L. timidus* distribution range will notably decrease. Based on the maps, these  
260 interpretations are also supported by the fuzzy logic indices summarized in Table 3.

261 The relationships between parapatric species in terms of favourability and their trends  
262 over the gradient defined by FOvI-L are displayed in Figure 3 (see also Table 3).

263 Localities that are simultaneously highly favourable to both *L. granatensis* and *L.*  
264 *europaeus* (FOvI-L  $> 0.8$ ), i.e., with ecogeographical conditions that actually favour the  
265 presence of both species, do not exist at present and are not expected to exist in future  
266 scenarios. Both species overlapped with FOvI-L  $> 0.2$  in only 3.2% of the study area  
267 (82 squares); this means that 96.8% of the study area is highly unfavourable ( $F < 0.2$ )  
268 to, at least, one of the species, i.e., they are territories with ecogeographical conditions  
269 that constraint the presence of, at least, one of the species. In the intervals with  
270 intermediate values of FOvI-L, *L. granatensis* attained higher favourability values than  
271 *L. europaeus*, suggesting that given equal population status (e.g., balanced densities) for

272 both species, if competitive relationships were established in these localities the former  
273 species may have some advantages over the latter. This situation is maintained in the  
274 future climatic scenario, although favourability for *L. granatensis* is expected to  
275 decrease slightly, with a subsequent reduction in overlap between species (Table 3).  
276 Regarding the biogeographical relationship between *L. europaeus* and *L. timidus*, the  
277 current favourability maps for these species overlapped by more than double compared  
278 to those for the previous pair of species. *L. timidus* attained higher favourabilities than  
279 *L. europaeus* in the intervals with intermediate values of FOvI-L. When models for  
280 these species were projected into the future climatic scenario, the situation was similar  
281 to that obtained for the present period, except for the areas with FOvI-L > 0.8 that  
282 generally shifted northward.

283 If the results of the interspecific interactions are considered, an uncertain area could be  
284 delineated where biotic interactions could limit species occurrence; this is the area with  
285  $0.2 < \text{FOvI-L} < 0.8$  (see Figure 3). This assumes 3.2% of the study area for *L.*  
286 *granatensis/L. europaeus* and 29.5% for *L. europaeus/L. timidus* in the models for the  
287 present period, and 2.2% and 21.5%, respectively, for models projected into the future.

288 Two extreme values can be estimated when assessing the sensitivity of the species to  
289 climate change. The first is defined by the rates of change for each single species  
290 assuming non-negative relationships between parapatric species, that is, those rates  
291 exclusively modulated by abiotic factors (see Table 3). When biotic interactions are  
292 considered, the other extreme value can be obtained by assuming that each species  
293 could be competitively excluded from the uncertainty area (see Table 3).

294

295 **DISCUSSION**

296 Our results focus on two issues: the methodology used and the conservation of the  
297 studied species in Europe. On the one hand, the analytical approach followed in this  
298 study is useful for a deeper assessment of the biogeographical relationship between  
299 parapatric species and its expected shifts under new scenarios according to global  
300 change. Even though this approach is based on the favourableness-severity hypothesis  
301 (Richerson & Lum 1980) and it was used in the context of competing species, under  
302 other theoretical frameworks it can be useful for exploring the biogeographical  
303 relationships of species, for example, when species are positively related (Callaway *et*  
304 *al.* 2002). On the other hand, the effects of climate change on the distribution of *L.*  
305 *timidus* predicted for 2080, especially when combined with potential exclusion by *L.*  
306 *europaeus*, should drive managers to consider global climate change as one of the  
307 factors involved in *L. timidus* decline in Europe, as already appears to be occurring in  
308 some contact areas (see Thulin 2003).

