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Modelling the influence of biotic factors on species distribution patterns

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1 **Modelling the influence of biotic factors on species distribution patterns**

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13 **ABSTRACT**

14

15 Biotic interactions can have large effects on species distributions yet their role in shaping species ranges
16 is seldom explored due to historical difficulties in incorporating biotic factors into models without *a*
17 *priori* knowledge on interspecific interactions. Improved SDMs, which account for biotic factors and
18 do not require *a priori* knowledge on species interactions, are needed to fully understand species
19 distributions. Here, we model the influence of abiotic and biotic factors on species distribution patterns
20 and explore the robustness of distributions under future climate change. We fit hierarchical spatial
21 models using Integrated Nested Laplace Approximation (INLA) for lagomorph species throughout
22 Europe and test the predictive ability of models containing only abiotic factors against models
23 containing abiotic and biotic factors. We account for residual spatial autocorrelation using a conditional
24 autoregressive (CAR) model. Model outputs are used to estimate areas in which abiotic and biotic
25 factors determine species' ranges. INLA models containing both abiotic and biotic factors had
26 substantially better predictive ability than models containing abiotic factors only, for all but one of the
27 four species. In models containing abiotic and biotic factors, both appeared equally important as
28 determinants of lagomorph ranges, but the influences were spatially heterogeneous. Parts of widespread
29 lagomorph ranges highly influenced by biotic factors will be less robust to future changes in climate,
30 whereas parts of more localised species ranges highly influenced by the environment may be less robust
31 to future climate. SDMs that do not explicitly include biotic factors are potentially misleading and omit
32 a very important source of variation. For the field of species distribution modelling to advance, biotic
33 factors must be taken into account in order to improve the reliability of predicting species distribution
34 patterns both presently and under future climate change.

35

36 **Keywords:** *biotic interactions; climate; competition; INLA; Order Lagomorpha;*
37 *species distribution modelling.*

38 1.1 INTRODUCTION

39 The factors shaping species spatial distributions are crucial for our understanding of patterns
40 of biodiversity, and, hence, are commonly studied. Species distributions are constrained by
41 abiotic conditions, for example, suitable climate, and biotic conditions, for example,
42 competitive interspecific interactions, as well as movement behaviour, such as dispersal or
43 colonisation (Soberon & Nakamura, 2009). Species Distribution Models (SDMs) are widely
44 used in ecology and typically relate species occurrences to (abiotic) environmental variables to
45 produce models of environmental suitability, which can be spatially or temporally extrapolated
46 to unsurveyed areas or into past or future conditions (e.g. Elith *et al.*, 2006). Most SDMs use
47 only environmental variables to predict species distributions and often do not offer credible
48 statistical tests of the relative influence of these abiotic factors. Typically, they also ignore
49 other key determinants of species ranges, most pertinently, biotic interactions, as including
50 these has tended to require *a priori* knowledge on species interactions (see Elith & Leathwick,
51 2009; Beale *et al.*, 2014).

52 Although macroclimate drives distribution patterns at large scales (Whittaker, 1975;
53 Pearson & Dawson, 2003; Thuiller *et al.*, 2003), there is growing evidence of the important
54 role of biotic interactions in delineating species' range extents (Jablonski, 2008; Wiens, 2011;
55 Wisz *et al.*, 2012). Biotic interactions can take place at local scales, for example, predation,
56 parasitism, competition and disturbance, or regional scales, for example, dispersal, speciation,
57 extinction and expansions or contractions of species ranges (Cornell & Lawton, 1992;
58 Amarasekare, 2003). Competitive interactions, in particular, tend to produce biogeographical
59 patterns in species distributions; species may meet at a sharp boundary with little or no overlap
60 (Flux, 2008). Parapatric distributions, whereby two species have separate, but contiguous
61 ranges, with no physical barrier between them and only co-occur, if at all, in a narrow contact
62 zone, may result from such competitive interactions (Bull, 1991, Gutiérrez *et al.*, 2014). In

63 order to fully understand species distributions, we need to recognise the role of biotic
64 interactions in shaping geographic ranges (Wiszniewski *et al.*, 2012) and develop novel SDM
65 techniques to disaggregate the effects of the abiotic environment and biotic interactions.

66 Despite the many limitations with current correlative SDM methods, they remain one of the
67 only methods to predict species distributions. Further, they have practical applications in
68 conservation management as well as providing insights into the past and future distributions of
69 organisms and the factors that shape their biogeography. However, if predictions do not
70 explicitly include biotic factors, they could potentially misinform conservation management
71 decisions. Accurate representations of species distributions are vital for the design and
72 implementation of appropriate conservation measures, e.g. protected areas, but SDMs are
73 unlikely to produce reliable predictions if they rely on abiotic factors alone (Hof *et al.*, 2012;
74 Kissling *et al.*, 2012).

75 Studies using SDMs are beginning to consider biotic interactions by including the
76 occurrence of other species' as additional covariates (e.g. Pellissier *et al.*, 2010) and this has
77 been central in improving performance (Araujo & Luoto, 2007; Mod *et al.*, 2015). Surrogates
78 for biotic-interaction gradients are also used; for example, habitat productivity, which is known
79 to be a basis of competition in plants (Maestre *et al.*, 2010), or species richness patterns. SDMs
80 may also be hybridised with dynamic models, such as BIOMOVE (Midgley *et al.*, 2010), but
81 these methods all require *a priori* ecological knowledge and can only be applied to one
82 interacting species' pair at a time (Wiszniewski *et al.*, 2012).

83 Markov Chain Monte Carlo (MCMC) simulations offer a flexible framework for species
84 distribution modelling (Beale *et al.*, 2014) but they come with a wide range of problems
85 regarding convergence, processing time and implementation (Beguin *et al.*, 2012). An
86 alternative for fitting such Bayesian hierarchical spatial models uses Integrated Nested Laplace

87 Approximation (INLA; Rue *et al.*, 2009) which does not require advanced programming skills,
88 yields comparable results to MCMC and is rapid (Beguin *et al.*, 2012). Both methods can model
89 spatial associations within the data using conditional autoregressive (CAR) models, but
90 because INLA substitutes accurate, deterministic approximations to posterior marginal
91 distributions in place of long MCMC simulations, in the majority of occasions INLA requires
92 less processing time to model spatial effects (Beguin *et al.*, 2012). However, INLA is not yet a
93 completely adequate replacement for MCMC because some models, for example observation
94 effort models (Illian, 2013), cannot be fitted with INLA but can with MCMC. More recently
95 ‘Joint SDMs’ have been introduced, which simultaneously estimate the ranges of multiple
96 coexisting species producing mixtures of possible species assemblages (Pollock *et al.*, 2014;
97 Harris, 2014). Joint SDMs are a substantial step forward, but most do not directly take into
98 account spatial autocorrelation. A major advantage of using INLA is the ability to account for
99 spatial autocorrelation with relative ease. SDM studies are especially sensitive to spatial
100 autocorrelation, which arises when nearby locations are not independent of each other
101 (Legendre, 1993), and if spatial autocorrelation is not considered it can result in misleading
102 and biased models (Lennon, 2000; Beale *et al.*, 2010).

