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Characterizing biotic interactions within the Order Lagomorpha using Joint Species Distribution Models at three different spatial scales

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Species Distribution Models (SDMs) rarely incorporate biotic interactions, even though the latter may have great impacts on biogeographical patterns, because interactions can be difficult to model in time and space. In addition, the resolution of input data can have dramatic effects on results, with coarser resolutions unlikely to capture climatic variation at small scales, particularly in mountainous regions. Joint SDMs can be used to explore distributions of multiple, coexisting species and characterize modelled biotic interactions; however, the influence of scale on predictions is yet to be tested. We produced Joint SDMs for European lagomorph species at 3 hierarchical resolutions and calculated residual and environmental correlations that could explain why species may or may not co-occur, thereby suggesting biotic interactions. European lagomorph species exhibited similar environmental and biotic responses at all 3 resolutions (50 km, 25 km, and 10 km), with models at finer resolutions producing more precise estimates but requiring considerable computing time. The majority of pairwise residual responses were negative, indicating that European lagomorph species co-occur less than expected given their similarity in environmental responses, and suggesting modelled biotic interactions consistent with those reported in the literature. Fine-scale data and models offer greater precision but are not always necessary for multi-species models. However, caution is advised when inferring biotic interactions using data and models based on a coarser scale.

Key words: competition, co-occurrence, Europe, hare, MCMC, lagomorph, probit regression, rabbit, species interactions

Species Distribution Models (SDMs) are a widely used analytical approach in modern ecology, particularly with respect to predicting the impacts of climate change; however, SDMs have well known limitations (see Elith and Leathwick 2009). Spatial scale, in terms of resolution, is a major concern when using SDMs, with large-scale environmental data likely too coarse to capture the effects of local climatic variation, especially in areas with large topographical variation (Dobrowski et al. 2009). Environmental and distributional data may be characterized by their extent, referring to the geographical area covered (for example, global, continental, or national), or by their resolution (or grain), which refers to the size of the grid cells in which data are sampled (Wiens 1989; Nystrom Sandman et al. 2013; Wisz et al. 2013). Extent and resolution may be linked, although a greater extent will not always lead to coarser resolution, but an increase in extent is likely to be associated with a decrease in resolution (Pearson and Dawson 2003).

Conducting studies at different spatial scales can lead to very diverse results (Wiens 1989; Hamer and Hill 2000). For example, change in biodiversity may be different in strength and direction using data collected at different scales (Keil et al. 2011) due to differential impacts of natural and anthropogenic drivers of ecological change (Moorcroft et al. 2001). Further, in using SDMs to project distributions under future climate scenarios, fine-scale climate projections have been shown to provide very different estimates of climate change impacts compared to their coarse-scale equivalents (Franklin et al. 2013). Notwithstanding, SDMs are often used without regard for the effect of scale (Elith and Leathwick 2009), even though differences among scales are frequently acknowledged. Bradter et al. (2013) advocated studies identifying the appropriate spatial scale of predictors in order to produce more accurate species distribution projections. However, how this identification is undertaken will most likely vary depending on the species and environmental variables in question.

Macroclimate is suggested to be one of the main drivers of distribution patterns at continental and global scales, whereas biotic interactions and microclimate may control distributions at community and landscape scales, with human impacts one of the factors explaining ranges at intermediate scales (Whittaker 1975; Pearson and Dawson 2003; Thuiller et al. 2003). However, there is growing evidence of a role for biotic interactions in shaping species distributions at the global scale (Jablonski 2008; Wiens 2011; Wisz et al. 2013). Historically, distributional studies have focused on interspecific competition (MacArthur 1972; Amarasekare 2003), but facilitation (mutualism), predation, parasitism, and disease, are now recognized as additional factors in species distribution patterns (Araujo and Rozenfeld 2014). Biotic interactions within trophic levels, such as competition and facilitation, are much harder to observe than interactions between trophic levels, for example predation, but are well known to produce sharp boundaries in species distributions with little or no overlap (Flux 2008).

