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Splitting hares: Current and future ecological niches predicted as distinctly different for two congeneric lagomorphs

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ABSTRACT

The congeneric lagomorphs *Lepus timidus* and *L. europaeus* share allopatric distributions in many areas of Europe characterised by competitive exclusion and hybridisation. We investigated prospects for these species under climate change in northern England uplands. We created ensemble models predicting niche realisation for these species, influenced by abiotic and biotic factors, estimating niche overlap in geo-environmental space. The two species occupy distinctly different niches, influenced more by vegetation preferences than climatic differences. The current climate niche for *L. timidus* featured higher elevations with cooler temperatures and 168 km^2 range extent. Its current habitat niche scale was larger at 269 km^2, comprised entirely of upland dwarf shrubs: heather, cotton grass, moorland grasses. By contrast, the current climate niche predicted *L. europaeus* occupying lowland areas with a milder climate and range extent of 252 km^2. Its current habitat niche was also greater, 401 km^2, being mostly improved grassland. Competition was presently limited. The current niche predictions showed very little geographic overlap between the species. Niche overlap measured by Schoener Index was low: current climate niche 0.16; current habitat niche 0.07. The future climate niches for 2050 (IPCC RCP2.6), predicted *L. timidus* range contracting to 19 km^2, on hilltops and *L. europaeus* range expanding to 765 km^2. Consequently *L. timidus* range would be wholly within the *L. europaeus* range. In many contact zones throughout Europe, *L. europaeus* outcompetes *L. timidus;* however, in the Peak District their distributions are largely distinct. Future replacement of *L. timidus* by *L. europaeus* may be engendered by dietary convergence, should a warmer climate cause a transition of upland dwarf shrub vegetation to grasses.

1. Introduction

1.1. Lagomorph niches and conservation status

Ecological niche models often predict opposing patterns of distribution and survival for two European lagomorph species: the mountain hare (*Lepus timidus)* and the European brown hare (*Lepus europaeus)* (Acevedo et al., 2012; Bisi et al., 2015; Leach et al. 2015a, 2015b, 2016, 2017). Despite differences in physiological adaptations and requirements, they often share distributions and compete for resources (Thulin 2003; Jansson et al., 2007). As herbivores both species are important to ecosystems for recycling vegetation nutrients, and are prey for carnivores and raptors (Harris and Yalden 2008; Barbar and Lambertucci (2018).

With a circumpolar distribution, *L. timidus* is adapted for cold temperatures and snow in hilly or mountainous areas, and is a habitat generalist, living upon boreal forest, mires, heaths and moorlands (Angerbjörn and Flux, 1995; Harris and Yalden 2008). The IUCN Red List status is Least Concern and population status is stable for *L. timidus* (Smith and Johnston 2019). Some populations are vulnerable, being quasi-cyclic (Newey et al., 2007) or limited by parasites, predation or starvation (Smith and Johnston, 2019). Climate change scenarios suggest *L. timidus* can be affected by changes in long-term weather patterns (Reid et al., 2021) and will move to higher latitudes and elevations (Anderson et al., 2009; Hof et al., 2012; Leach et al., 2015b), its range in Europe reducing by 70% (Acevedo et al., 2012).

By contrast *L. europaeus*, occupies temperate climate zones across Europe, is a habitat specialist, inhabiting grassland and agricultural

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environments, favouring cereal, root crops or grasses (Tapper and Yalden 2010). For *L. europaeus* the IUCN Red List status is Least Concern and population status is recorded as decreasing due to agricultural intensification (Hackländer and Schai-Braun 2019). Recently some populations have revived, enabled by agricultural improvements (Viviano et al., 2021). Forecasts for *L. europaeus* under climate change suggests little response (Bisi et al., 2015) or range expansion (Hof et al., 2012; Leach et al., 2015b; Caravaggi et al., 2017).

Together, these two species form a recognised model of interspecific competition: a mechanism which acts as a determinant of species distributions (Elton 1927). Competition frequently involves one species exploiting food or shelter resources, much more effectively than another. To survive, the less effective species must either move to a different habitat or adjust its diet away from the competitor (Krebs 2001). Historic studies have reported large areas of *L. timidus* range being superseded by *L. europaeus* as a result of competition for space and resources or interspecific hybridisation with introgression, e.g. populations in Sweden and Russia (Thulin 2003), and Ireland (Caravaggi et al. 2014, 2017). Where different habitats overlap, *L. timidus* maintains high elevations and deep forests, feeding on woody browse and excludes *L. europaeus.* Alternatively *L. europaeus* maintains its dominance over optimum grassland habitats, preferring a diet of soft greens, and may displace *L. timidus* (Flux and Angermann 1990; Thulin 2003; Jansson and Pehrson 2007). However the two species may exist in sympatry, such as in Italy where they share a spatially overlapping elevation gradient, though occupying different habitats: *L. europaeus* from 500m to 1500m a.s.l. upon arable land or sparsely vegetated areas; *L. timidus* from 1300m to 3000m in areas of dwarf mountain pine (Bisi et al. 2013, 2015; La Morgia and Venturino 2017; Naldi et al., 2020).

The species *L. timidus* is native to Great Britain though died out in England around 6000 BP (Harris and Yalden, 2008) though persisted in Scotland where it is now associated with upland heather moorlands (Hewson 1984, 1989). Because of heavy culling on some moors (Watson and Wilson 2018) and a large decline in abundance, the conservation status of the UK *L. timidus* population was downgraded to 'unfavourable-inadequate' (JNCC, 2019a).

In England *L. timidus* was reintroduced through translocations from Scotland by sporting landowners in the 1870s and now occupies some 250 km^2 of Peak District uplands. Population density has been estimated at 10 hares km^{-2} (Mathews et al., 2018). It is isolated by 300 km from its founder population. Surveys described *L. timidus* preferring habitats of heather, cotton grass (*Eriophorum* spp.), moorland grasses (*Deschampsia flexuosa, Nardus stricta, Festuca* spp.*, Juncus* spp.) and dwarf shrubs (*Empetrum nigrum, Vaccinium myrtillis*) (Mallon et al., 2003).

By contrast *L. europaeus* is thought to have been introduced to Great Britain during the Bronze Age (Thulin 2003) and certainly by Roman times (Harris and Yalden 2008) and now occupies arable landscapes. Once widespread, numbers have decreased by 80% since 1880 as a result of game-shooting and intensive farming practices, the last conservation assessment recording the species as in decline (UK BAP, 2007). There have been no recent assessments (JNCC, 2019b). Around the Peak District extensive surveys of *L. europaeus* during 2011–12 (Bolton 2013) recorded density amongst agricultural landscapes at 1.7 hares km^{-2}, though not in upland habitats. An extensive metapopulation facilitated inward and outward migration.

Within the UK competition between these two species has received little attention. Hewson (1976a) reported in Scotland that *L. timidus* maintained dominance upon heather moorland when *L. europaeus* was present. Within the Peak District, Yalden (1971) recorded a range overlap between *L. timidus* and *L. europaeus* between elevations of 280–500m; a rough boundary between arable and moorland ecosystems. The Peak District presents an ideal model environment, to provide an important understanding of competitive dynamics between these two species (Thulin 2003; Smith and Johnston, 2019).