103 Extending the use of hierarchical spatial models to project species distributions under future
104 climate scenarios is problematic as species interactions can be unstable in space or time (Wisz
105 *et al.*, 2012). Climatic changes may impact the distribution of interacting species which could,
106 in turn, alter interactions (Wisz *et al.*, 2012), but species interactions may also influence the
107 impacts of climate change, for example by altering community dynamics (Gilman *et al.*, 2010).
108 If interactions have minimal effects on predicted distributions then projection may be possible,
109 however, if interactions are influential then projection is difficult because the strength and/or
110 direction of these interactions is likely to change (Beale *et al.*, 2014). Due to the difficulties
111 with quantitatively modelling the multiple impacts of future change on interacting species,

112 proxies for studying climate change impacts, i.e. using measures which indicate change, for
113 example ecoregional climatic stability, can be useful in determining likely effects (Iwamura *et*
114 *al.*, 2010; Iwamura *et al.*, 2013; Watson *et al.*, 2013). Regions highly influenced by biotic
115 interactions with a low robustness to future climate change (or low climatic stability) may be
116 particularly susceptible to altered distributions and/ or interactions.

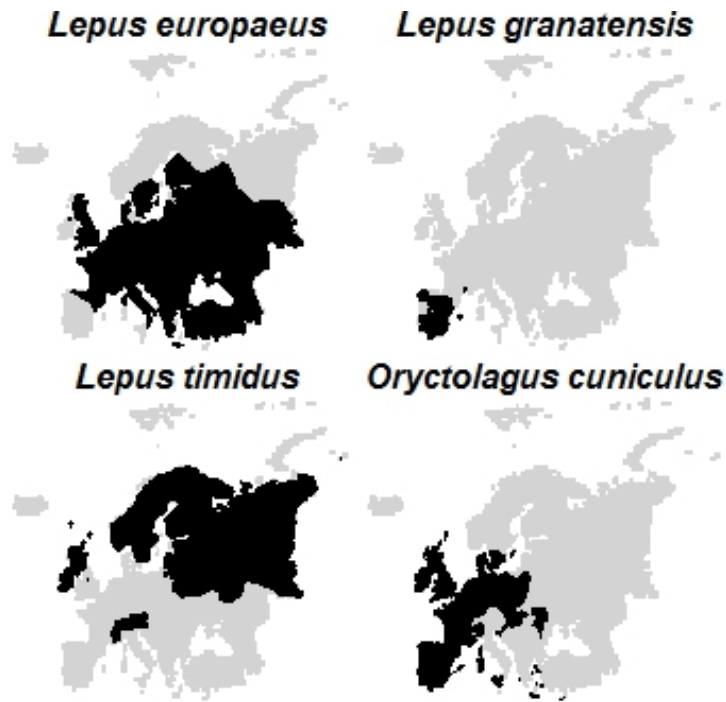
117 Here, we fit hierarchical spatial models using INLA to quantify the influence of biotic
118 factors on species distribution patterns and test the difference in predictive ability between
119 INLA models containing only abiotic factors and models containing abiotic and biotic factors.
120 Using a number of explanatory factors, including climatic variables, co-occurring species,
121 vegetation, topography and human influence, we aim to produce more reliable predictions of
122 species distributions as well as estimating the areas in which abiotic and biotic factors
123 determine species' ranges. *Post-hoc* tests exploring the climatic stability of these areas can
124 highlight, for example, if areas influenced to a greater extent by biotic factors are likely to be
125 less robust to future changes, and, therefore, direct future management actions towards either
126 the conservation of co-occurring species or the conservation of particular habitats. This
127 approach could be implemented widely, for a number of species, but here we use lagomorphs
128 in Europe, a fairly large spatial extent, as a test dataset because their biotic interactions are well
129 known (see Acevedo *et al.*, 2012 and Leach *et al.*, 2015a) and can, therefore, be easily
130 validated. There are six lagomorph species found throughout Europe (*Lepus castroviejoi*, *L.*
131 *corsicanus*, *L. europaeus*, *L. granatensis*, *L. timidus* and *Oryctolagus cuniculus*) and they
132 occupy a wide range of environmental conditions. We expect large influences of biotic factors
133 on lagomorph species distributions, and given the wide-ranging climatic conditions occupied,
134 we anticipate significant implications for conservation management in a changing climate. We
135 expect to recover competitive interactions between *L. europaeus* and *L. timidus*, given studies
136 in Ireland and across Europe (Thulin, 2003; Reid & Montgomery, 2007; Reid, 2011; Caravaggi

137 *et al.*, 2014; 2016), and also between *L. europaeus* and *L. granatensis*, given their parapatric
138 distributions and field studies in Iberia (Gortazar *et al.*, 2007).

139 1.2 MATERIALS AND METHODS

140 1.2.1 Species data

141 International Union for Conservation of Nature (IUCN) geographic range polygons for
142 European lagomorph species (Fig. 1) were rasterised in R version 3.1.1 at 30 arc-minute
143 resolution (~50km² grid cells), with a value of 1 for species presence and 0 for absence. IUCN
144 polygons have been used in a number of species distribution modelling studies to date (e.g.
145 Lawler *et al.*, 2009; Visconti *et al.*, 2015), and whilst they may have higher omission errors
146 (Graham & Hijmans, 2006; Murray *et al.*, 2011), the detailed construction of the polygons
147 together with the internal review process and expert assessments by the IUCN can lead to the
148 production of more realistic distribution models. To illustrate the consequences of using
149 different input data, species distributions models will be built with IUCN polygons and
150 compared to those built using point occurrence data. For this exercise, point data was
151 downloaded from the Global Biodiversity Information Facility (GBIF) Data Portal
152 (<http://data.gbif.org>) and prepared as per Leach *et al.* (2015b). Models for two highly range-
153 restricted species: *L. castroviejoi* and *L. corsicanus*, were extremely poor and are not
154 considered further.



155

156 **Fig. 1.** IUCN geographic range polygons (black) for the European lagomorph species
 157 modelled. *L. castroviejoi* and *L. corsicanus* models were extremely poor and so their ranges
 158 are not shown here.

