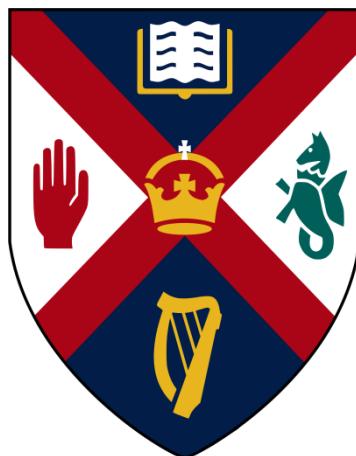


GLOBAL LAGOMORPH MACROECOLOGY: INTERSPECIFIC INTERACTIONS AND THE IMPACT OF CLIMATE CHANGE

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SUMMARY

Climate change is predicted to have huge impacts on the distribution of species, and the current rate of anthropogenically-driven climate change is of great concern to conservation biologists. Future climatic conditions are likely to affect all aspects of biodiversity from individuals to biomes, and although the field of climate change ecology is advancing, our knowledge of the impacts on biodiversity are hindered by methodological limitations. The main aim of this thesis was to assess the processes which contribute to the macroecology of the order Lagomorpha, in particular studying their interspecific interactions and the impact of climate change, whilst addressing methodological issues. Lagomorphs are comprised of 87 species of pikas, rabbits, hares and jackrabbits and are of great scientific and economic importance. They are especially important to study in terms of macroecology because they are extremely widespread, occupy a huge range of environmental conditions, a quarter of species are threatened and due to the relatively low number of species, compared to other mammalian orders, an entire trophic level can be studied providing significant insights into food webs. However, the factors which lead to the importance of the order also suggest likely vulnerability to future climate change. In this thesis, the responses to future climate change are assessed at a species-level for the entire order using species distribution modelling techniques and projected future climate scenarios. These techniques are then improved to include interspecific interactions in the modelling of distributions, as well as environmental factors. Two-thirds of species are likely to be affected by climate change, with larger leporid species predicted to shift polewards with little overall change in range extent, but, smaller lagomorph species like pikas are predicted to shift upwards in elevation with dramatic declines in range. Interspecific interactions are common in the order and therefore incorporating them into models is vital. Interspecific interactions and environmental factors are shown to be equal determinants of species ranges and appear to be similar in terms of strength and direction at numerous scales, but the effects are spatially heterogeneous. Combining improved species distribution models with network analysis techniques provides more reliable estimates of climate change impacts on a community-level, and suggests high turnover and substantial changes in ecological network properties for lagomorphs.

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CHAPTER 1

Introduction

1.1 Climate change

Observations of the physical evidence for global climate change has accumulated since the 1950s; there have been substantial increases in the temperature of Earth's atmosphere and ocean, large decreases in snowfall and sea ice extent and significant rises in sea level (IPCC, 2014). The Intergovernmental Panel for Climate Change (IPCC) Fifth Assessment Report states that the effects of anthropogenic greenhouse gas emissions, together with other anthropogenic drivers, are extremely likely to be the main causative factors in global climatic change. Increases in atmospheric carbon dioxide, methane and nitrous oxide driven by economic and human population growth have had dramatic impacts on natural and human systems across the world. If greenhouse gas emissions remain at the same level, or continue to increase, there will likely be further warming and more changes to the global climate system during the 21st Century (IPCC, 2014).

Observed changes include a 0.85°C increase in global land and ocean surface temperature between 1880 and 2012, a 0.11°C increase per decade in mean global sea temperature between 1971 and 2010 in the top 75 metres of water, a 3.5-4.1% per decade decrease in Arctic sea ice extent and a 0.19m global mean sea level rise between 1901 and 2010. In terms of future changes, it is predicted that the global mean surface temperature change between 2016 and 2035 will be between 0.3 and 0.7°C, with spatially variable, but overall increases in precipitation and sea level (Fig. 1.1). Recent studies have shown that increases in global mean surface temperature are causing an increased incidence of heat waves and extreme precipitation events, with 18% of daily precipitation extremes and 75% of daily hot extremes attributable to present warming of just 0.85°C (e.g. Fischer & Knutti, 2015). In addition, ocean temperature and acidification will likely increase and global sea level is predicted to rise substantially over the 21st Century (IPCC, 2014) with severe implications for deep sea ecosystems and communities (Thresher *et al.* 2015). It is likely that these changes will bring about: increased risk of severe human ill-health due to flooding and extreme heat; breakdown of infrastructure due to extreme weather events; loss of rural livelihoods and food insecurity; and loss of biodiversity and ecosystem services (IPCC, 2014).

Global Circulation Models (GCMs) simulate interactions between components of the climate system at global or regional scales and capture projections of future climate conditions in terms of temperature and precipitation. Climate models in the IPCC Fourth

Assessment Report describe possible, future situations or Special Report on Emissions Scenarios' (SRES), incorporating information on economic, population and technological growth, known as A1, A2, B1 and B2. Climate models in the Fifth Assessment Report were improved, especially in terms of precipitation predictions, but models of changes in temperature still perform best. The Fifth Assessment Report contains Representative Concentration Pathways (RCPs), rather than SRESSs, which describe four pathways for greenhouse gas emissions, air pollutants and land use: RCP2.6, RCP4.5, RCP6.0 and RCP8.5; each number represents total radiative forcing in watts per square metre by 2100. RCP8.5 is approximately equivalent to the SRES A2 scenario. Land use scenarios included in RCPs show a range of possible projections from reforestation to increased deforestation, whilst air pollutant emissions are assumed to decrease gradually following control and mitigation (IPCC, 2014). The stringent mitigation scenario (RCP2.6) indicates an increase in global mean surface temperature of 0.3-1.7°C by the end of the 21st Century; whereas the extreme scenario (RCP8.5) predicts a likely increase of 2.6-4.8°C.

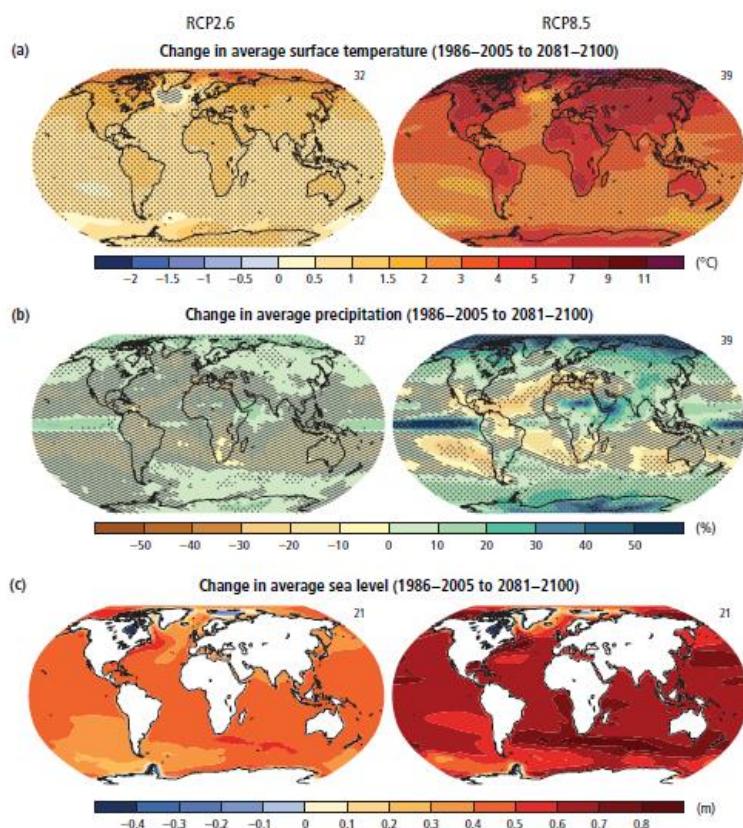


Fig. 1.1. Maps of Coupled Model Intercomparison Project 5 (CMIP5) multi-model mean changes in (a) surface temperature, (b) precipitation and (c) sea level. [Extracted from IPCC, 2014].

1.2 Effects of climate change on biodiversity

Climate change is predicted to have major impacts on the abundance and distribution of species and habitats, across marine, freshwater and terrestrial ecosystems (Parmesan & Yohe, 2003; Dawson *et al.*, 2011; Warren *et al.*, 2013). The effects of climate change on biodiversity are usually tested with metrics such as extinction risk, distribution and turnover (Collen & Nicholson, 2014), which are used to assess global biodiversity targets such as those agreed in the Convention on Biological Diversity (CBD). These metrics have been used to demonstrate a number of significant responses to projected climate change, including range shifts (Chen *et al.*, 2011), increases in elevation (Leach *et al.*, 2015a), phenological changes (Visser & Both, 2005), extinction risk (Thomas *et al.*, 2004), species turnover (Thuiller, 2004) and altered biodiversity patterns (Thuiller, 2007).

Although anthropogenically-driven climate change has been happening for decades, the accelerated rate of current change is of great concern to conservation biologists (Thuiller *et al.*, 2011). Species distributions may shift dramatically under future climate change due to the effects that increased temperature and precipitation have on physiological and ecological processes (Hansen *et al.*, 2006). Climate change components, including temperature, precipitation, extreme events, carbon dioxide concentrations and ocean dynamics, affect all aspects of biodiversity, from individual organisms, to populations, species, communities, ecosystems and biomes (Bellard *et al.*, 2012).

Climate change components are likely to alter genetic, physiological and phenological aspects at an individual level, with negative effects on allelic diversity, disease susceptibility and growing season length. Recruitment dynamics may be affected at the population level, and, at the species level, ecological niches and range size may be affected. Indeed, future climate change may have substantial effects on species niches i.e. the biotic and abiotic conditions under which a species can persist (Holt, 2009). Species are predicted to adapt their bioclimatic niche, migrate to maintain their current niche, or become range restricted and undergo population decline, local or global extinction (Holt, 1990; Wiens *et al.* 2010). Changes in climate may lead to a species being poorly adapted to a new set of environmental conditions, or climatic niche, potentially resulting in adaptive responses (Bellard *et al.* 2012). The mechanism by which adaptation happens may be through mutations of existing genotypes (Salamin *et*

al. 2010) or short-term, plastic adaptation (e.g. Charmantier *et al.* 2008). Species responses to climate change normally involve either spatial change, such as latitudinal shifts (Parmesan, 2006), temporal changes, such as flowering time (Parmesan, 2006) or “self” changes, such as physiological modification of diet or activity pattern (Johansen & Jones, 2011).

At higher biological levels, interspecific interactions, community productivity, ecosystem services and even biome integrity are likely to be affected (Bellard *et al.* 2012). Irreversible changes in biomes may result due to shifts in terrestrial systems, such as savannahs (Sala *et al.* 2000), exceeding their “tipping points” (Leadley *et al.* 2010). At the community level, the effects of climate change are mediated through altered environmental conditions which shape community structure, but temperature can also interact with community assembly to alter future compositions (Clements *et al.* 2013). Changes in community composition, for example number of species, due to climate change, or even invasive species or land use change, will have great consequences for community structure and ecosystem responses (Emmerson *et al.* 2005). However, idiosyncratic species or individual responses, which may or may not be linked to body size, complicate the prediction of community-level responses to future climatic conditions (Twomey *et al.* 2012).

Although the field of climate change ecology is advancing rapidly, substantial improvements still need to be made in our understanding of the effects of climate change on biodiversity (Bellard *et al.* 2012). Variability between climate models and emission scenarios can lead to great differences in projected species’ distributions (Beaumont *et al.* 2008), and together with the bias in taxa studied can lead to inconsistent estimation of the extent of biodiversity loss. Choice of scale, publication bias (non-reporting of positive effects) and inconsistency of biodiversity measures, such as extinction risk (Collen & Nicholson, 2014) can lead to vast overestimation of biodiversity loss (Bellard *et al.* 2012). However, one of the most important topics which must be addressed, and the greatest source of error in studying the effects of climate change on biodiversity, is the limitations of predictive tools, for example, Species Distribution Models (Guisan & Thuiller, 2005; Elith & Leathwick, 2007; Elith & Leathwick, 2009).

1.3 Predicting impacts of climate change on species distributions

Species Distribution Modelling (SDM), otherwise known as ecological niche modelling, is a widely used tool in ecology and conservation which quantifies patterns of species distributions (Elith & Leathwick, 2007; Franklin, 2010) based on statistical modelling (Franklin, 2010). SDM relates species occurrences at known locations to environmental variables in order to produce a model of environmental suitability. This model can then be fitted spatially to past, current, or future conditions to identify potentially suitable areas for the focal species (Guisan & Thuiller, 2005; Elith *et al.*, 2006; Warren & Seifert, 2011). These models can be used to predict distribution changes under different environmental conditions, for example, climate change (Wintle *et al.*, 2005), and may also be developed to include other ecological factors, such as interspecific interactions (Kissling *et al.*, 2011).

SDM is founded on the niche concept (Guisan & Zimmerman, 2000) and assumes that distributions are caused by environmental tolerances, i.e. the Grinnellian niche, whereby species occupy all of their suitable habitats; this is also referred to as the fundamental niche. However, species may be excluded from parts of their fundamental niche, for example, by biotic interactions or constraints such as elevation, leading to the concept of the realised niche (Hutchinson, 1957; Hutchinson, 1978; Guisan & Thuiller, 2005). Although SDM in theory does not predict the realised niche, it is assumed that the observed distributions, i.e. occurrence data, are already constrained by these factors and, therefore, SDM is in fact predicting Hutchinson's realised niche. The inclusion of parameters such as dispersal and biotic interactions (Wisz *et al.* 2012) leads to improved models of the realised niche, but in reality, estimating the realised niche can only be performed using mechanistic models which require highly detailed, but often unavailable, ecological information.

Nevertheless, SDM has been highly influential as it can be applied to a large number of species, in a variety of taxonomic groups, captures ecological processes in the relationships between occurrence data and spatial information, and uses readily accessible data (Bellard *et al.* 2012). SDM requires accurate, comprehensive species data, relevant and uncorrelated environmental data, an appropriate modelling algorithm, sufficient model evaluation and the selection of appropriate thresholds (Elith

& Leathwick, 2007). It can be performed using many different algorithms with at least nineteen in current use, of which Generalised Linear Models (GLMs) and MAXENT (based on the probability distribution of maximum entropy) are the most frequently applied (Aguirre-Gutierrez *et al.* 2013).

The limitations of SDM have been widely reviewed (Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Kramer-Schadt *et al.* 2013) and careful consideration is required before data can be analysed to produce useful analyses. Issues with input data include: sampling bias, choice of spatial scale, lack of information on absence, multicollinearity in environmental variables, lack of data for rare species and functionally irrelevant environmental predictors (Pearson *et al.* 2007; Elith & Leathwick, 2009). However, many of these issues can be tackled prior to model specification or during the modelling procedure. Sampling bias can be accounted for by weighting species data according to the bias of records or by sub-sampling (Araujo & Guisan, 2006). The resolution of species and environmental data should be consistent; correlated and irrelevant environmental predictors should not be used; species should only be assessed if sufficient records are available and lack of data on absence can be dealt with by rigorous model evaluation (Elith & Leathwick, 2009).

Models are also vulnerable to: spatial autocorrelation; uncertainty in future climate conditions; incorrect specification of thresholds for output predictions; insufficient independent evaluation; and difficulty in projection of distributions into novel conditions (Beaumont *et al.* 2008; Elith & Leathwick, 2009). Spatial autocorrelation, which arises when nearby locations are not independent of each other (Legendre, 1993), can be dealt with in certain modelling methods using intrinsic conditional autoregressive error structures, for example, Integrated Nested Laplace Approximation (INLA) and other Bayesian Species Distribution Modelling techniques. Data from global climate models can be averaged to reduce error (Pierce *et al.* 2009). Thresholds for producing binary predictions of presence and absence should be selected based on the question being addressed, but in some cases it may not be necessary to report binary predictions, and producing continuous scales of presence may be enough to guide conservation management action. Finally, model evaluation is very important and lack of independent data can be overcome by using expert evaluation together with model statistics to assess predictions (Anderson *et al.* 2003; Leach *et al.* 2015a).

Despite their many limitations, the correlative models discussed here remain one of the only methods to forecast or hindcast species distributions. Fortunately, most of the limitations of SDM can be mitigated using statistical techniques or new methods. Provided the methods are carefully considered and results are rigorously assessed SDM can be extremely useful in predicting the impacts of global climate change on biodiversity. Further, they have practical applications in conservation management as well as providing insights into the past and future distributions of organisms and the factors that shape their biogeography.

1.4 Order Lagomorpha

The order Lagomorpha is currently comprised of 87 species of pikas, rabbits, hares and jackrabbits. The order is thought to be closely related to rodents (Fritz *et al.* 2009), and at one point they were considered as the same order, but the presence of small peg-like teeth behind the incisors of lagomorphs is found in no other mammals and supports evidence for lagomorphs as a distinct lineage. Lagomorphs are an important mammalian group, both economically and scientifically, as they are a major human food resource, model laboratory animals in medical research, valued game species, pests of agricultural and national significance, ecosystem engineers and key elements in food webs providing prey for many carnivores. Lagomorphs are extremely widespread; they are native or introduced on all continents except Antarctica, occurring from sea level to >5,000m and from the equator to 80°N spanning a huge range of environmental conditions (Chapman & Flux, 2008).

The taxonomy of the Lagomorpha has been in a state of flux in recent decades but all species belong to two families: the Ochotonidae and the Leporidae. The Ochotonidae consists of a monotypic genus, *Ochotona*, containing 25 species of small, social, high-latitude and usually high-altitude, pikas. The Leporidae has 32 species of large, solitary, cursorial hares and jackrabbits in a single genus *Lepus* and 30 species of medium-sized, semi-social, rabbits (some of which are fossorial) comprising ten genera: *Brachylagus*, *Bunolagus*, *Caprolagus*, *Nesolagus*, *Oryctolagus*, *Pentalagus*, *Poelagus*, *Pronolagus*, *Romerolagus* and *Sylvilagus* (Fig. 1.2). Ochotonidae have hind legs of a similar length to their fore legs, rounded ears, a skull with no supraorbital bones and a short nasal region, whereas Leporidae have hind legs longer than fore legs, long ears, a skull with supraorbital bones and a long nasal region (Chapman & Flux, 2008).

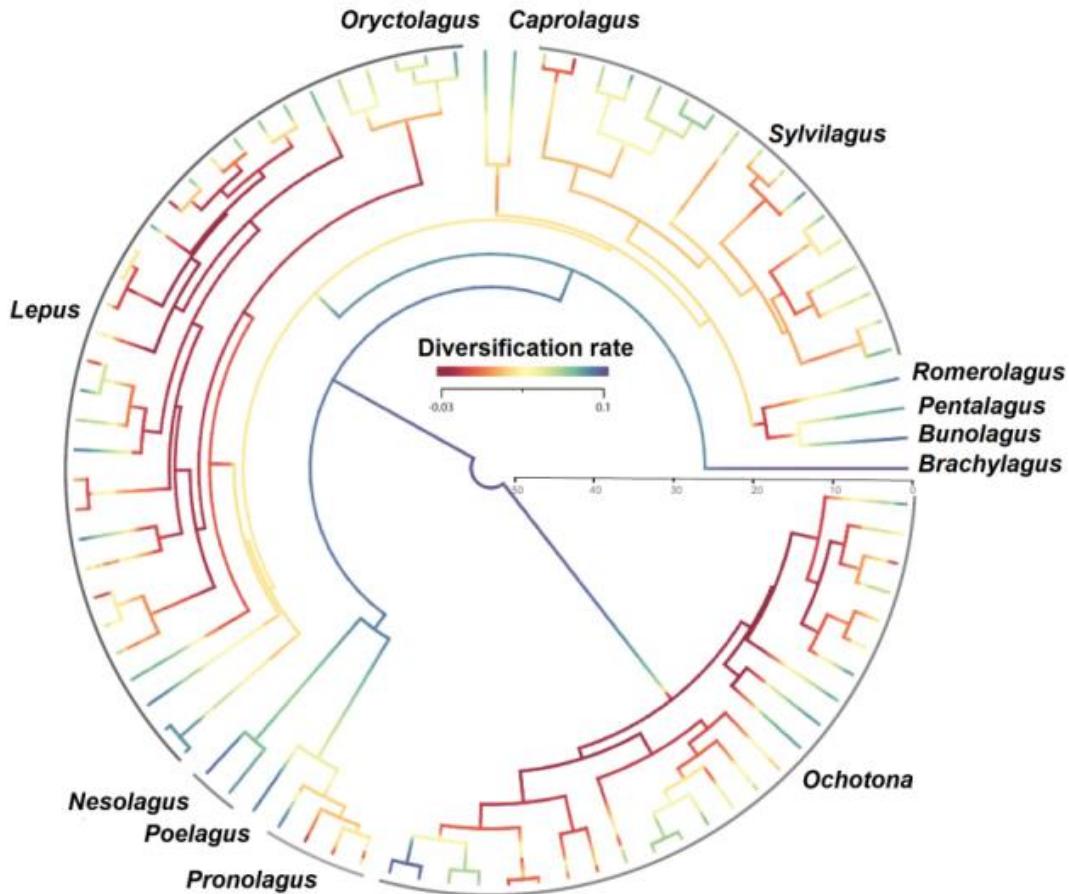


Fig.1.2. Diversification rate of lagomorph genera. [Extracted from Verde Arregoitia *et al.* 2015].

A quarter of lagomorphs are listed in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Fig. 1.3.; www.iucnredlist.org) with a notable number of highly range-restricted species including fourteen listed under the IUCN Criteria B, with an extent of occurrence estimated to be less than 20,000 km², and populations of more than a third declining. Recently, media attention has been drawn to the rediscovery of the critically endangered Ili pika *Ochotona iliensis* in China after 24 years without records (BBC, 2015a), and the elusive, data-deficient Annamite striped rabbit *Nesolagus timminsi* was found in Vietnam after being first discovered in 1999 (BBC, 2015b).



Fig. 1.3. Location of threatened lagomorph species. Closed circles represent critically endangered species and open circles endangered species. (1) *Lepus flavigularis*; (2) *Bunolagus monticularis*; (3) *Ochotona argentata*; (4) *Sylvilagus mansuetus*; (5) *Caprolagus hispidus*; (6) *Ochotona hoffmanni*; (7) *Ochotona iliensis*; (8) *Ochotona koslowi*; (9) *Pentalagus furnessi*; (10) *Romerolagus diazi*; (11) *Sylvilagus graysoni*; (12) *Sylvilagus insonus*; (13) *Sylvilagus robustus*. [Extracted from Lorenzo *et al.* 2015].

Climate change may have a huge impact on lagomorph distributions as they occupy such a vast array of habitats worldwide and are known to be vulnerable to environmental change from empirical studies. Many lagomorph species have very small geographical ranges, with one species (Silver pika *O. argentata*) occupying a single forest just over 4km² in China and another species (Volcano rabbit *Romerolagus diazi*) occupying four discontinuous habitat patches on volcano summits in Mexico. Pikas, as high-altitude specialists with very high body temperatures of 39.3-41.0°C (Smith, 1974), are extremely susceptible to changes in their environment, particularly ambient temperatures (Smith, 2008). A small change in climate may alter their habitat dramatically and lead to heat stress. Therefore, environmental change is predicted to have significant effects on lagomorphs, especially changes in climatic conditions (Ge *et al.* 2013; Mills *et al.* 2013), land use (Fa & Bell, 1990) and human disturbance (Schmidt *et al.* 2012). However, lagomorphs also show adaptability to changing environments; for example, some species which change pelage colour from brown to white during the autumn, appear to have a delayed moult due to climate change (Smith, 2008).

Environmental change is also likely to have significant effects on lagomorph interspecific interactions. Competition among species in the order can involve interference or exploitation for food or shelter (Vidus-Rosin *et al.* 2008). Interspecific

competition is common between lagomorph species and is often precipitated by the introduction of non-native species (e.g. the European rabbit *Oryctolagus cuniculus*, the European hare *Lepus europaeus*, and the eastern cottontail *Sylvilagus floridanus*), leading to suppression or expulsion of native lagomorphs from certain habitats due to dominant behaviour and adaptive capabilities of the antagonist (Hackländer *et al.* 2008). Intraspecific competition in lagomorphs (Somers *et al.* 2012) and competition with other herbivores (Hulbert & Andersen, 2001; Bakker *et al.* 2009), on the other hand, has rarely been reported. Parapatric species, those which have separate but contiguous ranges, are common in the order, especially in Europe (Acevedo *et al.* 2012a). Under future climate scenarios the Iberian hare *L. granatensis* is predicted to be the beneficiary in competition with *L. europaeus* in their zone of contact in northern Iberia, and interactions between the mountain hare *L. timidus* and *L. europaeus* are expected to contribute to the decline of the former in areas of co-occurrence in northern Europe (Acevedo *et al.* 2012a), for example, in Sweden (Thulin, 2003) and Ireland (Reid, 2011). Therefore, it is particularly important to consider interspecific interactions when studying the impacts of climate change on lagomorphs.

1.5 Aims and objectives

The main aim of this thesis was to examine the processes which contribute to the global distribution of lagomorphs including biogeography, macroecology and interspecific interactions. The research aimed to describe the response of the order to climate change at a species level and then in progressive steps which identify, incorporate and model interspecific interactions, develop methods to estimate community-level responses to projected change. An overview of the data used throughout this thesis, including details on data sources and manipulation, are provided in Chapter 2. The specific objectives of the project were to:

- Assess the projected change in lagomorph species distributions under projected future climate change. Determine species traits correlated with the responses to future climatic conditions, in terms of elevational change, poleward movement and range change (Chapter 3).