European lagomorphs exhibit strong competitive interactions and occupy a wide range of environmental conditions (Leach et al. 2015a). They occupy extreme elevations in the Alps, and are found across all European latitudes, from the Arctic Circle to the Mediterranean (Chapman and Flux 2008). In addition to the European rabbit, *Oryctolagus cuniculus*, there are 5 species of hare: the Apennine hare, *Lepus corsicanus*, and broom hare, *Lepus castroviejoi*, have highly restricted ranges, whereas the European hare, *Lepus europaeus*, mountain hare, *Lepus timidus*, and Iberian hare, *Lepus granatensis*, have much wider ranges. Competition between the latter 3 species is asymmetrical and in most cases, the ranges are parapatric (Acevedo et al. 2012a). For example, in the Iberian Peninsula, European hare densities decrease in areas where they contact Iberian hares (Gortázar et al. 2007; Acevedo et al. 2012a). In mainland Italy, the Apennine hare is decreasing as a result of multiple pressures, including habitat degradation, and probable competition with introduced European hares (Angelici et al. 2008). The Apennine hare competes with the introduced European hare, which is larger and has a higher reproductive rate than the Apennine hare (Angelici et al. 2010). When the 2 species occur in sympatry, the Apennine hare is found at higher altitudes, whilst in allopatry they occur in the same altitudinal range (Angelici and Luiselli, 2007). Mountain hare populations typically decline in contact with expanding European hare populations usually with upslope range contraction (Thulin 2003; Reid 2011).

In most of the European hare's native range, the mountain hare seems to be restricted to high elevations and forests, as it is driven away from lowland grassland plains (Thulin 2003, Flux 2008), but in Ireland, Finland, Russia, and Sweden, the European hare is found in sympatry with the mountain hare (Flux 2008). In Ireland, introduced European hares and endemic Irish hares, *Lepus timidus hibernicus*, occupy similar habitats in sympatry (Reid and Montgomery 2007). They would probably show strong interspecific competition if resources were limiting (Reid 2011), but this is highly unlikely as the majority of available habitat is grassland and thus optimal for both species. Nevertheless, the European hare has actively displaced the Irish hare within its core invasive range presumed related to competition for space and hybridization (Caravaggi et al. 2015, 2016a).

Hares and rabbits frequently co-occur but rarely interact. The European hare and rabbit form one of the most commonly studied and observed systems with respect to competition. Before anthropogenic introductions, the European hare was restricted to central Europe and the Asian steppes, and the European rabbit to the Iberian Peninsula (Flux 1994), but overlap in the ranges of these 2 species is now widespread, and coexistence occurs in many introduced populations (Flux 2008). In most areas of their range they graze side by side, showing significant dietary overlap (e.g., Katona et al. 2004).

Here, we produce Joint SDMs for European lagomorph species at 3 hierarchical resolutions: 50 km, 25 km, and 10 km grid cell resolutions. Although home ranges of

European hares and rabbits span up to 1 km^2 (Jones et al. 2009), these resolutions were chosen because environmental or species data are often collected at these levels for atlases and, therefore, these resolutions are frequently used to model species distributions. Model outputs were used to calculate residual and environmental correlations that can explain why species may or may not co-occur, and thus suggest modelled biotic interactions. We hypothesized that the strength of modelled biotic interactions varies with scale due to differential impacts of natural and anthropogenic drivers of ecological change at varying scales (Moorcroft et al. 2001). Modelled biotic interactions are likely to play a greater role at finer resolutions on a community and landscape scale, i.e., 10 km grid cell resolution (Whittaker 1975; Pearson and Dawson 2003; Thuiller et al. 2003).

MATERIALS AND METHODS

Species and environmental data.— International Union for Conservation of Nature (IUCN) geographic range polygons for each European lagomorph species (Fig. 1) were rasterized in R v.3.1.1 at 3 hierarchical resolutions: 50 x 50 km (n = 6,255 cells), 25 x 25 km (n = 23,118 cells), and 10 x 10 km (n = 224,691 cells), with a value of 1 for species presence and 0 for absence. IUCN polygons have been used in a number of SDM studies to date (e.g., Lawler et al. 2009; Visconti et al. 2015), and whilst they may have higher commission errors (Graham and Hijmans 2006), the detailed construction of the polygons together with the internal review process and expert assessments by the IUCN (see http://www.iucnredlist.org/technical-documents/red-list-training/iucnspatialresources for further information) can lead to the production of more realistic SDMs (Fourcade 2016). To illustrate the consequences in using different input data for lagomorph species distributions, Leach et al. (2016) compared models built with IUCN polygons to those built with point occurrence data. Predicted probabilities of presence were found to vary substantially between models. Although using IUCN polygons may result in false positives, in this case, point occurrence data resulted in false positive and false negative predictions of occurrence. For example, the Iberian hare is restricted to the Iberian Peninsula, yet models utilizing point occurrence incorrectly predicted areas in northern Europe to be suitable. In addition, the European hare and rabbit are distributed throughout central Europe extending into eastern Europe, yet models using point occurrence data predicted distributions skewed to western Europe. This reflects the sparse and biased nature of point occurrence data, whilst suggesting that IUCN polygons, at least for European lagomorphs, lead to more realistic species distribution models.