159

160 1.2.2 Environmental data

161 Current climate variables (~1950-2000) known to determine lagomorph species distributions
 162 were downloaded from WorldClim (www.worldclim.org) and resampled to the same resolution
 163 as the species data. Evapotranspiration was calculated using the Hargreaves equation (see
 164 Leach *et al.*, 2015b for more details) and annual water balance was calculated by subtracting
 165 annual evapotranspiration from mean annual precipitation. The number of months with a
 166 Positive Water Balance (PWB) was calculated by subtracting each monthly evapotranspiration
 167 from its corresponding monthly precipitation, then converting into a binary format, where a
 168 value greater than zero was given a value of one and a value less than zero was kept at zero,
 169 finally summing the twelve binary scores (Kremen *et al.*, 2008). Mean annual Normalised

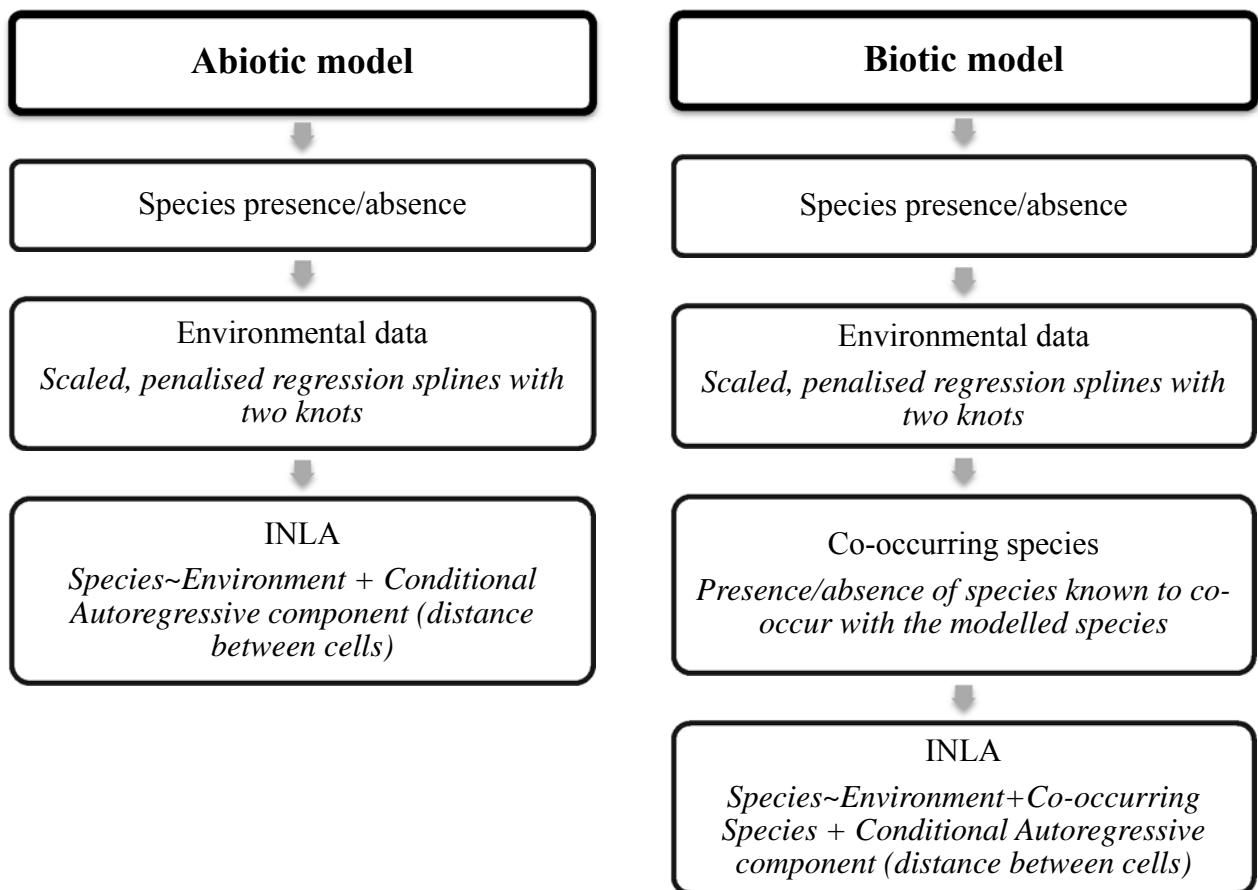
170 Difference Vegetation Index (NDVI) was calculated from monthly values which were
171 downloaded from the European Distributed Institute of Taxonomy (EDIT) Geoplatform
172 (<http://edit.csic.es/Soil-Vegetation-LandCover.html>). Hilliness, an index of surface roughness,
173 was calculated by finding the difference between maximum and minimum gradient values,
174 based on a global Digital Elevation Model at 30 arc-minute resolution (Newton-Cross *et al.*,
175 2007). Human Influence Index data were downloaded from the NASA Socioeconomic Data
176 and Applications Centre (SEDAC) website (<http://sedac.ciesin.columbia.edu/>; WCS CIESIN,
177 2005). Subsequently, correlated environmental variables (minimum precipitation, minimum
178 temperature, mean annual precipitation, mean annual temperature, solar radiation, annual water
179 balance and annual evapotranspiration) were removed, leaving the following: maximum
180 temperature, temperature seasonality, maximum precipitation, precipitation seasonality, PWB,
181 NDVI, Hilliness and Human Influence Index. All environmental variables were rescaled to
182 have a mean of zero and unit variance. Environmental data were extracted for each grid cell
183 across Europe and combined in a dataset with species presence/absence data.

184

185 **1.2.3 Model structure**

186 Hierarchical spatial models were fit using INLA (Fig. 2). Code and sample data are available
187 from: <https://github.com/katieleach/BioticSDMs>. Relationships between the response variable
188 and individual covariates were restricted to functional forms with simple shapes (Austin, 2002)
189 and the flexibility of these forms was part of the modelling approach. Each covariate was fitted
190 as a smooth term represented by a penalised regression spline with two knots to describe
191 biologically realistic unimodal response terms; regression splines were recombined to obtain
192 fitted values for environmental variables as per Beale *et al.* (2014). Greater or lesser flexibility
193 can be permitted by altering the number of knots in the spline terms. The spline models are
194 detailed further in the R script. Species known to co-occur with the target (modelled) species

195 i.e. response variable were included as biotic covariates in addition to the environmental
 196 variables. Residual spatial autocorrelation was accounted for using an intrinsic conditional
 197 autoregressive (iCAR) error structure. This represents a spatial random effect and accounts for
 198 spatially structured residuals, e.g. missing abiotic and biotic variables and processes, not
 199 modelled by the included covariates. A vague Gaussian prior was assumed for the model
 200 parameters and values of the shape parameters were defined so that the ratio of data points to
 201 the number of effective parameters was >20 ; for more details see Beguin *et al.* (2012).



202

203 **Fig. 2.** Conceptual diagram of abiotic and biotic models.

204 **1.2.4 Model evaluation**

205 Predictive ability of species distribution models is typically assessed using metrics such as Area
206 Under the Curve (AUC) or alternatives such as the True Skill Statistic (TSS) or Kappa values.
207 However, these metrics have been criticised when using presence/pseudo-absence data and
208 have limitations with respect to sensitivity, specificity, omission and commission errors
209 (Allouche *et al.*, 2006). These performance metrics require arbitrary designation of training
210 and test data, and comparison of values between models for hypothesis testing is difficult. In
211 Bayesian statistics, common methods of model evaluation include Bayesian Information
212 Criterion (BIC; unavailable in R-INLA), Deviance Information Criterion (DIC) and Watanabe-
213 Akaike information criterion (WAIC). But, all these methods over fit because of their
214 equivalence to cross-validation (Plummer, 2008; Gelman *et al.*, 2014). WAIC has recently been
215 made available in R-INLA for model comparison and is recommended because it is a more
216 fully Bayesian approach for out-of-sample prediction (Watanabe, 2010; Gelman *et al.*, 2014),
217 however, WAIC is not recommended for spatial analyses (Gelman *et al.*, 2014). DIC is known
218 to penalise for model complexity (Plummer, 2008), but Spiegelhalter *et al.* (2002) recommend
219 DIC for spatial analyses. Given that there is no perfect solution to date, we evaluate models
220 containing only abiotic factors against models containing both abiotic *and* biotic factors using
221 both WAIC and DIC.