309 **The methodological approach**

310 A key step in SDM involves taking into account biotic interaction; thus, changes in  
311 climate may not only directly alter the distribution of a species, but also indirectly alter  
312 it through affecting the distribution of other interactive species (Meier *et al.* 2011). Our  
313 study offers a new perspective on the role of interspecific interactions on shaping future  
314 distribution ranges in response to climate change. The methodological approach,  
315 previously described by Acevedo *et al.* (2010), allowed us: i) to determine the areas  
316 where the probability of competition between species is higher; and assuming equal  
317 population status for the species involved in the interaction, ii) to infer a directional  
318 hypothesis on the role of each species; and iii) to explore the spatial shifts in species  
319 interactions pattern under different scenarios, that is, to assess interspecific interactions

320 and how they would evolve under climate change scenarios (see Klanderud & Totland  
321 2005). It is an improvement over other approaches previously used in the context of  
322 SDM and climate change assessment which are mainly based on including the  
323 distribution data of the interacting species as predictors during the modelling processes.  
324 Clearly, the critical issue is not to determine whether biotic interactions have effects at  
325 biogeographical scales, but to quantify their magnitude (e.g., Leathwick & Austin  
326 2001). This key question is difficult to answer mainly because there is no validation  
327 data available by which to assess the predictions of the models under climate change  
328 conditions (Araújo *et al.* 2005). It is also often very difficult to distinguish spatial  
329 patterns generated by interspecific interactions from those caused by abiotic causes,  
330 historical factors or dispersal barriers (Wiens 1989). With our approach two extreme  
331 situations for each species can be determined, one in which no effects of interspecific  
332 interaction were considered when assessing shifts in the species distribution area due to  
333 climate changes, and another in which it was assumed that the species was totally  
334 excluded from potentially competitive exclusion areas (see also Araújo & Luoto 2007).  
335 In other words, it presents a range between no effects and the full effects of interspecific  
336 interactions. The real situation is likely to be between these extremes, although the exact  
337 outcome cannot be determined. The approach used allows the identification and  
338 mapping of the most probable areas for competitive exclusion, and so would be of use  
339 when designing subsequent studies on biotic interactions at local scales (Anderson *et al.*  
340 2002; Jiménez-Valverde *et al.* 2007). Even when the real distribution of the species in  
341 the future is unknown, with this approach a more detailed assessment can be made of  
342 the expected species distribution in response to change, based on the directional  
343 hypothesis about the role of each species and, when available, on previous knowledge



344 of species' relationships obtained from local studies. This is the case for hare species in  
345 Europe (see below), although this may not be possible for every species.

346 **On the hare species in Europe**

347 Our results on the effects of climate change on *L. granatensis* and *L. europaeus*  
348 distributions indicate slight northward shifts in their ranges by 2080 according to the A2  
349 emissions scenario. However, this situation does not apply to *L. timidus*, as the  
350 predictions suggest that its range will undergo notable reductions because of climate  
351 changes (Figure 2). First, these results are consistent with studies which have  
352 documented differences in sensitivity to climate change in relation to the ecoregion  
353 inhabited by the species; i.e., species from the Boreo-Alpine region were more sensitive  
354 to climate change than those inhabiting more temperate regions (Thuiller *et al.* 2005).  
355 Thus, species occurring in colder regions should be affected by climate change because  
356 of a loss of suitable habitat. Given this context, and consistent with previous studies, the  
357 future range of *L. timidus* in Europe is highly dependent on climate (Jansson & Pehrson  
358 2007; Anderson *et al.* 2009). When interspecific interactions were considered the  
359 expected effects of climate change on these species were even more pronounced (Table  
360 3); the real situation probably lies between these extremes, but unfortunately this cannot  
361 be determined at present as no validation data exist regarding the future.