- Assess published data on lagomorph interspecific interactions to determine whether they may contribute to the shaping of species distributions. Examine environment and/or species' trait relationships between interacting species and non-interacting species (Chapter 4).
- Quantify the influence of environmental *and* interspecific interaction effects on lagomorph species distributions using improved species distribution models. Explore whether the impacts of projected future climate change are greater in areas influenced by either environmental or interspecific interaction effects (Chapter 5).
- Determine the effect of scale on results from recently developed Joint Species Distribution Models which simultaneously model the range of multiple coexisting species, taking account of environmental *and* interspecific interaction effects. Explore trade-offs between precision of results and resolution of input data (Chapter 6).
- Assess changes in species assemblages under projected future climate conditions in terms of stability and structure using a combination of sophisticated Species Distribution Models and network analyses. Determine the influence of species traits on changes in network properties (Chapter 7).
- Discuss the impact of these results in mitigating climate change and develop recommendations for future research (Chapter 8).

CHAPTER 2

Methodology and Data

All chapters in this thesis are based on similar data. The purpose of this chapter is provide an overview of the origin of the data and how it was manipulated pre-analysis to avoid unnecessary repetition of methodological details in each chapter. Where the method of each chapter varies it is explicitly stated within chapter-specific methods sections.

2.1 Species point occurrence data

A total of 139,686 records including all 87 lagomorph species were either downloaded from the Global Biodiversity Information Facility (GBIF) Data Portal (<http://data.gbif.org>), collated from species experts or members of the IUCN Species Survival Commission (SSC) Lagomorph Specialist Group (LSG) and/or extracted from the literature for data deficient species as advised by experts.

Taxonomic accuracy was dealt with by checking all records against the latest IUCN taxonomy; if names did not match after cross-referencing with taxonomic synonyms and previous names they were rejected. In the taxonomy adopted for this research *Ochotona nigritia* and *Ochotona gaoligongensis* were classed as morphs of *Ochotona forresti*, *Ochotona muliensis* as a morph of *Ochotona gloveri*, *Ochotona himalayana* as a morph of *Ochotona roylei* and *Ochotona huangensis* as a morph of *Ochotona thibetana*, following the taxonomic expertise of Dr Andrey Lissovsky from the Zoological Museum of Moscow State University.

Spatial data accuracy was dealt with by removing any obviously erroneous records for the target species if they fell outside the extent of the IUCN geographic range polygon. In addition, occurrences recorded with a spatial resolution of >2km were removed and duplicate records were eliminated unless they were recorded in different temporal periods (pre-1950 and post-1950). This left 41,874 records of which 3,207 were pre-1950 and 38,667 were post-1950 (Fig. 2.1). Spatial and temporal bias in sampling was eliminated by only selecting the background data (a random sample of 10,000 points from the environmental layers describing pseudo-absences) from sites at which any lagomorph species had been recorded and ensuring there were the same proportion of pre-1950 to post-1950 background points as there were pre-1950 to post-1950 species records.

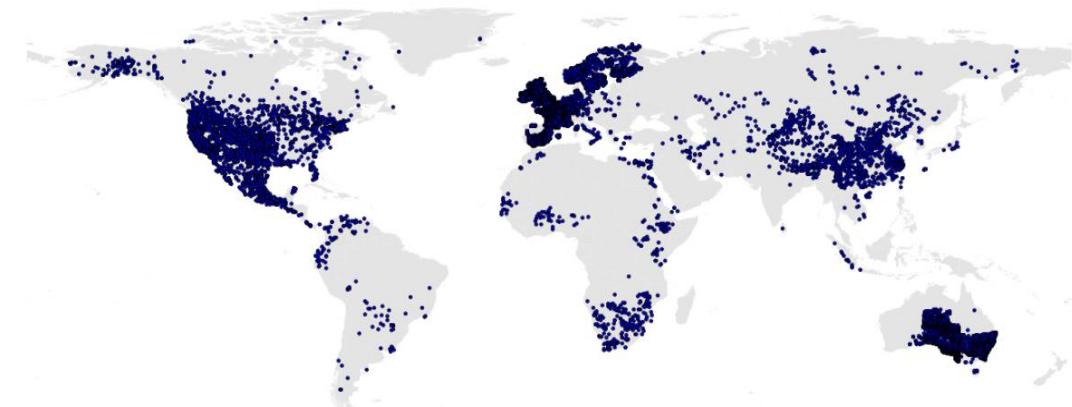


Fig. 2.1. Species point occurrence data for all 87 lagomorphs ($n=41,874$).

2.2 Species range data

IUCN species distribution polygons for the range of each lagomorph species were rasterised in R version 3.2.1 with a value of 1 for species presence and 0 for absence (Fig. 2.2). In Chapter 4 polygons for all 87 lagomorph species were rasterised at $\sim 1\text{km}^2$ grid cell resolution. In Chapter 5 polygons for European lagomorph species (*Lepus castroviejoi*, *L. corsicanus*, *L. europaeus*, *L. granatensis*, *L. timidus* and *Oryctolagus cuniculus*) were rasterised at $\sim 50\text{km}^2$ grid cell resolution. In Chapter 6 polygons for European lagomorph species were rasterised at three hierarchical resolutions: $\sim 50\text{km}^2$, $\sim 25\text{km}^2$ and $\sim 10\text{km}^2$ grid cells. Finally in Chapter 7 polygons for North and South American lagomorph species were rasterised at $\sim 50\text{km}^2$ grid cell resolution, but five highly range-restricted species were omitted, namely; *L. flavigularis*, *Romerolagus diazi*, *Sylvilagus cognatus*, *S. graysoni* and *S. insonus* as their ranges were $\leq 50\text{km}^2$ and, thus, typically occupied one or less grid cells.

IUCN geographic range polygons were used in later chapters because they captured species range extent more reliably for lagomorphs than point occurrence data. IUCN range maps for lagomorphs are detailed (for example, with high resolution of species range margins) while available point occurrence data was frequently low density and sparse in many regions (see Fig. 2.1) even (and in many cases) most notably, for very common species which have often gone unrecorded. Although, range maps have higher omission errors (Graham & Hijmans, 2006), this is more preferable for studies aiming to

capture interspecific interactions because only obvious potential interactions (co-occurrences) should be captured.

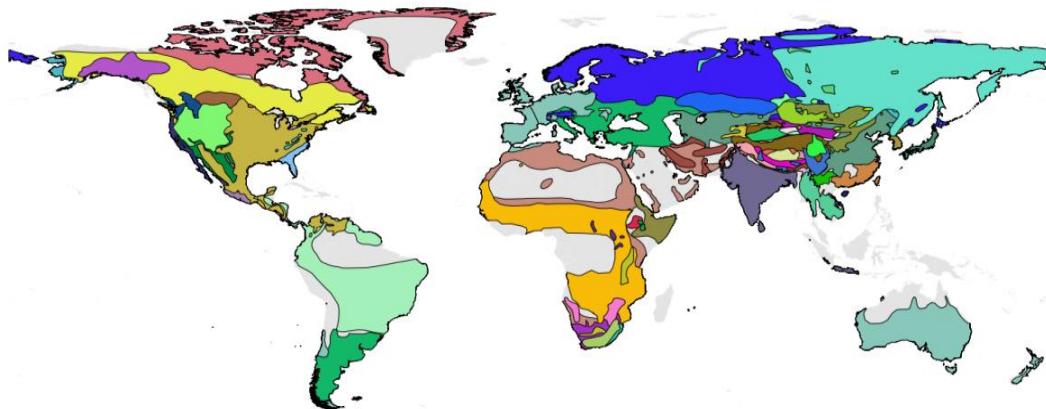


Fig. 2.2. Species range map data for all 87 lagomorphs.

2.3 Environmental data

Current climate data (~1950-2000) were downloaded from WorldClim (<http://www.worldclim.org>) at ~1km² grid cell resolution for Chapter 3, but resampled at ~50km² grid cell resolution for Chapters 5 and 7 and resampled at three hierarchical resolutions (~50km², ~25km² and ~10km²) for Chapter 6. Past climate data (~1900-1950) were downloaded from the R-GIS Data Portal (<http://r-gis.org>). 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 (°C), temperature seasonality (°C), maximum precipitation (mm), precipitation seasonality (mm), number of months with a Positive Water Balance (PWB), Normalised Difference Vegetation Index (NDVI), an index of hilliness and an index of human influence.

Evapotranspiration was calculated using the Hargreaves equation (Allen *et al.* 1998):

$$\text{Evapotranspiration} = 0.0023 \times (T_{\text{mean}} + 17.8) \times (T_{\text{max}} - T_{\text{min}})^{0.5} \times R_a$$

where,

$$R_a = ((24 \times 60)/\pi) \times G_{sc} \times d_r [(\omega_s \times \sin\varphi \times \sin\delta) + (\cos\varphi \times \cos\delta \times \sin\omega_s)] \times 0.408$$

$$G_{sc} = \text{solar constant} = 0.0820 \text{ MJ m}^{-2} \text{ min}^{-1}$$

$$d_r = \text{inverse relative distance Earth-Sun} = 1 + 0.033 \cos((2\pi/365) \times J)$$

$$\omega_s = \text{sunrise hour angle [rad]} = \arccos[-\tan(\varphi) \tan(\delta)]$$

$$\varphi = \text{latitude [radians]} \text{ (grid file in decimal degrees converted to radians)}$$

$$\delta = \text{solar decimation [rad]} = 0.409 \sin(((2\pi/365) \times J) - 1.39)$$

J = number of days in the year. J at the middle of the month is approximately given by $J = \text{INTEGER}(30.4 \text{ Month} - 15) = 15$ on average.

Annual evapotranspiration was taken as the sum of all monthly values calculated above, but later excluded due to high correlation with other variables. Annual water balance was calculated by subtracting annual evapotranspiration from mean annual precipitation. PWB was calculated by subtracting each monthly evapotranspiration from its corresponding monthly precipitation, and then converting these into a binary format, where a value greater than zero was given a value of one and a value less than zero was kept at zero (Kremen *et al.* 2008). The twelve binary files were then summed to calculate PWB.

Mean annual 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>). NDVI is commonly used to measure the density of plant growth and is obtained from National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) satellite images. A negative value indicates snow or ice, a value around 0 indicates barren areas, values between 0.2 and 0.3 indicate grassland, and values near 1 indicate rainforests (Holben, 1986).

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 (Newton-Cross *et al.*, 2007). Elevation was not included as a variable independently because organisms perceive climatic and habitat variables as proxies for elevation (Austin, 2002). Human Influence index data was downloaded from the Socioeconomic Data and Applications Centre (SEDAC) website

(<http://sedac.ciesin.columbia.edu/>). This was a composite of human population density, railways, roads, navigable rivers, coastlines, night-time lights, built-up areas and agricultural and urban land cover. Values within the index range from 0 to 64, where zero equalled no human influence and 64 represented maximum human influence (WCS-CIESIN, 2005). Solar radiation was calculated using the Spatial Analyst function in ArcGIS 10.1 (ESRI, California, USA). Solar radiation is defined as the total amount of incoming solar insolation (direct and diffuse), or global radiation, and was measured in watt hours per square meter or wh/m² (Fu & Rich, 2000), but later excluded due to high correlation with other variables.

Projected future climate data for Chapter 3 were obtained from the IPCC Fourth Assessment Report from the Climate Change, Agriculture and Food Security Global Circulation Models (CCAFS GCM) Data Portal (<http://www.ccafs-climate.org/data>) at ~1km² grid cell resolution and for the A2 emissions scenario. Climatic variables were averaged across the following GCMs: CCCma-CGCM3.1/T47, CNRM-CM3, CSIRO-Mk3.0, HadCM3 and NASA-GISS-ER, because Pierce *et al.* (2009) report that using data averaged across five GCMs is substantially better than any one individual model and significantly reduces model error. Future projections adopted the time periods: 2020s (average for 2010-2039), 2050s (average for 2040-2069) and 2080s (average for 2070-2099). Data from the A2 future climate change scenario was used because although it was originally described as “extreme climate change” it now appears to best represent the trend in observed climate.

In Chapter 7, IPCC Fifth Assessment Report Coupled Model Inter-comparison Project Phase 5 (CMIP5) future climatic data for the 2050s (average for 2041-2060) and 2070s (average for 2061-2080) were downloaded from WorldClim at ~1km² grid cell resolution and rescaled at ~50km². Data were downloaded for the Representative Concentration Pathway (RCP) 8.5 which indicates total radiative forcing of 8.5 watts per square metre by 2100, a mean average global temperature increase of 2°C by the 2050s and 3.7°C by the 2070s. Data were averaged across five GCMs from research stations across the world (CNRM-CM5, GFDL-CM3, GISS-E2-R, Had-GEM-ES and MIROC-ESM-CHEM) to again reduce model error following Pierce *et al.* (2009). All current and future environmental variables were rescaled to have a mean of zero and unit variance.

2.4 Species traits

Species trait data were downloaded from the PanTHERIA database (Jones *et al.* 2009) and missing data were added after searching the literature. Correlated traits were removed to reduce multicollinearity (i.e. tolerance <2 and VIF >5) and the final set of traits used were: activity cycle (nocturnal only, diurnal only, flexible), adult body mass (g), diet breadth (number of dietary categories eaten from: vertebrates, invertebrates, fruit, flowers/nectar/pollen, leaves/branches/bark, seeds, grass and roots/tubers), gestation length (days), habitat breadth (above ground-dwelling, aquatic, fossorial and ground-dwelling), home range (km²), litters per year, litter size, population density (n/km²) and age at sexual maturity in days (Fig. 2.3).

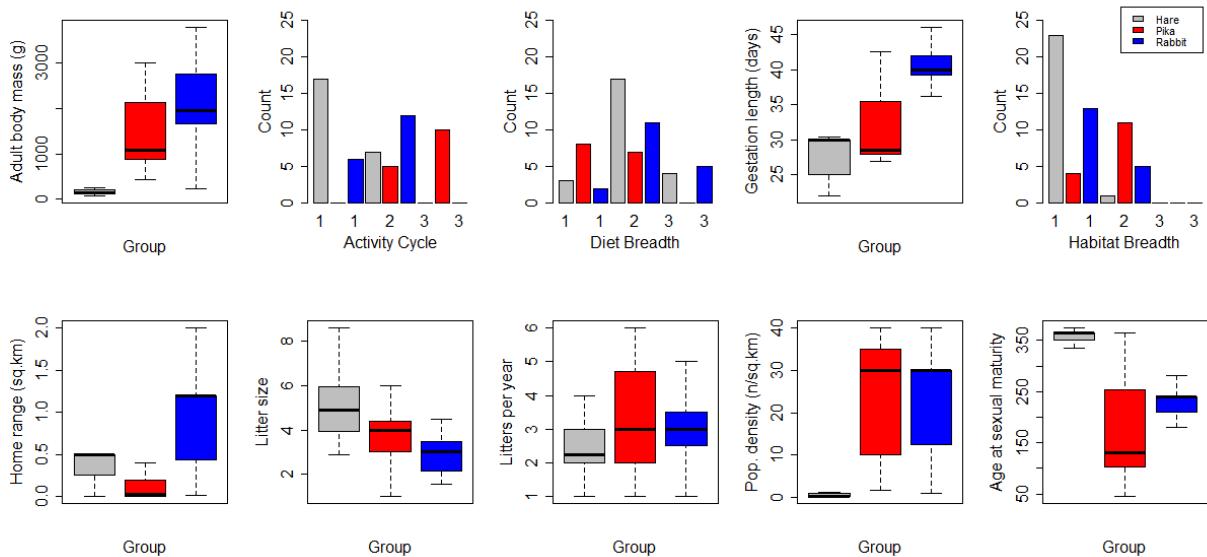


Fig. 2.3. Trait values for all three lagomorph groups (rabbits, hares & jackrabbits, and pikas). Pikas are shown in red, rabbits in blue and hares and jackrabbits in grey. Activity cycle, diet breadth and habitat breadth are categorical variables and are therefore represented as bar plots.

2.5 Phylogeny

A lagomorph phylogeny was extracted from the mammalian supertree provided by Fritz *et al.* (2009) for the 87 species taxonomy adopted in this research (Fig. 2.4). Likely clade memberships for five species not included in this phylogeny was determined from Ge *et al.* (2013) and were incorporated using phylogenetic assembly with soft taxonomic

inferences (PASTIS). Missing tips were grafted on using an expanded tree approach, rather than grafting directly at the tip of the existing tree; generating random phylogenies for each group, removing a random fraction of the existing branch length and scaling the simulated tree to have the same length as the fraction removed (Day *et al.* 2008).

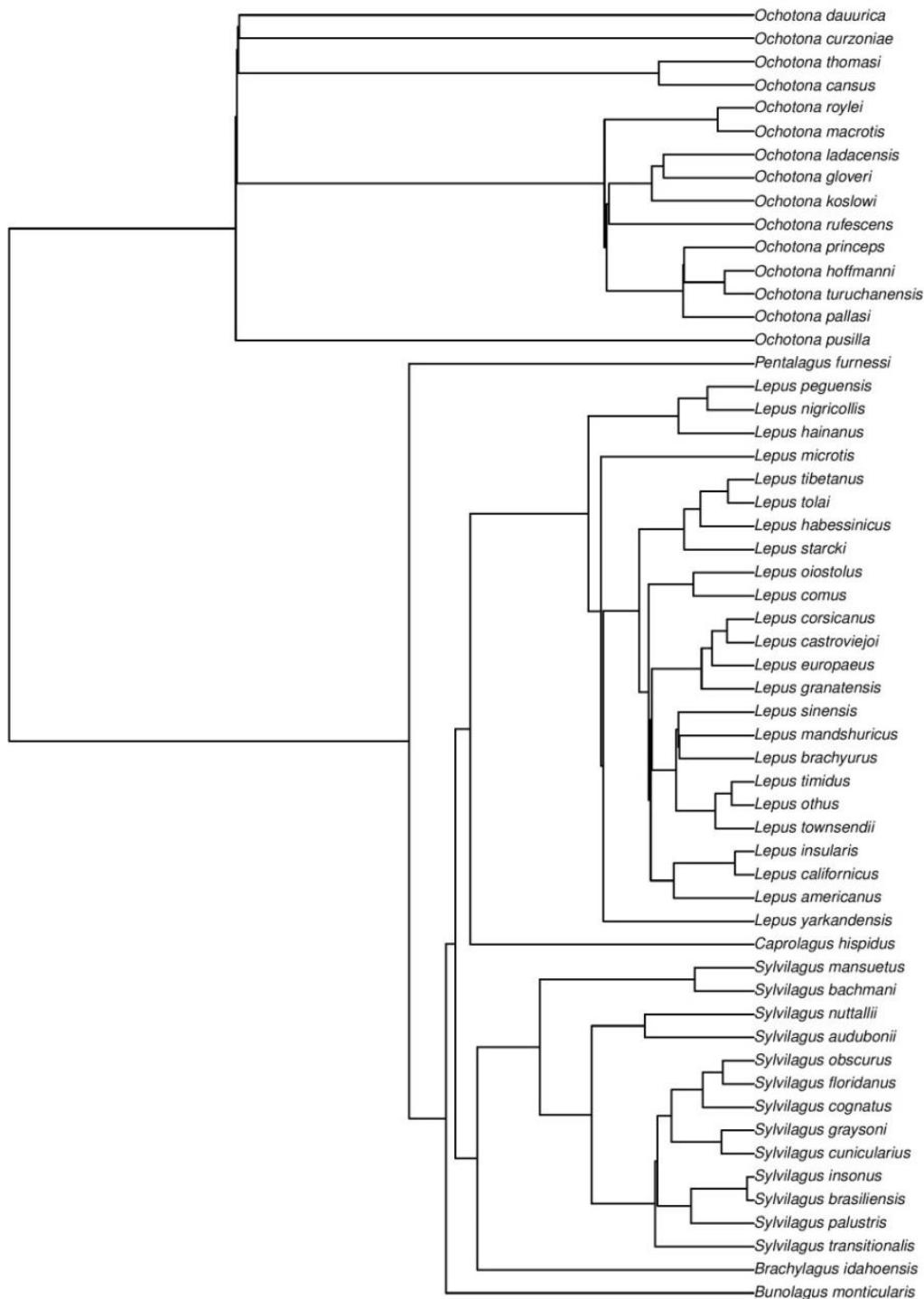


Fig. 2.4. Full lagomorph phylogeny for all 87 species.

CHAPTER 3

Responses to climate change are related to species traits in the order Lagomorpha

A manuscript based on this chapter has been published as:

Leach, K., Kelly, R., Cameron, A., Montgomery, W.I. & Reid, N. (2015) Expertly Validated Models and Phylogenetically-Controlled Analysis Suggests Responses to Climate Change are related to Species Traits in the order Lagomorpha. PLOS ONE. 10: e0122267. DOI: 10.1371/journal.pone.0122267

3.1 Abstract

Climate change during the last five decades has impacted significantly on natural ecosystems and the rate of current climate change is of great concern among conservation biologists. Species Distribution Models (SDMs) have been used widely to project changes in species' bioclimatic envelopes under future climate scenarios. Here, we aimed to advance this technique by assessing future changes in the bioclimatic envelopes of an entire mammalian order, the Lagomorpha, using a novel framework for model validation based jointly on subjective expert evaluation and objective model evaluation statistics. SDMs were built using climatic, topographical and habitat variables for all 87 lagomorph species under past and current climate scenarios. Expert evaluation and Kappa values were used to validate past and current models and only those deemed 'modellable' within our framework were projected under future climate scenarios (58 species). Phylogenetically-controlled regressions were used to test whether species traits correlated with predicted responses to climate change. Climate change is likely to impact more than two-thirds of lagomorph species, with leporids (rabbits, hares and jackrabbits) likely to undertake poleward shifts with little overall change in range extent, whilst pikas are likely to show extreme shifts to higher altitudes associated with marked range declines, including the likely extinction of Kozlov's Pika *Ochotona koslowi*. Smaller-bodied species were more likely to exhibit range contractions and elevational increases, but showed little poleward movement, and fecund species were more likely to shift latitudinally and elevationally. Our results suggest that species traits may be important indicators of future climate change and we believe multi-species approaches, as demonstrated here, are likely to lead to more effective mitigation measures and conservation management. We strongly advocate studies minimising data gaps in our knowledge of the order, specifically collecting more specimens for biodiversity archives and targeting data deficient geographic regions.

3.2 Introduction

The impact of climate change on species distributions has been modelled in a wide range of studies and a number of responses have been described (e.g. Parmesan & Yohe, 2003; Chen *et al.* 2011; Thuiller *et al.* 2011). Mammalian distributional changes have been well studied over the past decade and indicate that future climate change will have profound impacts (Moritz *et al.* 2008; Maiorano *et al.* 2011; Thuiller *et al.* 2011; Schloss *et al.* 2012). Mammals in the Western hemisphere are unlikely to keep pace with climate change, with 87% expected to undergo range contractions (Schloss *et al.* 2012), and mammals in Mediterranean regions, particularly endemic species, are predicted to be severely threatened by future climate change (Maiorano *et al.* 2011); shrews are especially vulnerable to future changes (Maiorano *et al.* 2011; Thuiller *et al.* 2011). These distributional responses have also been noted in studies of past climatic changes, for example, Moritz *et al.* (2008) found that from the early 20th century to the present day, small mammals in a North American national park substantially shifted their elevational range upwards corresponding to ~3°C increase in minimum temperatures. To date, very few SDM studies have included lagomorphs, but the American pika *Ochotona princeps* has been studied in detail and is predicted to decline in range (Calkins *et al.* 2012) and shift upslope (Beever *et al.* 2011) in response to future climate. The European rabbit *Oryctolagus cuniculus* and mountain hare *Lepus timidus* have also been studied but only in a subset of their range in Australia (Fordham *et al.* 2013) and Great Britain (Anderson *et al.* 2009).

The predicted impact of climate change on species distributions has only rarely been linked with species traits. Yet, species traits are widely accepted as potentially important indicators of responses to climate change and identifying such traits may be crucial for future conservation planning (Parmesan, 2006; Moritz *et al.* 2008; Angert *et al.* 2011). Traits that directly impact climatic conditions experienced by a species, for example, their activity cycle, are likely to be more important in mediating species responses to projected climate change than traits such as diet breadth. If species can broaden their occupied bioclimatic niche through trait plasticity, for example, altering their diel patterns of activity, then they may be less susceptible to future change (McCain & King, 2014). Mammalian species active during certain times of the day will experience a limited range of climatic conditions, whereas more flexible species can

select the conditions in which they are active (Nowak, 1991), and therefore, may be less susceptible to future change (McCain & King, 2014). Small body size, nocturnal behaviour and burrowing may have allowed mammalian species to ‘shelter’ from climatic changes during the beginning of the Cenozoic era, following the Cretaceous-Tertiary (K-T) mass extinction event (Robertson *et al.* 2004). Burrowing rabbits and pikas may be able to avoid the impacts of climate change by seeking underground refuge from extreme or fluctuating temperatures (Pike & Mitchell, 2013) and inhabiting thermally buffered habitats (Henry & Russello, 2013), whilst larger cursorial species, such as the hares and jackrabbits which, in the majority of cases, live above ground may have less variability in microclimate opportunities within which to shelter (Cardillo *et al.* 2005), but they may exhibit greater adaptation to prevailing climate, for example, pelage colour (Grange, 1932) and long extremities (e.g. the pinna of the ear) in desert environments (Dawson & Schmidt-Nielsen, 1966). Dispersal is also likely to be very important in future species distributions, especially in regions predicted to have higher climate velocities where species will require greater dispersal rates to track climatic changes. Larger species are likely to be more mobile, and, hence better prepared to track climatic change (Schloss *et al.* 2012).