1.2. Study objectives

Niche model theories describe the conditions within which species maintain populations at different locations (Franklin 2009; Peterson et al., 2011). Models suggest species exist in environments having combinations of abiotic factors, topography and climate, that enable physiological survival i.e. the fundamental niche (Guisan and Zimmermann, 2000); also described as the potential niche (Sillero 2011); or the climate/geomorphological niche (Peterson et al., 2011) and it is often considered that species express such preferences over large scales (countries or continents). Species occurrence may then be facilitated, constrained or "filtered" by biotic factors: food and shelter resources, competitors, predators, parasites, human influences, this being the realised niche (Guisan and Zimmermann, 2000; Sillero 2011); the occupied or biotically reduced niche in the terms of Peterson et al. (2011) and which may be conventionally regarded as habitats (Krebs 2001: 66). However filtering processes may not always act in such a formulaic sequential hierarchy (Guisan et al., 2017: 23) and ecological or stochastic processes may alter species distribution in unexpected ways. Statistical models reference occurrence records, combined with environmental variables, to explain how species occupy these niches (Guisan et al., 2017) and the extent to which similar species co-exist together (Broennimann et al., 2012). Such evaluations assess the sustainability of populations and prompt monitoring, legal protections, revision of land uses, identification of species invasions, reintroductions or translocations, or warnings of future threats (Franklin 2009).

The aims of this study were to:

1) Predict and compare the current climate niche and current habitat niche of both *L. timidus* and *L. europaeus* in northern England. We hypothesised that *L. timidus* would be associated with high elevations, a cold climate, upland heather moorland and bog vegetation and *L. europaeus* low elevations, warmer climate and grassland or woodland (Tapper and Yalden 2010);
2) Measure the extent of overlap between the two species in geographic and environmental space, to estimate the degree of competition. We did expect some competition, though were unsure how strong this might be;
3) Forecast the future climate niche for the year 2050. We anticipated that with warming climate, *L. timidus* would move to higher elevations, reducing its range. For *L. europaeus* we had no specific expectation.

2. Materials and methods

2.1. Study area

The study area encompassed the Peak District National Park, Northern England (Fig. 1). The landscape is dominated by peat uplands with vegetation of upland heath, dwarf shrubs including berries, bog grasses and mosses and grasslands. (Anderson and Shimwell 1981). Topography consists of plateau-like hills, ranging up to 631m (OS Explorer (2015). The uplands are surrounded by improved grassland areas, agriculture and cities.

2.2. Species records

Observations of species came from citizen-science sources, provided by walkers, wildlife enthusiasts, natural historians, landowners and environmental experts, sent by paper, post, email or mobile phone apps to one of eleven relevant regional or national biological recording centres (BRC's). The BRC's then provided to us records from 2001 to 2018 for *L. timidus* (8666 records) and *L. europaeus* (5994 records) (see Hare Data Sources). These records gave species locations from which to derive environmental data, define the study extent and provide sufficient sample and prevalence sizes for modelling (Guisan et al., 2017).

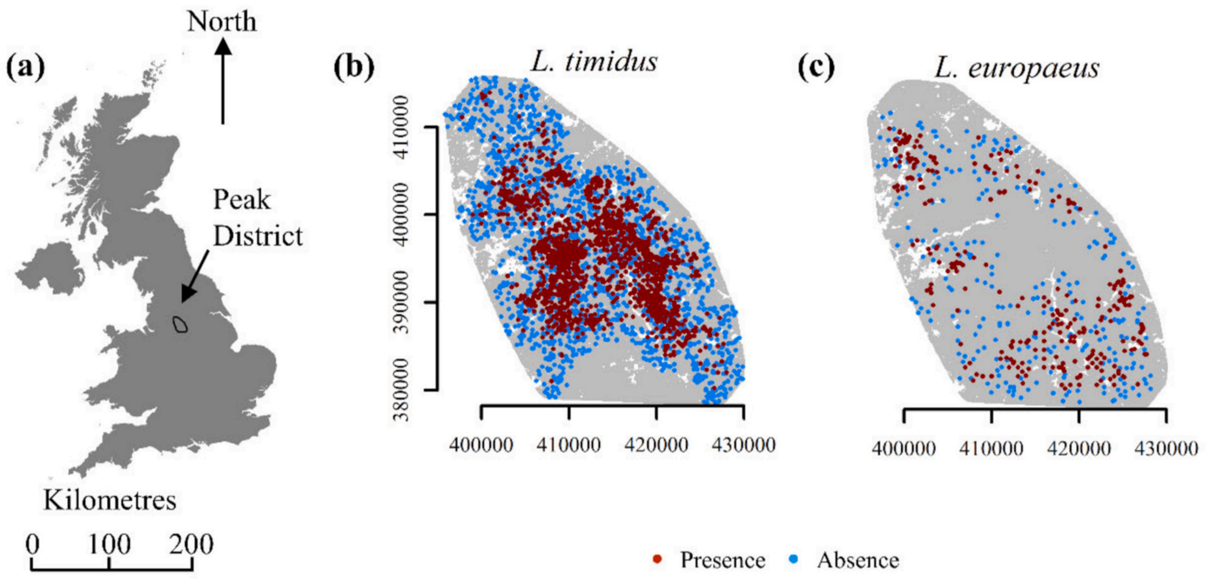


Fig. 1. Maps showing hare observation locations. **(a)** Great Britain, with Peak District; **(b)** Presence/pseudo absence data for *L. timidus;* **(c)** Presence/pseudo absence data for *L. europaeus*. Grey shape is study extent within Peak District National Park, UK, Latitude 53.3342° N, Longitude 1.7837° W. Map axes (b) and (c) represent Ordnance Survey Eastings and Northings taken from British National Grid 100 km tiles SK and SE with ticks at 10 km intervals.

To prepare the data set we considered sources of bias including autocorrelation, pseudo-replication, duplication or observer effects (Guisan et al., 2017). Within the records we assumed correct identification of species, except discarding 5 *L. timidus* records found >10 km from the study extent as mis-identifications. We kept observations recorded to the nearest 100m, excluding records accurate only to 1000m. We used kernel density plots to assess occurrence patterns for 2001 to 2018. For *L. timidus* in particular, these showed strong annual fluctuations, with a marked nadir during 2013 (Figure S1), less so for *L. europaeus* (Figure S2). We regarded likely causes as differences of observer effort, though ecological factors were possible. Indeed fifty percent of *L. timidus* records were contributed by the late Professor Derek Yalden, until he passed away in 2013 (Table S1). To mitigate for observer effort, maintain relevance to contemporary environmental data, and alleviate possible effects of hare population dynamics (Newey et al., 2007), we then used records for the last ten years. To reduce duplication or autocorrelation, we discarded records occurring within 100m of each other using function [ecospat.occ.desaggregation] in R package 'ecospat' (Di Cola et al., 2017). Thus the final data set consisted of 1690 *L. timidus* and 265 *L. europaeus* records (Fig. 1). Of these 4% *L. timidus* and 30% *L. europaeus* records were on or within 100m of roads. We acknowledged that using observations from roads might provide bias: roads being a potential deterrent or attractant to lagomorphs.

We defined potential pseudo-absences as any locations without a record for the respective species at the scale of 1 ha. We opted for ratios of 50/50 presence/absence, generating 1690 (*L. timidus*) and 265 (*L. europaeus*) pseudo-absence records. This ensured prevalence was above minimum sample sizes and ratios affecting modelling errors (Jimenez-Valverde et al., 2009; Guisan et al., 2017) and ratios would not influence the accuracy measure kappa, with TSS and AUC unaffected (Allouche et al., 2006). We restricted placement of pseudo-absence locations as randomly within a shape determined by designating, overlapping and dissolving 2000m circles around each species presence point, using R package 'dismo' using functions [circles] and [randomPoints] (Van Der Wal et al., 2009; Hijmans et al., 2017). Thus analysis utilised a randomly generated 1-ha scale grid with presence and absence points and environmental data per 1-ha.

We calculated a minimum convex polygon (MCP) of 639 km^2 based upon *L. timidus* BRC records and only employed *L. europaeus* records which occurred within this MCP. To account for environmental influences at MCP edges, we added a 2 km buffer, excluding water and urban features, to create a study extent of 805 km^2. This extent therefore encompassed the northern Peak District uplands which was the known range of *L. timidus*. By contrast *L. europaeus* could disperse in and out of the study area from surrounding populations. We assumed both hare species were at equilibrium with environmental conditions. Hares exhibit short natal dispersal ranges and fidelity to small home ranges (Harris and Yalden, 2008; Tapper and Yalden 2010). We assumed hare records were representative of home ranges and habitat utilisation.