362 We can interpret the predicted interactions based on previous knowledge about the  
363 ecology of the studied species. On the one hand, *L. granatensis* is expected to have  
364 some advantage over *L. europaeus* in their contact area since it is more favourable to the  
365 former (Figure 3A). In addition, data obtained from population monitoring has  
366 described an increasing population trend for *L. granatensis*, whereas *L. europaeus* is  
367 declining in their contact area (Gortázar *et al.* 2007), thus enhancing the potential  
368 advantage of *L. granatensis* over *L. europaeus*. In this context, the effects of biotic

369 interactions on *L. granatensis* could be considered negligible when the models are  
370 projected onto future scenarios. Therefore, the future distribution of *L. europaeus* is  
371 predicted to be negatively affected by *L. granatensis*, although it should be noted that *L.*  
372 *europaeus* has been suggested as a competitor able to force the exclusion of *L. timidus*  
373 in border distribution areas (Thulin 2003, and references therein). Thus, it is expected  
374 that *L. europaeus* would display an intermediate pattern between the reported extremes  
375 (Table 3), since even if the viability of the southern European populations from the  
376 Iberian Peninsula may be compromised, it is not expected that those of the north will be  
377 constrained by competition. Nevertheless, the last interpretation is not directly  
378 supported by our analysis; when the population status of both species was expected to  
379 be similar, then *L. timidus* seemed to be favoured over *L. europaeus* in their contact area  
380 (Figure 3B). In our opinion, a plausible explanation would be related to unbalanced  
381 densities between these species when they co-occur; *L. timidus* is usually found at lower  
382 densities than *L. europaeus* (Jansson & Pehrson 2007). Even if a territory is more  
383 favourable to *L. timidus*, differences in densities could drive a situation in which this  
384 species is disadvantaged compared to *L. europaeus* when resources become limited  
385 (Thulin 2003). However, in addition to resources, exclusion mediated by hybridization  
386 (see Rhymer & Simberloff 1996) can occur when species differ in density, especially in  
387 highly unbalanced situations. This was also suggested as a potential factor mediating the  
388 *L. europaeus/L. timidus* interactions (Thulin 2003; but see Jansson *et al.* 2007), and  
389 even explaining the ancestral local extinction of *L. timidus* in the Iberian Peninsula due  
390 to displacement by *L. granatensis* (e.g., Melo-Ferreira *et al.* 2007). These range  
391 replacements with hybridization have also important implications on the genetic  
392 composition of the involved species, as gene introgression should predominantly occur  
393 from the resident into the invading species (Currat *et al.* 2008). Finally, future

394 predictions for the distribution of *L. timidus* cannot be viewed with optimism; it is  
395 expected that by 2080 the distribution of this species will be reduced to 30% of its  
396 current range (72% under the most optimistic predictions) due to climate changes.  
397 According to our results, the future of this species will be compromised by climate  
398 change especially when biotic interactions with *L. europaeus* are taken into account.  
399 Thus, we suggest that climate change should be included among the factors to be  
400 monitored when addressing the conservation of *L. timidus* (Smith & Johnston 2008).

401

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561

562 Table 1. Explanatory variables used to model the hare species distributions.

<b>Code</b>	<b>Description</b>
LONG	Longitude (decimal degrees)
LAT	Latitude (decimal degrees)
ALT	Mean altitude (masl)
BIO1	Annual mean temperature
BIO2	Mean diurnal range (mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature seasonality (standard deviation *100)
BIO5	Max temperature of warmest month
BIO6	Min temperature of coldest month
BIO7	Temperature annual range (BIO5-BIO6)
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12	Annual precipitation
BIO13	Precipitation of wettest month
BIO14	Precipitation of driest month
BIO15	Precipitation seasonality (coefficient of variation)
BIO16	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter
T11	Post-flooding or irrigated croplands
T14	Rainfed croplands
T20	Mosaic Cropland (50-70%) / Vegetation (grassland, shrubland, forest) (20-50%)
T30	Mosaic Vegetation (grassland, shrubland, forest) (50-70%) / Cropland (20-50%)
T50	Closed (>40%) broadleaved deciduous forest (>5m)
T70	Closed (>40%) needleleaved evergreen forest (>5m)
T90	Open (15-40%) needleleaved deciduous or evergreen forest (>5m)
T100	Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)
T110	Mosaic Forest/Shrubland (50-70%) / Grassland (20-50%)
T120	Mosaic Grassland (50-70%) / Forest/Shrubland (20-50%)
T130	Closed to open (>15%) shrubland (<5m)
T140	Closed to open (>15%) grassland