222 1.2.5 Analysis

223 All analyses were carried out in R version 3.1.1. Separate models were fit for each lagomorph
224 species, with the abiotic *and* biotic model for one species defined as:

225

$$226 \quad \text{logit}(P_i) = e_0 + (e_1 \times \text{env1}_i + e_2 \times \text{env2}_i) + (b_1 \times \text{species1}_i + \dots b_2 \times \text{species2}_i) + SE_i$$

227 (**Equation 1**),

228

229 and the abiotic only model defined as:

230

$$231 \quad \text{logit}(P_i) = e_0 + (e_1 \times \text{env1}_i + \dots e_2 \times \text{env2}_i) + SE_i$$

232 (**Equation 2**),

233

234 where P_i was the probability of presence in cell i , e_0 was the intercept, e_1 and e_2 the estimated

235 parameters for abiotic factors, env1_i and env2_i the two spline bases for e_1 and e_2 in cell i , b_1

236 and b_2 the estimated parameters for biotic factors, species1_i and species2_i the two spline

237 bases for b_1 and b_2 in cell i , and SE was the estimated spatially explicit error term for cell i .

238 The total number of fixed-effect parameters differs between models due to differing numbers

239 of co-occurring species; however, there were always 17 fixed-effect abiotic parameters

240 (intercept plus two parameters for each abiotic factor – due to the two knots in the penalised

241 regression spline).

242 Equations 1 and 2 can be separated into multiple terms in order to explore the relative
 243 influence of abiotic and biotic factors in each cell. Contributions of each term to the model
 244 were calculated as follows: the contribution of the spatially explicit error term or spatially
 245 structured residuals in cell i , $SE_{COMP_i} = inv.logit(SE_i)$, the contribution of the abiotic
 246 component, $ENV_{COMP_i} = inv.logit(e_1 \times env1_i + \dots e_2 \times env2_i)$ and the contribution of the
 247 biotic component, $BIO_{COMP_i} = inv.logit(b_1 \times species1_i + \dots b_2 \times species2_i)$. The logit
 248 transform ensures that probabilities close to 0 or 1 are explained equally well by a number of
 249 components because the function is flat at extremes. Adapting equations from Beale *et al.*
 250 (2014), the proportion of the probability of presence explained by abiotic effects was calculated
 251 by:

252

$$253 \quad logit(Prop_{ENV_i}) = \frac{|P_i - SE_{COMP_i} - BIO_{COMP_i}|}{|P_i - SE_{COMP_i} - ENV_{COMP_i}| + |P_i - SE_{COMP_i} - BIO_{COMP_i}| + |P_i - BIO_{COMP_i} - ENV_{COMP_i}|}$$

254 **(Equation 3),**

255

256 And the proportion of the probability of presence explained by biotic factors:

257

$$258 \quad logit(Prop_{BIO_i}) = \frac{|P_i - SE_{COMP_i} - ENV_{COMP_i}|}{|P_i - SE_{COMP_i} - BIO_{COMP_i}| + |P_i - SE_{COMP_i} - ENV_{COMP_i}| + |P_i - BIO_{COMP_i} - ENV_{COMP_i}|}$$

259 **(Equation 4).**

260

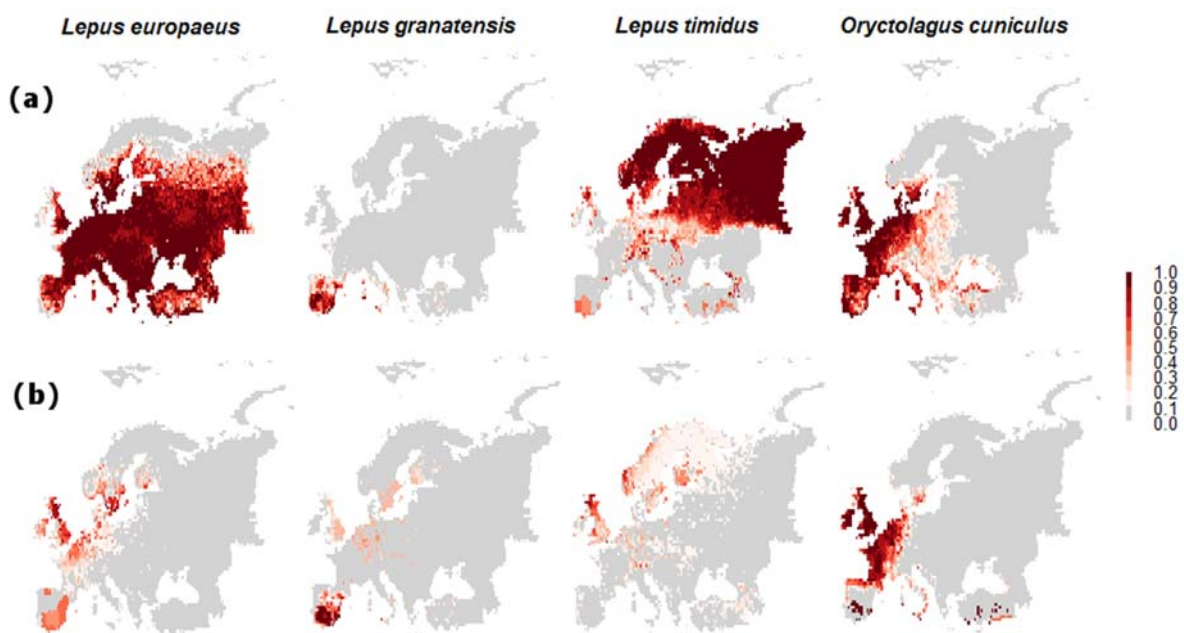
261 Outputs from the calculation of $Prop_{BIO_i}$ and $Prop_{ENV_i}$ were plotted spatially by
 262 reassigning coordinates to each grid cell. Marginal effect plots for environmental covariates

263 were produced using original variable values and predicted probability of presence values P_i
264 from INLA models. Marginal effect plots for biotic interactions were produced as boxplots due
265 to the binary input data.

266 Ecoregional climatic stability was defined as “the proportion of an ecoregion which was
267 predicted to be climatically stable under [future] climate change” (Iwamura *et al.*, 2013). The
268 climatic stability index was calculated by estimating the overlap between present and future
269 climatic envelopes for each ecoregion using results from seven global circulation models
270 (GCMs). It ranges from 0, no overlap between current and future climates, to 1, complete
271 overlap and high robustness to climate change (Watson *et al.*, 2013). Linear regressions were
272 performed to test the relationship between climatic stability and $Prop_{BIO_i}/Prop_{ENV_i}$ for each
273 species.