Past studies have modelled the response of large numbers of species to predicted climate change (Warren *et al.* 2013) or dealt with a few key species from a range of orders (Schloss *et al.* 2012). Lagomorphs due to their restricted diversity provide an opportunity to rigorously examine the response of every species yielding a detailed picture of change within an entire order for the first time. Crucially, the small number of lagomorph species, compared to other mammalian groups, means that datasets can be verified in detail, modelled individually and outputs expertly validated. Moreover, lagomorphs have a nearly global terrestrial distribution and occupy a wide range of biomes providing an opportunity to examine the response of similar species from tundra to desert and islands to mountain summits.

Here, we assess the projected change in the bioclimatic envelopes of all ‘modellable’ lagomorph species under future climate change using a framework for model validation based jointly on subjective expert evaluation cross-validated with objective model evaluation statistics. We predict lagomorph species distributions will increase in elevation and poleward movement under future climate change, but with significant

differences between pikas, rabbits, hares and jackrabbits due to dissimilarities in species traits, for example, body size. Lagomorph morphological and life history traits are correlated with the predicted responses to future climate change in order to test this hypothesis. We posit that flexibility in activity cycle and larger body sizes, which may lead to greater mobility, will result in species being less vulnerable to future climatic changes and better able to track climate niches.

3.3 Methods

3.3.1 *Species distribution modelling*

Species Distribution Models (SDMs) were run using MAXENT version 3.3.3k (Elith *et al.* 2006; Phillips *et al.* 2006). Models were built using two different sets of input data: i) pre- and post-1950 data, or ii) post-1950 data only. The ‘samples with data’ (SWD) input format in MaxEnt was used for data entry, pairing pre-1950 species point occurrence records with mean climatic variables from 1900-1949 and post-1950 species point occurrence records with mean data from 1950-2000. Species occurrence and environmental data are described in sections 2.1 and 2.3. The models were validated using either 10 replicate bootstrapping for species with low numbers of records (<30) or 4-fold cross-validation for species with high numbers of records (≥ 30). More than 30 records were needed for 4 fold cross-validation as this equates to ~ 8 points per replicate, which has been deemed adequate for modelling some species distributions (Pearson *et al.* 2007), bootstrapping was used with <30 records as this maximised the points used for both training and testing. Ten bootstrap replicates were needed to minimise computational power and maximise accuracy. Linear, quadratic and product feature types were used. The 10 percentile training presence threshold was applied to define likely presence and absence of each species.

Records for each species were associated with global land cover data downloaded from the European Space Agency (ESA) GlobCover 2009 Project (<http://due.esrin.esa.int/globcover/>) and any land class not occupied by the target species was marked as unsuitable. Model outputs restricted to suitable land classes, i.e. climate and habitat model, and unrestricted climate-only models were evaluated by experts. A minimum convex polygon of the species occurrence records, buffered by a

dispersal value specific to each species which was verified by experts from the IUCN Species Survival Commission (SSC) Lagomorph Specialist Group (LSG), was used to remove areas of over-prediction. This meant that the suitable area within reach of each species was predicted, and led to more conservative outputs than just simply predicting suitable area. Although this assumes occurrence records are complete, it was a reasonable way to correct for potential biogeographic over-prediction and a similar method was advocated by Kremen *et al.* (2008). Annual dispersal distances were elicited from each species expert during the model evaluation procedure (see Appendix 1). Dispersal distances were either observed by lagomorph experts (personal observations), documented in the literature, or for species where no data were available, the group average was calculated (e.g. Asian pikas or African hares).

Non-native ranges for the only three invasive lagomorphs, European hare *L. europaeus*, Eastern cottontail *S. floridanus* and European rabbit *O. cuniculus*, were not modelled because invasive species are not at equilibrium with the environment and their niches cannot be transferred in space and time (Gallien *et al.* 2012). Mountain hare *Lepus timidus* populations in Ireland and mainland Eurasia were modelled separately due to the distinct morphological, phenotypic, behavioural, ecological and genetic differences between the Irish sub-species *L. t. hibernicus* and other mountain hares e.g. Reid *et al.* (2010), but the outputs for each geographic region were subsequently combined to produce a single species model reflecting the current classification of *L. t. hibernicus* as an endemic sub-species.

3.3.2 Model evaluation

A bespoke website (lagomorphclimatechange.wordpress.com) was created to allow each species expert to review the output of their allocated species. Expert evaluation, whereby an acknowledged expert on each species judges model predictions for current and past distributions, can be a useful tool prior to making future extrapolations (Anderson *et al.* 2003). A framework combining expert evaluation with reliable model evaluation metrics allows species distribution models to be assessed before they are used in future projections to infer likely future changes in distribution.

Forty-six lagomorph experts, including 20 members of the IUCN Species Survival Commission (SSC) Lagomorph Specialist Group (LSG) and 26 recognised lagomorph

researchers selected on recent publications, were paired to species (see Appendix 2, Table 2.1) and asked to assess whether model projections accurately, roughly or did not capture the current and past range of each species i.e. good, medium or poor respectively according to the criteria in Anderson *et al.* (2003). Experts were asked to select the most accurate representation of the current and past range from the following models: i) pre- and post-1950 input data showing the suitable bioclimatic envelope, ii) pre- and post-1950 input data showing the suitable bioclimatic envelope restricted to suitable habitat, iii) post-1950 input data only showing the suitable bioclimatic envelope, or iv) post-1950 input data only showing the suitable bioclimatic envelope restricted to suitable habitat.

Independent model evaluation in SDMs often uses the Area Under the Curve (AUC) value but has been heavily criticised (Lobo *et al.* 2008). AUC is not advocated for model evaluation because Receiver Operating Characteristic (ROC) curves cannot be built for presence/absence or presence/pseudo-absence data (Allouche *et al.* 2006) and AUC values can be influenced by the extent of model predictions (Lobo *et al.* 2008). There are also known limitations with using alternative metrics (Allouche *et al.* 2006) such as sensitivity (proportion of presences which are correctly predicted), specificity (proportion of absences which are correctly predicted) or True Skill Statistic (a prevalence independent metric calculated using sensitivity and specificity). Misleading commission errors, which can arise from species not being at equilibrium with the environment, can affect such metrics. On the other hand, Kappa is an objective measure of prediction accuracy based on input species records and background points adjusted for the proportion of correct predictions expected by random chance (Monserud & Leemans, 1992). Kappa utilises commission and omission errors (Manel *et al.* 2001), although it does not take into account prevalence like the True Skill Statistic (Allouche *et al.* 2006), and can sometimes produce misleading commission errors (Peterson *et al.* 2011), it has widely accepted thresholds which can be useful in model evaluation (Landis & Koch, 1977; Fleiss *et al.* 1981; Altman, 1991). There are documented flaws with all possible model evaluation statistics. However, Kappa is now commonly used in model evaluation e.g. Estes *et al.* (2013) and here has been paired with an expert validation approach for added reliability.

The ‘accuracy’ function in the SDMTools package (Van der Wal *et al.* 2014) in R version 3.0.2 was used to calculate the Area under the Curve (AUC) value, omission rate, sensitivity, specificity, proportion correct, Kappa and True Skill Statistic for completeness, but only Kappa was taken forward for use in the model validation framework. The optimum threshold was taken as Kappa >0.4 as this value has been advocated in a range of previous studies (Landis & Koch, 1977; Altman, 1991; Allouche *et al.* 2006). Models that had Kappa >0.4 and those that were ranked as either good or medium by expert evaluation were defined as “modellable” because they demonstrate good model fit and predictive ability; these species were carried forward for projection and further analysis. Those models with a Kappa <0.4 or ranked as poor by expert evaluation were defined as “unmodellable”, with poor model fit and predictive ability, and were rejected from further analysis (see Appendix 2, Fig. 2.1). Hereafter, species are referred to as “modellable” or “unmodellable” as explicitly defined above.

3.3.3 Future predictions

The model settings, for example, the input data used (pre- or post-1950) or restriction/no restriction to occupied land classes, which provided the optimal outcome i.e. the highest Kappa value and best expert evaluation, were used to project modellable species bioclimatic envelopes under future climate during the 2020s, 2050s and 2080s. Future predictions were clipped to the buffered minimum convex polygon of the target species further buffered by the dispersal distance (kilometres/year) of each species multiplied by the number of years elapsed from the present (1950-2000) taken as 1975. Predicted range size, mean latitude and minimum, mean and maximum elevation for each species and each time period were calculated. Model outputs for each species can be found in Appendix 1; unmodellable species projections are included for reference only.

3.3.4 Statistical analysis

To illustrate projected changes in the distribution of lagomorph species, the difference in predicted species richness per cell was calculated between the 1930s (1900-1949) and 2080s (2070-2099). The difference in model output metrics (range size, mean latitude and minimum, mean and maximum elevation) was calculated between the 1930s and 2080s. Change in range size was expressed in percentage change but change

in latitude was represented as degree movement towards the poles and change in elevation in metres. Generalised Least Square (GLS) models, with an autoregressive moving average (ARMA) correlation structure, were used to test the differences in temporal trends for range change, poleward movement and elevation between lagomorph groups: 1) pikas, 2) rabbits and 3) hares and jackrabbits. ARMA was used to explicitly account for the non-independent nature of the time-series periods. This required use of the ‘nlme’ package in R version 3.0.2 (Pinheiro *et al.* 2014). Phylogenetic Generalized Least-Squares (PGLS) regressions were performed to test whether changes in model predictions varied with morphological or life history traits. For further details on traits and the phylogeny see sections 2.4 and 2.5. PGLS analysis was run using the ‘caper’ package in R (Orme *et al.* 2012) to fit a linear model which takes into account phylogenetic non-independence between data points. The implementation of this method is described in Freckleton *et al.* (2002). Outliers were removed prior to analysis, because species with large residuals may overly influence the results of the regression, and they were identified as those with a studentized residual >3 units following Cooper *et al.* (2012). All models exhibited normally distributed residuals tested using Shapiro-Wilk. The scaling parameter lambda varies from 0, where traits are independent of phylogeny, to 1 where species’ traits covary in direct proportion to their shared evolutionary history (Freckleton *et al.* 2002). We estimated lambda for each model and tested whether it was significantly different from 0 or 1 during the PGLS analysis. All subset regressions were run using the ‘dredge’ function in the ‘MuMIn’ (Barton, 2013) package in R, using AICc as the rank estimate, and then model averaging was used to describe the effect of each variable.

3.4 Results

There was a high degree of agreement between expert model classification and Kappa values. However, experts were often more critical; for example, they classified 25 species models as ‘poor’ but these species had a mean Kappa of ~ 0.6 (Fig. 3.1). Fifty-eight species (67%) were deemed modellable with expert validation classed as medium or good and Kappa >0.4 and 29 species (33%) were rejected as unmodellable with expert validation classed as poor and/or Kappa <0.4 . Unmodellable species were 4

times more likely to be listed by the IUCN as Data Deficient than modellable species, with 8 unmodellable species (28%) listed as threatened. The majority of species with small sample sizes were classed as unmodellable; the median number of occurrence points for modellable species was 36 and for unmodellable 13. Hereafter, all results are presented for modellable species only, and, therefore, are a highly conservative estimate of the impact of climate change on the order Lagomorpha as a whole.

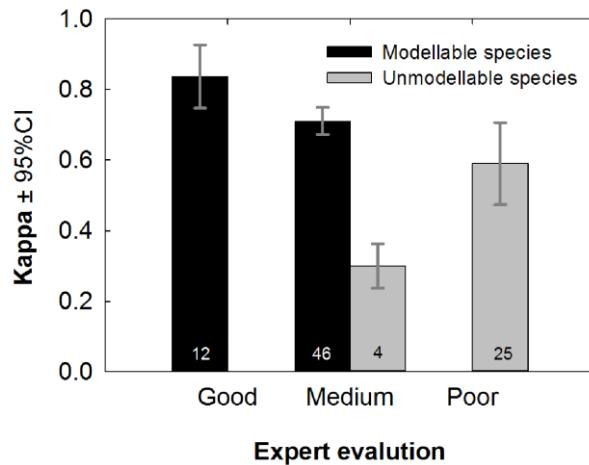


Fig. 3.1. Agreement between expert evaluation and model accuracy. Mean Kappa $\pm 95\%$ confidence intervals within the categories assigned by expert evaluation. Black bars indicate species that were deemed “modellable” and retained for further analyses, whereas grey bars indicate “unmodellable species” that were rejected. Sample sizes (i.e. numbers of species) are shown in the bars.

Global changes in predicted lagomorph species richness suggest that almost a third of the Earth’s terrestrial surface (31.5 million km²) currently occupied by lagomorphs is predicted to experience loss of lagomorph species by the 2080s (Fig. 3.2, also see Appendix 2, Fig. 2.2). Areas along the northern border of China become increasingly unsuitable, potentially losing up to 10 species by 2080, including the woolly hare *L. oiostolus* and Glover’s pika *O. gloveri* which are predicted to undergo dramatic movements to higher elevations. In contrast, predicted species gains were notable across: (a) northern Eurasia, due to poleward movement of the mountain hare *L. timidus*; and, (b) North America, where some regions e.g. the Upper Missouri catchment of Montana and North Dakota were predicted to gain up to 5 species. This includes the desert and eastern cottontails *S. audubonii* and *S. floridanus* respectively, which are predicted to exhibit strong poleward movements. The majority of African lagomorph

species were classed as unmodellable and as such Fig. 3.2 is largely data deficient for the continent.

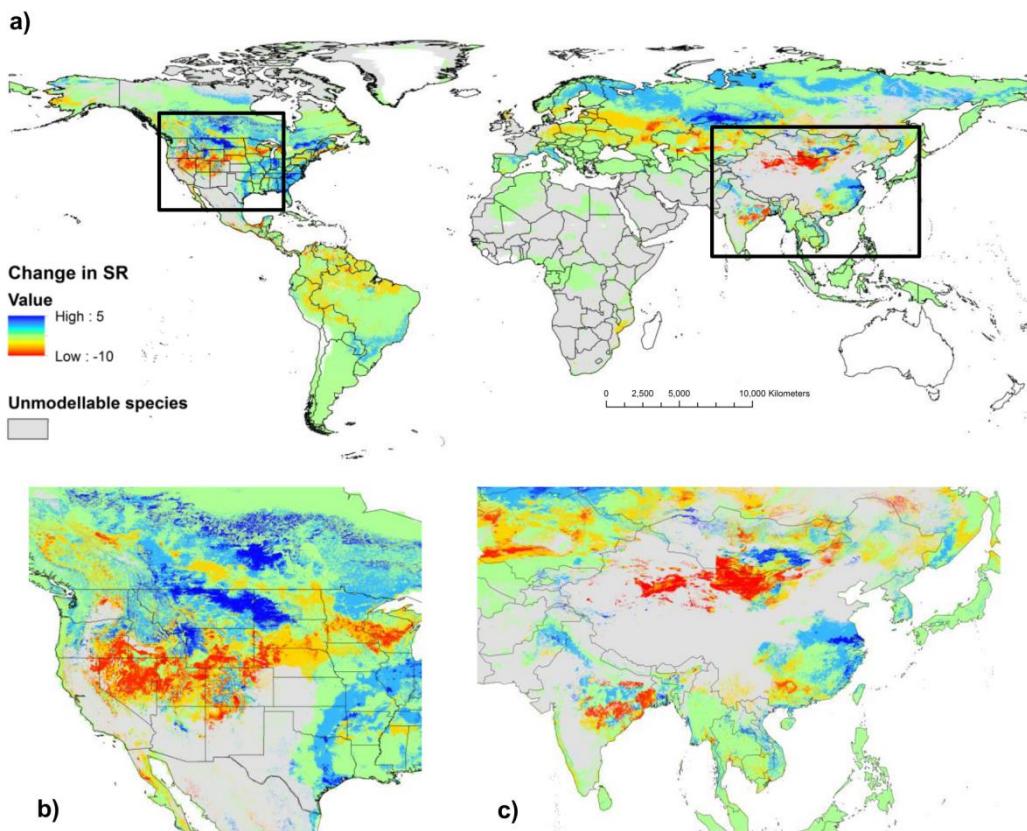


Fig. 3.2. Change in predicted lagomorph species richness from the 1930s to 2080s. (a) Global patterns in predicted species loss and gain showing details in (b) North America and (c) Asia. Light grey indicates areas occupied by “unmodellable” species with uncertain outcomes.

Thirty-six lagomorph species are predicted to experience range loss (63%), 48 poleward movements (83%) and 51 elevational increases (88%). However, 22 (38%) species are predicted to increase their range, 7 (12%) decrease in elevation and 10 (17%) move away from the poles due to future climatic changes. Thirty-five species (60%) are predicted to undergo range declines *and* either poleward movements *or* elevational increases. On average, all three groups of lagomorphs exhibited significant poleward shifts ($F_{df=1,234}= 13.5$, $p<0.001$) and elevational increases ($F_{df=1,234}= 44.2$, $p<0.001$) by 2080 (Fig. 3.3, also see Appendix 2, Table 2.2). The average poleward shift for the order was 1.1° and elevational shift 165m. Pikas exhibited the most substantial mean increase in elevation becoming increasingly isolated on mountain summits (e.g.

the Rockies in North America and the Tibetan Plateau and high Himalayas) resulting in a significant 31% range contraction ($F_{df=1,234} = 3.7, p=0.03$), but showed little poleward movement. In addition, lagomorph species occupying islands ($n=6$) will, on average, lose 8km² of their ranges compared to 0.2km² gained by continental species ($n=52$), whilst mountain dwelling species ($n=24$) will lose 37km² of their ranges compared to 25km² gained by lowland species ($n=34$).

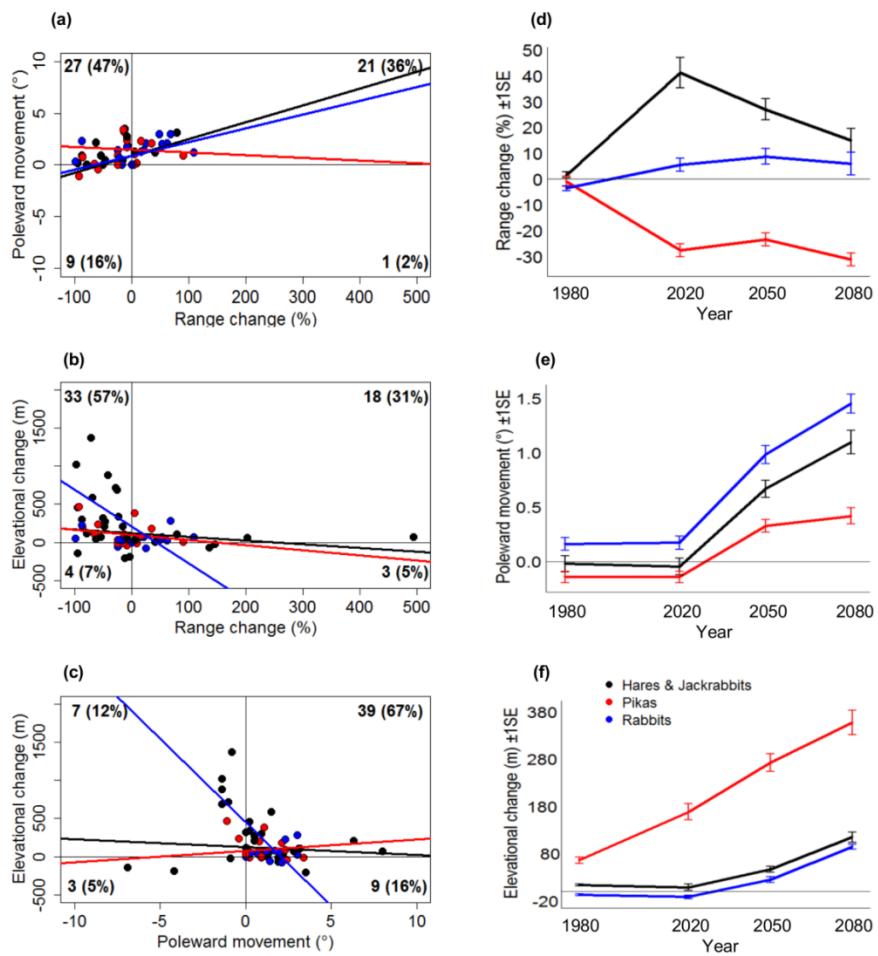


Fig. 3.3. Characterisation of predicted lagomorph bioclimatic envelope change. Scatterplots show the linear relationship between range change (%) and (a) poleward movement (°), (b) elevational change (m) and (c) poleward movement and elevational change. The numbers of species in each quadrant that exhibited positive or negative change on each axis are shown with percentages in parentheses. Temporal trends for (d) range change, (e) poleward movement and (f) elevational change ± 1 standard error for each species group; pikas (red), rabbits (blue) and hares and jackrabbits (black).

PGLS models indicate that members of each group were capable of showing a variety of responses i.e. species of pika, rabbits, hares or jackrabbits exhibited both increases and decreases in each response variable. There was a significant positive relationship between predicted range change and adult body mass ($\beta=0.258$, $F_{df=4,52}=2.308$, $p=0.021$) with hares and jackrabbits generally increasing their range by 2080 and pikas exhibiting range contraction (Fig. 3.4; also see Appendix 2, Table 2.3). Adult body mass was positively associated with predicted poleward movement ($\beta=0.196$, $F_{df=5,49}=1.989$, $p=0.047$) and inversely related to predicted elevational change ($\beta= -0.183$, $F_{df=2,50}=2.019$, $p=0.043$). The average adult body mass for lagomorph species living in mountainous regions was 836g, compared to 1.8kg in lowland areas. The number of litters a species produces per year was positively related to predicted latitudinal and maximum elevational shifts ($\beta=0.215$, $F_{df=5,49}=2.731$, $p=0.006$ and $\beta=0.160$, $F_{df=2,53}=1.746$, $p=0.081$ respectively) with more fecund species being capable of more extreme upward movement or poleward shifts. There was also a positive relationship between species dietary niche and the degree of predicted poleward shift ($\beta=0.181$, $F_{df=5,49}=2.190$, $p=0.029$). No significant relationships were found between activity cycle and predicted changes in species distribution.

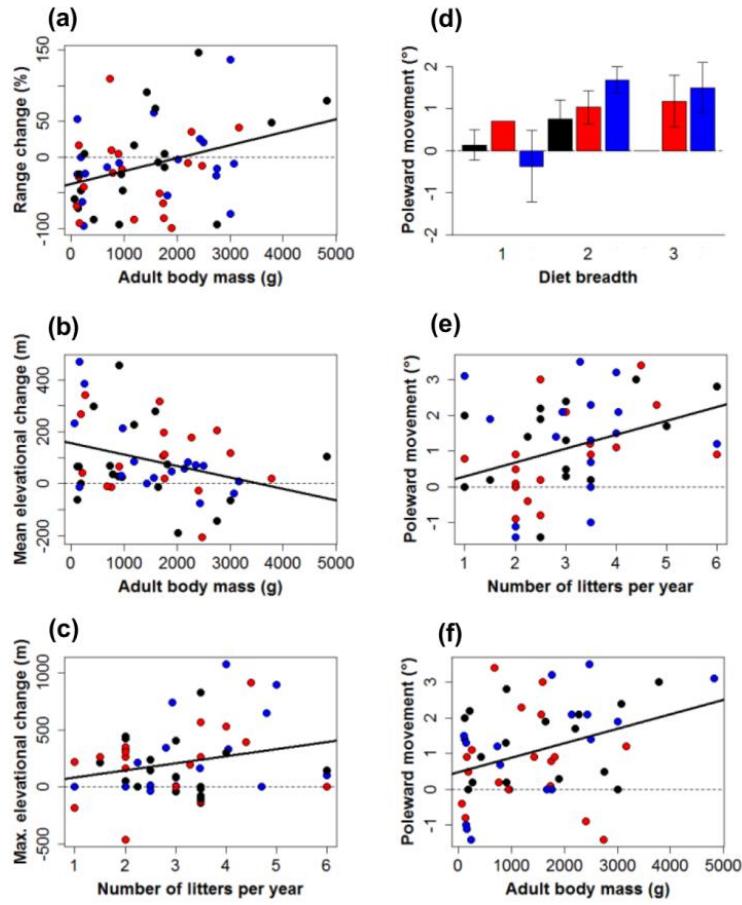


Fig. 3.4. Relationships between species traits and responses to future climate change. The ability of species' traits to predict changes in (a) range (b) mean elevation (c) maximum elevation and (d) (e) (f) poleward movement under future climate (between ~1930s and ~2080s) for each group; pikas (red), rabbits (blue) and hares and jackrabbits (black). Diet breadth is a categorical variable and is therefore represented as a bar plot (± 1 standard error) with sample sizes (i.e. numbers of species) shown above the bars. Only significant predictors of change are shown here. The dashed line at zero indicates no change in the response variable.