T150	Sparse (>15%) vegetation (woody vegetation, shrubs, grassland)
T180	Closed to open (>15%) vegetation (grassland, shrubland, woody vegetation) on regularly flooded or waterlogged soil - Fresh, brackish or saline water
T190	Artificial surfaces and associated areas (urban areas >50%)
T200	Bare areas
T210	Water bodies

563

564 Table 2. Variables included in the logistic regressions for the studied hare species in  
 565 Europe (estimate / Wald test values / *p*-value: \* $<0.05$ ; \*\* $<0.01$ ; \*\*\* $<0.001$ ). Variables  
 566 marked with “*FDR*” were those excluded after false discovery rate analyses, and thus  
 567 were not included in the final models. Variables coded as in Table 1.

Variables	<i>Lepus granatensis</i>	<i>L. europaeus</i>	<i>L. timidus</i>
LONG	-0.609 / 45.529 / ***	0.156 / 120.858 / ***	-0.056 / 6.237 / *
LAT	-0.736 / 17.019 / ***		0.167 / 25.16 / ***
BIO1			-0.098 / 87.23 / ***
BIO3	-0.486 / 18.955 / ***	<i>FDR</i>	
BIO4		-0.001 / 21.676 / ***	
BIO5			0.041 / 23.355 / ***
BIO6		<i>FDR</i>	
BIO7	<i>FDR</i>		
BIO11		<i>FDR</i>	
BIO12		<i>FDR</i>	
BIO15	-0.205 / 45.482 / ***	-0.088 / 185.019 / ***	
BIO17	-0.042 / 13.173 / ***		0.011 / 24.01 / ***
T11	0.144 / 7.02 / ***	<i>FDR</i>	
T14	<i>FDR</i>	0.023 / 17.361 / ***	-0.107 / 59.053 / ***
T30	0.076 / 3.99 / *		
T50	0.045 / 7.025 / ***		-0.026 / 5.458 / *
T70		<i>FDR</i>	-0.05 / 9.457 / **
T90		-0.019 / 12.244 / ***	
T100		<i>FDR</i>	
T110	<i>FDR</i>		
T120	-0.163 / 11.238 / ***		-0.1 / 20.997 / ***
T140		<i>FDR</i>	<i>FDR</i>
T150		-0.085 / 119.854 / ***	-0.104 / 107.186 / ***
T180		-0.065 / 22.62 / ***	
T190	<i>FDR</i>	<i>FDR</i>	
T200	<i>FDR</i>		

T210		-0.041 / 21.278 / ***	-0.053 / 17.13 / ***
<i>Intercept</i>	63.519 / 39.387 / ***	3.399 / 50.549 / ***	-8.854 / 9.167 / **

568

569

570 Table 3. Rates of increase (*I*, expansion [+]) or net loss [-]), overlap (*O*), maintenance  
 571 (*M*) and shifting (*S*) of favourability predicted for the future projection (2080 and A2  
 572 emissions scenario) in relation to models calibrated for the present period. *Lepus*  
 573 *granatensis*/*L. europaeus* and *L. europaeus*/*L. timidus* represent the fuzzy overlap index  
 574 between these species.