274 **1.3 RESULTS**

275 Predicted probabilities of presence for four European lagomorph species varied substantially
276 between INLA models built with IUCN geographic range polygons (Fig. 3a) and those built
277 with point occurrence data (Fig. 3b). Although using IUCN data may result in false positives,
278 in this case, point occurrence data resulted in false positive and false negative predictions of
279 occurrence. For example, the range of *L. granatensis* is restricted to the Iberian Peninsula yet
280 models utilising point occurrence predicted areas in Northern Europe to be suitable;
281 erroneously. In addition, *L. europaeus* and *O. cuniculus* are distributed throughout Central
282 Europe extending into Eastern Europe, yet models using point occurrence data predicted
283 distributions skewed to Western Europe. This reflects the sparsity and biased nature of point
284 occurrence data, whilst suggesting that IUCN polygons, at least for this taxon, lead to more
285 realistic species distribution models. However, it is possible that the disparity within species
286 between Fig. 3a and Fig. 3b may in fact be a result of differences in rate of movement within
287 the observed area of occurrence for spatially autocorrelated (Fig. 3a) and uncorrelated
288 distribution patterns (Fig. 3b), with rates likely to be larger for animal species, i.e. lagomorphs,
289 than plants.



290

291 **Fig. 3.** Predicted probability of presence using (a) IUCN geographic range polygons as species
 292 input data, and (b) using point occurrence data.

293

294 Evaluation of the predictive ability of INLA models for four lagomorph species in Europe,
 295 as assessed using both WAIC and DIC (which both showed similar results), indicated that those
 296 incorporating both abiotic *and* biotic factors were substantially better for all species except *L.*
 297 *timidus* (Table 1). For this species, the abiotic only model had much higher WAIC and DIC
 298 values, potentially indicating little influence of biotic factors on its distribution. The difference
 299 in WAIC and DIC values for full and abiotic only models of *L. europaeus* and *O. cuniculus*
 300 suggested that they differed with a high degree of confidence. Although, the difference was
 301 smaller for *L. granatensis*, a Δ WAIC/DIC of \sim 150 suggests models with abiotic and biotic
 302 factors had better predictive power.

303

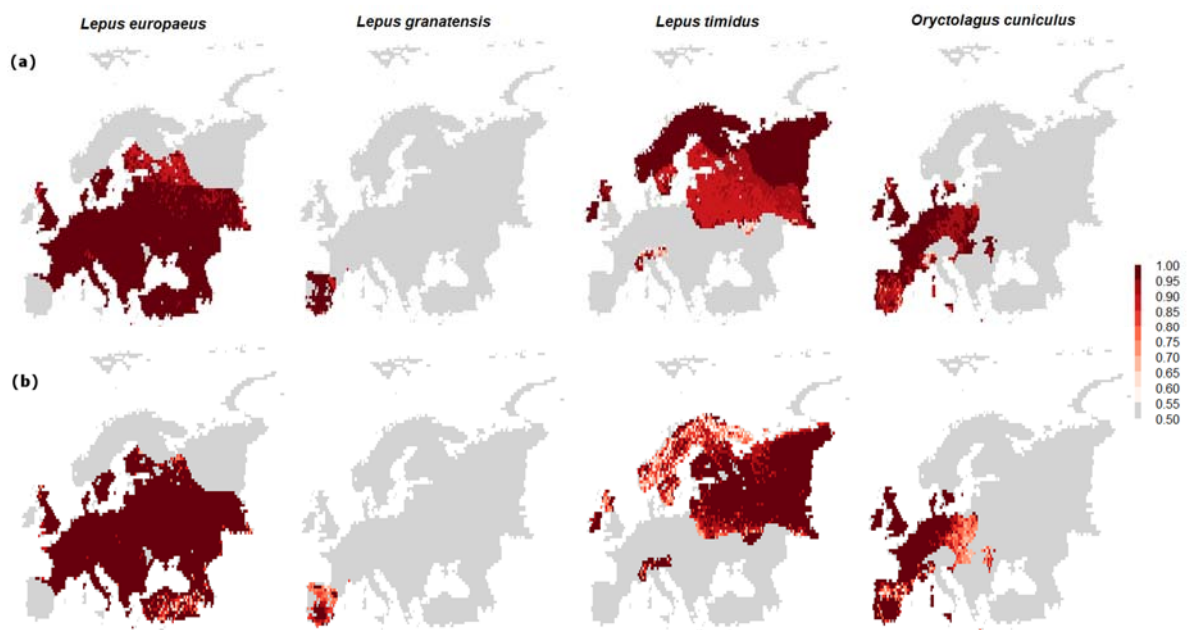
304 **Table 1.** Predictive ability of INLA models with abiotic and biotic factors compared to models
 305 with only abiotic factors. Watanabe-Akaike information criterion (WAIC) and deviance
 306 information criterion (DIC) were used to assess predictive ability, where a lower value
 307 indicates better predictive power (*) and a greater Δ WAIC/DIC suggests greater differences
 308 between the two models.

Species	DIC values			WAIC values		
	Abiotic + Biotic	Abiotic only	Δ DIC	Abiotic + Biotic	Abiotic only	Δ WAIC
<i>Lepus europaeus</i>	2765.06*	3363.69	598.63	2778.80*	3372.87	594.07
<i>Lepus granatensis</i>	420.91*	576.34	155.43	431.32*	581.86	150.54
<i>Lepus timidus</i>	3095.65	2584.00*	-511.65	3095.58	2757.06*	-338.52
<i>Oryctolagus cuniculus</i>	1880.04*	2204.49	324.45	1891.10*	2210.25	319.15