Current climate variables (~1950-2000) were downloaded from WorldClim (www.worldclim.org) and resampled to the same resolution 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 annual evapotranspiration from mean annual precipitation. The number of months with a Positive Water Balance (PWB) was calculated by subtracting each monthly evapotranspiration from its corresponding monthly precipitation, then converting into a binary format, where a value greater than 0 was given a value of 1 and a value less than 0 was kept at 0, and finally summing the 12 binary scores (Kremen et al. 2008). Mean annual Normalized Difference Vegetation Index (NDVI) was calculated from monthly values which were downloaded from the European Distributed Institute of Taxonomy (EDIT) Geoplatform (http://edit.csic.es/Soil-Vegetation-LandCover.html). Hilliness, an index of surface roughness, 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. 2007). Human Influence Index data were downloaded from the NASA Socioeconomic Data and

Applications Centre (SEDAC) website (http://sedac.ciesin.columbia.edu/; WCS CIESIN 2005). Subsequently, correlated environmental variables (minimum precipitation, minimum temperature, mean annual precipitation, mean annual temperature, solar radiation, annual water balance, and annual evapotranspiration) were removed, leaving the following: maximum temperature, temperature seasonality, maximum precipitation, precipitation seasonality, PWB, NDVI, Hilliness, and Human Influence Index. Environmental variables were centered on 0 and scaled by their standard deviations.

The environmental variables chosen ultimately for modelling were known to determine distributions of European lagomorph species. Leach et al. (2015b) found the following variables were important in describing the distribution of more than 1 European lagomorph: Hilliness, Human Influence Index, maximum temperature, NDVI, precipitation seasonality, temperature seasonality, and water balance. Altitude, maximum precipitation, and precipitation seasonality were significantly important in describing the distribution of the Iberian hare; precipitation and temperature seasonality in describing the distribution of the European hare; and maximum temperature in describing the distribution of the mountain hare (Acevedo et al. 2012a, b). In addition, temperature seasonality was the most influential environmental variable for predicting the distributions of European and mountain hares (Caravaggi et al. 2016a, b).

Model structure.— We used the code provided in Pollock et al. (2014) to produce Joint SDMs at the 3 hierarchical resolutions. Joint SDMs simultaneously estimate the ranges of multiple coexisting species producing mixtures of possible species assemblages (Pollock et al. 2014; Harris 2014). Pollock et al. (2014) used a hierarchical, multivariate, probit regression model to include multiple species into a single SDM, with 1 model run per spatial scale. The model response is species occurrence represented by a matrix with dimensions of sites by species. The response is predicted by a data matrix with dimensions of sites by environmental variables. The number of dependent and independent variables did not vary across model runs. Interactions between species will cause un-modelled (i.e., unaccounted for) dependence in the residuals of the model, but these residual correlations can provide insight into the abiotic and biotic factors driving species co-occurrence patterns.

Models were fitted using the MCMC Bayesian modelling software JAGSv3.4.0 run through Rv3.1.1 via the R2jags packagev0.5-6. For all 3 resolutions, we ran 2 chains for 850,000 generations with the first 150,000 discarded as burn-in in order to reach an asymptote and with the remaining samples thinned by a factor of 1,000 meaning we retained 985 samples per chain for post-processing. We used vague priors for all model parameters and considered models to be converged once all elements of the parameter and correlation matrices had potential scale reduction factor values close to 1. This convergence diagnostic value suggests that each of the sets of simulated observations is close to the target distribution (Brooks and Gelman 1998).

Species pairs were then examined after the models were fitted. Residual and environmental correlations for species pairs were decomposed from model outputs and used to explain why species may or may not co-occur. The model outputs include predicted probabilities of presence for each species in each grid cell, regression coefficients for the response of each species to each environmental variable, and species-by-species grids with correlation due to similar environmental responses and residual correlations. Environmental correlations between species are a function of those species' scaled regression coefficients and the covariance's of the environmental variables. Positive environmental correlations suggest shared environmental responses, with strong negative or positive residual correlations potentially suggesting evidence for biotic interactions (Fig. 2; see right quadrants).

RESULTS

For a particular species pair, the direction of environmental and residual correlation coefficients were largely similar at all spatial resolutions examined (Fig. 3). The majority of species pairs shared environmental responses; however, the mountain hare's environmental correlation coefficients were negatively related to those of the European rabbit and the European hare, suggesting that the mountain hare has strikingly different environmental responses. In addition, most species pairs had negative residual correlations, indicating that species co-occurred less than expected given the similarity in environmental responses (Table 1). Nevertheless, models at finer resolutions took considerably longer to run using a high performance desktop computer (64-bit, two 3.10GHz processors and 192GB RAM); the 50 km model took ~3 days, 25 km took ~3 months, and 10 km took ~6 months. Regression coefficients to show which environmental variables were driving the positive and negative correlations between species are given in Supplementary Data S1.