Model	Without biotic interaction				With biotic interaction			
	<i>I</i>	<i>O</i>	<i>M</i>	<i>S</i>	<i>I</i>	<i>O</i>	<i>M</i>	<i>S</i>
<i>L. granatensis</i>	0.065	0.866	0.959	0.041	-0.064	0.911	0.889	0.047
<i>L. europaeus</i>	-0.052	0.835	0.886	0.062	-0.281	0.842	0.688	0.031
<i>L. timidus</i>	-0.283	0.717	0.717	0.000	-0.696	0.646	0.304	0.000
<i>L. granatensis</i> / <i>L. europaeus</i>	-0.227	0.418	0.523	0.250				
<i>L. europaeus</i> / <i>L. timidus</i>	-0.228	0.593	0.660	0.112				

575

576

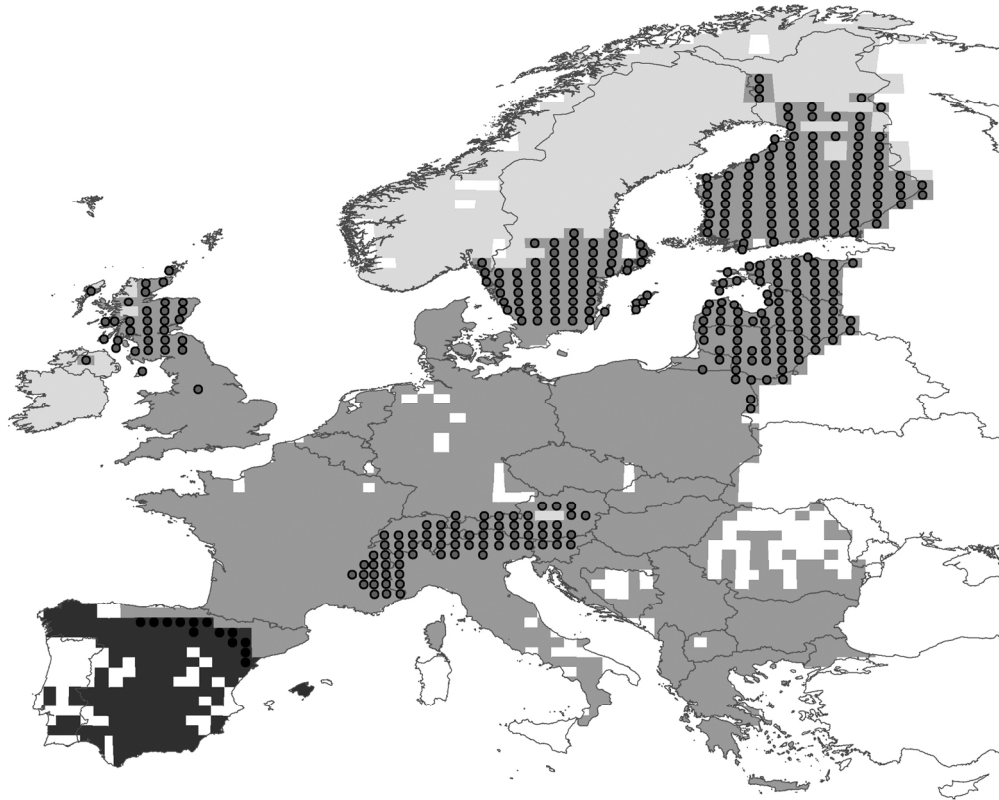


577 **FIGURE LEGENDS**

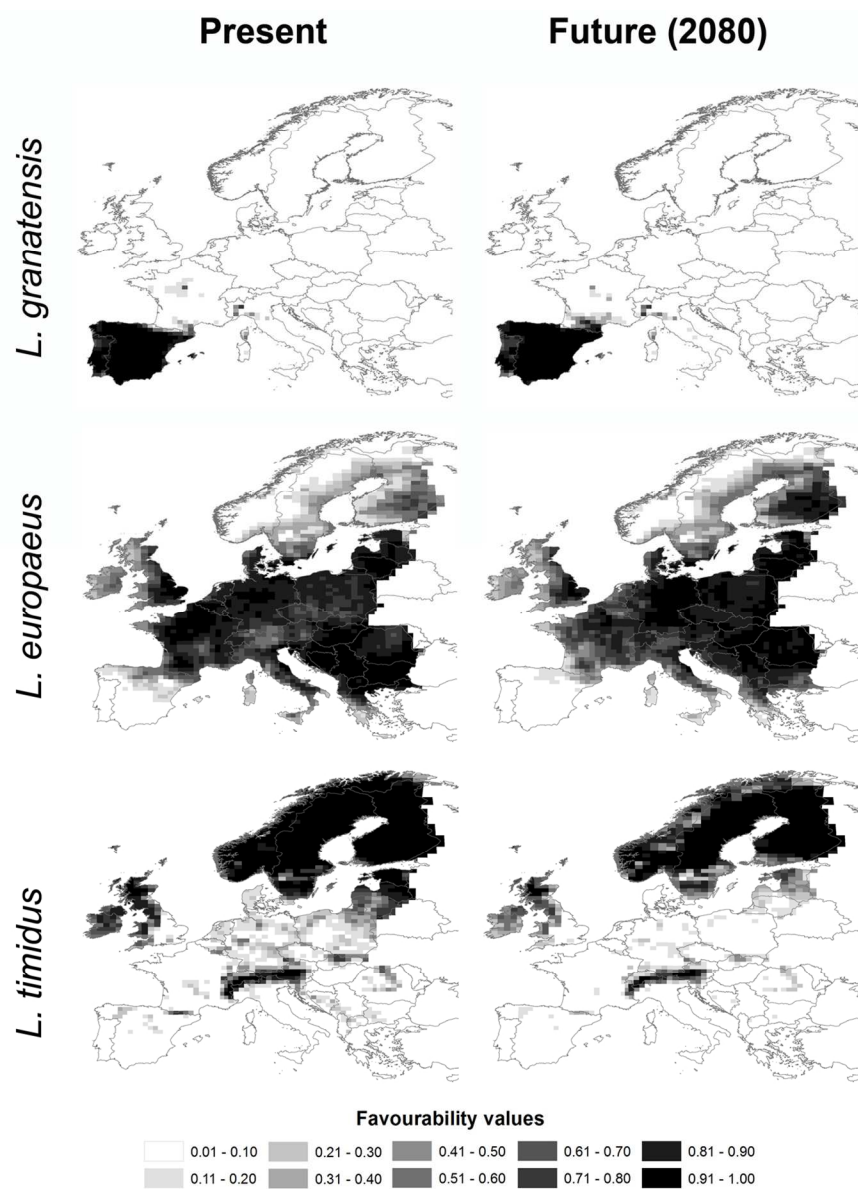
578 Figure 1. Distribution areas (from dark grey to bright grey) of *Lepus granatensis*, *L.*  
579 *europaeus* and *L. timidus* in Europe. Points depict areas where more than one species  
580 co-occurs, *L. granatensis* and *L. europaeus* (black points) or *L. europaeus* and *L.*  
581 *timidus* (grey points). Data were obtained from The Atlas of European Mammals  
582 (Mitchell-Jones *et al.* 1999).

583 Figure 2. Favourability and projections of favourability (for 2080) in Europe for *Lepus*  
584 *granatensis*, *L. europaeus* and *L. timidus*. Colours are graduated from black (the most  
585 favourable areas) to white (the most unfavourable areas).

586 Figure 3. Biogeographical relationships between parapatric hare species in Europe: a)  
587 *Lepus granatensis* (squares and solid line) versus *L. europaeus* (black squares and  
588 dotted line), and b) *L. europaeus* (black squares and dotted line) versus *L. timidus*  
589 (circles and dotted line). Variations of mean favourability scores along the gradients  
590 defined by the absolute local overlap values are displayed. The gradients are divided  
591 into natural intervals, and mean favourability values (95% confidence intervals) are  
592 shown. The number of sampling sites at each interval is also shown in columns.  
593 Intervals are defined (intermittent vertical lines) in the charts and mapped.

