

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

37

36 Keywords:

biotic interactions; climate; competition; INLA; Order Lagomorpha; species distribution modelling.

38 1.1 INTRODUCTION

39 The factors shaping species spatial distributions are crucial for our understanding of patterns of biodiversity, and, hence, are commonly studied. Species distributions are constrained by 40 abiotic conditions, for example, suitable climate, and biotic conditions, for example, 41 competitive interspecific interactions, as well as movement behaviour, such as dispersal or 42 colonisation (Soberon & Nakamura, 2009). Species Distribution Models (SDMs) are widely 43 used in ecology and typically relate species occurrences to (abiotic) environmental variables to 44 45 produce models of environmental suitability, which can be spatially or temporally extrapolated to unsurveyed areas or into past or future conditions (e.g. Elith et al., 2006). Most SDMs use 46 47 only environmental variables to predict species distributions and often do not offer credible statistical tests of the relative influence of these abiotic factors. Typically, they also ignore 48 other key determinants of species ranges, most pertinently, biotic interactions, as including 49 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; Wisz et al., 2012). Biotic interactions can take place at local scales, for example, predation, 55 parasitism, competition and disturbance, or regional scales, for example, dispersal, speciation, 56 57 extinction and expansions or contractions of species ranges (Cornell & Lawton, 1992; Amarasekare, 2003). Competitive interactions, in particular, tend to produce biogeographical 58 59 patterns in species distributions; species may meet at a sharp boundary with little or no overlap (Flux, 2008). Parapatric distributions, whereby two species have separate, but contiguous 60 ranges, with no physical barrier between them and only co-occur, if at all, in a narrow contact 61 62 zone, may result from such competitive interactions (Bull, 1991, Gutiérrez et al., 2014). In

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

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

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 for biotic-interaction gradients are also used; for example, habitat productivity, which is known 78 79 to be a basis of competition in plants (Maestre et al., 2010), or species richness patterns. SDMs may also be hybridised with dynamic models, such as BIOMOVE (Midgley et al., 2010), but 80 81 these methods all require a priori ecological knowledge and can only be applied to one interacting species' pair at a time (Wisz et al., 2012). 82

Markov Chain Monte Carlo (MCMC) simulations offer a flexible framework for species distribution modelling (Beale *et al.*, 2014) but they come with a wide range of problems regarding convergence, processing time and implementation (Beguin *et al.*, 2012). An 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 spatial associations within the data using conditional autoregressive (CAR) models, but 89 because INLA substitutes accurate, deterministic approximations to posterior marginal 90 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 coexisting species producing mixtures of possible species assemblages (Pollock et al., 2014; 96 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 and biased models (Lennon, 2000; Beale et al., 2010). 102

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 impacts of climate change, for example by altering community dynamics (Gilman et al., 2010). 107 108 If interactions have minimal effects on predicted distributions then projection may be possible, however, if interactions are influential then projection is difficult because the strength and/or 109 direction of these interactions is likely to change (Beale et al., 2014). Due to the difficulties 110 with quantitatively modelling the multiple impacts of future change on interacting species, 111

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

Here, we fit hierarchical spatial models using INLA to quantify the influence of biotic 117 factors on species distribution patterns and test the difference in predictive ability between 118 119 INLA models containing only abiotic factors and models containing abiotic and biotic factors. Using a number of explanatory factors, including climatic variables, co-occurring species, 120 121 vegetation, topography and human influence, we aim to produce more reliable predictions of species distributions as well as estimating the areas in which abiotic and biotic factors 122 determine species' ranges. *Post-hoc* tests exploring the climatic stability of these areas can 123 124 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 in Europe, a fairly large spatial extent, as a test dataset because their biotic interactions are well 128 129 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. corsicanus, L. europaeus, L. granatensis, L. timidus and Oryctolagus cuniculus) and they 131 occupy a wide range of environmental conditions. We expect large influences of biotic factors 132 133 on lagomorph species distributions, and given the wide-ranging climatic conditions occupied, we anticipate significant implications for conservation management in a changing climate. We 134 135 expect to recover competitive interactions between L. europaeus and L. timidus, given studies in Ireland and across Europe (Thulin, 2003; Reid & Montgomery, 2007; Reid, 2011; Caravaggi 136