309

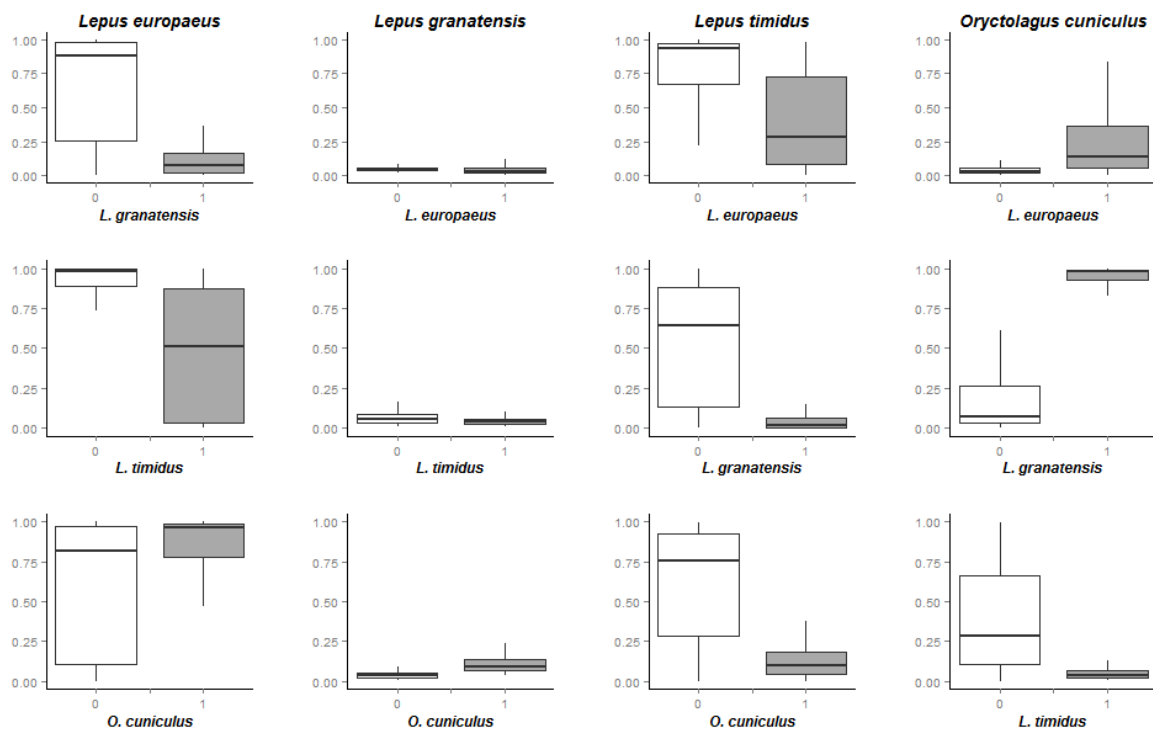
310 The average influences of abiotic and biotic factors on predicted distributions were largely
311 comparable for all species, with the average proportion of ranges explained by abiotic effects
312 0.916 and the average proportion explained by biotic factors 0.915, however, the range of *L.*
313 *granatensis* was explained to a greater extent by abiotic effects (0.907 vs. 0.824) and the range
314 of *O. cuniculus* explained to a greater extent by biotic factors (0.873 vs. 0.925). Though, the
315 proportion of species' presence explained by abiotic (Fig. 4a) and biotic factors (Fig. 4b) varied
316 considerably over space. For example, the range of *L. timidus* was influenced to a greater extent
317 by potential interspecific interactions and to a lesser extent by abiotic factors at its southern
318 range edge, whilst the range of *O. cuniculus* was influenced more by potential interspecific
319 interactions in the western part of its distribution than abiotic factors.

320



321
322 **Fig. 4.** Proportion of predicted probability of presence explained by (a) abiotic factors or (b)
323 biotic factors mapped spatially. These maps were clipped to the IUCN geographic range
324 polygons.

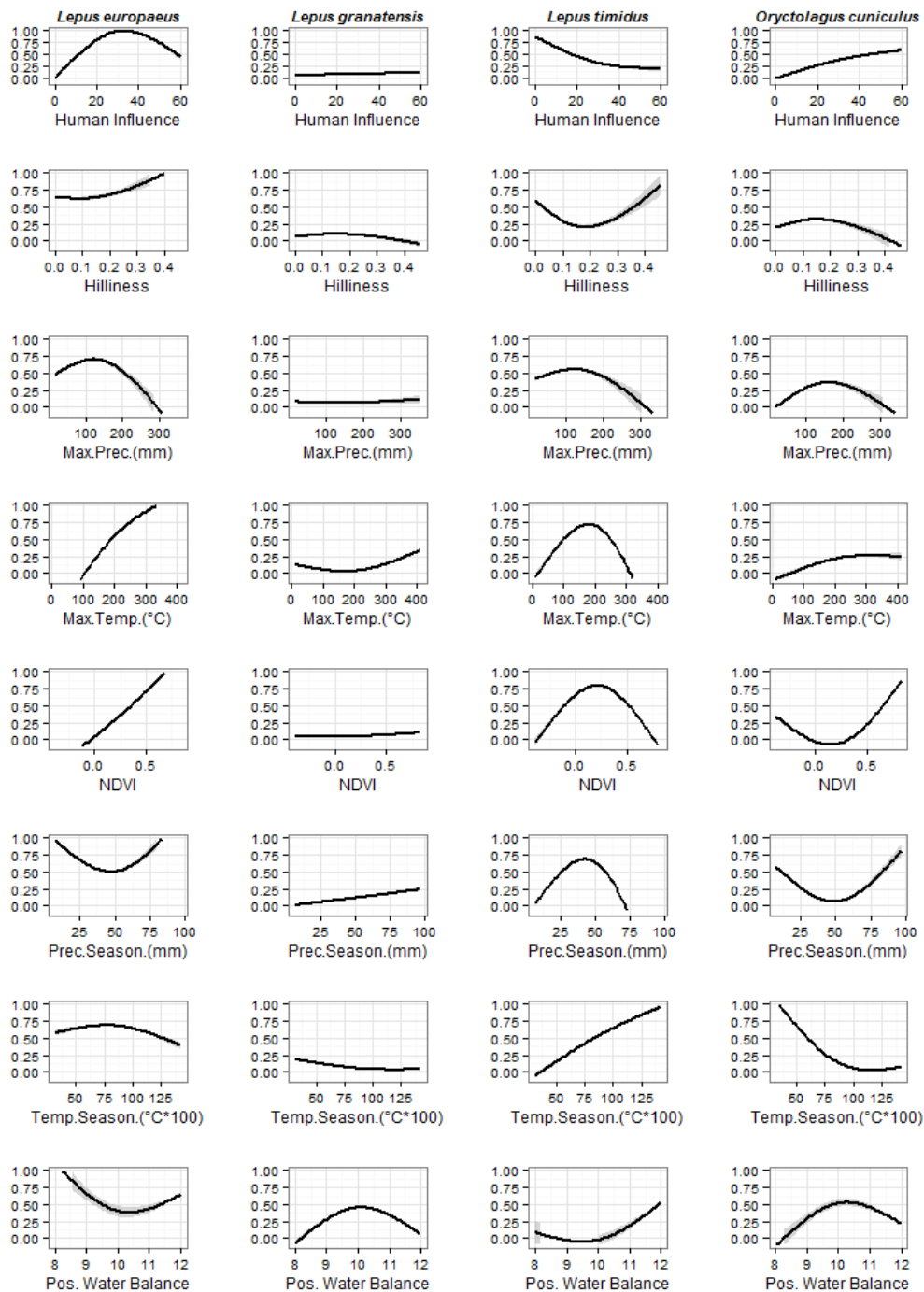
325 Our models suggest the potential for mutualistic as well as competitive interactions within
 326 European lagomorph species. *L. granatensis* and *O. cuniculus*, as well as *L. europaeus* and *O.*
 327 *cuniculus*, had higher probabilities of presence where they co-occur with each other, indicating
 328 possible mutualism (Fig. 5). Whereas *L. europaeus* had a higher probability of presence in the
 329 absence of *L. granatensis* and *L. timidus*, *L. granatensis* and *L. timidus* had higher probabilities
 330 in the absence of *L. europaeus*, and *O. cuniculus* had higher predicted probabilities of presence
 331 in the absence of *L. timidus* and *vice versa*, indicating possible competition (Fig. 5).
 332



333
 334 **Fig. 5.** Marginal effect plots showing the influence of biotic factors, i.e. co-occurring species
 335 (where 0 indicates absence and 1 presence), on predicted probabilities of presence for all
 336 combinations of species.