3.5 Discussion

The Lagomorpha as a whole are predicted to exhibit much greater poleward (mean \pm 95%CI = $1.1^\circ \pm 0.5^\circ$) and elevational shifts (165m \pm 73m) by 2100 than calculated in a recent meta-analysis collating information on a wide variety of taxonomic groups (Parmesan & Yohe, 2003). On average birds, butterflies and alpine herbs were predicted to shift $\sim 0.8^\circ$ poleward and increase in elevation by ~ 90 m by 2100. Thuiller *et al.* (2011) found that mammals were less vulnerable to change than other groups, but more than 50% of shrews could lose more than 30% of their suitable climatic space. In comparison, our study shows that only 34% of modellable lagomorphs will lose more than 30% of their suitable climatic space, but lagomorphs appear to show more notable changes in elevation and poleward movement. A study by Schloss *et al.* (2012) found that, in some scenarios, 50% of mammal species in North and South America will be unable to keep pace with future climate change and our results indicate that lagomorphs follow similar trends, but with more substantial poleward and elevational shifts. Furthermore, our results are conservative estimates due to the exclusion of unmodellable species, most notably African species. Parts of Africa are expected to become drier and warmer under future climate, with substantial increases in arid land (IPCC, 2007) which will likely lead to negative consequences for lagomorphs not assessed here. Our results are also conservative due to the exclusion of most Data Deficient lagomorph species (as classified by the IUCN) which are highly likely to be threatened with extinction (Bland *et al.* 2015). We strongly advocate studies minimising data gaps in our knowledge of the order, specifically collecting more specimens for biodiversity archives and targeting data deficient geographic regions.

In contrast, a recent study of empirical climate studies by McCain & King (2014) has shown that only about 50% of, mostly North American, mammal species respond to climate change by shifting in latitude and elevation. Results of four lagomorph studies are included which show that the pygmy rabbit *Brachylagus idahoensis* undergoes extirpation and contraction due to climatic changes (Larrucea & Brussard, 2008), the ranges of the snowshoe hare *L. americanus* and collared pika *O. collaris* do not change (Franken & Hik, 2004; Jannett *et al.* 2007) and the American pika *O. princeps* mostly undergoes extirpation and upslope contraction, but some sites within the range show no change (Moritz *et al.* 2008; Beever *et al.* 2011). Although we find that more than 50%

of lagomorphs respond to climate change, our results are largely congruent with these empirical studies, indicating range contraction in *O. princeps* and *B. idahoensis*, and little change in the ranges of the *L. americanus* and *O. collaris*.

Pikas are predicted to show elevational rather than latitudinal shifts because these high-altitude specialists are known to be extremely susceptible to increases in temperature or unpredictable seasonality, which could potentially lead to heat stress (Smith, 1974). On the other hand leporids, typically being lowland species, exhibited less substantial increases in elevation but greater poleward shifts, for example, *L. timidus*. This is probably due to the high sensitivity of its boreo-alpine niche to changes in temperature (Acevedo *et al.* 2012a). Indeed, even *L. t. hibernicus* which inhabits temperate grasslands, unlike other mountain hares, is predicted to experience a contraction from the south-east to the north-west of Ireland. As global temperatures increase, northern latitudes will become more climatically suitable for southern leporids and, therefore, species bioclimatic envelopes will track poleward to match. Rabbits, hares and jackrabbits were thus predicted to exhibit little overall change in the total extent of their ranges. The majority of the modellable rabbit species were from the genus *Sylvilagus* inhabiting south and eastern USA and Mexico; a region projected to become generally drier (Liverman & O'Brien, 1991) inducing latitudinal shifts in species to track suitable habitats or vegetation. Thus, by shifting their ranges poleward, leporids are predicted to be able to maintain or increase their range extent suggesting they are considerably less sensitive to projected climate change than pikas.

PGLS models estimated lambda to be close to zero for changes in range, poleward movement and elevation shifts indicating that observed trends were independent of phylogeny (Freckleton *et al.* 2002). Smaller species, principally pikas and some rabbits, were typically more likely to make elevational shifts in range whilst larger species, principally hares and jackrabbits, had a greater tendency for poleward shifts. This relationship has also been described in empirical climate studies e.g. McCain & King (2014) and is probably due to the large number of small-bodied mountainous species ($n=24$) which have less opportunity to shift latitudinally because they are confined to high-elevation areas that contract upslope as climate changes. An elevational shift is almost always accompanied by a range decline, whereas a latitudinal shift could be accompanied by declines, increases or no change in range. Only when a species occupies high latitudes, edges of continents or islands will latitudinal shifts cause drastic range

declines. A 1m elevational shift is equivalent to a 6km latitudinal shift (Parmesan & Yohe, 2003), so it is easier for smaller species to shift altitudinally rather than latitudinally. This could be explained due to a relationship between adult body mass and dispersal distance, which was used to clip model projections, but a Spearman's Rank correlation suggested no correlation between these two variables in our dataset ($rs[30,002] = 0.077, p=0.565$). Trait analyses also showed a significant positive relationship between fecundity and extreme elevational or poleward movement which is comparable to a study by Moritz *et al.* (2008), who found that fecund small mammals in Yosemite National Park, USA, were more likely to expand their ranges upward than less fecund counterparts. We found no association between activity cycle and vulnerability to climate change in the Lagomorpha as hypothesized and also reported in McCain & King (2014), but this may be due to the varied nature of lagomorph activity. The activity of the European hare is known to be less consistent and partially diurnal in the summer (Schai-Braun *et al.* 2012) and *O. princeps* also shows seasonal changes in activity patterns (Conner, 1983). However, we acknowledge the potential drawbacks of linking traits to modelled distributional changes rather than empirical-based studies, i.e. non-independence of trait results; nevertheless, the analysis presented here facilitates the understanding of the traits which could potentially lead to vulnerability to future climate change.

The uncertainties in SDM using projected future climate scenarios are well described (Kramer-Schadt *et al.* 2013). Models are vulnerable to sampling bias (Elith & Leathwick, 2009), spatial scale issues bias (Elith & Leathwick, 2009), lack of data for rare species (Pearson *et al.* 2007), uncertainty regarding future climate conditions (Beaumont *et al.* 2008) and insufficient independent evaluation bias (Elith & Leathwick, 2009). We have tackled these explicitly by accounting for sampling bias by restricting the set of background points used, using data with the highest spatial resolution available (30 arc-second) and selecting species records to match, bootstrapping models for rare species with few records, averaging climatic data from five global circulation models and using a framework of joint expert and metric-driven model validation to segregate current distribution model outputs into those that were modellable and unmodellable before subsequent projection and analysis. However, our predictions could still be potentially confounded by species-area relationships (Bellard *et al.* 2012) and biological interactions (Wisz *et al.* 2012).

Regardless of individual model outcomes, the overall trends observed across the order Lagomorpha as a whole are compelling. This study did not take account of shifts in habitats, vegetation or human impact in response to climate change, but we have shown that adaptation to future climate conditions may be possible as some species were predicted to exhibit poleward movements, with only modest shifts in range or elevation e.g. *S. floridanus* and the Appalachian cottontail *S. obscurus*.

The predicted changes in climatic conditions are likely to have greater impacts on isolated lagomorph populations, i.e. those on islands and in high-altitude systems. If changes continue at the rate currently predicted until the 2080s, then there may be no climatically suitable range available for some montane or isolated species e.g. the Tres Marias cottontail *S. graysoni* or black jackrabbit *L. insularis*. Conservation strategies, such as assisted migration, could be the only option for these highly range-restricted species. Furthermore, conservation management will need to focus on small-bodied mammals as these are predicted to show more dramatic responses to changing climate. Small mammals are key in food webs sustaining predator populations, impacting plant communities by grazing and soil biology and hydrology by burrowing. Thus, fundamental shifts in lagomorphs globally may cause trophic cascade effects, especially in northern latitudes such as the cyclic systems of the Arctic.

The advancing knowledge of past extinction rates for the Lagomorpha (Ge *et al.* 2012), along with better bioclimatic envelope modelling, could aid the prediction and prevention of future extinctions. Our models suggest that *O. koslowi* may become extinct by the 2080s as the elevational increases required to maintain its current bioclimatic envelope disappear as it reaches the maximum elevation available. We have shown here how expert validation can be effectively integrated into the model evaluation process in order to improve model predictions and advocate use of this framework in future SDM studies. Assessment of vulnerability to climate change is needed urgently to identify how and to what extent species, taxa, communities and ecosystems are susceptible to future changes, taking into account likely changes to vegetation, human pressures and interspecific interactions, and to direct conservation management in an efficient and effective manner. Multi-species approaches are likely to lead to more effective mitigation measures and contribute to our understanding of the general principles underpinning the biogeographical and ecological consequences of climate change impacts.

CHAPTER 4

Competitive interactions in the order Lagomorpha

A manuscript based on this chapter has been published as:

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4.1 Abstract

In addition to abiotic determinants, biotic factors, including competitive, interspecific interactions, limit species' distributions. Environmental changes in human disturbance, land use and climate are predicted to have widespread impacts on interactions between species, especially in the order Lagomorpha due to the higher latitudes and more extreme environmental conditions they occupy. We reviewed the published literature on interspecific interactions in the order Lagomorpha, and compared the biogeography, macroecology, phylogeny and traits of species known to interact with those of species with no reported interactions, to investigate how projected future environmental change may affect interactions and potentially alter species' distributions. Thirty-three lagomorph species have competitive interactions reported in the literature; the majority involve hares (*Lepus* sp.) or the eastern cottontail rabbit *Sylvilagus floridanus*. Key regions for interactions are located between 30-50°N of the Equator, and include eastern Asia (southern Russia on the border of Mongolia) and North America (north western USA). Closely related, large-bodied, similarly sized species occurring in regions of human-modified, typically agricultural landscapes, or at high elevations are significantly more likely to have reported competitive interactions than other lagomorph species. We identify species' traits associated with competitive interactions, and highlight some potential impacts that future environmental change may have on interspecific interactions. Our approach using bibliometric and biological data is widely applicable, and with relatively straightforward methodologies, can provide insights into interactions between species. Our results have implications for predicting species' responses to global change, and we advise that capturing, parameterising and incorporating interspecific interactions into analyses (for example, species distribution modelling) may be more important than suggested by the literature.

4.2 Introduction

Biotic interactions underpin a wide range of ecosystem processes and can occur between individuals of the same species (intraspecific interactions), or among individuals belonging to different species (interspecific interactions; Connell, 1983; Chase *et al.* 2002). Interactions can take place at the local scale, for example, predation, parasitism, competition, and disturbance, or at the regional scale, for example, dispersal, speciation, extinction, and expansions or contractions of species' ranges (Cornell & Lawton, 1992; Amarasekare, 2003). Competitive interactions are variously defined, but most definitions incorporate limited resources, for example: "the negative effects that one organism has upon another by consuming or controlling access to a resource that is limited in availability" (Keddy, 2001). Strong competitive interspecific interactions at the same trophic level are likely due to occupied or partially occupied niche space which influences species' coexistence (Cornell & Lawton, 1992). Competition can be symmetrical, whereby there are equivalent negative effects, or asymmetrical, whereby there is a clear winner or loser (Connell, 1983; Schoener, 1983). Three mechanisms are known: 1) interference competition is when an individual directly affects another, for example, by using aggression (Birch, 1957); 2) exploitation competition is when individuals interact indirectly, usually competing for a common, limited resource (Keddy, 2001); and 3) apparent competition is when two individuals that do not compete directly for resources affect each other indirectly, by being prey for the same predator (Chaneton & Bonsall, 2000; Hatcher *et al.* 2006; DeCesare *et al.* 2010).

Competitive interactions tend to produce biogeographical patterns in species' distributions. Competing species may meet at a sharp boundary with little or no overlap, whereas non-competing species' ranges may show complete overlap (Flux, 2008). Parapatry is when two species have separate but contiguous ranges, with no physical barrier between them, and only co-occur, if at all, in a narrow contact zone (Bull, 1991; Gutiérrez *et al.* 2014). Ranges of allopatric species are separated by a geographic barrier and, therefore, there can be no interspecific interaction. Sympatric species share the same geographical space, but may compete for access to similar habitats or resources. Alternatively, species occupying overlapping niches may not compete, so that their coexistence is possible due to the partitioning of resources. Exploitation competition may be evident if, for example, habitat use between species is comparable; abrupt habitat shifts

at their point of contact in sympatry are likely to mirror the response to competition (Vidus-Rosin *et al.* 2011).

Traits of competitively interacting species have been studied in great detail (e.g. Schoener, 1982; Luiselli, 2006). Phylogenetic relatedness and its association with competition are often studied. Darwin (1859) suggested that closely related species are more likely to exhibit competition because they occupy similar ecological niches. Close relatedness of interacting species has since been shown experimentally (Violle *et al.* 2011), but does not hold for some taxa, for example, green algae (Venail *et al.* 2014). Species with larger body masses are more competitive because they are able to utilise a larger share of resources (Brown & Maurer, 1986) and similarly sized species are typically more likely to interact (Leyequien *et al.* 2007). Environmental traits can also influence competitive interactions, for example, competition is more likely in urban environments with higher human population densities (Shocat *et al.* 2006), and past climatic changes have probably caused large impacts on species' distributions and, therefore, on interspecific interactions (Koblmüller *et al.* 2012). Interactions between species are more common at high elevations perhaps due to limited resources (Jankowski *et al.* 2010), and are likely more vulnerable to change due to the predicted effects of climate change at such elevations (Chen *et al.* 2011), potentially changing species' ranges both directly and indirectly. Thus, environmental change, caused by human disturbance, changes in climate, or changes in land use, may have direct or indirect effects on the strength of biotic interactions, thus informing our interpretation of their likely influence on species' distributions.

Interactions between species are extremely difficult to identify and quantify in the wild. In the majority of cases, interactions are inferred from parapatry or species replacement, but this inference is not conclusive, and interactions could be a result of hybridisation or adaptation to different habitats with no geographic overlap (Huey, 1979). Consequently, the impacts of global change on biotic interactions have rarely been studied (McCann, 2007), but they are likely to be significant, due to related changes in phenology, behaviour, physiology, abundance and the co-occurrence of multiple species throughout biomes (e.g. Tylianakis *et al.* 2008). Competitive interspecific interactions may be altered by changes in dominant plants or animals under future environmental change; for example, increases in mean global temperatures could affect seed dehiscence times and change competition between mammalian seed predators and invertebrate seed dispersers (Ness & Bressmer,

2005). In a hypothetical situation in which species A, B and C are positioned along a resource gradient, with species A occupying the upper end (a region of high resource availability), species C occupying the lower end (a region of low resource availability), and species B occupying a niche between the two, any response to future environmental change involving an increase in the availability of resources may lead to selection favouring the more extreme species (A and C) and, hence, may lead to the expansion of their distributions (impacting species B). For example, species B could broaden its niche space, or new species could invade and occupy niche vacancies left by shifts in species A and/or C. However, if environmental change were to reduce the availability of resource types, the ranges of all three species may contract, which could increase the intensity of competition, and possibly lead to local extirpations at their contact zones, or total extinction(s) (Post, 2013).

We collate, review and assess all published data on lagomorph interspecific interactions, from both experimental evidence and inference from parapatry or species replacement, and examine the potential relationships between the environment and species' traits within different types of interaction. We aim to investigate how future environmental change may affect such interactions and potentially alter species' distributions. We use a combination of bibliometric analyses and biological data to assess traits associated with competitive interactions in an entire mammalian order, the Lagomorpha. We predict greater competition between lagomorph species at higher elevations, due to restrictions in suitable habitat and in the range of potentially interacting species found in mountainous terrain, and in human-converted habitats, which are frequently inhabited by lagomorphs due to the availability of food (e.g. grasses or crops) and shelter (e.g. field margins and hedgerows providing cover). We expect the restricted range of food available in and the uniformity of anthropogenic landscapes to intensify competitive interactions. We also hypothesise that competitive interactions are more likely to occur between closely related species (i.e. those with shorter-than-average pairwise phylogenetic distances) with a small difference in body mass (i.e. those relatively similar in size).

4.3 Methods

4.3.1 Capturing competitive interactions

Data on interspecific interactions involving only lagomorphs were captured using the Web of Knowledge, searched using the terms “lagomorph AND interaction” or “lagomorph AND competition”. Additional search terms included pairwise combinations of all species whose IUCN range polygons overlapped (using both scientific and common names) to identify the possibility of interactions not returned in the initial search. All 3,741 possible pairs of the 87 species in our taxonomy were classified as: 1) allopatric, i.e. exhibiting no range overlap, and lacking any published evidence of interspecific interactions; 2) sympatric (i.e. with partially coincident geographical ranges, defined as overlap in their IUCN range polygons), but with no known interaction; or 3) sympatric with interaction reported in the literature. Using bibliometric information competitive interactions were classed as either exploitation or interference.

Information on interactions may be biased by body size or taxonomic group due to variable research effort (Brooke *et al.* 2014), and some pairwise interactions are likely to be undocumented in the literature to date; thus, the current study may have been vulnerable to type II errors or false negatives in identifying species’ interactions. Moreover, there may have been a bias towards species showing interactions, due to researchers’ preference for reporting significant effects: so-called ‘publication bias’ (Connell, 1983). To take this potential bias into consideration, instead of assuming no competition between species for which there was no evidence of interaction, we defined category 2) as ‘sympatric with no known interaction’.

4.3.2 Spatial analysis

Rasterised species range data (see section 2.2) were summed to show the global distribution of possible interactions between species known to interact with at least one other species. The invasive range of *Sylvilagus floridanus* in Italy was not included because IUCN polygons were only available for its native distribution. Mean elevation (m) and latitude (°) occupied by each pair of species known to interact were calculated at ~1km² grid cell resolution.

4.3.3 Species' traits and environmental data

Phylogenetic distance, the amount of time since the most recent common ancestor of both species existed (Vellend *et al.* 2011), as a proxy for phenotypic differences between two species (Cavender-Bares *et al.* 2009), was quantified for each pair (including allopatric, sympatric with no known interaction and sympatric with interaction), to investigate whether closely related species were more likely to interact competitively. Pairwise phylogenetic distances were calculated using the 'ape' package (Paradis *et al.* 2013) for R version 3.1.1 and the phylogeny described in section 2.5.

Ecoregional climatic stability data was provided by Takuya Iwamura (Iwamura *et al.* 2013), and was defined as "the proportion of an ecoregion which is predicted to be climatically stable under [future] climate change." The climatic stability index is calculated by estimating the overlap between present and future climatic envelopes for each ecoregion, using results from seven global circulation models. It ranges from 0 (no overlap between current and future climates) to 1 (complete overlap and high robustness to climate change; Watson *et al.* 2013). For each species, the percentage of occurrence records in human-converted habitats was included as a coarse measure of the threat to each species from human activities, following Hoekstra *et al.* (2005). Converted habitats included cultivated or managed land and artificial surfaces; areas were derived from a modified version of the Global Land Cover 2000 dataset (Anonymous, 2003). The occurrence data used in this calculation is described in section 2.1. Species' traits and environmental data considered (examined) but not included in the analysis were: activity cycle, body length, body mass at birth, diet breadth, elevational change (1930-2080), gestation length, habitat breadth, home range size, land use change (1980-2050), land use change (1980-2070), litter size, litters per year, poleward movement (1930-2080), population density, range decline (1930-2080). Species' traits are described in section 2.4.

4.3.4 Statistical analyses

A linear regression was performed in R version 3.1.1 to test the relationship between the dependent variable, elevation (m), and the number of possible pairwise interactions (rasterised data from section 4.3.2). A Generalized Linear Model was used to evaluate differences between pairs of species allocated to the three interaction types: 1) allopatric,

2) sympatric with no known interaction and 3) sympatric with interaction, using species' traits and environmental data described in section 4.3.3 as explanatory variables.

4.4 Results

4.4.1 Spatial patterns of interspecific interactions

Of the 3,741 possible pairs between the 87 species of lagomorph, 3,489 were classed as allopatric, 219 were classed as sympatric with no known interaction, and 33 were classed as sympatric with documented interaction; of the 33 species involved in the 33 documented interactions, nine were pikas, eight were rabbits and 16 were hares (Table 4.1). The distribution of documented interspecific interactions was not uniform but clustered in eastern Asia (exclusively pikas) and North America (rabbits, hares and jackrabbits; Fig. 4.1a). Six of the interactions involved interference competition, and five of these (83%) involved *S. florianus*. The global distribution of documented lagomorph interactions (Fig. 4.1b) showed that in large areas (~69% of the total global range of the order Lagomorpha), no pairwise interactions exist (Fig. 4.1c); lagomorph species were 2.2 times more likely to occur in allopatry than in sympathy, and 3.1 times more likely to be involved in just one pairwise interaction than in multiple interactions. The mean number of potential pairwise interactions globally was 1.51 ± 0.78 (SD). Only small areas of the globe contained the highest concentrations of possible interactions; for example, there were six possible pairwise species interactions in a 6,000 km² area in southern Russia on the border of Mongolia (Fig. 4.1c), with interactions clustered around 30-50°N of the Equator (Fig. 4.1d). There was a significant positive association between the number of possible pairwise interactions and elevation ($F_{3,49917} = 731.8, p < 0.001$; Fig. 4.2).

Table 4.1. Summary of the 33 competitive interactions documented in the order Lagomorpha, involving 33 species. Type of competitive interaction (exploitation or interference), resource competing for, and a citation for the interaction are also listed. Invasive interactions are highlighted in bold.

Competition	For...	Species	Replaced by...	Citation
Exploitation	Habitat	<i>Brachylagus idahoensis</i>	<i>Lepus californicus</i>	Pierce <i>et al.</i> 2011
Exploitation	Habitat	<i>Brachylagus idahoensis</i>	<i>Sylvilagus audubonii</i>	Pierce <i>et al.</i> 2011
Exploitation	Habitat	<i>Bunolagus monticularis</i>	<i>Lepus capensis</i>	Duthie, 1989
Exploitation	Habitat	<i>Lepus alleni</i>	<i>Lepus californicus</i>	Chapman & Flux, 1990
Exploitation	Habitat	<i>Lepus americanus</i>	<i>Lepus townsendii</i>	Leopold, 1947
Exploitation	Habitat	<i>Lepus americanus</i>	<i>Sylvilagus nuttallii</i>	Frey & Malaney, 2006
Exploitation	Habitat	<i>Lepus callotis</i>	<i>Lepus californicus</i>	Best & Henry, 1993
Exploitation	Habitat	<i>Lepus capensis</i>	<i>Lepus habessinicus</i>	Flux, 2008
Exploitation	Habitat	<i>Lepus capensis</i>	<i>Lepus europaeus</i>	Chapman & Flux, 1990
Exploitation	Habitat	<i>Lepus corsicanus</i>	<i>Lepus europaeus</i>	Angelici <i>et al.</i> 2008
Exploitation	Habitat	<i>Lepus europaeus</i>	<i>Lepus tolai</i>	Sokolov <i>et al.</i> 2009
Exploitation	Habitat	<i>Lepus europaeus</i>	<i>Lepus granatensis</i>	Gortázar <i>et al.</i> 2007
Exploitation	Habitat	<i>Lepus habessinicus</i>	<i>Lepus microtis</i>	Chapman & Flux, 1990
Exploitation	Habitat	<i>Lepus habessinicus</i>	<i>Lepus saxatilis</i>	Chapman & Flux, 1990
Exploitation	Habitat	<i>Lepus habessinicus</i>	<i>Lepus fagani</i>	Chapman & Flux, 1990
Exploitation	Habitat	<i>Lepus mandshuricus</i>	<i>Lepus tolai</i>	Chapman & Flux, 1990, Smith & Xie, 2008
Exploitation	Habitat	<i>Lepus microtis</i>	<i>Lepus saxatilis</i>	Flux, 2008
Exploitation	Habitat	<i>Lepus timidus</i>	<i>Lepus europaeus</i>	Thulin, 2003; Reid, 2011
Exploitation	Habitat	<i>Lepus townsendii</i>	<i>Lepus californicus</i>	Flinders & Chapman, 2003
Exploitation	Habitat	<i>Ochotona cansus</i>	<i>Ochotona curzoniae</i>	Chapman & Flux, 1990
Exploitation	Habitat	<i>Ochotona daurica</i>	<i>Ochotona curzoniae</i>	Zhang <i>et al.</i> 2001
Exploitation	Habitat	<i>Ochotona koslowi</i>	<i>Ochotona curzoniae</i>	Buchner, 1894
Exploitation	Habitat	<i>Ochotona koslowi</i>	<i>Ochotona ladacensis</i>	Buchner, 1894
Exploitation	Habitat	<i>Sylvilagus audubonii</i>	<i>Lepus californicus</i>	AMCELA <i>et al.</i> 2013
Exploitation	Habitat	<i>Sylvilagus audubonii</i>	<i>Lepus callotis</i>	Best & Henry, 1993
Exploitation	Habitat	<i>Sylvilagus brasiliensis</i>	<i>Lepus europaeus</i>	Novilla & Ojeda, 2008
Exploitation	Shelter	<i>Ochotona hyperborea</i>	<i>Ochotona alpina</i>	Chapman & Flux, 1990
Interference	Habitat	<i>Brachylagus idahoensis</i>	<i>Sylvilagus floridanus</i>	Pierce <i>et al.</i> 2011
Interference	Habitat	<i>Ochotona pusilla</i>	<i>Ochotona pallasi</i>	Sokolov <i>et al.</i> 2009
Interference	Habitat	<i>Sylvilagus bachmani</i>	<i>Sylvilagus floridanus</i>	Chapman & Verts, 1969
Interference	Habitat	<i>Sylvilagus brasiliensis</i>	<i>Sylvilagus floridanus</i>	Chapman & Flux, 1990
Interference	Habitat	<i>Sylvilagus nuttallii</i>	<i>Sylvilagus floridanus</i>	Genoways & Jones, 1972
Interference	Habitat/food	<i>Sylvilagus transitionalis</i>	<i>Sylvilagus floridanus</i>	Litvaitis, 2008; Probert & Litvaitis, 1996