2.3. Environmental parameters

We assessed environmental factors hypothesised to influence occurrence of *L. timidus* and *L. europaeus*. Predictor variables were prepared within ArcMap 10.6.1 (ESRI, USA) and R (R Core Team, 2011) referencing Bivand et al., (2013); Wegmann et al., (2016); Guisan et al., (2017).

Current climate niche predictors were based upon climate and topography. Climate predictors were the WorldClim set of metrics (Fick and Hijmans 2017): temperature, rainfall and solar radiation. These were downloaded at 1 km scale, resampled using bilinear interpolation with the ArcGIS (ESRI, USA) resampling tool, providing smoothed 1-ha size values. Topography predictors were derived from OS 50m digital terrain model (Digimap 2019), used to calculate elevation, slope and aspect values. In addition the uplands contained micro-topographical features: extensive networks of peat gullies, anthropogenically caused by acid rain erosion (Bonn et al., 2009). These were used by *L. timidus* for shelter and movement. Gullies information was sourced as OS Vector data (Digimap 2019) with a 50m buffer applied.

Current habitat niche predictors consisted of vegetation providing food and shelter resources, roads indicating human activity, and the presence of the competitor species. Vegetation productivity indices were derived from Landsat 8 scenes (Path203/Row023, 4th May 2016), downloaded using the EarthExplorer tool of the United States Geological Survey (USGS; www.earthexplorer.usgs.gov), and resampled to 1-ha. Bands were subject to signal enhancement, to represent Normalised Difference Vegetation Index (NDVI), Normalised Difference Water Index (NDWI), Simple Ratio (SR) and Soil Adjusted Vegetation Index (SAVI). Bands were analysed in R with at-sensor reflectance and tasselled cap transformation, representing vegetation brightness, greenness and wetness (Wegmann et al., 2016; Guisan et al., 2017). To assess the importance of habitat and vegetation types, we also created a detailed bespoke landcover map, combining the UK landcover map (Rowland et al., 2017), with data from aerial images (Digimap 2019). From the UK landcover map (Rowland et al., 2017) we included polygons for pertinent lowland categories: arable, broadleaved or coniferous woodland, improved grassland (managed or unmanaged pasture comprising *Lolium* spp and clover (*Trifolium repens),* used for sheep farming), inland rock, neutral grassland, suburban, urban, or water. However those UK landcover map (Rowland et al., 2017) types which represented upland areas (64% of the study extent) appeared homogeneous e.g. bog. Such areas consist of ecotones of young and mature heather (*Calluna vulgaris*), cotton grass (*Eriophorum* spp.), moorland grasses (*Nardus stricta, Deschampsia flexuosa, Festuca* spp.*, Molinia caerulea* etc*)*, and berries (*Empetrum nigrum, Vaccinium* spp.), pertaining to *L. timidus* food and shelter (Hewson 1962, 1989). Therefore we assembled new map data to represent these vegetation categories by supervised classification of aerial images (Wegmann et al., 2016) taking 10,527 samples, supported by 440 ground-referenced photographs, using random forest classification to create an upland vegetation raster, with 82% accuracy (Table S2; Figure S3). Each hectare was classified to its largest single dominant vegetation type, though other types might have been present. The upland vegetation raster and lowland polygons were then combined to one single map. Individual landcover classes were used as binary categorical predictors. Road information was sourced as OS Open Roads data (Digimap 2019) with a 50m buffer applied. Maps of historical *L. timidus* and *L. europaeus* records suggested a small range overlap, therefore we included the presence of each species as a predictor to the other.

Future climate niches were projected using the IPCC Fifth Assessment Report Coupled Model Intercomparison Project Phase 5 (Taylor et al., 2011) future climatic data for the Representative Concentration Pathway (RCP) 2.6 for 2050 (averaged across 2041–2060) downloaded from WorldClim at 1 km^2 grid cell resolution and resampled with bilinear interpolation to 1-ha scale. RCP 2.6 indicates a mean average global temperature increase of 2 °C by 2050. Variables were averaged across five Global Circulation Models (GCMs), CNRM-CM5, GFDL-CM3, GISSE2-R, Had-GEM-ES and MIROC-ESM-CHEM. The RCP 2.6 climate scenario is considered the mildest and least likely of global warming scenarios. Attempts to model with higher RCPs, predicted near binary absence (*L. timidus*) and presence (*L. europaeus*) which was less informative. These future climate niche projections also included the same topographical predictor variables and values as for the current climate niche i.e. elevation, slope and aspect derived from OS 50m digital terrain model and gullies information from OS Vector data (Digimap 2019). To be consistent with the current climate niche, the future climate niche did not include any vegetation information, which was of course unknown.

2.4. *Ecological niche modelling*

Niche modelling analysis followed Guisan et al. (2017) using 'biomod2' (Thuiller et al., 2014), 'ecospat' (Di Cola et al., 2017) and 'ade4' (Dray and Dufour 2007) packages in R. Predictors were normally distributed, though some were skewed, and were evaluated for collinearity with Pearson correlation coefficients using function [layerStats] from R Package 'raster' (Hijmans 2019). Strongly correlated predictors having Pearson coefficient $r > 0.75$ were removed (Guisan et al., 2017). Where choices arose, we retained those relevant to lagomorph ecology (Table 1) (Harris and Yalden 2008). For climate niche models we retained nine abiotic variables: BIO 6 minimum temperature of coldest month, BIO 7 temperature annual range, BIO 8 mean temperature of wettest quarter, BIO 9 mean temperature of driest quarter, BIO 12 annual precipitation, BIO 15 precipitation seasonality, aspect, gullies and slope (Table 1, Figure S4). For the habitat niche models we retained the following biotic variables: NDVI, brightness, wetness, all landcover types, roads and the presence of respective lagomorph species (Table 1, Figure S5).

Table 1
The models and variables used to predict hare ecological niches.

Species	*Lepus timidus*	*Lepus europaeus*
Species Occurrence Data	BRC data 1690 presences 1690 pseudo-absences	BRC data 265 presences 265 pseudo-absences
	Current climate niche	
	BIO.6 Min temp of coldest month	
	BIO.7 Temp annual range	
	BIO.8 Mean temp of wettest quarter	
	BIO.9 Mean temp of driest quarter	
	BIO.12 Annual precipitation	
	BIO.15 Precipitation seasonality	
	Aspect	
	Gullies	
	Slope	
	Current habitat niche	
	NDVI	
	Brightness	
	Wetness	
	Arable	
	Berries	
	Broadleaved woodland	
	Coniferous woodland	
	Cotton Grass	
	Young heather	
	Mature heather	
	Improved grassland	
	Moorland grasses	
	Roads	
	L. timidus or *L. europaeus*	
	Future climate niche	
	BIO.6 Min temp of coldest month	
	BIO.7 Temp annual range	
	BIO.8 Mean temp of wettest quarter	
	BIO.9 Mean temp of driest quarter	
	BIO.12 Annual precipitation	
	BIO.15 Precipitation seasonality	
	Aspect	
	Gullies	
	Slope	