337
 338 In terms of abiotic factors, *L. europaeus* was positively associated with NDVI (high
 339 productivity landscapes) and maximum temperature, and more likely to be found in areas of

340 approximately 100mm maximum precipitation, with little precipitation seasonality (Fig. 6 &
341 Table 2). *L. granatensis* was associated with high maximum temperatures above 20°C. *L.*
342 *timidus* was positively associated with temperature seasonality, as well as low human influence
343 and extremely hilly areas. *O. cuniculus* was more likely to be present in flat landscapes, at low
344 and high NDVI values i.e. semi-arid regions in Iberia and the Mediterranean, and high
345 productivity landscapes i.e. farmland, and in areas with approximately 150mm maximum
346 precipitation.



347

348 **Fig. 6.** Marginal effect plots showing the relationships between environmental covariates and
 349 predicted probabilities of species presence. Grey shaded regions show 95% credible intervals
 350 and solid lines the mean estimate.

351 **Table 2.** Parameter estimates for abiotic effects on the predicted probabilities of presence of
 352 European lagomorph species plus 2.5% and 97.5% credible intervals. Significant parameter
 353 estimates, i.e. those with credible intervals that do not cross 0.5, are shown in bold.

Effect		<i>Lepus europaeus</i>	<i>Lepus granatensis</i>	<i>Lepus timidus</i>	<i>Oryctolagus cuniculus</i>
Human Influence	Mean	<0.001	0.067	0.844	0.117
	97.5%	0.071	0.913	0.876	0.152
	2.5%	<0.001	0.003	0.805	0.016
Hilliness	Mean	0.502	0.496	0.513	0.509
	97.5%	0.508	0.500	0.516	0.512
	2.5%	0.496	0.492	0.510	0.505
Max. Prec. (mm)	Mean	0.943	0.944	0.055	0.941
	97.5%	0.969	0.999	0.060	0.951
	2.5%	0.927	0.921	0.047	0.930
Max. Temp. (°C)	Mean	0.704	0.787	<0.001	<0.001
	97.5%	1.000	1.000	<0.001	<0.001
	2.5%	0.522	0.717	<0.001	<0.001
NDVI	Mean	0.648	0.495	0.474	0.588
	97.5%	0.669	0.515	0.490	0.603
	2.5%	0.624	0.474	0.458	0.573
Prec. Season. (mm)	Mean	0.970	<0.001	0.932	0.989
	97.5%	0.999	0.012	0.958	0.999
	2.5%	0.960	<0.001	<0.001	0.015
Temp. Season. (°C)	Mean	0.000	0.485	0.524	0.503
	97.5%	0.328	1.000	0.533	0.516
	2.5%	0.000	0.000	0.517	0.493
Positive Water Balance	Mean	0.839	0.364	0.019	0.133
	97.5%	0.985	0.722	0.090	0.468
	2.5%	0.161	0.111	0.010	0.031

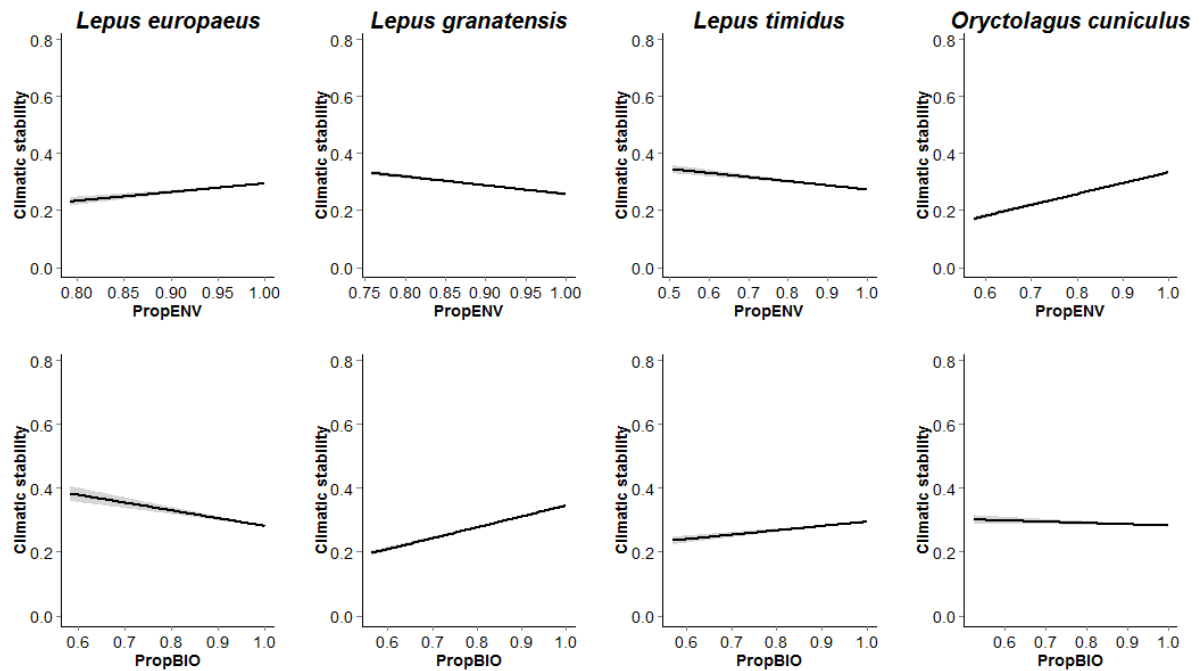
354

355

356 The relationship between climatic stability and the proportion of the range influenced by
 357 abiotic or biotic factors varied for each species. *L. europaeus* showed a similar response to *O.*
 358 *cuniculus*, and *L. granatensis* a similar response to *L. timidus* despite the geographically
 359 distinct distributions (Fig. 7). For *L. europaeus* and *O. cuniculus* areas highly influenced by
 360 abiotic factors were positively related to climatic stability (average slope = 0.342), i.e. these

361 areas are likely to become more climatically stable in the future, whereas areas for those species
 362 highly influenced by biotic factors were negatively associated with climatic stability (average
 363 slope = -0.142), i.e. these areas are likely to become less climatically stable in the future. For
 364 *L. granatensis* and *L. timidus* areas influenced by abiotic factors are predicted to be less stable
 365 under future climates (average slope = -0.227) and areas influenced by biotic factors more
 366 stable (average slope = 0.240).

367



368

369 **Fig. 7.** Relationship between climatic stability and the proportion of predicted probability of
 370 presence explained by abiotic (PropENV) or biotic factors (PropBIO) for each species. The
 371 grey areas surrounding fitted linear regression lines indicate credible intervals.