- 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 European lagomorph species (Fig. 1) were rasterised in R version 3.1.1 at 30 arc-minute 142 resolution (~50km² grid cells), with a value of 1 for species presence and 0 for absence. IUCN 143 144 polygons have been used in a number of species distribution modelling studies to date (e.g. Lawler et al., 2009; Visconti et al., 2015), and whilst they may have higher omission errors 145 (Graham & Hijmans, 2006; Murray et al., 2011), the detailed construction of the polygons 146 together with the internal review process and expert assessments by the IUCN can lead to the 147 production of more realistic distribution models. To illustrate the consequences of using 148 149 different input data, species distributions models will be built with IUCN polygons and compared to those built using point occurrence data. For this exercise, point data was 150 151 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 rangerestricted species: L. castroviejoi and L. corsicanus, were extremely poor and are not 153 considered further. 154



155

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

159

160 **1.2.2 Environmental data**

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

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

184

185 **1.2.3 Model structure**

Hierarchical spatial models were fit using INLA (Fig. 2). Code and sample data are available 186 from: https://github.com/katieleach/BioticSDMs. Relationships between the response variable 187 and individual covariates were restricted to functional forms with simple shapes (Austin, 2002) 188 189 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 fitted values for environmental variables as per Beale et al. (2014). Greater or lesser flexibility 192 193 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

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



202

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 Under the Curve (AUC) or alternatives such as the True Skill Statistic (TSS) or Kappa values. 206 207 However, these metrics have been criticised when using presence/pseudo-absence data and have limitations with respect to sensitivity, specificity, omission and commission errors 208 (Allouche et al., 2006). These performance metrics require arbitrary designation of training 209 and test data, and comparison of values between models for hypothesis testing is difficult. In 210 211 Bayesian statistics, common methods of model evaluation include Bayesian Information Criterion (BIC; unavailable in R-INLA), Deviance Information Criterion (DIC) and Watanabe-212 Akaike information criterion (WAIC). But, all these methods over fit because of their 213 equivalence to cross-validation (Plummer, 2008; Gelman et al., 2014). WAIC has recently been 214 made available in R-INLA for model comparison and is recommended because it is a more 215 216 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 containing only abiotic factors against models containing both abiotic and biotic factors using 220 221 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 | $logit(P_i) = e_0 + (e_1 \times env1_i + e_2 \times env2_i) + (b_1 \times species1_i + \cdots + b_2 \times species2_i) + SE_i$ |
| 227 | (Equation 1), |
| 228 | |
| 229 | and the abiotic only model defined as: |
| 230 | |
| 231 | $logit(P_i) = e_0 + (e_1 \times env1_i + \dots + e_2 \times env2_i) + SE_i$ |
| 232 | (Equation 2), |
| 233 | |
| 234 | where P_i was the probability of presence in cell <i>i</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>i</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>i</i> , and SE was the estimated spatially explicit error term for cell <i>i</i> . |

The total number of fixed-effect parameters differs between models due to differing numbers of co-occurring species; however, there were always 17 fixed-effect abiotic parameters (intercept plus two parameters for each abiotic factor – due to the two knots in the penalised regression spline). 242 Equations 1 and 2 can be separated into multiple terms in order to explore the relative influence of abiotic and biotic factors in each cell. Contributions of each term to the model 243 were calculated as follows: the contribution of the spatially explicit error term or spatially 244 structured residuals in cell i, $SE_{COMP_i} = inv. logit(SE_i)$, the contribution of the abiotic 245 component, $ENV_{COMP_i} = inv. logit(e_1 \times env1_i + \cdots + e_2 \times env2_i)$ and the contribution of the 246 biotic component, $BIO_{COMP_i} = inv.logit(b_1 \times species1_i + \cdots b_2 \times species2_i$. The logit 247 transform ensures that probabilities close to 0 or 1 are explained equally well by a number of 248 components because the function is flat at extremes. Adapting equations from Beale et al. 249 (2014), the proportion of the probability of presence explained by abiotic effects was calculated 250 251 by:

252

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

254 (*Equation* 3),

255

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

257

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

260

Outputs from the calculation of $Prop_{BIO_i}$ and $Prop_{ENV_i}$ were plotted spatially by reassigning coordinates to each grid cell. Marginal effect plots for environmental covariates were produced using original variable values and predicted probability of presence values P_i from INLA models. Marginal effect plots for biotic interactions were produced as boxplots due to the binary input data.