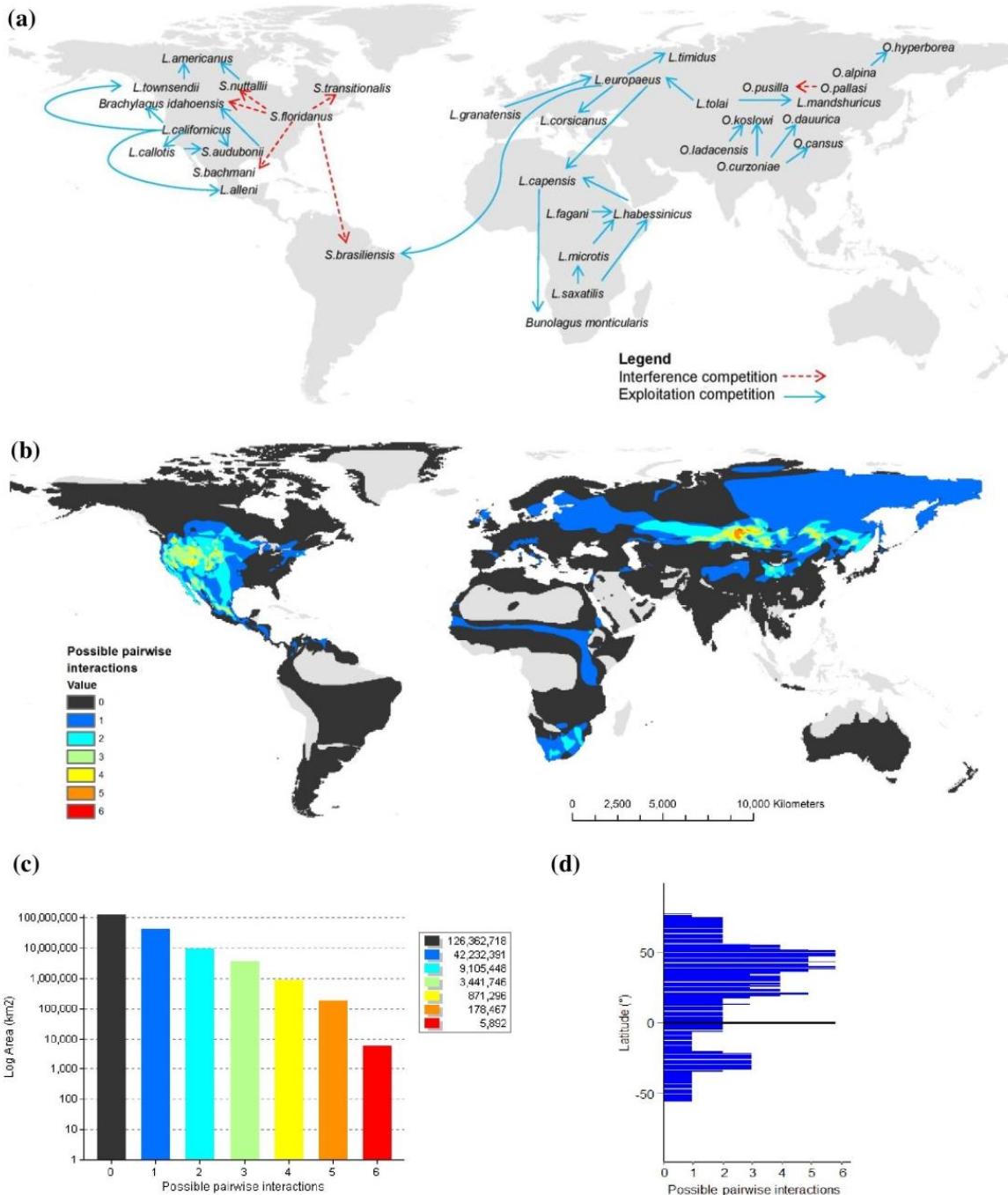


Fig. 4.1. (a) Documented competitive interactions in the order Lagomorpha shown in their approximate geographic locations. Red arrows (dashed) indicate interference competition, blue arrows indicate exploitation competition. **(b)** Global distribution of possible pairwise interactions between the 33 species in the order Lagomorpha. Pale grey areas indicate places where no lagomorph species are found. **(c)** Histogram of the area occupied by possible pairwise interactions between species documented to interact with others. **(d)** Histogram of the latitudes occupied by possible pairwise interactions between species known to interact with others; the bold line represents the Equator. In **(b)**, **(c)** and **(d)**, zero possible pairwise interactions indicate the occurrence of one species not documented to interact with others.

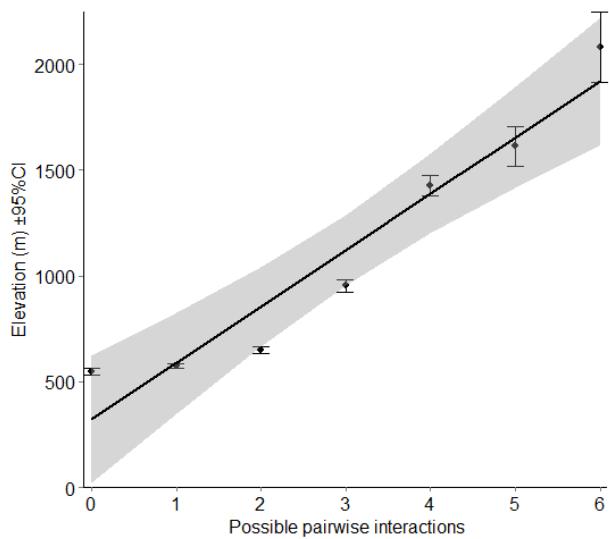


Fig. 4.2. Relationship between possible pairwise interactions between species of Lagomorpha with documented interactions and elevation (m), with $\pm 95\%$ confidence error bars. The grey area surrounding the fitted linear regression line indicates the 95% confidence limits.

4.4.2 *Linking interactions to species' traits and environmental change*

Sympatric pairs of species with documented pairwise interactions had significantly shorter phylogenetic distances between them than pairs of species that occurred in sympatry but had no known interaction ($F_{2, 3738} = 19.8, p < 0.001$; Fig. 4.3a, see Appendix 3, Fig. 3.1). Thus, within the order Lagomorpha, sympatric species with documented competitive interactions were 2.3 times more closely related than sympatric species with no known interaction.

The mean body mass of pairs of interacting sympatric species was significantly greater ($F_{2, 3738} = 22.3, p < 0.001$) than that of pairs of sympatric species that had no known interaction (Fig. 4.3b, Appendix 3, Table 3.1). The mean body mass of pairs of allopatric species was lower than both. However, whilst interacting species tended to be heaviest, analysis of the difference in body mass between species in each pair showed that pairs of interacting species were significantly closer in mass than pairs of allopatric species and sympatric species with no known interaction (Fig. 4.3c, Appendix 3, Table 3.1). There was no difference in mean ecoregional climatic stability between the pairwise interaction types ($F_{2, 3738} = 0.03, p = 0.969$; Fig. 4.3d, Appendix 3, Table 3.1). The mean ecoregional climatic

stability index value for the order Lagomorpha was 0.46 ± 0.14 , which is similar to, but slightly higher than, the global average of 0.42 ± 0.03 .

Pairs of sympatric species were more likely to occur in regions of high human population density, but due to the variability in human population density in regions supporting lagomorphs, the difference between sympatric groups was not significant (Fig. 4.3e, Appendix 3, Table 3.1). However, there was a significant difference in mean human population density between the ranges of pairs of allopatric species and those of sympatric species with a known interaction ($F_{2,3738} = 5.02, p < 0.001$; Fig. 4.3e, Appendix 3, Table 3.1). Interacting pairs of sympatric species occurred significantly more frequently in human-converted habitats than pairs of sympatric species with no known interaction ($F_{2,3738} = 6.3, p = 0.002$), and pairs of sympatric species with no known interaction were significantly more frequently found in human-converted habitats than pairs of allopatric species ($F_{2,3738} = 6.3, p = 0.002$; Fig. 4.3f, Appendix 3, Table 3.1).

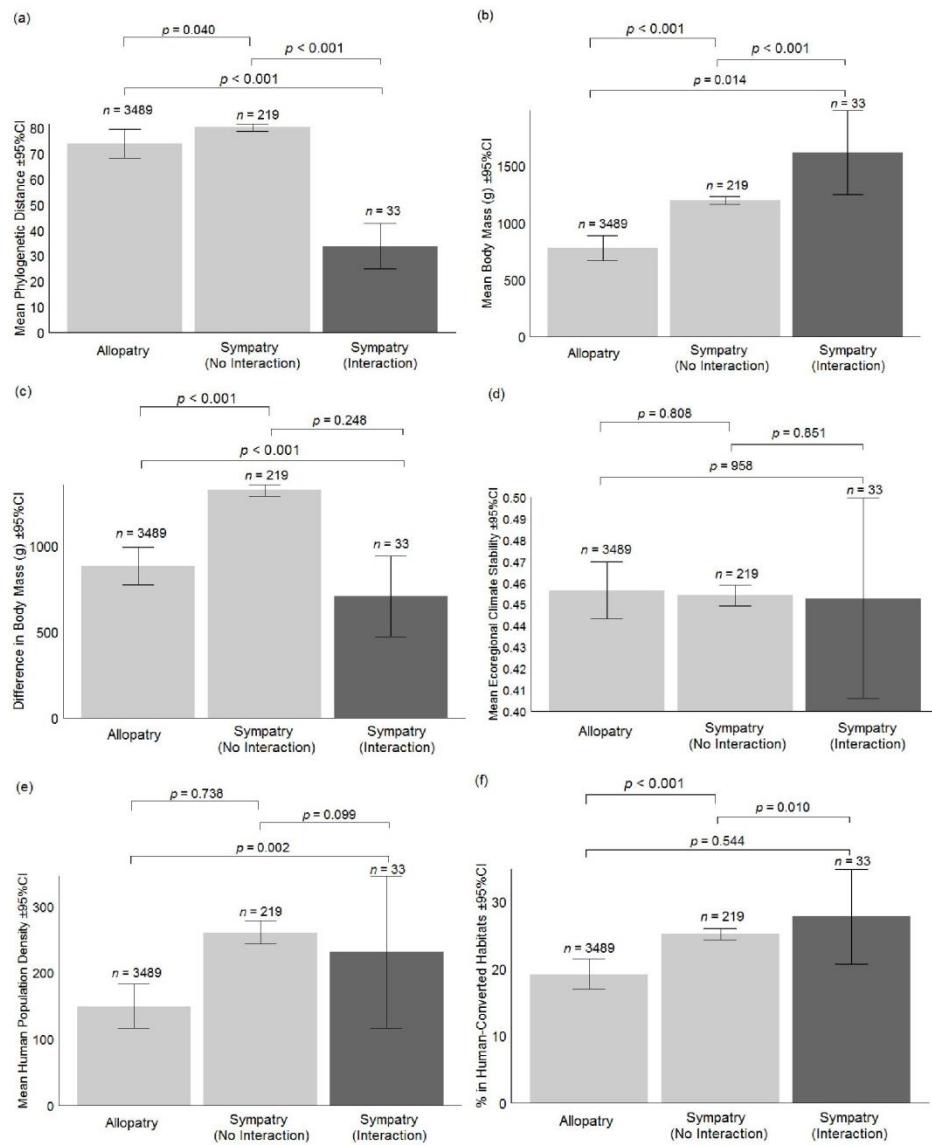


Fig. 4.3. Mean phylogenetic distance **(a)**, mean body mass **(b)**, difference in body mass between each species in an interacting pair **(c)**, mean ecoregional climate stability **(d)**, mean human population density **(e)** and mean percentage of occurrence records in human-converted habitats **(f)** ±95% confidence intervals, for lagomorph species in allopatry (light grey), sympatry with no known interaction (light grey) and sympatry with an interaction (dark grey).

4.5 Review and Discussion

Closely related, large-bodied, similarly-sized species occurring in regions of human-modified, typically agricultural landscapes, or at high elevations, were significantly more likely to exhibit competitive interactions than other species within the order Lagomorpha. The greatest changes in species' ranges are likely to occur either at high elevation, where the effects of climate warming are pronounced (Chen *et al.* 2011), or in human-modified habitats, which are already subject to significant threats and pressures (McCarthy *et al.* 2010). This suggests that interacting species, which are found more commonly in human-modified habitats and at high elevation, are likely to be highly susceptible to future environmental changes. Moreover, the average ecoregional climatic stability index for regions inhabited by lagomorphs, although slightly higher than the global average, indicates only medium robustness of those regions to future changes in climatic conditions. Larger mammalian species are predicted to be especially vulnerable to future climatic changes (McCain & King, 2014). Many of the responses to climate change in large mammals, e.g. the Eurasian elk *Alces alces*, are in fact positive, but large species are nevertheless vulnerable to change. In addition, we expect closely related species to show similar responses to environmental change, although idiosyncratic responses are predicted to be more likely (Tafani *et al.* 2013).

4.5.1 Experimental evidence of competition

Thirty-three pairwise interspecific interactions were identified within the order Lagomorpha, but the evidence for the majority of these competitive interactions was from opportunistic, isolated field observations inferred from parapatry or species replacement. Only one study to date (Probert & Litvaitis, 1996), provides experimental evidence of competition in lagomorphs: interference competition between *S. floridanus* and the New England cottontail *S. transitionalis*, due to their utilisation of the same habitat and food resources (e.g. Johnston, 1972), has led to the expansion of the former and a decline in abundance of the latter. It is possible that *S. floridanus* is a better competitor than *S. transitionalis* due to inbreeding in transplanted locations which, by increasing the genetic variability of offspring, has functionally enabled occupation of a broad range of habitats (Litvaitis *et al.* 2008) and also because it is approximately 20% larger. The experimental

trial by Probert and Litvaitis (1996), however, showed that *S. floridanus* was dominant in only 42% of trials, suggesting that factors other than physical dominance may explain their colonisation of habitats. *S. floridanus* is likely to be dominant because it uses open habitats (Smith & Litvaitis 2000), can detect predators at greater distances (Smith & Litvaitis, 1999), and has better dispersal capabilities (Probert & Litvaitis, 1996) than *S. transitionalis*.

Interference competition, as recorded by Probert and Litvaitis (1996), is attributable only to a very small proportion of reported pairwise interactions between lagomorph species. This suggests that most species lack aggressive antagonistic behaviour towards other lagomorphs. Most notably, *S. floridanus* exhibits strong evidence for interference competition by commonly displacing other species from shared habitats (Litvaitis *et al.* 2008). Our results suggest that *S. floridanus* occupies a region of average climate stability (~ 0.36), with higher than average mean human population density (267 individuals/km²) and higher than average occurrence within human-converted habitats (44%). Occupation of areas vulnerable to anthropogenic change may lead to heightened aggression in competitive interactions between *S. floridanus* and other lagomorphs, e.g. pygmy rabbits *Brachylagus idahoensis*, brush rabbits *S. bachmani*, forest rabbits *S. brasiliensis*, mountain cottontails *S. nuttallii* and *S. transitionalis*, but further comparative analysis of species' traits may be required to identify the mechanisms behind its uniquely exploitative, competitive interactions.

4.5.2 Inferred competition based on parapatry or species replacement

Competitive interactions are not easily identified in the wild, and even when they are, most competition is inferred from parapatry or species replacement. Due to limited data, we considered two species to be competitively interacting even if there was only one record providing supporting evidence, i.e. either an experimental study or inference from parapatry or species replacement. However, the weaknesses of inferring competition should be noted. Parapatric distributions and species replacement are consistent with intraspecific competition, but evidence is far from conclusive. Huey (1979) states that parapatry is often used as evidence for competition, and parapatric distributions can in fact result from intense interspecific competition, but they may also arise from hybridisation or

from adaptation of species to different habitats that do not overlap geographically. Nevertheless, with scarcely any experimental demonstration of competitive interactions in lagomorphs, information on parapatric distributions and species replacement is all we have at present to review competition within the order.

Hares of the genus *Lepus* are typically allopatric, but in a few notable cases they exhibit parapatry. For example, in Europe there are five *Lepus* species: the Apennine hare *L. corsicanus* and broom hare *L. castroviejoi* have restricted allopatric ranges, whereas the European hare *L. europaeus*, mountain hare *L. timidus* and Iberian hare *L. granatensis* have much wider ranges. Competition between the latter three species is asymmetrical and in most cases the ranges are parapatric (Acevedo *et al.* 2012a). In the contact zone between *L. granatensis* and *L. europaeus*, there is a decrease in abundance of the latter (Gortázar *et al.* 2007), *L. europaeus* competes with *L. corsicanus* (Angelici *et al.* 2008) and there tends to be contraction of *L. timidus'* range, in extent and elevation, in contact zones with *L. europaeus* (Thulin, 2003; Reid, 2011). In most of *L. europaeus'* native range, *L. timidus* 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, *L. europaeus*, which was introduced in the late 19th and early 20th centuries, is found in sympatry with the mountain hare (Flux, 2008). In Ireland, introduced *L. europaeus* and endemic Irish hares *L. t. hibernicus* occupy similar habitats in sympatry (Reid & 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, *L. europaeus* has actively displaced *L. t. hibernicus* within its core invasive range, creating a zone of *L. europaeus* allopatry (Caravaggi *et al.* 2014).

'Extinction by hybridisation' was originally described by Rhymer and Simberloff (1996) as a possible effect of hybridisation between native and introduced species. If there were a large number of hybrid events between female *L. timidus* and male *L. europaeus*, then species-specific litters would be lost in *L. timidus* populations, causing a loss of range and decline in population density (Thulin, 2003). In Sweden, where the two species hybridise in sympatry, the mitochondrial DNA (mtDNA) from *L. timidus* is transferred to *Lepus europaeus*, but this pattern gradually disappears in areas of allopatry (Thulin & Tegelström, 2002). Only one researcher to date (Lind, 1963) has examined competition between *L. timidus* and *L. europaeus*; competitive exclusion of *L. timidus* and significant

differences in food preference and habitat utilisation were found. However, *L. europaeus* and *L. timidus* have often been observed feeding side by side (Hewson, 1990).

Species displacement through hybridisation is not a new phenomenon restricted to secondary contact after anthropogenic introductions of alien species into the ranges of old adversaries; 'ancient hybridisation' is prevalent within the order Lagomorpha such that many species actually share mitochondrial or nuclear haplotypes revealing the 'ghosts of a hybrid past' (Paulo Célio Alves, *pers. comms.* citing Wilson & Bernatchez, 1998). *L. timidus* mtDNA lineages are found throughout Europe within *L. europaeus*, *L. granatensis* and *L. castroviejoi* (Melo-Ferreira *et al.* 2009). Such ancient hybridisation is likely to have occurred during the last glacial maximum when *L. timidus*' range would have extended further south than today. Moreover, *L. europaeus*, *L. granatensis* and *L. corsicanus* are also known to have hybridised in ancient times (Pietri *et al.* 2011). The phenomenon is pervasive, being present also in Asia (Liu *et al.* 2011) and North America. For example, snowshoe hare *L. americanus* mtDNA lineages in the Greater Pacific Northwest exhibit hybrid introgression from black-tailed jackrabbits *L. californicus*, despite the minimal overlap of their current geographic ranges (Cheng *et al.* 2014; Melo-Ferreira *et al.* 2014). For the purposes of this study, ancient hybridisation and introgression will not be considered any further as they do not represent on-going competitive behavioural interactions.

The majority of competitive interactions occurred between hares in the genus *Lepus* and involved a few key species, e.g. *L. europaeus*. Replacement of white-sided jackrabbits *L. callotis* by *L. californicus* and desert cottontails *S. audubonii* has been observed (Best & Henry, 1993); antelope jackrabbits *L. alleni* have been replaced by *L. californicus* in some habitats (Chapman & Flux, 1990); *L. americanus* in Wisconsin, USA were replaced by white-tailed jackrabbits *L. townsendii* (Leopold, 1947); and *L. townsendii* were replaced by *L. californicus* (Flinders & Chapman, 2003). The Abyssinian hare *L. habessinicus* and *L. europaeus* replace the cape hare *L. capensis* in some habitats (Chapman & Flux, 1990; Flux, 2008), but *L. habessinicus* has been replaced by the African savannah hare *L. microtis*, scrub hare *L. saxatilis* and Ethiopian hare *L. fagani* in others (Chapman & Flux, 1990). *L. microtis* is replaced by *L. saxatilis* (Flux, 2008), and the Manchurian hare *L. mandshuricus* and *L. europaeus* are replaced by the Tolai hare *L. tolai* in Russian Asia (Fadeev, 1966; Chapman & Flux, 1990; Smith & Xie, 2008; Sokolov *et al.* 2009). Competition amongst hares is inferred

in many cases because a species is observed occupying the preferred habitat of another species in its absence, but it can also be inferred due to the rare and transient nature of sympatric hare co-occurrence (Flux, 1981). Hare species often exhibit parapatric distributions and only tend to occur, if at all, temporarily in the same habitat (Acevedo *et al.* 2012a). Despite a lack of any experimental demonstration of competitive exclusion in lagomorphs, this may nevertheless be a very powerful determinant of geographical and local ranges (Flux, 1981; Thulin, 2003).

Large areas, globally, were occupied by lagomorphs for which there was no evidence of interaction, suggesting that allopatry or parapatry is the usual situation, and that interspecific contact is globally restricted and occurs only in relatively narrow contact zones. However, our spatial analysis would not reveal that species could occupy the same range but be functionally separated by habitat, e.g. *L. timidus* and *L. europaeus* are separated by elevation within parts of their contact zone (Thulin, 2003). Thus, not all sympatric species will have the opportunity to interact directly and, if they do, interactions may occur in a smaller range than that suggested by our spatial analysis. In addition, population dynamics rather than competition may cause a decline in the abundance of one species, leading to movement of the more abundant species and hence replacement of one species by another in a particular habitat.

Hares and rabbits frequently co-occur, but rarely interact. *L. europaeus* and *Oryctolagus cuniculus* form one of the most commonly studied and observed systems with respect to competition. Before anthropogenic introductions, *L. europaeus* was restricted to central Europe and the Asian steppes, and *O. cuniculus* to the Iberian Peninsula (Flux, 1994), but overlap in the ranges of these two species is now widespread, and coexistence occurs in many introduced populations (Flux, 2008). Allopatry is seen at regional scales due to habitat preferences (e.g. Petrovan *et al.* 2011), and there is widespread belief that the species avoid each other (e.g. Cox, 1976). However, in most areas of their range they graze side by side, showing significant dietary overlap (e.g. Katona *et al.* 2004). Various reports from the early 20th century note physical attacks of rabbits on hares both in captivity and in the wild (Gayot, 1868; Millais, 1906), but more recent observations indicate that aggressive antagonism is rare (e.g. Flux, 2008).

Rabbits from other genera, for example *Bunolagus*, *Poelagus* and *Pronolagus*, coexist with hares without physical aggression, and there appear to be no antagonistic interactions between rabbits and jackrabbits (Orr, 1940; Flux, 2008). However, competition with *L. californicus* may affect the distribution of *S. audubonii* (AMCELA *et al.* 2013) and competition may have occurred in at least some areas between *S. nuttallii* and *L. americanus* (Frey & Malaney, 2006), although more studies are needed to confirm this interaction. Leporids, for example *L. californicus*, *S. floridanus* and *S. audubonii*, may compete with *Brachylagus idahoensis* for burrows (e.g. Pierce *et al.* 2011), *L. capensis* may displace the riverine rabbit *Bunolagus monticularis* in marginal habitat (Duthie, 1989) and competition between introduced *S. floridanus* in Italy and *L. europaeus* and *O. cuniculus* is likely, due to marked differences in habitat selection for feeding and resting in sympatric and allopatric areas (Vidus-Rosin *et al.* 2011; 2012), but has yet to be observed (e.g. Bertolino *et al.* 2013). In addition, aggressive competitive interactions are documented between *S. floridanus*, *S. bachmani* and *S. nuttallii* in North Dakota, USA (Chapman & Verts, 1969; Genoways & Jones, 1972) and between *S. floridanus* and *S. brasiliensis* in expanding savannah and scrub habitats of South America (Chapman & Flux, 1990).

Two species of pika in North America, the American pika *Ochotona princeps* and the collared pika *O. collaris*, show no overlap in range, whereas the ranges of the twenty-three Asian pikas exhibit large degrees of overlap, yet most have no reported interaction in the published literature. The plateau pika *O. curzoniae* excludes the Daurian pika *O. daurica* and the Gansu pika *O. cansus* from open alpine meadows (Chapman & Flux, 1990; Su, 2001; Zhang *et al.* 2001), and Kozlov's pika *O. koslowi* is excluded from the Guldsha valley, Pakistan, by *O. curzoniae* and the Ladak pika *O. Ladacensis* (Buchner, 1894). In sympatric areas, alpine pikas *O. alpina* and northern pikas *O. hyperborea* compete for shelter, and *O. hyperborea* are smaller in sympatry than in allopatry (Chapman & Flux, 1990). Interference competition has been reported between Pallas's pikas *O. pallasi* and steppe pikas *O. pusilla* in peak population years (Sokolov *et al.* 2009). *O. pallasi* is more successful due to its aggressiveness and dispersal ability (Smirnov, 1974).