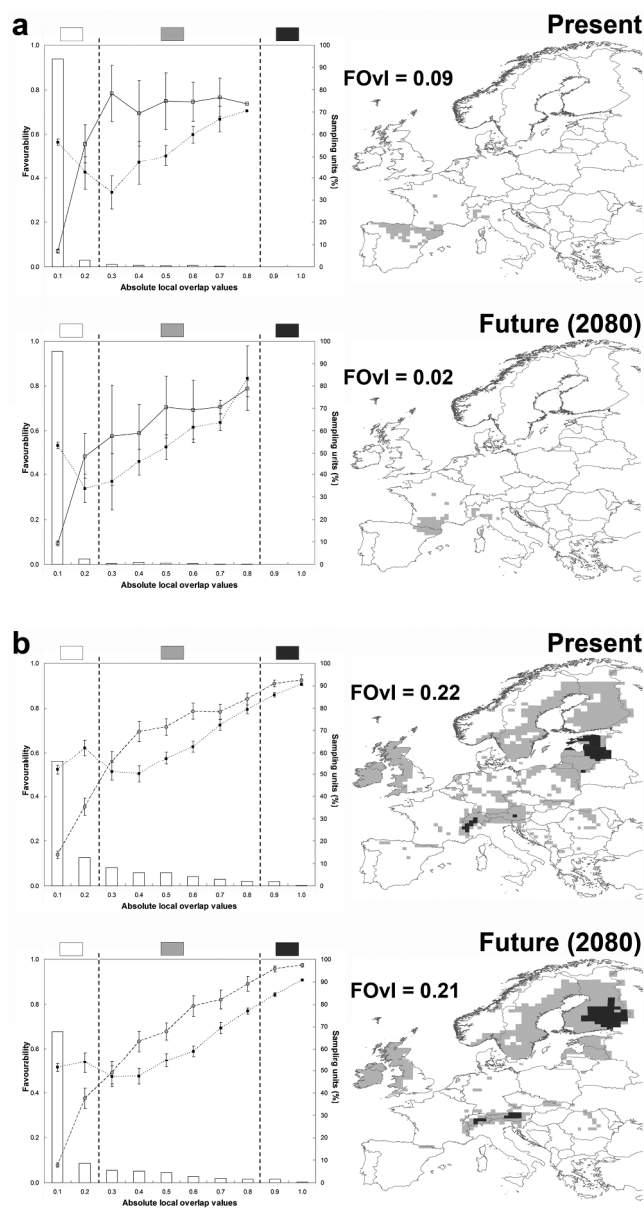


Distribution areas (from dark grey to bright grey) of *Lepus granatensis*, *L. europaeus* and *L. timidus* in Europe. Points depict areas where more than one species co-occurs, *L. granatensis* and *L. europaeus* (black points) or *L. europaeus* and *L. timidus* (grey points). Data were obtained from The Atlas of European Mammals (Mitchell-Jones et al. 1999).  
150x120mm (300 x 300 DPI)



Favourability and projections of favourability (for 2080) in Europe for *Lepus granatensis*, *L. europaeus* and *L. timidus*. Colours are graduated from black (the most favourable areas) to white (the most unfavourable areas).

108x150mm (300 x 300 DPI)



Biogeographical relationships between parapatric hare species in Europe: a) *Lepus granatensis* (squares and solid line) versus *L. europaeus* (black squares and dotted line), and b) *L. europaeus* (black squares and dotted line) versus *L. timidus* (circles and dotted line). Variations of mean favourability scores along the gradients defined by the absolute local overlap values are displayed. The gradients are divided into natural intervals, and mean favourability values (95% confidence intervals) are shown. The number of sampling sites at each interval is also shown in columns. Intervals are defined (intermittent vertical lines) in the charts and mapped.

150x279mm (300 x 300 DPI)