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

274 **1.3 RESULTS**

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

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

293

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

303

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

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

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

320

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

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

332

333

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

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

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

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

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

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

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The relationship between climatic stability and the proportion of the range influenced by abiotic or biotic factors varied for each species. *L. europaeus* showed a similar response to *O. cuniculus*, and *L. granatensis* a similar response to *L. timidus* despite the geographically distinct distributions (Fig. 7). For *L. europaeus* and *O. cuniculus* areas highly influenced by abiotic factors were positively related to climatic stability (average slope = 0.342), i.e. these areas are likely to become more climatically stable in the future, whereas areas for those species highly influenced by biotic factors were negatively associated with climatic stability (average slope = -0.142), i.e. these areas are likely to become less climatically stable in the future. For *L. granatensis* and *L. timidus* areas influenced by abiotic factors are predicted to be less stable under future climates (average slope = -0.227) and areas influenced by biotic factors more stable (average slope = 0.240).

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Fig. 7. Relationship between climatic stability and the proportion of predicted probability of presence explained by abiotic (PropENV) or biotic factors (PropBIO) for each species. The 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 in models built solely with abiotic variables, for all but one lagomorph, suggesting the potential 374 375 for interspecific drivers in determining species distribution patterns. Abiotic factors alone are likely to build a better model for the mountain hare, L. timidus, due to its distribution being 376 primarily driven by cooler temperatures at high latitudes and elevations. For the majority of 377 lagomorph species in Europe, abiotic factors and interspecific interaction effects appeared 378 379 equally important in determining their ranges. Our models suggest directional associations consistent with field-based observations reported in the literature between L. granatensis and 380 L. europaeus (Gortazar et al., 2007), L. europaeus and L. timidus (Thulin, 2003; Reid & 381 Montgomery, 2007; Reid, 2011; Caravaggi et al., 2014; 2016) and O. cuniculus and L. timidus 382 (though this latter relationship has not been empirically documented their ranges show 383 384 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 used to attribute causation; underlying mechanisms, for example, the strength and direction of 388 389 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 albiventer) are known to exhibit mutualism in some locations (Khanal, 2007), and also do not 392 393 consider that possible mutualistic relationships could be due to competitive interactions of species in the same niche, not reaching equilibrium. 394

The influence of biotic factors was spatially heterogeneous. For example, it is predicted that biotic factors disproportionately influenced the southern range of *L. timidus*, a predominately high latitude species which overlaps with its competitor *L. europaeus*, a predominately temperate climate, lowland farmland species at its southern range margin (Thulin, 2003). The western regions of the range of *O. cuniculus* were also suggested to be disproportionately influenced by biotic factors presumably where it overlaps with other lagomorphs.

401 Environmental covariates identified as important to the predicted presence of European lagomorphs in our models were largely supported in the literature. O. cuniculus prefers flat 402 landscapes (Fa et al., 1999; Tapia et al., 2010), and L. europaeus and O. cuniculus occupy 403 404 landscapes of differing productivity and vegetation (Smith & Boyer, 2008; Smith & Johnston, 2008). In addition, L. europaeus and O. cuniculus prefer less seasonal and lower levels of 405 precipitation (Rödel & Dekker, 2012), whereas L. granatensis is only found in areas of 406 407 relatively high temperatures (Alves & Rocha, 2003). L. timidus occupies regions with high winter snowfall (Angerbjorn & Flux, 1995), and, therefore, tolerates large seasonal variations 408 409 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, especially with the inclusion of biotic factors which may introduce the potential for 412 413 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 (e.g. Watson et al., 2013). We show that areas of O. cuniculus and L. europaeus ranges 415 influenced by biotic factors will be less robust to future changes in climate, whereas areas of 416 417 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, 2003) and cold temperatures in Northern Europe (Thulin, 2003), probably explains why the 420 421 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 small changes to temperature or precipitation. The widespread lagomorphs, L. europaeus and 424 O. cuniculus, on the other hand, are predicted to be less robust to future climatic changes in 425 areas determined by biotic factors. This may lead to substantial changes in future distributions, 426 given that these species co-occur with most other lagomorph species in Europe, and may lead 427 to altered interactions, for example one of the more range-restricted species may outcompete 428 one of the widespread species in the future, potentially changing the direction of interactions. 429 430 The effects on range-restricted species, e.g. L. castroviejoi and L. corsicanus, are still unknown, but we expect them to be particularly sensitive to projected changes due to the restricted 431 climatic envelopes that they occupy. On the basis of these results we suggest that the 432 433 management of L. timidus and L. granatensis in the future is directed towards habitat conservation in areas of climate particularly favoured by these species, whereas for L. 434 europaeus and O. cuniculus conservation strategies should be directed at areas where these 435 436 species overlap with co-occurring lagomorphs, for example conservation of O. cuniculus in Iberia, France and the UK, and L. europaeus in the UK, Central Europe and the more southerly 437 regions of its overlap with L. timidus. 438

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

447 **1.4.1 Conclusions**

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

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