Niche models used presences and pseudo-absences for each species and relevant predictor layers (Table 1). Predictive models were assembled in 'biomod2' (Thuiller et al., 2014) which hosts a series of process steps within the function [BIOMOD_ModelingOptions] to enable use of algorithms. For these we employed three with standard settings: General Linear Model (quadratic models, no interaction terms, testing on AIC); Random Forest (500 trees, 5 nodes); MAXENT (Phillips et al., 2006) (200 iterations with linear or quadratic features). Nine runs were conducted with cross-validation, 70/30 training/test data; performance monitored with kappa, TSS (Allouche et al., 2006) and AUC scores (Fielding and Bell 1997). Because each algorithm may perform differently with different environmental predictors, making evaluation and comparison difficult, we created ensemble models retaining all information from the candidate algorithms following Thuiller et al. (2009) and Guisan et al. (2017), using function [BIOMOD_EnsembleModeling] within 'biomod2'. We chose between committee and weighted mean averaged models considering test scores for kappa, TSS and AUC. Predictor variables were ranked on average importance values for the GLM. The influence of each predictor was portrayed with evaluation strip charts (Elith et al., 2005). For each ensemble model we used optimised TSS value to determine probability threshold, predicting climate and habitat niches (Franklin 2009) using function [find.optim.stat] within 'biomod2' (Guisan et al. 17: 259). Using function [extract] in 'raster' we then measured the size of predicted niches for each species. We calculated min, max and mean abiotic values and vegetation productivity values for each species. For each landcover class we measured how much the models predicted as occupied. The future climate niche model applied the ensemble model values derived from the current climate model, to predict future climate values, forecasting for the year 2050 and quantifying range change (Fick and Hijmans 2017; Guisan et al., 2017). Some future climate variables had ranges outside those used to calibrate the current climate models. Therefore for the future climate niche models, we recorded how many variables were invoked to form predictions, thereby indicating where predictions might be uncertain, determined with the function argument [build.clamping.mask] in 'biomod2'.

Geographic overlaps were calculated from prediction maps. Elevation overlaps were assessed with Welch's *t*-test for difference. Environmental niche overlap assessment followed Broennimann et al. (2012) predicting niche occupancy in environmental space, thereby removing geographic bias. This method was designed to detect niche overlaps in current environments. We assessed both the climate and habitat niches. Multivariate analysis of these factors applied principal components analysis to species presence points only, determining two leading components within 'ecospat' using function [ecospat.sample.envar] (Di Cola et al., 2017) and function [dudi.pca] in R package 'ade4' (Dray and Dufour 2007). Overlap of niches were tested for equivalency and similarity using Schoener and Hellinger indices (Broennimann et al., 2012) using functions including [ecospat.niche.similarity.test] in 'ecospat' (Di Cola et al., 2017).

3. Results

For both lagomorphs in all niches, ensemble modelling achieved high test scores and credible predictions of probability of occurrence (Franklin 2009; Guisan et al., 2017) (Table S3). Evaluations of maximised TSS scores provided thresholds for current climate, current habitat and future climate niches (Table 2) predicting distinctly different species niches (Fig. 2).

3.1. *Lepus timidus predicted niches*

The current climate niche was predicted at 168 km^2 comprising the highest elevations in the centre of the study extent (Fig. 2). Referring to GLM models, the strongest abiotic predictors associated *L. timidus* presence with a narrow temperature range (BIO 7), the wettest quarter (BIO 8), the coldest temperature of the coldest month (BIO 6), less precipitation (BIO 12) and with no apparent association for topography (Table 3, Table 4, Figure S6).

In the current habitat niche, the predictors influencing *L. timidus* presence were mid-ranges of vegetation productivity: brightness and NDVI (Table 3, Table 5, Figure S6). Broadleaved and coniferous woodland and improved grassland suggested slight negative associations. Neither roads, nor the presence of *L. europaeus* were important predictors.

The current habitat niche was predicted as actually being 60% larger than the current climate niche, 269 km^2 (Table 6, Fig. 2). More than half of the landcover occupied by *L. timidus* was young or mature heather; moorland grasses or cotton grass made up the remainder. The current habitat niche model predicted 80% utilisation of available heather landcover (Table 6).

Table 2
TSS and threshold scores for the models when projected using weighted mean ensemble modelling.

Model	Max TSS	Threshold
L. timidus current climate niche	0.66	0.57
L. timidus current habitat niche	0.46	0.49
L. timidus future climate niche	0.09	0.07
L. europaeus current climate niche	0.73	0.54
L. europaeus current habitat niche	0.44	0.37
L. europaeus future climate niche	0.04	0.23

The future climate niche predicted for *L. timidus* a range reduction of 88% to 19 km^2, remaining only on high elevation areas (Fig. 2). The future probability of occurrence threshold was very low (Table 2). Suitable areas were mostly predicted in those locations where the model referenced at least seven abiotic variables, having ranges used to calibrate current climate niche models (Fig. 2; Figure S7).

3.2. *Lepus europaeus predicted niches*

The current climate niche predicted a wide lowland area of 252 km^2 encircling the uplands (Fig. 2). Referring to GLM models, the main abiotic predictors for *L. europaeus* were less precipitation (BIO 12), a colder mean temperature of the wettest quarter (BIO 8) and warmer temperatures of the driest quarter (BIO 9), (Table 3, Table 4, Figure S6).

The current habitat niche was determined by vegetation productivity measures wetness and NDVI (Table 3, Table 5, Figure S6). The only important landcover predictors reported a disinclination towards cotton grass and a slight preference for improved grassland. There was a slight association with the presence of *L. timidus*. Roads provided a slight association, which we attribute to sample bias.

The current habitat niche was 401 km^2, again larger than the current climate niche by 59% (Table 6, Fig. 2). Of this, improved grassland and moorland grasses accounted for more than 70%, woodlands at least 14% and heather 10% including slightly on to the hills. Utilisation of available improved grassland was 100%.

The future climate niche predicted expansion by *L. europaeus* across the whole study extent to 765 km^2, more than 3 times its current climate niche, and including all hill tops (Fig. 2). The predicted future probability of occurrence threshold was low (Table 2). Suitable areas were predicted by five or more abiotic variables (Figure S7).

3.3. *Niche overlap*

Summed kernel density plots of all years' records for *L. timidus* and *L. europaeus* showed significant weak negative correlation (Pearson $r_{\text{timidus europaeus}}$ t = −55.6, df = 81002, correlation = −0.19, *P*-value<0.001) (Fig. 3). Comparing current climate niches, there was an overlap of just 0.2 km^2 between the species. For current habitat niches, there was overlap by 38.4 km^2; 14% of *L. timidus* range and 9% of *L. europaeus* range (Fig. 2). The future climate niche space predicted *L. timidus* range wholly within and comprising 3% of *L. europaeus* range (Fig. 2).

The elevation ranges (Fig. 4) in the current climate niche predicted *L. timidus* occurring at mean elevation 491m, moving in future up to 573m. For L. *europaeus* current climate niche mean elevation was 298m, moving in future to 369m (Fig. 4). Assessment with Welch's *t*-test of mean elevation ranges between species showed these as significantly different (Table 7). Note these forecasts are based on relationships with climate and topographical variables, without reference to vegetation.

Based on occurrence points, *L. timidus* was present at temperatures ~1° colder than *L. europaeus*, with 241 mm more annual precipitation (Table 4). Principal components analyses of abiotic variables on combined species occurrence points showed climatic variables more influential than topography; and of biotic variables, vegetation productivity indices were most important (Table 8). Kernel density plots of principal components axes showed the two species occupying separate niches (Fig. 5). Overlap indices showed the niches as very different: current climate niche Schoener D = 0.16, Hellinger I = 0.31; current habitat niche Schoener D = 0.07, Hellinger I = 0.20. Both metrics are probability scales from 0 (no overlap) to 1 (complete overlaps).