A variety of pairwise responses were evident from the models. The broom hare co-occurred more than expected with the European hare and rabbit at all spatial scales given shared environmental responses and suggesting the potential for facilitative interactions. The Apennine and Iberian hares co-occurred less than expected with the European hare and rabbit given shared environmental responses, suggesting the potential for competitive interactions. European hares and rabbits co-occurred more than expected given their shared environmental responses, whereas European hares and mountain hares occupy very different environments and were less likely to co-occur than expected. The European rabbit and mountain hare also occupy very different environments and were less likely to co-occur than expected (Fig. 4). No species pairs occupied the upper left quadrant of Fig. 4, i.e., species with distinct environments did not co-occur more than expected. The strength of environmental and residual correlations was similar across different scales, although credible intervals were substantially narrower at finer resolutions, i.e., 10 km grid cells (by 75.8% on average when compared to those associated with the 50km resolution) and, therefore, provided greater precision (Fig. 4).

Co-occurrence patterns varied substantially between spatial scales (Fig. 5). There was no evidence for co-occurrence between mountain and European hares at the 50 km and 25 km scales, but models at the 10 km scale predict co-occurrence between these species with greater accuracy. In probit regression models, the mean of the normal distribution is an analogue of the linear predictor; therefore, a large positive value indicates high probability of presence and a large negative value indicates a low probability of presence. Therefore, patterns extending into the upper right quadrant of Fig. 5 indicate co-occurrence between those species, for example the mountain hare and European rabbit.

DISCUSSION

Lagomorphs occupy a considerable range of environmental conditions (Chapman and Flux 2008), from the Arctic Circle, Scandinavia, and the mountains of northern Scotland where cold temperatures and high precipitation are common, to the Iberian Peninsula and the Mediterranean with semi-arid environments. So initially, it may be surprising that most species shared environmental responses. However, *within*-species variation can be large due to the huge range of environments each occupies. The Iberian hare occupies the whole of the Iberian Peninsula experiencing concomitant variation in climate from lowland coastal regions to high elevation arid regions inland (Acevedo et al. 2012b). In contrast, *between*-species variation can also be large with some species occupying distinct environmental conditions, for example, the mountain hare and the European rabbit and hare. The former has a high latitudinal and elevational range, and occurs in areas with lower temperatures, compared to the European rabbit and hare; therefore, we would expect the mountain hare to demonstrate very different environmental responses (Thulin 2003).

Our analysis suggested that the majority of residual correlation coefficients were negative, and thus, species co-occurred less than expected given their shared environmental responses. Strong negative residual correlations indicate the possibility of competitive interactions for lagomorphs in Europe consistent with published sources, specifically: Iberian and European hares (Gortázar et al. 2007; Acevedo et al. 2012a), Apennine and European hares (Angelici and Luiselli, 2007; Angelici et al. 2008, 2010), and mountain and European hares (Thulin 2003; Reid 2011; Caravaggi et al. 2015). Thirty-three lagomorph species are known to have competitive interactions reported in the literature, with closely related, large-bodied, similarly sized species, occurring in regions of human-modified, typically agricultural landscapes or at high elevations, such as Apennine, European, Iberian, and mountain hares, significantly more likely to have reported competitive interactions than other lagomorph species (Leach et al. 2015a). In addition, the models suggest a facilitative interaction between European hares and rabbits. Evidence for biotic interactions between these 2 species has been debated, but the current general consensus is that they co-occur without competition (Flux 2008), comparable to our results. It should be noted that these are hypotheses of species interactions that need to be tested empirically and confirmed using natural history data. Unexplained residual variance between some species pairs, however, may not be explained by modelled biotic interactions if key determinants of the extent of their ranges have been left out of our models (i.e., other environmental variables not included could account for the unexplained residual variation). For example, minimum temperature is known to be a key determinant of distributions of European lagomorph species (Leach et al. 2015b) but was left out of the models in this study due to high multicollinearity with other environmental variables, notably maximum temperature, causing undue model leverage.

Co-occurrence in terms of overlapping species presence can change substantially at finer resolutions. Mountain and European hares, and European hares and rabbits, exhibited more overlap in their ranges at finer resolutions, whereas Apennine hares and European rabbits, and mountain hares and European rabbits, showed less overlap at finer resolutions. Species exhibiting less overlap occupied high elevational ranges in the Alps, Apennines, and Scottish Highlands, indicating again that finer resolutions capture small changes in microclimatic variation in mountainous regions (Dobrowski et al. 2009), and suggesting that models at finer resolutions may be more appropriate for species found in these areas.