372 1.4 DISCUSSION

373 Predictive ability was substantially better in models built using abiotic *and* biotic factors, than
374 in models built solely with abiotic variables, for all but one lagomorph, suggesting the potential
375 for interspecific drivers in determining species distribution patterns. Abiotic factors alone are
376 likely to build a better model for the mountain hare, *L. timidus*, due to its distribution being
377 primarily driven by cooler temperatures at high latitudes and elevations. For the majority of
378 lagomorph species in Europe, abiotic factors and interspecific interaction effects appeared
379 *equally* important in determining their ranges. Our models suggest directional associations
380 consistent with field-based observations reported in the literature between *L. granatensis* and
381 *L. europaeus* (Gortazar *et al.*, 2007), *L. europaeus* and *L. timidus* (Thulin, 2003; Reid &
382 Montgomery, 2007; Reid, 2011; Caravaggi *et al.*, 2014; 2016) and *O. cuniculus* and *L. timidus*
383 (though this latter relationship has not been empirically documented their ranges show
384 significant overlap and biotic interactions are both possible and probable, particularly at the
385 southerly range edge of *L. timidus*). In addition, a potential mutualistic interaction is suggested
386 between *O. cuniculus* and *L. granatensis*, which to the best of our knowledge has not yet been
387 reported. However, these correlative analyses may only identify associations which cannot be
388 used to attribute causation; underlying mechanisms, for example, the strength and direction of
389 interspecific competition, can only be established using field observations and/or hypothesis
390 testing experiments (Beale *et al.*, 2014). Furthermore, these results do not consider the
391 influence of additional biotic factors, for example pikas (*Ochotona roylei*) and birds (*Pnoepyge*
392 *albiventer*) are known to exhibit mutualism in some locations (Khanal, 2007), and also do not
393 consider that possible mutualistic relationships could be due to competitive interactions of
394 species in the same niche, not reaching equilibrium.

395 The influence of biotic factors was spatially heterogeneous. For example, it is predicted that
396 biotic factors disproportionately influenced the southern range of *L. timidus*, a predominately

397 high latitude species which overlaps with its competitor *L. europaeus*, a predominately
398 temperate climate, lowland farmland species at its southern range margin (Thulin, 2003). The
399 western regions of the range of *O. cuniculus* were also suggested to be disproportionately
400 influenced by biotic factors presumably where it overlaps with other lagomorphs.

401 Environmental covariates identified as important to the predicted presence of European
402 lagomorphs in our models were largely supported in the literature. *O. cuniculus* prefers flat
403 landscapes (Fa *et al.*, 1999; Tapia *et al.*, 2010), and *L. europaeus* and *O. cuniculus* occupy
404 landscapes of differing productivity and vegetation (Smith & Boyer, 2008; Smith & Johnston,
405 2008). In addition, *L. europaeus* and *O. cuniculus* prefer less seasonal and lower levels of
406 precipitation (Rödel & Dekker, 2012), whereas *L. granatensis* is only found in areas of
407 relatively high temperatures (Alves & Rocha, 2003). *L. timidus* occupies regions with high
408 winter snowfall (Angerbjorn & Flux, 1995), and, therefore, tolerates large seasonal variations
409 in temperature. Also, *L. timidus* is known to occupy high elevations, especially in the Alps, and
410 inhabits areas of low human influence (Thulin, 2003).

411 Projecting species distributions under future climate scenarios is inherently challenging,
412 especially with the inclusion of biotic factors which may introduce the potential for
413 multicollinearity (Kissling *et al.*, 2012). Associating proxies for climate change with the results
414 of spatial hierarchical models can provide insight into the potential impacts of future change
415 (e.g. Watson *et al.*, 2013). We show that areas of *O. cuniculus* and *L. europaeus* ranges
416 influenced by biotic factors will be less robust to future changes in climate, whereas areas of
417 *L. granatensis* and *L. timidus* ranges highly influenced by the environment will be less robust
418 to future climate. The narrow climatic conditions occupied by the latter two species and the
419 uniqueness of these conditions within Europe, i.e. high temperatures in Iberia (Alves & Rocha,
420 2003) and cold temperatures in Northern Europe (Thulin, 2003), probably explains why the
421 areas influenced by abiotic factors are less robust – these particularly arid and arctic ecoregions

422 are highly susceptible to even small changes in climate (Beaumont *et al.*, 2011), and the species
423 found here, which are adapted to these narrow conditions, may therefore struggle to cope with
424 small changes to temperature or precipitation. The widespread lagomorphs, *L. europaeus* and
425 *O. cuniculus*, on the other hand, are predicted to be less robust to future climatic changes in
426 areas determined by biotic factors. This may lead to substantial changes in future distributions,
427 given that these species co-occur with most other lagomorph species in Europe, and may lead
428 to altered interactions, for example one of the more range-restricted species may outcompete
429 one of the widespread species in the future, potentially changing the direction of interactions.
430 The effects on range-restricted species, e.g. *L. castroviejoi* and *L. corsicanus*, are still unknown,
431 but we expect them to be particularly sensitive to projected changes due to the restricted
432 climatic envelopes that they occupy. On the basis of these results we suggest that the
433 management of *L. timidus* and *L. granatensis* in the future is directed towards habitat
434 conservation in areas of climate particularly favoured by these species, whereas for *L.*
435 *europaeus* and *O. cuniculus* conservation strategies should be directed at areas where these
436 species overlap with co-occurring lagomorphs, for example conservation of *O. cuniculus* in
437 Iberia, France and the UK, and *L. europaeus* in the UK, Central Europe and the more southerly
438 regions of its overlap with *L. timidus*.

439 Although our species-specific results are consistent with environmental and interspecific
440 effects reported in the literature, given unbiased and adequate point occurrences with reliable
441 data on observer effort, models could be improved (see Royle *et al.*, 2007; Beale *et al.*, 2014).
442 Here, we concentrated on determining interspecific interaction effects at the same trophic level
443 with congeneric species (for simplicity), but future improvements might also include top-down
444 (predator-prey), bottom-up (plant-grazer) and host-parasite interactions as these are equally, if
445 not more likely, to have strong impacts on species distributions (Kissling *et al.*, 2012).

446

447 **1.4.1 Conclusions**

448 The approach demonstrated here allowed biotic factors to be included in modelling species
449 distributions, without the need for *a priori* knowledge on species interactions. SDMs that do
450 not explicitly include biotic, as well as abiotic factors are missing a large source of variation
451 that appears, for European lagomorphs, equally important in determining species distributions.
452 Even though the results are limited to European lagomorphs and the approach might not be
453 relevant for some taxa, for example plants, it is likely that it can be applied to a wide range of
454 species given adequate species occurrence and environmental data. In addition, through the
455 production of accurate species distribution models, built with abiotic and biotic factors,
456 effective and appropriate conservation measures can be suggested. However, these approaches
457 must be extended to model rare, and/or highly range-restricted species which are likely to be
458 particularly vulnerable in the future, yet are seldom included due to sparse data and poor model
459 performance. The evaluation of risk to future conservation status of a species by extrapolation
460 under future climate scenarios of SDMs that do not include biotic factors is likely to result in
461 biased and unrealistic results (except in those cases where the effect of biotic interactions is
462 small, which we suspect likely to be the case for a minority of species only). Species
463 distributions largely defined by biotic interactions cannot be extrapolated without
464 simultaneously extrapolating the distribution of all potentially interacting species, including
465 top-down and bottom-up processes. Even if the statistical challenges of creating such complex
466 models are overcome, they are unlikely to account for changes in the strength and direction of
467 biotic interactions in the future because species range determinants are likely to have
468 multivariate influences. Thus, the development of Joint SDM approaches and network analysis
469 to quantify the strength of biotic interactions at all trophic levels accounting for spatial
470 autocorrelation whilst minimising computational power is needed.

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476

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