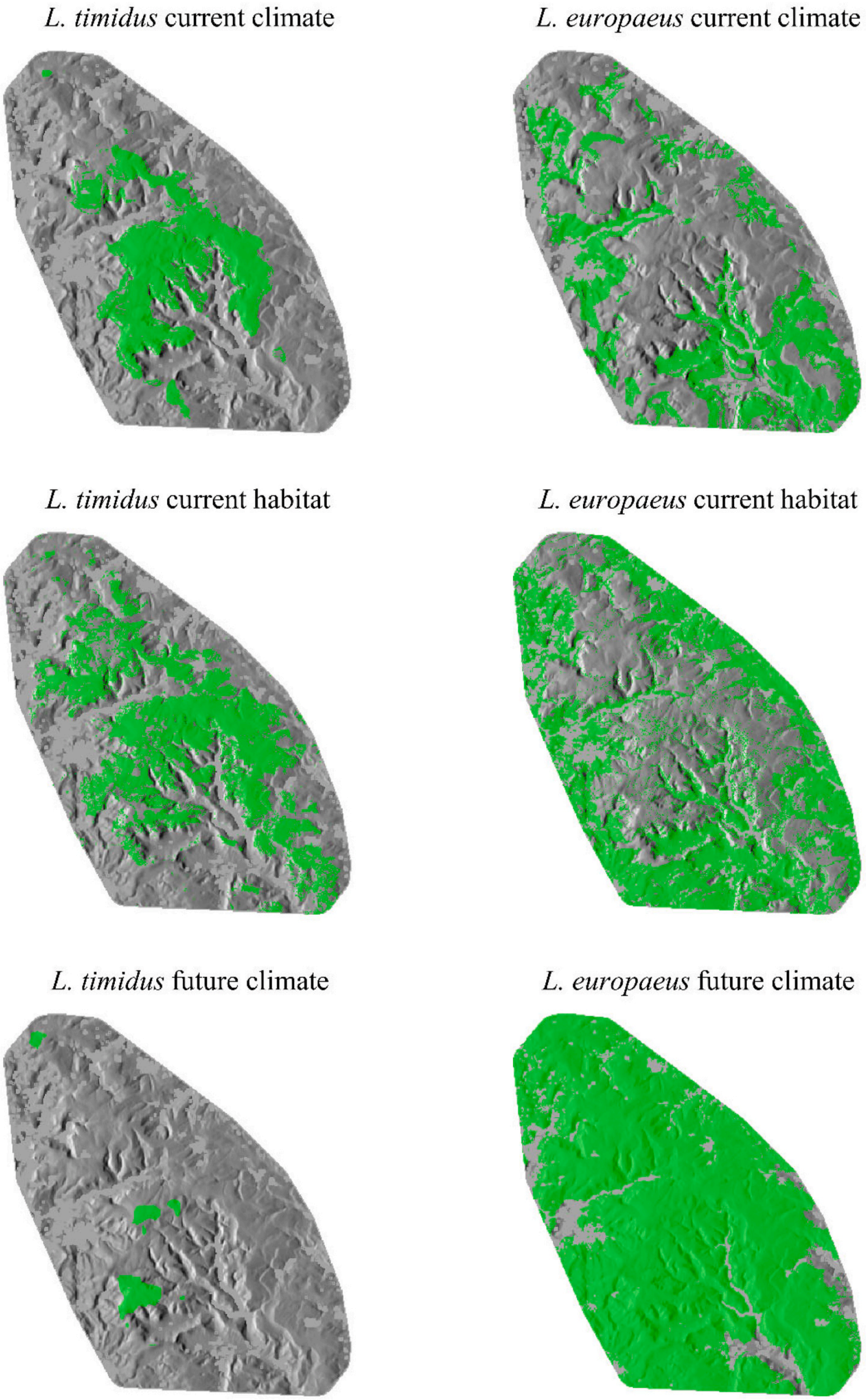


Fig. 2. Threshold maps showing current climate (year 2020) niche and current habitat niche, and future climate (year 2050) niche for *L. timidus* and *L. europaeus*. Background hill shade based on elevation data. Green overlain shapes are predicted niches. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

4.1. Two separate species, two separate niches

This study predicted two congeneric lagomorph species occupying distinctly different ecological niches in close geographic proximity with virtually no overlap. For both, their current climate niches predicted by temperature, precipitation and topography, were actually much smaller than their habitat niches predicted by vegetation productivity and composition. We found *L. timidus* occupied high elevation areas characterised by colder temperatures and higher precipitation levels. The landcover for *L. timidus* predominantly consisted of upland dwarf shrub vegetation: heather, cotton grass and moorland grasses. By contrast *L. europaeus* occupied lower elevation areas, just 1° Celsius warmer, with

Table 3

Variable importance was calculated with 3 permutations in biomod2, reporting by algorithm (GLM, Generalised linear model; RF, Random Forest and MAXENT). Variable importance is predicted by shuffling a single variable, then computing simple Pearson's correlation between reference predictions and the 'shuffled' one. The highest values show the more influence the variable has on the model, normalised to 100% i.e. 1.0 is most, 0.0 is no influence. Method does not account for interactions. (From package 'biomod2′, Thuiller et al., 2014). Each model is ranked by GLM score.

L. timidus current climate niche				*L. europaeus* current climate niche			
VARIABLE	GLM	RF	MAXENT	VARIABLE	GLM	RF	MAXENT
BIO.7	0.47	0.20	0.31	BIO.12	0.54	0.13	0.21
BIO.8	0.23	0.13	0.17	BIO.8	0.20	0.11	0.10
BIO.6	0.18	0.05	0.06	BIO.9	0.16	0.20	0.27
BIO.12	0.08	0.09	0.05	BIO.15	0.06	0.20	0.12
BIO.15	0.04	0.21	0.07	BIO.7	0.02	0.11	0.14
ASPECT	0.00	0.01	0.00	GULLIES	0.01	0.00	0.02
SLOPE	0.00	0.05	0.02	BIO.6	0.00	0.08	0.06
BIO.9	0.00	0.26	0.32	ASPECT	0.00	0.05	0.02
GULLIES	0.00	0.00	0.00	SLOPE	0.00	0.12	0.07
L. timidus current habitat niche				*L. europaeus* current habitat niche			
VARIABLE	GLM	RF	MAXENT	VARIABLE	GLM	RF	MAXENT
BRIGHTNESS	0.52	0.36	0.29	WETNESS	0.47	0.28	0.17
NDVI	0.32	0.29	0.12	COTTON.GRASS	0.19	0.03	0.06
BROADLEAF	0.04	0.02	0.01	NDVI	0.08	0.20	0.12
IMPROVED.GRASS	0.04	0.08	0.08	IMPROVED.GRASS	0.07	0.16	0.15
WETNESS	0.04	0.11	0.08	CONIFEROUS	0.06	0.03	0.06
CONIFEROUS	0.02	0.04	0.01	ROADS	0.05	0.09	0.09
ROADS	0.01	0.01	0.01	MATURE.HEATHER	0.03	0.02	0.05
L.europaeus	0.01	0.00	0.04	BERRIES	0.03	0.01	0.00
MOOR.GRASSES	0.00	0.02	0.10	*L.timidus*	0.02	0.01	0.05
MATURE.HEATHER	0.00	0.04	0.11	BRIGHTNESS	0.00	0.13	0.07
BERRIES	0.00	0.00	0.00	ARABLE	0.00	0.00	0.00
ARABLE	0.00	0.00	0.00	BROADLEAF	0.00	0.00	0.03
COTTON.GRASS	0.00	0.01	0.07	YOUNG.HEATHER	0.00	0.01	0.07
YOUNG.HEATHER	0.00	0.03	0.08	MOOR.GRASSES	0.00	0.02	0.07

Table 4

Mean abiotic variable values for each species, at their respective locations. Temperatures are ^{o}C, precipitation mm.

	L. timidus			*L. europaeus*		
	Min	Mean	Max	Min	Mean	Max
BIO.6 min temp, coldest month	−2.20	−1.83	−0.92	−2.13	−1.47	−0.88
BIO.7 temp annual range	17.20	17.91	19.47	17.60	18.55	19.64
BIO.8 mean temp wettest quarter	3.08	3.55	4.25	3.20	3.95	5.95
BIO.9 mean temp driest quarter	9.17	11.53	13.06	10.42	12.26	13.21
BIO.12 annual precipitation	997.20	1395.40	1664.40	926.90	1154.00	1595.46
BIO.15 precipitation seasonality (CV)	17.83	21.17	22.78	16.60	19.63	22.12
Slope	0.14	6.79	30.78	0.22	8.25	23.47
Aspect^{o}		229			221	
Species locations at gullies		43%			34%	

Table 5

Ranges of vegetation productivity at the two species' locations.