Using rasterized IUCN geographic range polygons to build SDMs may lead to outputs particularly vulnerable to false positives (Murray et al. 2011), and potentially influence our interpretation of ‘interaction’; 2 species with identical range extents may never meet because of habitat partitioning, especially when separated by elevational gradients. Another potentially confounding effect is that models built with point-occurrence data will have been downloaded at a specific time and, therefore, may not reflect ecology based on long-term climate trends. To the best of our knowledge this has not yet been addressed within the field of Species Distribution Modelling. However, neither the use of range maps nor point occurrence data is without error (Pineda and Lobo 2012), and the relationship with scale may in fact be an artefact of coarse input data, regardless of resolution. In this study, we preferred to accept the risk of omission errors over commission errors because only the interactions with most confidence are likely to be captured by the models. Nonetheless, we suggest that when deciding what input data are to be used, the purpose of the study and quality of the data available should be considered.

Joint SDMs run at fine-scale resolutions had extremely long processing times using a high performance desktop computer, and although they produced estimates of residual and environmental correlation coefficients with greater precision, the strength and direction of correlations were similar, and in most cases identical, at all scales. This contradicts our hypothesis that the strength of modelled biotic interactions varies with scale. Predicted probabilities of occurrence were more precise at finer resolutions for some species, agreeing with our hypothesis that modelled biotic interactions play a greater role at finer resolutions, but for others an increase in spatial resolution resulted in little change to these values. If the aim is to accurately infer biotic interactions, modelling at finer resolutions is recommended. However, if only the strength and direction of environmental and residual correlations is of interest, then a coarser resolution may be adequate in the interest of saving processing time. Coarse resolution data may be just as useful in terms of accuracy (not precision), so it may not always be necessary to collect fine-resolution species occurrence data that could require considerable effort.

Scale is highly important when modelling multi-species distributions, but will nearly always result in a compromise between processing time and precision of results. The strength and directions of estimated correlations from joint SDMs were similar across scales, but with greater precision at finer resolutions, especially with respect to predicted probabilities of occurrence. Fine-scale models and data collection may not always be necessary for multi-species models; however, caution is advised when seeking to accurately infer biotic interactions using coarse data, especially when the species in question occupies mountainous regions.

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SUPPLEMENTARY DATA

Supplementary Data S1. Regression coefficients between European lagomorph species and environmental variables at 3 hierarchical resolutions.

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FIGURE LEGENDS

Figure 1. IUCN geographic range polygons for European lagomorph species.

Figure 2. Diagrammatic interpretation of negative and positive residual and environmental correlations. These interpretations may become less reliable with weaker correlation coefficients.

Figure 3. Network diagrams representing modelled environmental and residual correlation between European lagomorph species at 3 different scales: (a) 50 km, (b) 25 km and (c) 10 km. Black edges indicate positive correlations between species and red edges indicate negative correlations. Each edge is labelled with its correlation coefficient. Only significant correlations, i.e., those for which the credible intervals do not cross 0, are shown. Species pairs without connecting edges do not have spatially overlapping ranges.

Figure 3. Modelled environmental and residual correlations between European lagomorph species pairs at 3 different scales: (a) 50 km, (b) 25 km and (c) 10 km. Error bars represent 95% credible intervals.

Figure 5. Co-occurrence patterns for all combinations of European lagomorph species using predicted probabilities of co-occurrence from Joint SDMs at 3 different scales: 50 km (grey), 25 km (blue) and 10 km (red). Large positive values indicate high probability of presence and large negative values low probability of presence – for further explanation please see the Results section.

TABLES

Table 1. Modelled environmental and residual correlations between pairs of European lagomorph species at 3 hierarchical resolutions. NS indicates a species pair with credible intervals overlapping 0, i.e., non-significant. Interpretations are based on Fig. 2.