Two invasive interactions were identified in our literature review: between *L. europaeus* and *L. timidus* in Sweden and Ireland (Thulin, 2003; Reid, 2011), and between *L. europaeus* and *S. brasiliensis* in Argentina (Novillo & Ojeda, 2008). Inclusion of these species into the analysis did not have substantial effects on the overall patterns observed; however, we did

find that these invasive interactions occupied regions with higher than average human population density and human-converted habitats, and regions which were on average more climatically unstable. Other researchers have found increased occurrence of invasive species in areas of high human population density (e.g. McKinney, 2001), and our finding indicates that the interactions between these lagomorph species pairs may be heavily influenced by future human disturbance as well as by climatic changes (e.g. Schmidt *et al.* 2012). Invasive interactions between *S. florianus* and native Italian lagomorphs are also possible; however at present there is no available IUCN polygon for the invasive range and competition is yet to be observed (e.g. Bertolino *et al.* 2013).

Our results have implications for predicting lagomorph responses to global change, and suggest that capturing, parameterising and incorporating interspecific interactions into analyses may be more important than suggested by the literature, for example, when applying species distribution modelling (Acevedo *et al.* 2012a). Future behavioural observation studies should focus on areas of sympatry, particularly those areas in which *Lepus* species occur in a narrow contact zone or in species-rich regions (most notably, the hotspots in southern Russia on the border of Mongolia and north western USA), to increase our knowledge of competitive interactions in the order Lagomorpha. The combination of bibliometric analyses and biological data used in this study allowed us to identify traits associated with competitively interacting species and highlight the potential impacts of future environmental change. This approach is widely applicable, and with relatively straightforward methodologies, can provide significant insights into interactions between species.

CHAPTER 5

Environmental and interspecific drivers of species distribution patterns

A manuscript based on this chapter has been submitted as:

Leach, K., Lennon, J., Montgomery, W.I. & Reid, N. (*under review*) Environmental and interspecific drivers of species distribution patterns: potential impacts of future climate change. *Global Ecology & Biogeography*.

5.1 Abstract

To date, the majority of Species Distribution Models (SDMs) use only abiotic variables to predict species distributions. Biotic interactions can have large effects on species distributions yet their role in shaping species ranges is seldom explored. Improved SDMs, which account for biotic variables, are needed to fully understand species distributions. Here, we aim to disaggregate the environmental and interspecific interaction effects determining the ranges of European lagomorph species and explore the potential impacts of future climate change. We fit hierarchical spatial models using Integrated Nested Laplace Approximation (INLA) for lagomorph species throughout Europe. Environmental covariates are included using regression splines. Species distributions are used as both response variables and explanatory covariates. We account for residual spatial autocorrelation using a conditional autoregressive (CAR) model. Model outputs are used to estimate the proportion of the probability of presence explained by either interspecific interactions or environmental effects. INLA models containing both abiotic and biotic factors had substantially better predictive ability, measured using the Watanabe-Akaike information criterion (WAIC), than models containing only abiotic factors, for all but one lagomorph. In models containing both abiotic and biotic factors, environmental and interspecific effects appeared equally important as determinants of lagomorph ranges, but the influences of environmental and interspecific interactions were spatially heterogeneous. Regions of widespread lagomorph distributions influenced strongly by environmental variables were more robust to future climatic change than areas influenced strongly by interspecific interactions. SDMs that do not explicitly include biotic factors are potentially misleading and omit a very important source of variation. Inclusion of biotic factors in the projection of SDMs under future climate scenarios is challenging, but necessary; without this approach it will not be possible to advance the reliability of predicting future species distribution patterns.

5.2 Introduction

The factors shaping species spatial distributions are crucial for our understanding of patterns of biodiversity, and, hence, commonly studied. Species distributions are constrained by abiotic conditions, for example, suitable climate, and biotic conditions, for example, competitive interspecific interactions, as well as movement behaviour, such as dispersal or colonisation (Soberon & Nakamura, 2009). Most Species Distribution Models (SDMs) use only climatic variables to predict species distributions and often do not offer credible statistical tests of the relative influence of environmental (climatic) factors. Typically, they often ignore other key determinants of species ranges, most pertinently, biotic interactions (Beale *et al.*, 2014). Studies using SDMs are beginning to consider biotic interactions by including the occurrence of other species' as additional covariates (e.g. Pellissier *et al.*, 2010) and this has been central in improving performance (Araujo & Luoto, 2007; Mod *et al.*, 2015). 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 better SDM techniques to disaggregate the effects of the abiotic environment and biotic interactions.

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). MCMC algorithms give exact results and are flexible for a wide range of models, but have very low computational speed (Beguin *et al.*, 2012). An alternative for fitting such Bayesian hierarchical spatial models uses Integrated Nested Laplace Approximations (INLA; Rue *et al.* 2009) which does not require advanced programming skills, yields comparable results to MCMC (Beguin *et al.*, 2012) and is rapid. INLA substitutes accurate, deterministic approximations to posterior marginal distributions in place of long MCMC simulations. In addition, conditional autoregressive (CAR) models, which model spatial associations within the data, are difficult to implement for complex hierarchical models using MCMC techniques due to a whole suite of problems related to convergence and computation time, but they can be fitted with relative ease using INLA (Beguin *et al.*, 2012). SDM studies are especially sensitive to spatial autocorrelation, which arises when nearby locations are not independent of each other (Legendre, 1993), and if spatial autocorrelation is not considered it can result in misleading and

biased models (Lennon, 2000; Beale *et al.*, 2010). However, INLA is not yet a completely adequate replacement for MCMC because some models, for example observation effort models (Illian, 2013), cannot be fitted with INLA but can with MCMC.

Extending the use of hierarchical spatial models to project species distributions under future climate scenarios is problematic as species interactions can be unstable in space or time (Wisz *et al.*, 2012). 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 direction of these interactions is likely to change (Beale *et al.*, 2014). Climatic changes may impact the distribution of interacting species which could, 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). Due to the difficulties with quantitatively modelling the multiple impacts of future change on interacting species, 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 interspecific 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 and disaggregate the influence of environmental and interspecific interaction effects on the distributions of lagomorph species throughout Europe. We test the difference in predictive ability between INLA models containing only environmental factors and models containing environmental and biotic factors. European lagomorph data is sufficiently reliable and of higher quality than global datasets, and represents an area and group of species in which evidence of competition is strongest, hence forming a useful test dataset for this methodology. We hypothesise that interspecific interactions should have strong effects on species distributions, especially for lagomorphs in Europe. Using a number of explanatory factors, including climatic variables, co-occurring species, vegetation, topography and human influence, we aim to produce more reliable predictions of species distributions as well as estimating the areas in which both environmental and interspecific interactions strongly determine species' ranges. We then use post-hoc tests

with ecoregional climatic stability data and projected future climatic variables to explore the impacts that future climate change may have in areas of predicted presence influenced predominately by either environmental or biotic factors.

5.3 Methods

5.3.1 Model structure

Hierarchical spatial models were fitted using INLA and the ‘R-INLA’ package (<http://www.r-inla.org/download>) in R version 3.1.1 following Beguin *et al.* (2012). Species range and environmental data are described in sections 2.2 and 2.3. Model predictive ability is typically assessed using metrics such as Area Under the Curve (AUC) or alternatives such as the True Skill Statistic (TSS) or Kappa values. However, these metrics have been criticised when using presence/pseudo-absence data and have limitations with respect to sensitivity, specificity, omission and commission errors (Allouche *et al.*, 2006). These performance metrics require arbitrary designation of training and test data, and comparison of values between models for hypothesis testing is difficult. In Bayesian statistics, the most common method of model evaluation is the Deviance Information Criterion (DIC), however, this metric penalises model complexity and encourages overfitting (Plummer, 2008). Therefore, we tested model predictive ability using the Watanabe-Akaike information criterion (WAIC) for models containing only environmental factors and models containing both environmental *and* biotic factors. WAIC is a generalisation of AIC and includes a leave-one-out cross validation prediction component which directly tests the predictive ability of models, and at the same time allows model comparative evaluation (like ordinary AIC) by comparing the WAIC values between models. WAIC has recently been made available in R-INLA for model comparison and is recommended because it is a more fully Bayesian approach for out-of-sample prediction which adjusts for overfitting (Watanabe, 2010; Gelman *et al.*, 2014).

Relationships between the response variable and individual covariates were restricted to functional forms with simple shapes (Austin, 2002) and the flexibility of these forms was part of the modelling approach. Each covariate was fitted as a smooth term represented by a regression spline to describe biologically realistic unimodal

response terms. Greater or lesser flexibility can be permitted by altering the number of knots in the spline terms. We used two knots and then recombined regression splines following code in Beale *et al.* (2014) to obtain fitted values for environmental variables. Biotic covariates included only those species known to co-occur with the target (modelled) species i.e. response variable. 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. Values of the shape parameters were defined so that the ratio of data points to the number of effective parameters was >20 following Beguin *et al.* (2012).

5.3.2 Analysis

All analyses were carried out in R version 3.1.1. The full, environmental *and* biotic model was defined as:

$$P_{\text{PRES}} i = \text{Intercept} + (\text{env}_1 + \dots + \text{env}_x) + (\text{species}_1 + \dots + \text{species}_x) + \text{SE} \quad (\text{Equation 1})$$

where $P_{\text{PRES}} i$ was the probability of presence in cell i , env_x was the fitted value for the environmental variable following recombination of regression splines, species_x was the probability of presence of a co-occurring species and SE was the estimated spatially explicit error term. Contributions of each term to the model were calculated as follows: the contribution of the spatially explicit error term in cell i , $\text{SE}_{\text{COMP}i} = \text{inv.logit}(\text{SE})$, where inv.logit represents an inverse logit function, the contribution of the environmental component, $\text{Env}_{\text{COMP}i} = \text{inv.logit}(\text{env}_1 + \dots + \text{env}_x)$ and the contribution of co-occurring species or interspecific effects, $\text{Int}_{\text{COMP}i} = \text{inv.logit}(\text{species}_1 + \dots + \text{species}_x)$. Adapting equations from Beale *et al.* (2014), the proportion of the probability of presence explained by environmental effects was calculated by:

$$\text{Prop}_{\text{ENV}}^i = \frac{|\text{P}_{\text{PRES}} i - \text{SE}_{\text{COMP}i} - \text{Int}_{\text{COMP}i}|}{|\text{P}_{\text{PRES}} i - \text{SE}_{\text{COMP}i} - \text{Env}_{\text{COMP}i}| + |\text{P}_{\text{PRES}} i - \text{SE}_{\text{COMP}i} - \text{Int}_{\text{COMP}i}| + |\text{P}_{\text{PRES}} i - \text{Int}_{\text{COMP}i} - \text{Env}_{\text{COMP}i}|} \quad (\text{Equation 2}),$$

And the proportion of the probability of presence explained by interspecific interactions:

$$\text{Prop}_{\text{INT}}^i = \frac{|\text{P}_{\text{PRES}i}\text{-SE}_{\text{COMP}i}\text{-Env}_{\text{COMP}i}|}{|\text{P}_{\text{PRES}i}\text{-SE}_{\text{COMP}i}\text{-Int}_{\text{COMP}i}| + |\text{P}_{\text{PRES}i}\text{-SE}_{\text{COMP}i}\text{-Env}_{\text{COMP}i}| + |\text{P}_{\text{PRES}i}\text{-Int}_{\text{COMP}i}\text{-Env}_{\text{COMP}i}|}$$

(Equation 3).

Marginal effect plots for environmental covariates were produced using original variable values and predicted probability of presence values $P_{\text{PRES}i}$ from INLA models. Significant covariates are those >0.5 and for which the 95% credible intervals did not cross 0.5. Marginal effect plots for interspecific interactions were produced as boxplots due to the binary input data. Spatially-corrected tests were used to identify differences in boxplots in order to understand the influence of co-occurring species' (Osorio & Vallejos, 2014).

Ecoregional climatic stability data was provided by Takuya Iwamura (Iwamura *et al.* 2013) and defined as "the proportion of an ecoregion which was predicted to be climatically stable under [future] climate change." The climatic stability index was calculated by estimating the overlap between present and future 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 overlap and high robustness to climate change (Watson *et al.* 2013). The difference in climatic stability between areas strongly influenced by *PropEnv* compared to areas strongly influenced by *PropInt* was tested for each species. Wilcoxon rank sum tests were used for non-normal data which was not spatially autocorrelated, whereas if the data was spatially autocorrelated then Wilcoxon rank sum tests were performed on the residuals of a spatial autoregressive model. Cells were classed as highly influential if they had a value in the top 10th percentile. The environmental covariate with the highest average fitted value, whose credible intervals do not cross 0.5, was identified as most important for that particular species. By calculating the difference between the current (~1950-2000) and 2070 values (also downloaded from WorldClim) for these important covariates it is possible to identify areas potentially susceptible to future climatic changes. The difference in climatic changes between areas strongly influenced by *PropEnv* compared to areas strongly influenced by *PropInt* was tested as above for each species.

5.4 Results

The predictive ability of models for two highly range-restricted species, *L. castroviejoi* and *L. corsicanus*, was extremely poor, therefore, these species were not considered further. The evaluation of predictive ability for the remaining four widespread species, using WAIC, indicated that INLA models comprising both abiotic *and* biotic factors were substantially better for all species except one, *Lepus timidus* (Table 5.1). The change in WAIC between models was very large and showed that the full and abiotic only models differed with a high degree of confidence (Table 5.1).

Table 5.1. Predictive ability of INLA models with environmental and biotic factors compared to models with only environmental variables. Watanabe-Akaike information criterion (WAIC) was used to assess predictive ability, where a lower value indicates better predictive power and a greater Δ WAIC suggests greater differences between the two models.

Species	Watanabe-Akaike information criteria (WAIC) values		
	Abiotic + Biotic	Abiotic only	Δ WAIC
<i>Lepus europaeus</i>	2778.80	3372.87	594.07
<i>Lepus granatensis</i>	431.32	581.86	150.54
<i>Lepus timidus</i>	3095.58	2757.06	-338.52
<i>Oryctolagus cuniculus</i>	1891.10	2210.25	319.15
Overall mean	2049.20	2230.51	181.31

On average the range of *O. cuniculus* was explained to a greater extent by interspecific interactions than environmental variables. For the remaining species, the average influences of environmental and interspecific constraints were largely comparable (Fig. 5.1). However, the proportion of species' presence explained by environmental and interspecific variables varied over space, shown by mapping values spatially and by the distribution of values in density plots; for example, the range of *L. timidus* was influenced to a greater extent by interspecific interactions and to a lesser extent by environmental factors at its southern range edge (Fig. 5.1), whilst the range of *O. cuniculus* was influenced more by interspecific interactions in the western part of its distribution than environmental variables (Fig. 5.1).

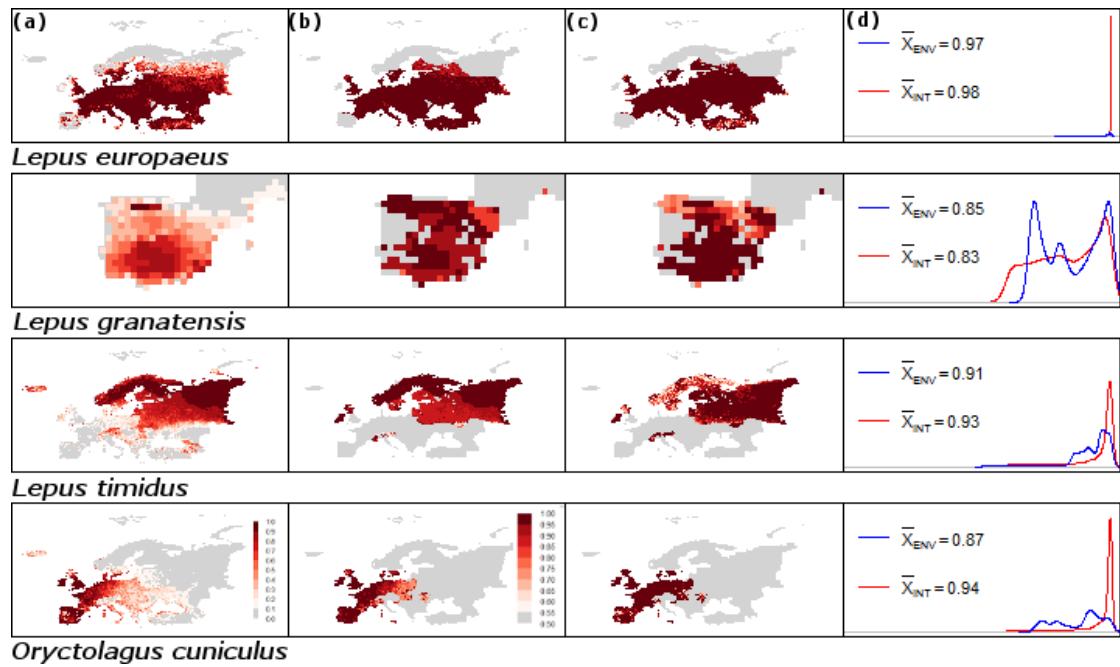


Fig. 5.1. (a) Predicted probability of species presence and proportion of predicted probability of presence explained by (b) environmental effects or (c) interspecific interactions mapped spatially. The distributions of values for these maps are also represented as density plots: (d) \bar{X}_{ENV} represents the average proportion explained by environmental factors, whereas \bar{X}_{INT} represents the average proportion explained by interspecific interactions. Parts (b) and (c) are clipped to the IUCN geographic range polygons for presentational purposes only.

Our models indicate mutualistic as well as competitive interactions within European lagomorph species. *L. granatensis* had significantly higher probability of presence in the presence of *O. cuniculus* ($F_{(26.6)} = 8.9$, $p=0.006$; spatially-corrected t-test (Osorio & Vallejos, 2014); Fig. 5.2), and *O. cuniculus* had higher predicted probabilities of presence in the presence of *L. granatensis* ($F_{(31.4)} = 7.4$, $p=0.011$), but also in the absence of *L. timidus* ($F_{(13.2)} = 5.5$, $p=0.035$). There was a higher probability of presence of *L. europaeus* in the absence of *L. granatensis* and *L. timidus* ($F_{(102.3)} = 5.3$, $p=0.023$; $F_{(43.9)} = 9.6$, $p=0.003$ respectively).

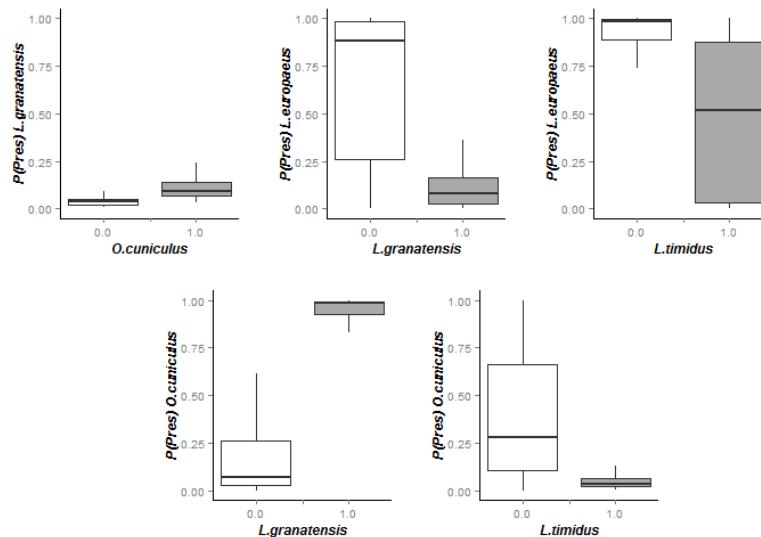


Fig. 5.2. Influence of co-occurring species' on predicted probability of presence. Only significant results, following spatially corrected t-tests, are shown in this figure.

The influences of environmental covariates on probabilities of presence are described in Table 5.2 and significant covariates are plotted in Fig. 5.3. *L. europaeus* was positively associated with NDVI (high productivity landscapes), in areas of approximately 100mm maximum precipitation, with high water balance levels and little precipitation seasonality. *L. granatensis* prefers high maximum temperatures, above 20°C. *L. timidus* was most likely to be associated with areas of approximately 40mm difference in precipitation seasonality and low temperature seasonality (most likely due to winter snowfall in northern or highland regions), 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, presumably in Iberia and the Mediterranean, and high productivity landscapes i.e. farmland, in areas with approximately 150mm maximum precipitation and little temperature seasonality i.e. consistently mild climates.

Table 5.2. Parameter estimates for environmental effects on the predicted probability of presence of European lagomorph species plus credible intervals. Environmental covariates of highest importance for each species are shown in bold.

Effect		<i>L. europaeus</i>	<i>L. granatensis</i>	<i>L. timidus</i>	<i>O. cuniculus</i>
Human Influence	Median	<0.001	0.067	0.844	0.117
	97.5%	0.071	0.913	0.876	0.152
	2.5%	0.524	0.501	0.501	0.503
Hilliness	Median	0.502	0.496	0.513	0.509
	97.5%	0.508	0.500	0.516	0.512
	2.5%	0.497	0.501	0.503	0.501
NDVI	Median	0.648	0.495	0.474	0.588
	97.5%	0.669	0.515	0.490	0.603
	2.5%	0.500	0.502	0.517	0.498
Max. Prec.	Median	0.943	0.944	0.055	0.941
	97.5%	0.969	0.999	0.060	0.951
	2.5%	0.502	0.501	0.508	0.502
Max. Temp.	Median	0.704	0.787	<0.001	<0.001
	97.5%	1.000	1.000	<0.001	<0.001
	2.5%	0.525	0.502	0.572	0.522
Prec. Season.	Median	0.970	<0.001	0.932	0.989
	97.5%	0.999	0.012	0.958	0.999
	2.5%	0.494	0.501	0.500	0.500
Temp. Season.	Median	0.000	0.485	0.524	0.503
	97.5%	0.328	1.000	0.533	0.516
	2.5%	0.520	0.501	0.492	0.497
Positive Water Balance	Median	0.839	0.364	0.019	0.133
97.5%	0.985	0.722	0.090	0.468	
2.5%	0.499	0.500	0.489	0.497	

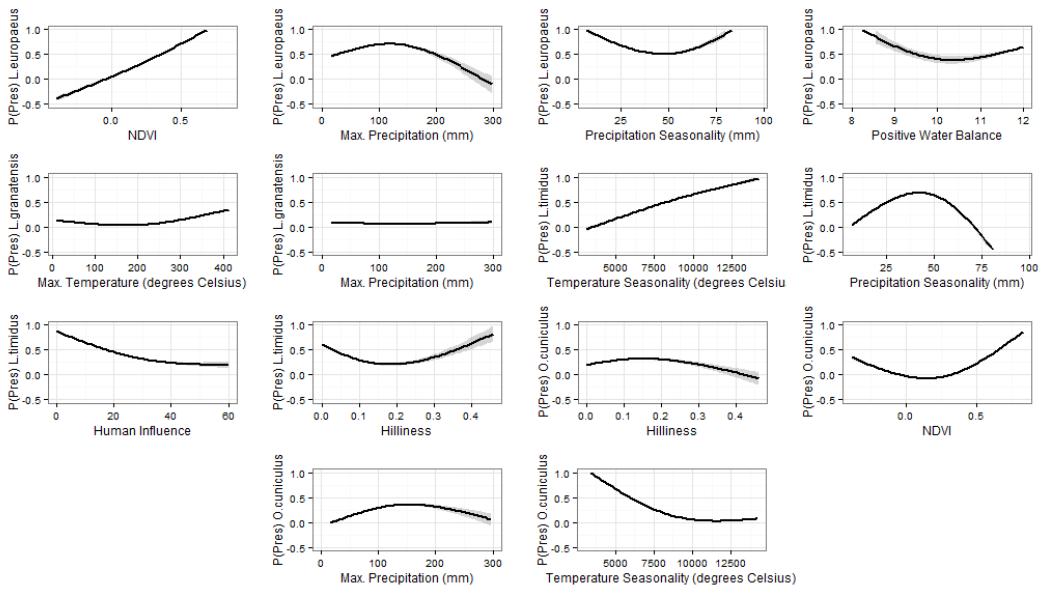


Fig. 5.3. Marginal effect plots for significant relationships between environmental covariates and predicted probabilities of species presence. Grey shaded regions show 95% credible intervals and solid lines show the mean estimate.

Predicted climatic stability was significantly higher (or ecoregions were more robust to future climatic changes) in the top 10th percentile of regions influenced most by environmental effects compared to interspecific interactions for *O. cuniculus* ($W=196203, p<0.001$) and *L. europaeus* ($W=50235, p=0.02$), but were not significantly different for *L. timidus* ($W=7648, p=0.403$; Fig. 5.4). Statistical significance could not be tested for *L. granatensis* because there was no overlap in regions highly influenced by interspecific interactions or environmental effects. The mean climatic stability index value across the ranges of all European lagomorphs ($\bar{x} = 0.34 \pm 0.08$ (SD)) was lower than the global average ($\bar{x} = 0.46 \pm 0.14$ (SD)).