	L. timidus			*L. europaeus*		
	Min	Mean	Max	Min	Mean	Max
Brightness	0.83	0.95	1.47	0.85	1.01	1.2
Wetness	0.08	0.26	0.43	0.01	0.20	0.36
NDVI	−0.07	0.00	0.05	−0.08	−0.03	0.04

less precipitation. Its preferred landcover was improved grassland. Woodland and heather areas were also important. Whilst the margins of difference for preferred climate variables were small, they predicted strikingly separate niches across the landscape. Referencing climate values for RCP 2.6 for 2050, the *L. timidus* future climate niche was predicted to shrink to small patches at high elevations. The *L. europaeus* future climate niche was predicted to expand to higher elevations, encompassing the uplands, completely covering the range of *L . timidus*. Interspecies competition in terms of overlaps of geographic and environmental niche ranges was presently very low and yet inferred to increase in future.

4.2. Reasons for niche preferences

Environmental forces are often complex and difficult to categorise or explain (Sillero 2011). There are subtle reasons for niche differences between these two lagomorphs. Our study predicted both species actually occupied much larger habitat niches than climate niches. This is a different outcome to the perhaps conventional expectation that the habitat, i.e. realised niche, may be a limited version or subset of the climate, i.e. fundamental niche (Guisan and Zimmermann, 2000; Sillero 2011). This finding reflects the view that ecological forces may indeed act stochastically (Guisan et al., 2017: 23). Both species were in effect tolerating wider climatic ranges than suggested by the current climate niche models. Across the entire study extent the climate variables reported small variations which were not of critical physiological

Table 6

Geographic occupation of current climate and habitat niches by *L. timidus* and *L. europaeus* for each landcover type.

		L. timidus				*L. europaeus*			
Landcover	Total Available	Climate niche	Habitat niche			Climate niche	Habitat niche		
	km^2	km^2	km^2	% of total available	% of climate niche	km^2	km^2	% of total available	% of climate niche
Arable	3.0	0.0	0.0	0%	–	0.3	2.3	78%	900%
Berries	7.4	1.0	0.1	1%	8%	3.2	0.8	11%	25%
Broadleaf	47.0	0.0	0.2	0%	1500%	26.3	30.0	64%	114%
Coniferous	33.6	1.2	0.2	1%	16%	18.2	27.0	80%	148%
Cotton grass	81.7	32.2	33.2	41%	103%	10.3	0.1	0%	1%
Improved grassland	205.9	0.2	0.0	0%	0%	97.2	205.8	100%	212%
Mature heather	143.5	58.3	115.8	81%	199%	25.2	10.7	7%	43%
Moorland grasses	201.2	41.1	54.5	27%	133%	51.9	94.0	47%	181%
Young heather	82.2	34.2	65.1	79%	190%	20.2	30.8	37%	152%
Total	805.5	168.1	268.9	33%	160%	252.8	401.5	50%	159%

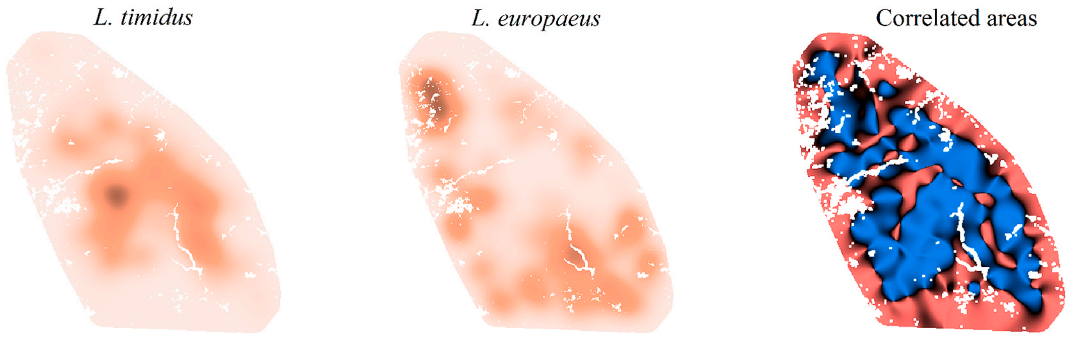


Fig. 3. Kernel density plots of summed (2000–2018) records for *L. timidus* and *L. europaeus* with darker areas indicating higher density. Correlated areas chart: blue = *L. timidus*; red = *L. europaeus*; correlated areas ("contact zones") indicated by shading increasing to black. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

importance to lagomorphs, yet could still indicate strong preferences, e.g. the widest temperature variation BIO 9 (mean temperature, driest quarter) ranged from 5.1 °C to 13.8 °C, the narrowest BIO 6 (min temperature coldest month) ranged from −2.2 °C to −0.8 °C; BIO 12 (annual precipitation) ranged 689–1666 mm. The small climatic variations showed distinct steep local changes, resembling the hilly topography. Consequently, these values were sufficiently different to predict two separate climate niches for the two species. By contrast the biotic vegetation productivity variables (NDVI, tasselled cap brightness and tasselled cap wetness) showed midrange values covering a much wider geographical extent, with less severe graduations, thereby predicting much larger habitat niches.

Considering abiotic and biotic factors, it therefore appears the two species occupied separate niches because vegetation productivity, composition and associated dietary preferences, were more important than climate influences. Of note, the lagomorphs' different biotic niches were predicted by alternate aspects of vegetation productivity. Brightness (i.e. less exposed soil) and NDVI (i.e. actively photosynthesising plant growth) were most important for *L. timidus,* whereas, for *L. europaeus*, it was wetness (i.e. drier soil and vegetation moisture content). This then provided contrasting differences to the consequent proportion of vegetation types in the respective habitat niches of each species.

For *L. timidus,* the majority of its habitat niche was heather, with other upland bog vegetation also important (cotton grass and moorland grasses). This was consistent with reported dietary and shelter preferences for *L. timidus* in the UK (Hewson 1962, 1976b, 1989). In the Peak District, much heather resource exists because of grouse moor management (Anderson and Shimwell 1981). Other large areas of uplands are subject to blanket bog restoration: gully blocking to retain water and planting of upland dwarf shrubs (Bonn et al., 2009). These human interventions provide the vegetation that support the presence of *L. timidus*.

The habitat niche for *L. europaeus* was different: mostly improved grassland areas, with moorland grass, woodland and some heather also being important. This reflected the reported preferences of *L. europaeus,* favouring mixed agrarian landscapes: crops, cereals or grasses (Harris and Yalden, 2008; Tapper and Yalden, 2010).