Species 1	Species 2	Environmental correlation			Residual correlation			Interpretation
		50 km	25 km	10 km	50 km	25 km	10 km	
Apennine hare	European hare	0.406	0.435	0.664	0.773	0.380	0.470	Potential facilitative interaction
Apennine hare	European rabbit	0.575	NS	0.711	0.496	NS	0.145	Potential facilitative interaction
Corsican hare	European hare	0.268	0.199	0.273	-0.611	-0.460	-0.629	Potential competitive interaction
Corsican hare	European rabbit	0.469	NS	0.463	-0.140	NS	-0.073	Potential competitive interaction
European hare	Mountain hare	-0.911	-0.899	-0.890	-0.208	-0.331	-0.175	Distinct environments, co-occur less than expected
European hare	European rabbit	0.799	0.810	0.806	0.612	0.554	0.641	Potential facilitative interaction
Iberian hare	European hare	0.657	0.722	0.775	-0.361	-0.416	-0.332	Potential competitive interaction
Iberian hare	European rabbit	0.815	0.856	0.894	-0.370	-0.456	-0.304	Potential competitive interaction
Mountain hare	European rabbit	-0.613	-0.737	-0.616	-0.304	-0.381	-0.301	Distinct environments, co-occur less than expected

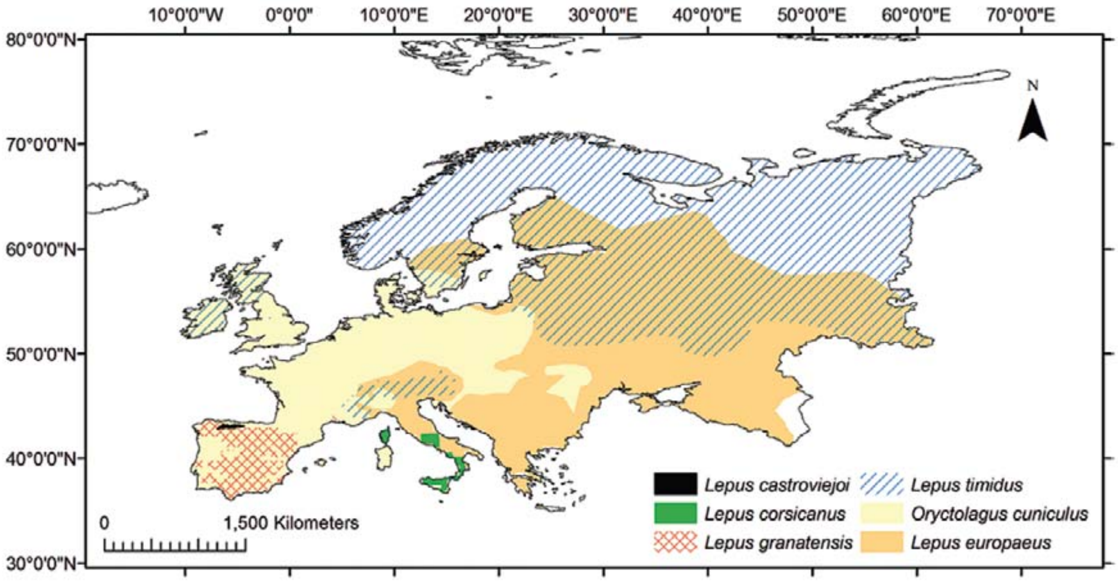


Figure 4. IUCN geographic range polygons for European lagomorph species.