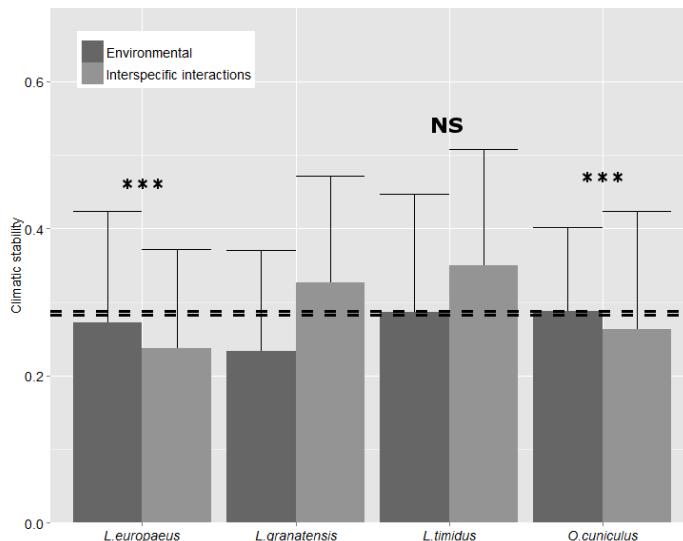


Fig. 5.4. Climatic stability in the top 10th percentile of regions influenced by environmental effects (dark grey) or interspecific interactions (light grey) ± standard deviations. Results from spatially corrected tests showing differences between environmental and interspecific interaction effects are indicated above each set of bars. The average climatic stability across Europe is shown by the dashed 95% confidence intervals.

Maximum annual precipitation was identified as the single most influential environmental variable in models of *L. granatensis* and *L. europaeus* whilst precipitation seasonality was most important for *L. timidus* and *O. cuniculus* (see Table 5.2). The difference (Δ) between current (~1950-2000) and future (2070) values of projected maximum annual precipitation averaged across all cells in Europe is 7.815 mm, whereas for precipitation seasonality it is 0.537 mm. Projected change in precipitation seasonality was significantly higher in the top 10th percentile of regions influenced most by interspecific interactions compared to environmental effects for *L. timidus* ($W=213379, p<0.001$), and higher in regions influenced most by environmental effects for *O. cuniculus* ($W=157460, p=0.002$; Fig. 5.5a). Projected change in maximum precipitation was not significantly different between regions influenced most by interspecific interactions and regions strongly influenced by environmental effects for *L. europaeus* ($W=62374, p=0.178$; Fig. 5.5b). Again, statistical significance could not be tested for *L. granatensis* because there was no overlap in regions highly influenced by interspecific interactions or environmental effects.

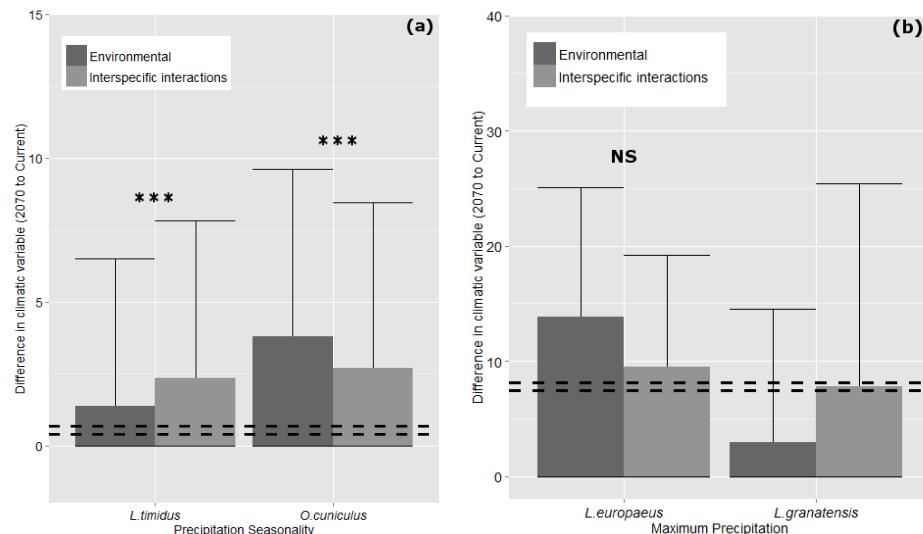


Fig. 5.5. Difference between current (~1950-2000) and future (2070) values of most important climatic variables, (a) precipitation seasonality and (b) maximum precipitation, in the top 10th percentile of regions influenced by environmental effects (dark grey) or interspecific interactions (light grey) ± standard deviations. Results from spatially corrected tests showing differences between environmental and interspecific interaction effects are indicated above each set of bars. The average difference in each climatic variable across Europe is shown by the dashed 95% confidence intervals.

5.5 Discussion

Predictive ability is substantially better in models built using environmental *and* biotic factors, than in models built solely with environmental variables, for all but one lagomorph, suggesting evidence for interspecific drivers of species distribution patterns. Environmental factors alone are likely to build a better model for the mountain hare, *L. timidus*, due to its distribution being primarily driven by elevation and cooler temperatures. For the majority of lagomorph species in Europe, environmental effects and interspecific interactions appeared *equally* important in determining their range. Our results suggest significant directional associations (consistent with field-based observations reported in the literature) between *L. granatensis* and *L. europaeus* (Gortázar *et al.*, 2007), *L. europaeus* and *L. timidus* (Thulin, 2003; Reid, 2011; Caravaggi *et al.* 2014) and *O. cuniculus* and *L. timidus* (though this latter relationship has not been empirically documented, their ranges show significant overlap and biotic interactions are both possible and probable, particularly at the southerly range edge of *L. timidus*). In addition, there appears to be a mutualistic interaction between *O. cuniculus* and *L. granatensis*, which to the best of our knowledge has not yet been reported. However, these correlative analyses only identify associations which cannot be used to attribute causation; underlying mechanisms, for example, the strength and direction of interspecific competition, can only be established using field observations and/or hypothesis testing experiments (Beale *et al.*, 2014).

The influence of interspecific effects was spatially heterogeneous. For example, interspecific interactions 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 disproportionately influenced by interspecific interactions presumably where it overlaps with other lagomorphs.

Environmental covariates identified as important to the predicted presence of European lagomorphs were largely supported in the literature. *O. cuniculus* prefers flat landscapes (Fa *et al.*, 1999; Tapia *et al.*, 2010), and *L. europaeus* and *O. cuniculus* occupy 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 precipitation (Rödel & Dekker, 2012), whereas *L. granatensis* is only found in areas of relatively high temperatures (Alves & Rocha, 2003). *L. timidus* occupies regions with high winter snowfall (Angerbjorn & Flux, 1995), and, therefore, tolerates large seasonal variations in precipitation and temperature. *L. timidus* is known to occupy high elevations, especially in the Alps, and inhabits areas of low human influence due to its very northern range (Thulin, 2003).

Projecting species distributions under future climate scenarios is inherently challenging, especially with the inclusion of biotic variables which may introduce the potential for multicollinearity (Kissling *et al.*, 2012). Associating proxies for climate change with the results of spatial hierarchical models can provide insight into the potential impacts of future change (e.g. Watson *et al.*, 2013). We show that regions in which species presence was strongly influenced by environmental effects were significantly more robust to future climatic changes, i.e. more climatically stable, than areas highly influenced by interspecific interactions. Regions highly influenced by interspecific interactions are less climatically stable and, therefore, more susceptible to future change. The effects on range-restricted species are still unknown, but we expect them to be particularly sensitive to projected changes due to the restricted climatic envelopes that they occupy. Furthermore, mean climatic stability values within the ranges of European lagomorphs were lower than the global mean suggesting that these species may be particularly vulnerable to global change which is likely to have greater (and earlier) effects on range-restricted species, however it could suggest that these species are adapted for survival in areas of fairly low climatic stability. Our analyses also suggest that regions of *L. timidus*' range influenced most by interspecific interactions are likely to undergo relatively more change in precipitation seasonality by 2070, whereas for *O. cuniculus* there will be more change in precipitation seasonality in parts of its range influenced strongly by environmental effects. Despite being a widespread species capable of proliferating in human-modified ecosystems (i.e. agriculturally intense farmlands), and thus expected to be fairly robust to future change, *O. cuniculus*, which prefers drier, less seasonal regions (Rödel & Dekker, 2012) may be more vulnerable to future changes than previously anticipated. In addition, the interaction between *L. timidus* and *L. europaeus* may be particularly susceptible to future climatic

changes if areas influenced by interspecific interactions are likely to undergo large changes in precipitation seasonality.

Although our species-specific results are consistent with environmental and interspecific effects reported in the literature, given adequate point occurrences with reliable data on observer effort, models could easily be improved (see Royle *et al.*, 2007; Beale *et al.*, 2014). 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 shaping species distributions (Kissling *et al.*, 2012).

SDMs that do 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. Therefore, 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 biased and unrealistic results (except in those cases where the effect of biotic interactions is small, which we suspect is unlikely for the majority of species). Species distributions largely defined by biotic interactions cannot be extrapolated without simultaneously extrapolating the distribution of all potentially interacting species, including top-down and bottom-up processes. Even if the statistical challenges of creating such complex models are overcome, they are unlikely to account for changes in the strength and direction of biotic interactions in the future as species range determinants are likely to have 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 autocorrelation whilst minimising computational power, is needed.

CHAPTER 6

Importance of scale in Joint Species Distribution Models

A manuscript based on this chapter has been submitted as:

Leach, K., Montgomery, W.I. & Reid, N. (*under review*) Splitting hares over the importance of scale in Joint Species Distribution Models for European lagomorphs: trade-offs between resolution, accuracy and precision. *Ecography*.

6.1 Abstract

Spatial scale is a major concern inherent in Species Distribution Models (SDM). 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. SDMs rarely incorporate biotic interactions even though they are known to have great impacts on biogeographical patterns. Joint SDMs are an important tool for exploring distributions of multiple coexisting species; however, scale may have a major influence on predictions. We produce Joint SDMs for all European lagomorph species at 50km², 25km² and 10km² grid cell resolutions to test the effect of scale on results. Model outputs are used to calculate residual and environmental correlation coefficients which can be used to explain why species may or may not co-occur, suggesting potential biotic interactions. Joint SDMs can produce very precise estimates of residual and environmental correlations on a continental and fine scale resolution, but require a considerable amount of time and processing power to run on a standard, high performance, desktop computer and produce similar results, in terms of strength and direction, to models run at coarser resolutions. The influence of scale on co-occurrence patterns was considerable: at finer resolutions some species show more overlap, whereas others displayed less. Pairwise species environmental correlation coefficients, however, were consistent among most European lagomorph species except those involving *Lepus timidus*. The majority of pairwise residual correlation coefficients were negative, indicating species co-occur less than expected given their similarity in environmental responses and suggesting the possibility of biotic interactions. Accurate and precise inference of biotic interactions may only be possible at finer resolutions, but collection of finer resolution mammal and bird atlas data across Europe, for example, may not be worth the 25 fold increase in effort given that coarser data yields similar results.

6.2 Introduction

Scale is very important in all aspects of ecology. Environmental and distributional data may be characterised by their extent referring to the geographical area covered (for example, continental or national), or by their resolution (or grain) which refers to the size of the grid cells in which data are sampled, such as 1km² (Wiens, 1989; Nystrom Sandman *et al.*, 2013; Wisz *et al.*, 2013). Extent and resolution may be linked, although a greater extent does not always lead to coarser resolution, an increase in extent is likely to be associated with a decrease in resolution (Pearson & Dawson, 2003).

Spatial scale, in terms of resolution, is a major concern when using Species Distribution Models (SDMs) as large-scale environmental data may be too coarse to capture the effects of climatic variation, for example, at smaller scales, especially in areas with large topographical variation (Dobrowski *et al.*, 2009). Using coarse resolution data may result in poor predictive power of models on a more local scale. On the other hand, upscaling models based on data from a limited area, for broader interpretation is also likely to be problematic (Osborne & Suarez-Seoane, 2002), and conducting studies at different spatial scales can lead to very diverse results (Wiens, 1989; Hamer & Hill, 2000). For example, change in biodiversity may be different in strength and direction using data collected on different scales (Keil *et al.*, 2011) due to differential impact 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 are shown to provide very different estimates of climate change impacts compared to their coarse-scale equivalents (Franklin *et al.*, 2013). SDMs are often used without regard for the effect of scale (Elith & Leathwick, 2009) even though differences between scales are frequently acknowledged. Bradter *et al.* (2013) advocate studies identifying the appropriate spatial scale of predictors in order to produce more accurate predictions of species distributions. However, how this is done most likely will vary depending on the species and environmental variables in question.

Macroclimate is suggested to drive distribution patterns at continental and global scales, whereas biotic interactions may control distributions at community and landscape scales, with human impacts explaining ranges at intermediate scales

(Whittaker, 1975; Pearson & Dawson, 2003; Thuiller *et al.*, 2003). However, there is growing evidence for the effect of biotic interactions in shaping species distributions on a global extent (Jablonski, 2008; Wiens, 2011; Wisz *et al.*, 2013). Historically, distributional studies have focused on interspecific competition (MacArthur, 1972; Amarasekare, 2003), but it is now recognised that facilitation (mutualism), predation, parasitism and disease may also drive species distribution patterns (Araujo & 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).

Integrating biotic interactions into species distribution modelling is of great importance in improving the accuracy of predictions (Kissling *et al.*, 2012). A range of tools are currently available, for example, integrating pairwise dependencies: SDM studies including the occurrence of other species' as additional covariates (e.g. Pellissier *et al.*, 2010) have led to improvements in the performance of models (Araujo & Luoto, 2007; Mod *et al.*, 2015), but these only model unidirectional interactions (Kissling *et al.*, 2012). Surrogates for biotic-interaction gradients are also useful; for example, habitat productivity, which is known to be a basis of competition in plants (Maestre *et al.*, 2010), or species richness patterns. SDMs may be hybridised with dynamic models, such as BIOMOVE (Midgley *et al.*, 2010), but these require *a priori* ecological knowledge and can only be applied to one interacting species' pair at a time (Wisz *et al.*, 2013).

A more recent, substantial step forward has been made with Joint SDMs which simultaneously estimate the ranges of multiple coexisting species producing mixtures of possible species assemblages (Pollock *et al.*, 2014; Harris, 2014). Pollock *et al.* (2014) use a hierarchical, multivariate, probit regression model to include multiple species into a single SDM. Interactions between species will cause un-modelled (i.e. not accounted 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 (Pollock *et al.*, 2014). Joint SDMs are often run using Markov Chain Monte Carlo (MCMC) simulations which give exact results and offer a flexible framework for a wide range of models (Beale *et al.*, 2014; Pollock *et al.*, 2014). However, this approach has a number of

problems regarding convergence, processing time and implementation (Beguin *et al.*, 2012).

Here, we test the effect of scale on the results of Joint SDMs using data at 50km², 25km² and 10km² grid cell resolutions and European lagomorphs as a test dataset. We hypothesised greater confidence in residual correlation coefficients (i.e. evidence of biotic interactions) when using data at finer resolutions. We also expected lengthier processing times than for coarser data using a high performance, desktop computer. Therefore, we describe a trade-off between precision of results, sampling effort and processing time when using Joint SDMs.

6.3 Methods

6.3.1 Model structure

We used the code provided in Pollock *et al.* (2014) to produce Joint SDMs at three hierarchical resolutions: 50km², 25km² and 10km². Species range and environmental data is described in sections 2.2 and 2.3. Species co-occurrence is modelled using multivariate probit regression parameterised indirectly with a latent variable formulation. The response is species occurrence (number of sites x number of species), and this is predicted by a data matrix, number of sites x number of environmental variables. Further details and description of Joint SDMs can be found in Pollock *et al.* (2014). Models were fitted using the MCMC Bayesian modelling software JAGS version 3.4.0 run through R version 3.1.1 via the R2jags package version 0.5-6 (Su & Yajima, 2015). For all three resolutions, we ran two chains for 850,000 iterations with the first 150,000 discarded as burn-in and the remaining samples thinned by a factor of 1,000. We used the same priors for all parameters as Pollock *et al.* (2014) and considered models to be converged once all elements of the parameter and correlation matrices had potential scale reduction factor values close to one. This convergence diagnostic value suggests that each of the sets of simulated observations is close to the target distribution (Brooks & Gelman, 1998).

Residual and environmental correlations were decomposed from model outputs and can be used to explain why species may or may not co-occur. Outputs can be roughly

divided into four categories (Fig. 6.1): positive environmental correlation suggests shared environmental responses, whereas strong negative/ positive residual correlation may suggest evidence for biotic interactions or perhaps indicate that not all relevant abiotic variables were incorporated in the model to explain the environmental niche space of all species.

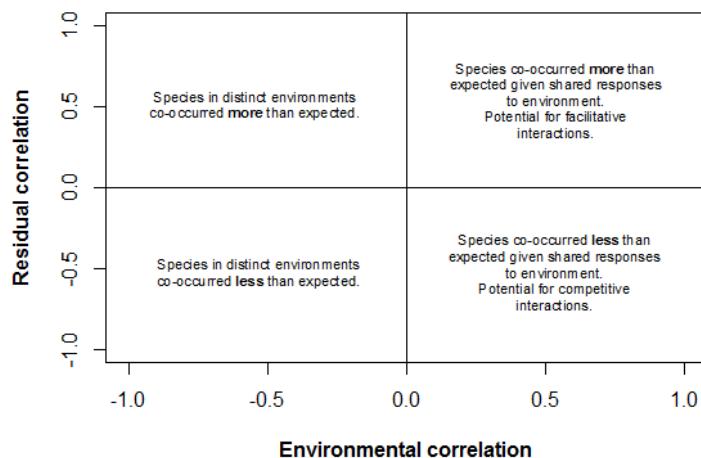


Fig. 6.1. Diagrammatic interpretation of negative and positive residual and environmental correlations. These interpretations may become less reliable with weaker correlation coefficients.

6.4 Results

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 50km² model took ~3 days, 25km² took ~3 months and 10km² took ~6 months. Nevertheless, the directions of environmental and residual correlation coefficients were similar at all spatial scales examined (Fig. 6.2). The majority of species pairs, i.e. seven of nine (78%), shared environmental responses exhibiting positive pairwise environmental correlation coefficients. *Lepus timidus* was strikingly different from all other species as its northerly distribution was allopatric with many of the more southerly Mediterranean species (thus they did not exhibit any pairwise relationship), whilst its environmental correlation coefficients were negatively related with *L. europaeus* and *Oryctolagus cuniculus*. The strength and direction of residual correlation coefficients was similar

across scales, but the majority of species pairs had negative residual correlations, indicating that species co-occurred less than expected given the similarity in their environmental responses.

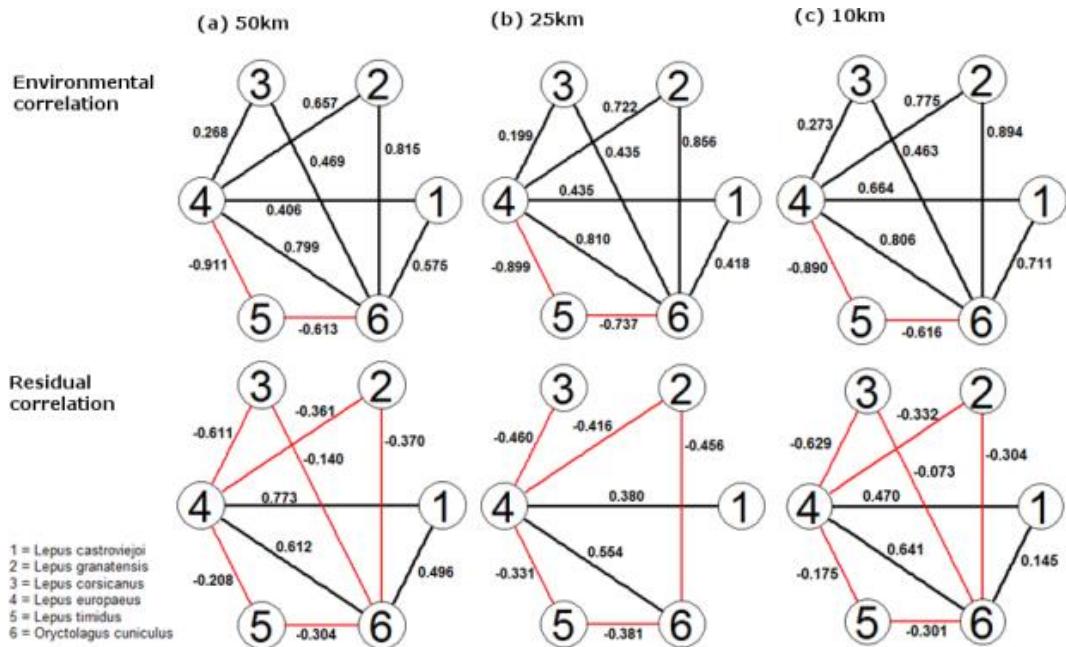


Fig. 6.2. Network diagrams representing modelled environmental correlation and residual correlation between European lagomorph species at three different scales: 50km² (a), 25km² (b) and 10km² (c) grid cells. Black edges are positive correlations between species and red edges are negative correlations. Each edge is labelled with its correlation coefficient. Edge thickness represents correlation strength. Only correlations in which the credible intervals did not cross zero are shown.

Although the strength of environmental and residual correlations remained similar across different scales, at finer resolutions i.e. 10km² grid cells, credible intervals were substantially narrower (by 75.8% on average when compared to those associated with the 50km² resolution) and, therefore, provided greater precision (Fig. 6.3). A variety of pairwise responses were evident: for example, *L. timidus* and *L. europaeus* occupy very different environments and are less likely to co-occur than expected; *L. corsicanus* and *L. europaeus* co-occur less than expected given their shared environmental responses; and *L. europaeus* and *O. cuniculus* co-occur more than expected given their shared environmental responses (Fig. 6.3). Species in the lower quadrants of Fig. 6.3 have the potential to exhibit competitive interactions, i.e. *L. corsicanus* and *L. europaeus*, whereas

species in the upper quadrants may show facilitative interactions, i.e. *L. europaeus* and *O. cuniculus*. Species in the lower left quadrant i.e. *L. europaeus* and *L. timidus*, are likely to exhibit habitat filtering in parts of their range and competitive interactions in other parts. No species pairs occupied the top left quadrant having distinct environments, yet co-occurring more than expected.

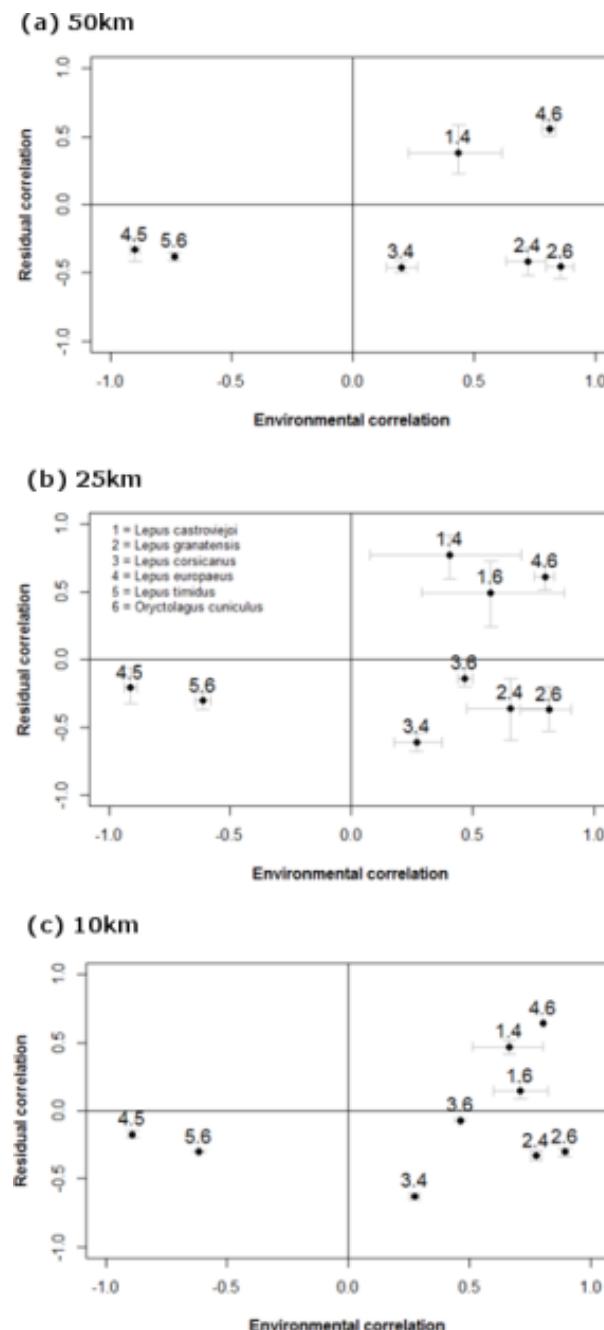


Fig. 6.3. Modelled residual correlation and environmental correlation between European lagomorph species pairs at three different scales: 50km² (a), 25km² (b) and 10km² (c) grid cells. Error bars represent 95% credible intervals.

Mean pairwise environmental correlation coefficients typically became more negative when spatial scale was decreased, with greatest change between the 25km² and 10km² scales, indicating an increase in environmental correlation at finer scales, i.e. increased sharing of environmental responses. Conversely, mean pairwise residual correlation coefficients typically became more positive at smaller spatial scales, indicating a decrease in residual correlation i.e. species co-occurred less than expected given environmental responses at finer resolutions. The greatest impact of altering spatial scale was observed in species pairs involving the range restricted species *L. castroviejoi* (Table 6.1).