Differences in niche preferences, and by implication diet, may be explained by vegetation qualities and productivity: energy content, moisture, digestibility of secondary compounds, terpenes, phenolic resins, and selected in an order of preference by lagomorphs (Hulbert et al., 2001; Rödel et al., 2004). The preference of *L. timidus* is grasses: *Deschampsia flexuosa, D. caespitosa, Nardus stricta, Festuca, Agrostis* spp. especially for females in summer (Harris and Yalden 2008). However, when winter grass nutritional quality is poor, *L. timidus* switches to a 90% heather diet, less digestible but tolerable. (Hewson 1962; Hulbert et al., 2001; Harris and Yalden 2008). Between the two species, *L. timidus* may be better able to detoxify phenolics occurring in shrubs and trees (Iason and Palo 1991). By contrast *L. europaeus* favours grass resources throughout the year until there is no other option. It depends on weeds in agricultural lands (Reichlin et al., 2006). Thus, whilst *L. europaeus* may venture to utilise upland grasses, when these fall senescent in winter, instead of switching to heather in the manner of *L. timidus,* (Hulbert et al., 2001), *L. europaeus* chooses improved grasslands at low elevations. Absent competition, *L. europaeus* can broaden its dietary niche to selectively include shrubs (Green et al., 2013), possibly as a last resort (Rödel et al., 2004; Harris and Yalden 2008). Other

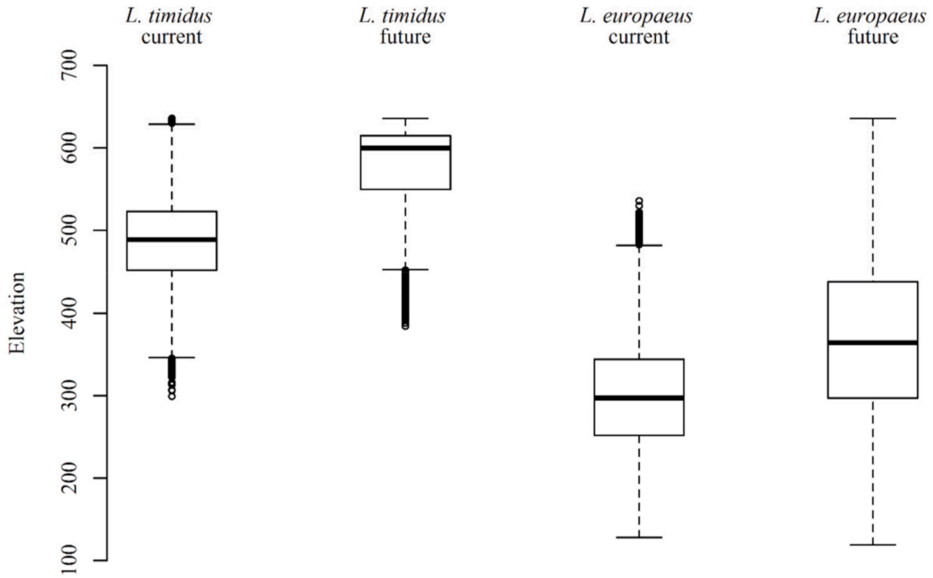


Fig. 4. Boxplots showing predicted elevation ranges for *L. timidus* and *L. europaeus* based on current and future climate niche threshold maps.

Table 7
Welch's *t*-test comparisons of predicted mean elevations (m) of hare species for current and future climate niches.

Comparison	t	df	*P*-value
L. timidus current vs *L. timidus* future	−56.8	2356	<.05
L. timidus current vs *L. europaeus* current	−313.7	38985	<.05
L. europaeus current vs *L. europaeus* future	−130.3	63858	<.05
L. timidus future vs *L. europaeus* future	−143.7	2180	<.05

Table 8
Percent contribution of each variable to principle components 1 and 2 used in the niche overlap models, values in bold as contributors.

Variable	Climate niche		Variable	Habitat niche	
	PCA 1	PCA 2		PCA 1	PCA 2
BIO.6	**11.8**	**21.6**	NDVI	**27.2**	6.6
BIO.7	**15.2**	**11.2**	BRIGHTNESS	1.9	**37.5**
BIO.8	**15.4**	5.0	WETNESS	**27.1**	1.0
BIO.9	**13.7**	0.1	ARABLE	0.1	0.0
BIO.12	**24.1**	0.1	BERRIES	0.0	0.0
BIO.15	**18.3**	4.6	BROADLEAF	0.0	1.9
ASPECT	0.0	**19.2**	CONIFEROUS	0.1	3.2
GULLIES	1.3	1.3	COTTON.GRASS	2.5	1.7
SLOPE	0.3	**37.0**	YOUNG.HEATHER	1.9	1.1
			MATURE.HEATHER	4.3	**18.8**
			IMPROVED.GRASS	**28.1**	0.0
			MOOR.GRASSES	1.9	**28.1**
			ROADS	4.8	0.1

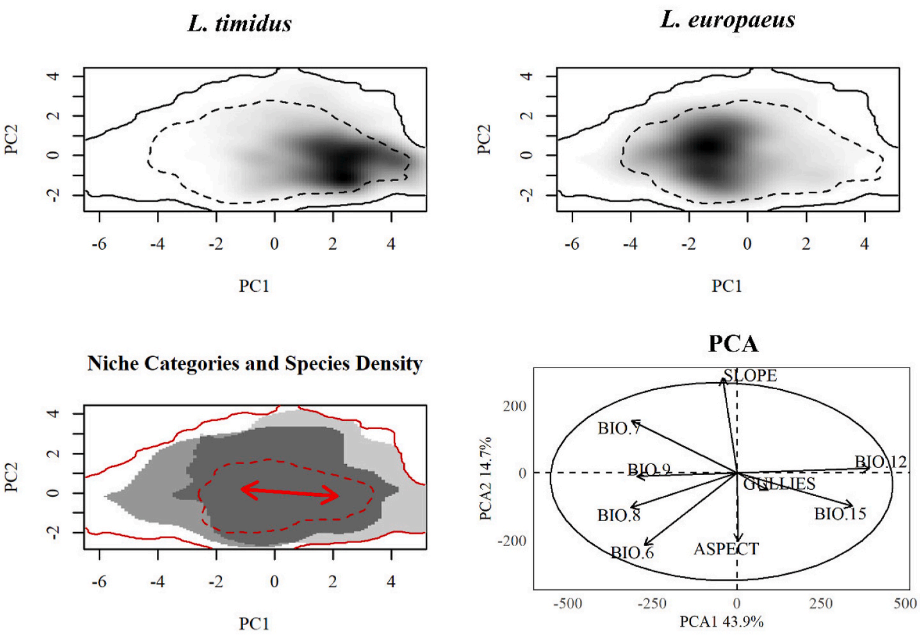
studies suggest *L. europaeus* adapts its diet when food availability is limited (Puig et al., 2017). Yet, there is ample supply of lowland improved grassland in the Peak District, providing a distinct niche for *L. europaeus*.

4.3. Level of interspecies competition

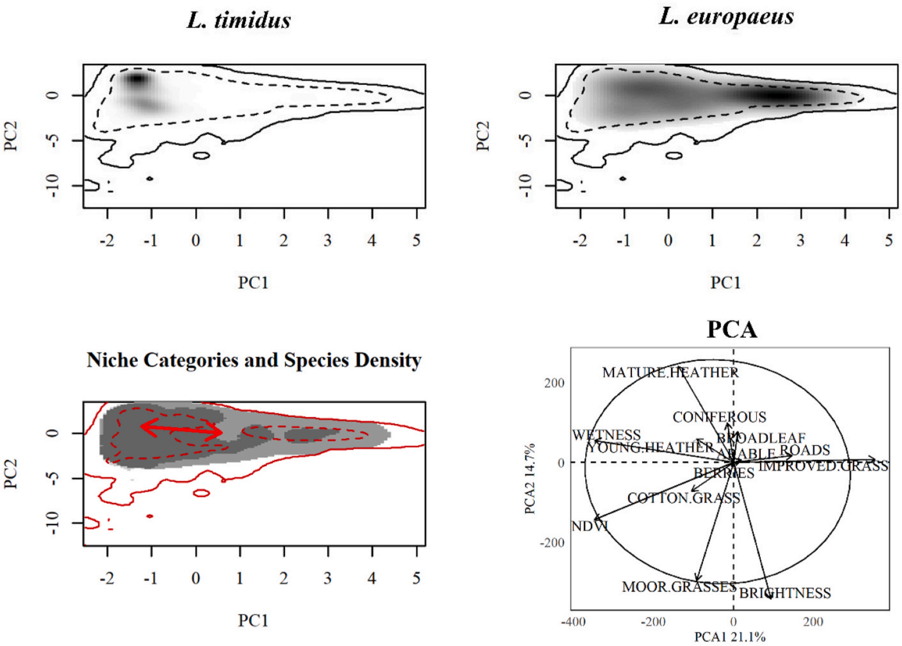
We inferred that both abiotic and biotic factors combined to determine distinct species ranges, with very small overlaps between the two. For *L. timidus*, a boreal species adapted for harsh winter climates, it was anticipated that its climate niche would occur on hilltops with the coldest wet conditions. The seasonally white pelage of *L. timidus* has high densities of air-filled hairs providing insulation that allows it to utilise colder areas during winter (Zimova et al., 2018). The heavily furred hind feet of *L. timidus* are helpful for digging through snow to reach heather (Jansson and Pehrson 2007; Harris and Yalden 2008). Yet, although *L. europaeus* does not share these adaptations, physiologically it can survive very cold habitats at high elevations (>2000m a.s.l.) during winter (Green et al., 2013; Puig et al., 2017). In snowscapes, *L. europaeus* restricts its diet to taller vegetation that remains visible (Green et al., 2013); but in the Peak District, only heather and berry shrubs of low height are available. So whilst *L. europaeus* could theoretically endure the cold climate of the high elevations of the Peak District, it is less well suited than *L. timidus* and may avoid the energy costs of searching for less preferable forage in poor weather or under snow, by remaining at lower, warmer elevations. Indeed where both species share territory, *L. timidus* copes more effectively with cold snow conditions (Jansson and Pehrson 2007). There may also be competitive exclusion by *L. timidus*, though the mechanism is unclear (Reid and Montgomery 2007).