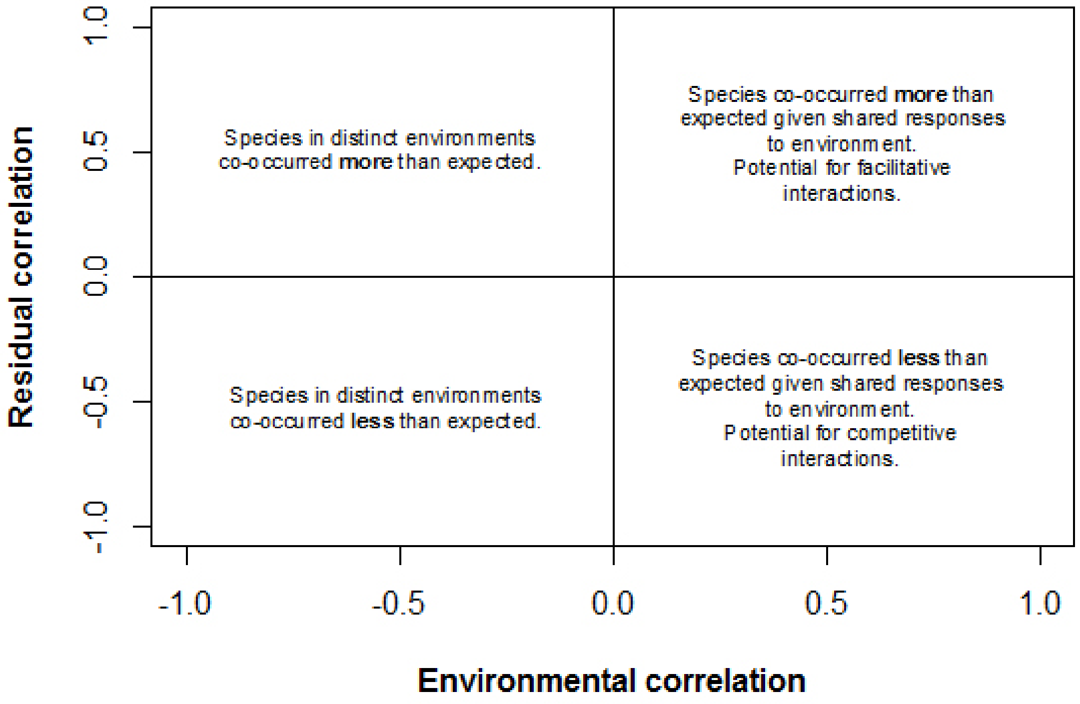


Figure 5. Diagrammatic interpretation of negative and positive residual and environmental correlations. These interpretations may become less reliable with weaker correlation coefficients.

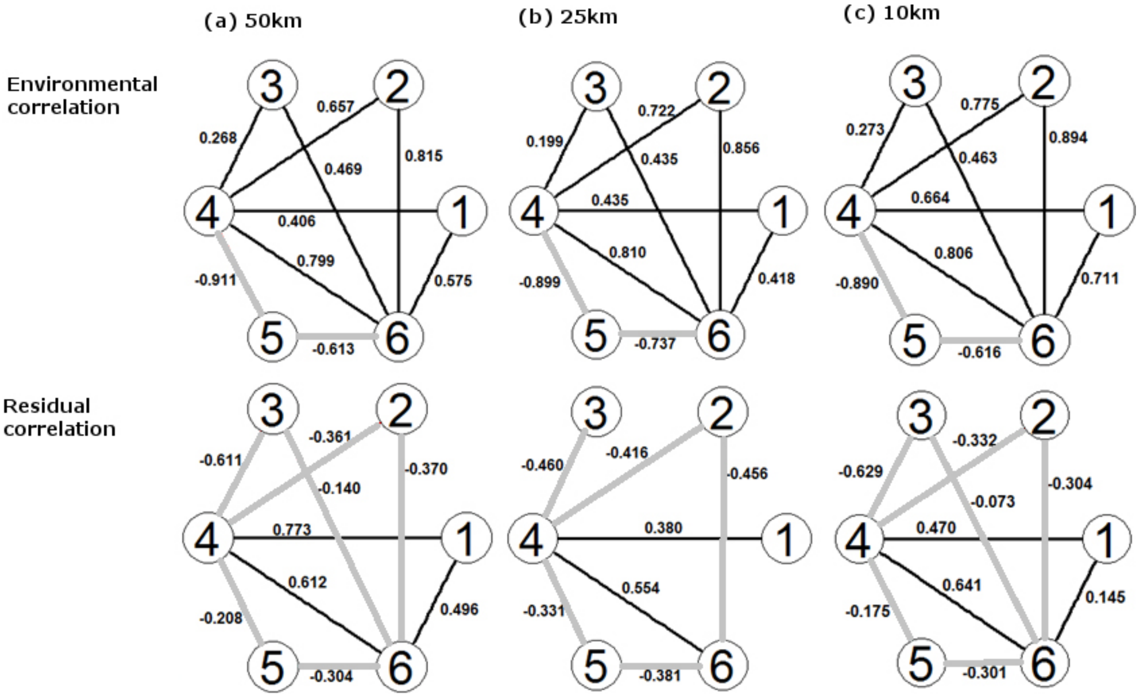
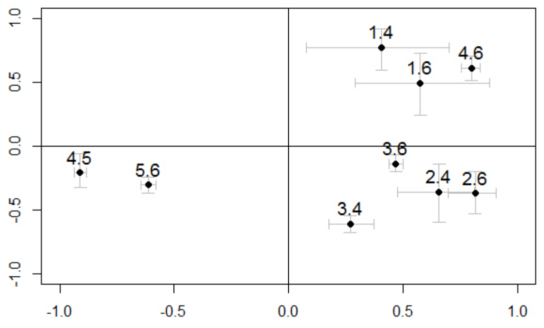
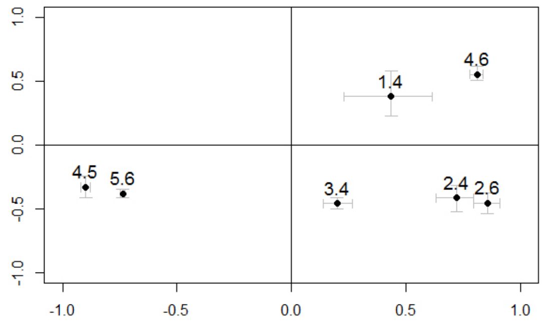


Figure 3. Network diagrams representing modelled environmental and residual correlation between European lagomorph species at 3 different scales: (a) 50 km, (b) 25 km and (c) 10 km. Black edges indicate positive correlations between species and red edges indicate negative correlations. Each edge is labelled with its correlation coefficient. Only significant correlations, i.e., those for which the credible intervals do not cross 0, are shown. Species pairs without connecting edges do not have spatially overlapping ranges.