Grasslands were outside the habitat niche of *L. timidus,* consistent with reports of it typically occupying heather moorland, tundra or forest (Angerbjörn and Flux 1995). Surprisingly our niche models also predicted that in woodlands, *L. timidus* were absent, and yet *L. europaeus* were present. This is different to other localities in Europe, where *L. timidus* often utilises woodlands, feeding on *Salix*, *Sorbus*, *Betula, Juniperus, Populus* and *Vaccinium* spp. (Hewson 1962; Angerbjörn and Flux 1995; Jansson and Pehrson 2007; Rehnus et al., 2013). Although this situation was recorded differently in Scotland wherein amongst mixed habitats, *L. timidus* was specifically shown to prefer heather moorland over newly planted Scots pine (*Pinus sylvestris*) woodland (Rao et al., 2003). Separate records across Europe describe *L. europaeus* pushing *L. timidus* out of forests (Flux and Angermann 1990); *L. europaeus* present in forests where clear-cuts promoted grass growth (Jansson and Pehrson 2007) or, otherwise, where *L. timidus* was absent (Rödel et al., 2004). Therefore, we are uncertain whether *L. timidus* avoids Peak District woodlands as its own preference or whether *L. europaeus* excludes them. This intriguing interspecies dynamic invites further study.

Competition occurs where dietary preferences converge. In these circumstances, *L. europaeus* often dominates, though this may depend upon local species densities (Acevedo et al., 2012). In Sweden, Jansson and Pehrson (2007) described how *L. europaeus* displaced *L. timidus* facilitated by warmer winters which increased grass availability in forests. In Ireland, the introduced *L. europaeus* outcompetes the native



(a) Current climate niche



(b) Current habitat niche

Fig. 5. Niche overlap density and PCA plots **(a)** Current climate **(b)** Current habitat. Density plots show ranges for *L. timidus* and *L. europaeus*, based on the first two principal components. The solid and dotted line show 100% and 50% available environmental space. Bottom left charts: Light grey area indicates the native niche for *L. timidus* only, dark grey area (centre) common (stable, shared) niche between *L. timidus* and *L. europaeus*; and medium grey area native niche for *L. europaeus* only. The red arrow indicates the difference in the centroid of the niche, mapping between species. The PCA charts bottom right portray the niche variables plotted on the first two axes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

L. timidus hibernicus subspecies, which feeds mainly on grasses (Caravaggi et al. 2014, 2017). By comparison, in the Peak District, the separate improved grassland which abuts the distinctly different heather moorland and the alternate dietary preferences allow the two lagomorph species to thrive in close proximity, seemingly without competition. These findings are consistent with those of Hewson (1976a) who reported that *L. europaeus* only invaded heather ranges when *L. timidus* numbers were very low. Flux and Angermann (1990) also described separate dietary niches for both these hare species.

4.4. *Future niches under climate change*

The future climate niche scenarios predicted that, by 2050, *L. timidus* would occupy a reduced geographic range of smaller patch sizes at higher elevations, consistent with studies elsewhere (Anderson et al., 2009; Leach et al., 2016; Rehnus et al., 2018). The persistence of *L. timidus* may depend on available vegetation under warmer climates. Policies and investments support both grouse moor management and blanket bog restoration, providing heather resource. However, heather requires drier soil structures. Climate forecasts for England are for wetter winters and driers summers. Notwithstanding human intervention, there is much uncertainty regarding future vegetation composition

(Bonn et al., 2009). Otherwise, to survive, *L. timidus* must adapt its diet (Harris and Yalden, 2008). There are scant opportunities for *L. timidus* to disperse elsewhere. Peripheral areas comprise only small patches of heather moorland and are several kilometres away. There are large areas of intervening agriculture and roads: a difficult migration for a species whose natal dispersal range is less than 1 km (Angerbjörn and Flux, 1995). Notwithstanding these challenges, the warming climate also reduces snow cover, thereby increasing the vulnerability of *L. timidus* to predators, because of the camouflage mismatch arising from its white winter pelage (Zimova et al., 2020). The increasing number of wildfires inevitably also threatens hares on the uplands (Albertson et al., 2010).

By contrast, we predict by 2050 the widespread expansion of *L. europaeus* to higher elevations. Being descended from central European and Asian species, *L. europaeus* may be physiologically better able to thrive in warmer temperatures (Caravaggi et al., 2017). However, our habitat niche model and dietary evidence suggests *L. europaeus* relies on grasses. Its spread to hilltops would require upland dwarf shrub vegetation succumbing to warmer climate, the failure of human upland management interventions and a transition to grassland communities. Regardless, the dietary preference of *L. europaeus* allows it to migrate to prolific lowland agricultural landscapes of northern England.

The relationship between these species depends on whether vegetation availability and dietary requirements converge. Should the two species' climatic niches merge as predicted and the upland vegetation change, this is likely to precipitate competition or hybridisation (Thulin 2003). This might occur remarkably swiftly (Caravaggi et al., 2017). We recommend ongoing monitoring of the respective niches and competitive dynamics of both lagomorph species.

Hare Data Sources

Brown and mountain hare records were kindly provided by British Trust for Ornithology, RECORD LRC (Cheshire), Derbyshire Mammal Group, Derbyshire Wildlife Trust, Greater Manchester Local Records Centre, Moors for the Future, Liverpool Museum, National Biodiversity Atlas, Sheffield Biological Records Centre, Sorby Natural History Society and West Yorkshire Ecology.

Data availability

Species records remain copyright with the Biological Record Centres listed under Hare Data Sources.

WorldClim data is open access and available from htttps://www.worldclim.org.

Both Ordnance Survey data and aerial images may be sourced from Edina, National Data Centre, University of Edinburgh, UK.

Ordnance Survey map and topography data are available from https://www.ordnancesurvey.co.uk. Aerial images are supplied by Getmapping plc, Fleet, Hampshire UK.

Author contributions

Carlos P.E. Bedson: Conceptualisation, data curation, formal analysis, writing-original draft preparation, writing - reviewing and editing. **Christian Devenish:** Formal analysis, validation. **Elias Symeonakis:** Software, validation. **David Mallon:** Validation. **Neil Reid**: Conceptualisation. **W. Edwin Harris:** Conceptualisation. **Richard Preziosi:** Supervision. All authors were involved with Writing - Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2021.103742.

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