(a) 50km



(b) 25km



(c) 10km

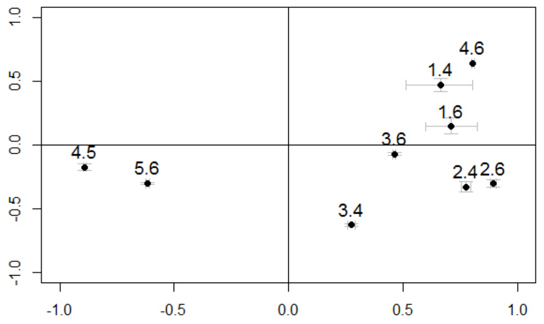


Figure 6. Modelled environmental and residual correlations between European lagomorph species pairs at 3 different scales: (a) 50 km, (b) 25 km and (c) 10 km. Error bars represent 95% credible intervals.

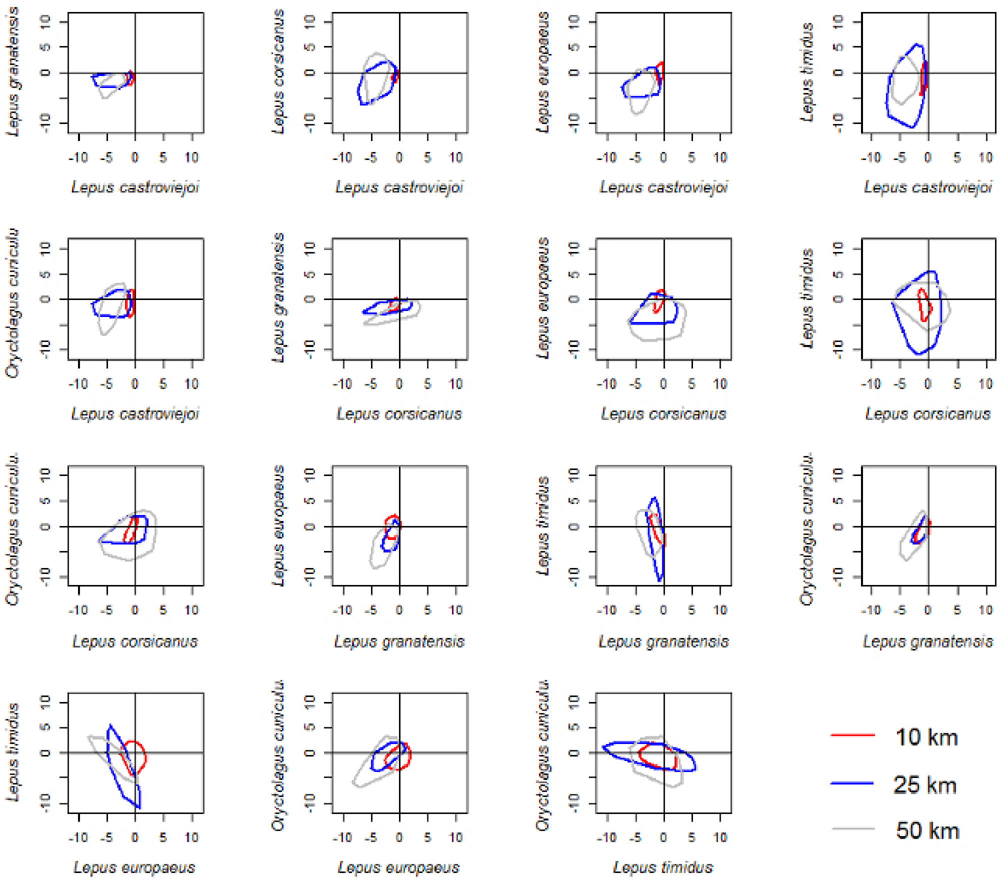


Figure 5. Co-occurrence patterns for all combinations of European lagomorph species using predicted probabilities of co-occurrence from Joint SDMs at 3 different scales: 50 km (grey), 25 km (blue) and 10 km (red). Large positive values indicate high probability of presence and large negative values low probability of presence – for further explanation please see the Results section.