Table 6.1. Change in position on x-axis (environmental correlation) and y-axis (residual correlation) between scales expressed as a % for each species pair. Negative numbers indicate an increase in correlation, whereas positive numbers represent a decrease.

Species pair	50km to 25km		25km to 10km		Mean change	
	Environ. correlation	Residual correlation	Environ. correlation	Residual correlation	Environ. correlation	Residual correlation
<i>L. castroviejoi</i> & <i>L. europaeus</i>	-7.14	50.84	-52.64	-23.68	-29.89	13.58
<i>L. castroviejoi</i> & <i>O. cuniculus</i>	27.30	61.90	-70.10	23.28	-21.40	42.59
<i>L. granatensis</i> & <i>L. europaeus</i>	-9.89	-15.24	-7.34	20.19	-8.62	2.48
<i>L. granatensis</i> & <i>O. cuniculus</i>	-5.03	-23.24	-4.44	33.33	-4.73	5.05
<i>L. corsicanus</i> & <i>L. europaeus</i>	25.75	24.71	-37.19	-36.74	-5.72	-6.01
<i>L. europaeus</i> & <i>L. timidus</i>	1.32	-59.13	1.00	47.13	1.16	-6.00
<i>L. europaeus</i> & <i>O. cuniculus</i>	-1.38	9.48	0.49	-15.70	-0.44	-3.11
<i>L. timidus</i> & <i>O. cuniculus</i>	-20.23	-25.33	16.42	21.00	-1.91	-2.17
Mean change	1.34	3.00	-19.23	8.60	-8.94	5.80

Co-occurrence patterns varied substantially between spatial scales but typically exhibited similar relationships, with greater precision at 10km² (Fig. 6.4). Species occurrence is shown by predicted probabilities of occurrence greater than zero; as a result species will co-occur in the upper right hand quadrant. As an example, the co-occurrence pattern between *L. europaeus* and *L. timidus* at the 50km² and 25km² scales, does not feature convex hulls in the upper right hand quadrant, i.e. there is no evidence for co-occurrence. However, at the 10km² scale we predict co-occurrence between these species. These patterns differed greatly for different combinations of species and at different scales.

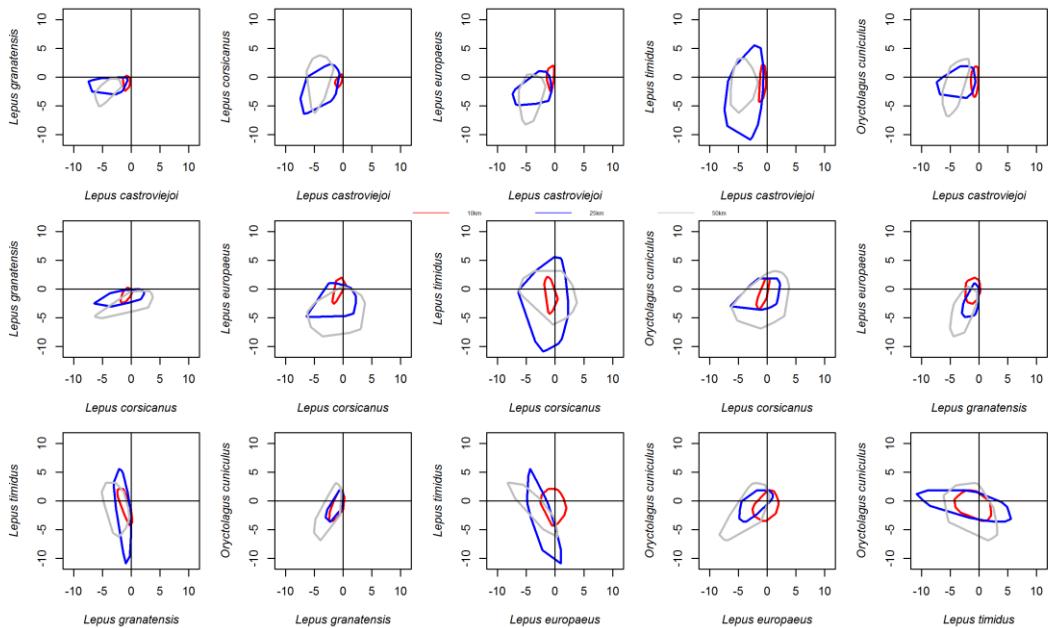


Fig. 6.4. Co-occurrence patterns for all combinations of European lagomorph species using predicted probabilities of occurrence from Joint Species Distribution Models at three different scales: 50km² (grey), 25km² (blue) and 10km² (red). A value greater than zero indicates species occurrence; therefore, convex hulls in the upper right hand quadrant indicate co-occurrence.

6.5 Discussion

Joint SDMs ran 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. Predicted probabilities of occurrence were more precise at finer resolutions for some species, but for others an increase in spatial resolution resulted in little change to these values. Therefore, if the aim is to accurately infer biotic interactions then modelling at finer resolutions is recommended. However, if only the strength and direction of environmental and residual correlations is of interest then coarser grid cell 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 is not always necessary to collect fine resolution occurrence data which could require up to 25 times more effort in the present case.

Most lagomorph species pairs in Europe shared environmental responses, except *L. timidus* with *L. europaeus* and *O. cuniculus*. Lagomorphs occupy a considerable range of environmental conditions (Chapman & Flux, 2008), from northern Scotland where cold temperatures and high rainfall are common, to the Iberian Peninsula with semi-arid environments, so it may be surprising that most species shared environmental responses. However, this could be explained by the variety of environments occupied within ranges; for example, the Iberian hare *L. granatensis* occupies the whole of the peninsula experiencing great variation in climate (Acevedo *et al.*, 2012b), and similar variation can be seen across most other lagomorph ranges. It is not surprising that the range of *L. timidus* exhibited very distinct environmental conditions; with its high latitudinal and elevational range it is likely that the environmental responses are very different to other species (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 observations in the literature: *L. granatensis* and *L. europaeus* (Gortázar *et al.*, 2007), *L. corsicanus* and *L. europaeus* (Angelici *et al.*, 2008) and *L. europaeus* and *L. timidus* (Thulin, 2003; Reid,

2011; Caravaggi *et al.* 2014). In addition, the models indicate a facilitative interaction between *O. cuniculus* and *L. europaeus*. Evidence for biotic interactions between these two species has been highly debated, but the current general consensus is that they co-occur without competition (Flux, 2008), comparable to the results of our analysis. Unexplained residual variance between some species pairs, however, may not be explained by potential 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).

Despite similar correlations across scales, at finer resolutions sharing of environmental responses increased and co-occurrence decreased, particularly for the highly range restricted species *L. castroviejoi*. This species occupies the Cantabrian Mountains in the Iberian Peninsula (Acevedo *et al.*, 2012b). Increasing resolution may capture small changes in microclimatic variation often seen in areas with large topographical variation (Dobrowski *et al.*, 2009) and thus result in this species sharing more similar environments with co-occurring species. However, because the range of this species is so small, ~5,000km² (Ballesteros, 2003), at finer resolutions the number of grid cells increases, separating it from species it was thought to co-occur with and generally resulting in less overlap in species ranges.

Co-occurrence in terms of overlapping species presence can alter substantially at finer resolutions. *L. timidus* and *L. europaeus*, and *L. europaeus* and *O. cuniculus*, exhibited more overlap in their ranges at finer resolutions, whereas *L. timidus* and *L. corsicanus*, *O. cuniculus* and *L. corsicanus*, and *O. cuniculus* and *L. timidus*, 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) suggesting that finer resolution models for species found in these areas are more appropriate. Using rasterised IUCN geographic range polygons is particularly vulnerable to false positives (Murray *et al.*, 2011) potentially influencing our interpretation of ‘interaction’; two species with identical range extents may never meet because of habitat partitioning, especially when separated by elevational gradients. Neither method, using range maps or point occurrence data is without error (Pineda & Lobo, 2012) and the relationship with scale may in fact be an artefact of coarse input data, regardless of resolution, but in this study omission errors were more

preferable to commission errors because only the interactions we are most confident are likely to be captured by our models. However, we suggest that when deciding what input data to be used, the purpose of the study and quality of the data available be considered.

An alternative approach to minimise processing time could be to use Integrated Nested Laplace Approximations (INLA), which would substitute long MCMC simulations for accurate, deterministic approximations to posterior marginal distributions and potentially allow a greater number of models to be run at finer resolutions. Conditional autoregressive (CAR) models, which model spatial associations within the data, are also difficult to implement for complex hierarchical models using MCMC techniques, but they can be fitted with relative ease using INLA to account for spatial autocorrelation in model residuals (Beguin *et al.*, 2012). SDM studies are especially sensitive to spatial autocorrelation, which arises when nearby locations are not independent of each other (Legendre, 1993), and if spatial autocorrelation is not accounted for it can result in misleading and biased models (Lennon, 2000; Beale *et al.*, 2010). However, at present, hierarchical multivariate probit regression models cannot be run using INLA because it breaks the assumption that an observation only depends on one linear predictor (Harvard Rue, *pers. comm.*).

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.

CHAPTER 7

Assessing biological influences on the stability and structure of ecological networks under climate change

A manuscript based on this chapter has been submitted as:

Leach, K., Montgomery, W.I. & Reid, N. (*under review*) Assessing biological influences on the stability and structure of ecological networks. Global Change Biology.

7.1 Abstract

Species distributions are defined by abiotic environmental factors, such as climate, and biotic factors, such as interspecific interactions. Global climatic change is expected to alter species distributions dramatically. Despite the potentially large effects that biotic interactions may have on species distributions, their role in shaping species ranges is seldom explored. Understanding the impacts of climate change on species community structure will be important in predicting change, but species interactions are notably difficult to model due to their highly complex nature. Community responses to climate change are likely driven by variations in species co-occurrence leading to changes in current species interactions and the emergence of novel systems. We used a combination of Species Distribution Modelling (SDM) and network analyses to assess the stability and structure of ecological networks among 23 species of North and South American lagomorphs under projected changes in climate. We examined changes in a number of network properties including complexity, stability, structure, species' importance, transfer of information (communication) and the number of associations between species. We also investigated the influence of species traits on changes in network properties. SDMs projected high species turnover between the present day (2008) and the 2050s. The number of species associations is projected to increase substantially under future climate scenarios with increased network stability, increased communication between species, decreased species' importance and less structure in ecological networks. However, we found no significant influence of species traits on changes in lagomorph ecological network structure or properties. Nevertheless, projected climate change will likely have tremendous impacts on lagomorph ecological communities, including potentially advantageous effects such as increased stability and adverse effects such as substantial changes in species composition.

7.2 Introduction

There is an urgent need to understand how projected climate change will impact biotic interactions and future ecological communities. Species assemblages form extremely complex ecological interaction networks within and between trophic levels, and are likely to alter dramatically under future climate change (Albouy *et al.* 2014). Reorganisation of networks is completely dependent on individual species responses to climatic change. Novel systems may emerge with species that have never interacted before due to new spatial co-occurrences (Gilman *et al.* 2010) or previously interacting species may no longer co-occur in the future (Schweiger *et al.* 2008), leading to novel assemblages. The impact of climate change on species assemblages has rarely been studied but is likely extensive (Tylianakis *et al.* 2008). For example, seed dehiscence time could be affected by increases in temperature, which could in turn alter competition between seed predators and dispersers (Ness & Bressmer, 2005).

Ecological networks provide a means by which to study species assemblages either within trophic levels, for example interspecific interactions, or between trophic levels, for example food webs. In ecological networks, the nodes usually represent species and the edges (connecting lines) interactions between species. Networks are usually complex with species typically linked to many others either directly or indirectly (Montoya & Solé, 2002; Williams *et al.* 2002). Looking at snapshots of ecological networks or food webs through time can provide great insight into the potential expected change and how network properties may alter (Albouy *et al.* 2014).

Network properties may include simple metrics like degree distribution, which is the number of species associations or connections. Species with a high degree distribution may exhibit this property just by being very widespread or abundant; for example, abundant species are likely to have more predators than rare ones but these species may also have many connections because they are crucially important within the network (Montoya *et al.* 2006). Degree distribution may decrease under future climate change if species richness declines with local extinctions, but such effects are likely spatially heterogeneous (Albouy *et al.* 2014).

Network properties can include more advanced measures, such as complexity, clustering and nestedness. In theory, complexity in ecological networks equates to fragility, lowered resilience, decreased persistence, and lower resistance to change which may lead to extinction susceptibility or invasion by other species, but this is

seldom seen in real-world networks. If all species are closely associated, a disturbance in the network will likely affect a greater number of species. In the real-world, however, many disturbances affect species every day and they nonetheless persist (Montoya *et al.* 2006). Clustering in networks is caused by close links to many species and important classes tend to have densely linked groups of species (Montoya *et al.* 2006); for example, fish that feed from several trophic levels (Hall & Raffaelli, 1991) and host-parasitoid systems (Memmott *et al.* 1994). In reality, and especially in ecological networks, densely clustered networks are the norm (Montoya *et al.* 2006). Nestedness is widely reported in ecological species interaction networks (e.g. Bascompte *et al.* 2003) and occurs when specialist species interact with subsets of species, that in turn interact with more generalist species (Jordano *et al.* 2006; Almeida-Neto *et al.* 2008). Nestedness leads to high robustness to extinction if specialists have a higher risk of extinction (Memmott *et al.* 2004) and can lead to lower rates of interspecific competition (Bastolla *et al.* 2009). This is due to differences in abundances of interacting species (Lewinsohn *et al.* 2006), higher extinction rates when specialists interact with specialists (Ollerton *et al.* 2003) or complementarity of species traits (Santamaria & Rodriguez-Girones, 2007).

It is also extremely important to consider network structure when interpreting community responses under future climate change (Fortuna *et al.* 2010) and metrics such as assortativity coefficients and modularity values allow us to explore this further. Assortativity may result if associations between species are dense within groups, but sparse between groups (a traditional view of nodes in a network). However, if species are less likely to be connected within groups than between groups, a network is disassortative (Clauset *et al.* 2008). Modularity is a similar metric which measures how strongly a network is divided into communities; high modularity results from dense associations within groups and sparse associations between groups. Networks with a low number of associations and a high number of modules or communities, tend towards increased nestedness, i.e. increased stability, whereas, at high connectivities the reverse is observed (Fortuna *et al.* 2010). Alternative network properties consider the transfer of information through nodes. Low communicability between nodes or species in a network, whereby communication or association depends on all routes connecting those species and not just the shortest path, can lead to vulnerability such as higher susceptibility to changes in climate, and lower resilience (Estrada, 2011).

Communication between species is also imperative in determining how central or important a species is in the network. Central species may facilitate or inhibit communication between other species and their importance is measured by metrics such as betweenness centrality (Freeman, 1979; Estrada, 2011). Loss of central species from ecological networks due to range changes under future climate scenarios may result in dramatic consequences for other associated species.

Two of the ‘top 100’ fundamental ecological questions identified by Sutherland *et al.* (2012) concern the influence of species traits on network structure, and the ability of community responses and environmental change to be predicted from species traits (Sutherland *et al.* 2012). It is possible that traits may lead us to identify species predisposed to cause disturbance in networks (Montoya *et al.* 2009), given that phylogeny often predicts network structure (Rezende *et al.* 2007), but very little research has been carried out to date, with most studies looking at body size effects on food webs (Woodward *et al.* 2005).

We attempt to link species traits with predicted future changes in network properties in order to understand whether particular traits disproportionately impact network stability, using North and South American lagomorphs as a case study. Throughout the Americas, lagomorphs occupy a huge range of latitudes, elevations and habitats, from the Arctic tundra to the Amazon rainforest, and from the heights of the Rocky Mountains to the depths of Death Valley. There are 28 lagomorph species throughout the Americas exhibiting substantial species trait variation including two pikas, eight hares and jackrabbits and eighteen rabbits (Chapman & Flux, 2008). In addition, previous studies have mapped several notable species interaction hotspots particularly in North America (Leach *et al.* 2015b). Using sophisticated SDMs projected into the most up-to-date future climate scenarios combined with network analyses, we infer change in species assemblages and assess how their stability is likely to alter. We hypothesised that lagomorph network structure is likely to change dramatically under future global climate change as species distributions shift geographically and change in extent, and we also expected network stability to decrease as species comprising communities struggle to cope with rapid change.

7.3 Methods

7.3.1 Species Distribution Modelling

Species Distribution Models (SDMs) were fitted using Integrated Nested Laplace Approximation (INLA) and the ‘R-INLA’ package (<http://www.r-inla.org/download>) in R version 3.2.1 following Beguin *et al.* (2012) and extrapolated for the 2050s and 2070s. Species range and environmental data are described in sections 2.2 and 2.3. 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 not modelled by the included covariates. A vague Gaussian prior was assumed for the model parameters. Values of the shape parameters were defined so that the ratio of data points to the number of effective parameters was >20 following Beguin *et al.* (2012).

Projected species range extents were clipped by potential dispersal distances (following Chapter 3 and Leach *et al.* 2015a) and converted to binary data using the 10th percentile omission threshold in the ‘SDMTools’ R package version 1.1-221 (Van der Wal *et al.* 2014). Species turnover between time periods was calculated using the ‘betapart’ package version 1.3 and Sorenson’s measure of beta diversity (Baselga & Orme, 2012; Baselga *et al.* 2013).

7.3.2 Pairwise species associations

The strength and direction of pairwise species associations at each time period were estimated from model outputs using the ‘sppairs’ package (<https://github.com/mjwestgate/sppairs>; Lane *et al.* 2014). Odds ratios, which are used to infer the degree of association between two binary variables, were calculated using logistic regression and the rarity cut-off was set to zero to include all species.

7.3.3 Statistical analyses

A variety of functions written in MatLab, capable of dealing with large data matrices like those in network analysis, were used to analyse change in ecological networks between the present day (2008), 2050s and 2070s. We calculated degree distribution (number of associations per species), density of the network (ratio of the number of edges to the number of possible edges), complexity (average number of links per species; otherwise known as linkage density), the clustering coefficient (ratio of existing links connecting

node neighbours to the maximum possible number of these neighbouring links), nestedness (a proxy for stability calculated using code from www.bascompte.net which is derived from Almeida-Neto *et al.* 2008), assortativity coefficient (Pearson correlation coefficient of degree between pairs of linked nodes; preference for nodes to attach to others that are similar in some way), communicability (derived from a contour plot of the adjacency matrix between nodes) and betweenness centrality (the number of shortest paths from all vertices which pass through a specified node; an indicator of node importance). We then used the software Gephi to assign modularity values to each network. These are calculated using the fraction of edges that connect communities following Newman & Girvan (2004).

We investigated correlates of network properties using Bayesian Phylogenetic Mixed Models (BPMMS) following Botero *et al.* (2013) and Verde Arregoitia *et al.* (2015) which incorporated phylogenetic information as a covariance matrix. We fitted models using the ‘MCMCglmm’ R package version 2.21 (Hadfield, 2014) for each network measure, for example, change in degree distribution between the present day and 2070s, with species traits as possible correlates and 2.5 million iterations with a burn-in of 500,000 and thinning value of 2,000. Trait data are described in section 2.4. The lagomorph phylogeny is described in section 2.5.

7.4 Results

Species turnover in North and South American lagomorph species is likely to be high between the present day and the 2050s (mean= 0.288 ± 0.003 ; Fig. 7.1a) and 2070s (mean= 0.292 ± 0.002 ; Fig. 7.1b), especially in Arctic high latitude and in northern South America. There was patchy, but little turnover predicted between the 2050s and 2070s (mean= 0.029 ± 0.001 ; Fig. 7.1c).

An increase in ecological associations between lagomorph species was predicted under future climate scenarios (Fig. 7.2a-c). However, there was high turnover in species relationships; between the present day and by the 2050s there is predicted to be 19 species associations lost and 56 gained (Fig. 7.2d), between the present day and the 2070s there is predicted to be 20 associations lost and 57 gained (Fig. 7.2e), and between the 2050s and the 2070s there is predicted to be 8 associations lost and 8 (different associations) gained (Fig. 7.2f).

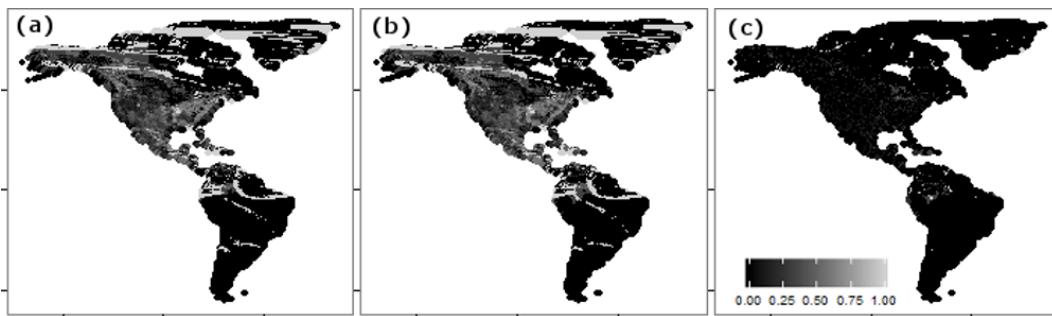


Fig. 7.1. Species turnover in North and South American lagomorphs. Turnover is calculated using Sorenson's index of beta diversity for changes in species compositions between the present day and the 2050s, the present day and 2070s, and between the 2050s and 2070s; shown in parts (a), (b) and (c) respectively. A light grey value indicates high species turnover.

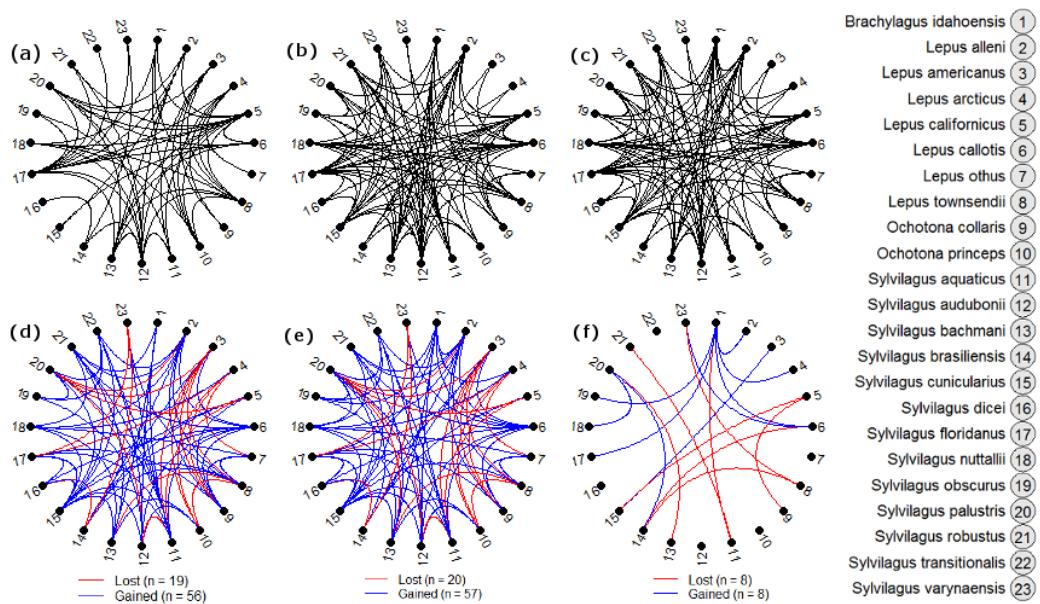


Fig. 7.2. Ecological association networks for North and South American lagomorph species. Associations are shown based on (a) the present distribution of 23 species, (b) the distribution as projected in the 2050s and (c) the 2070s. Associations lost (red) or gained (blue) between the present day and the 2050s, the present day and 2070s, and between the 2050s and 2070s are shown in parts (d), (e) and (f) respectively.

With the increase in ecological associations predicted under future climate scenarios, there is also an increase in network density, an increase in complexity, increased clustering, increased assortativity and increased nestedness between the present day and the 2050s and 2070s, but again there is little change between the 2050s and 2070s (Table 7.1).

Table 7.1. Global network metrics for ecological association networks based on distributions in the present day (2008), 2050s and 2070s. Definitions are provided in the Methods.

Network Metric	Present	2050s	2070s
Number of associations	56	93	93
Density	0.002	0.004	0.004
Complexity	0.212	0.352	0.352
Clustering coefficient	0.429	0.582	0.562
Assortativity coefficient	-0.090	-0.080	-0.126
Nestedness	0.340	0.522	0.528

Network structure was predicted to change dramatically under future climate from four distinct communities described during the present day (Fig. 7.3a) to three in the 2050s (Fig. 7.3b) and two in the 2070s (Fig. 7.3c). The four communities identified during the present were representative of Northern (orange community in Fig. 7.3a), Central (green), Eastern (yellow) and Southern (blue) lagomorph species groups (Fig. 7.3a). By the 2050s, the Eastern species group merges with several other communities (blue) while other species move between different communities (Fig. 7.3b); by the 2070s, the Central and Southern communities (blue) merge (Fig. 7.3c). The black-tailed jackrabbit *Lepus californicus*, desert cottontail *Sylvilagus audubonii* and robust cottontail *S. robustus* shift into a community with more Northern species, whilst the Southern community (antelope jackrabbit *L. alleni*, white-sided jackrabbit *L. callotis* and many of the other *Sylvilagus* spp.) merge with more northerly species including the snowshoe hare *L. americanus* and collared pika *Ochotona collaris*.

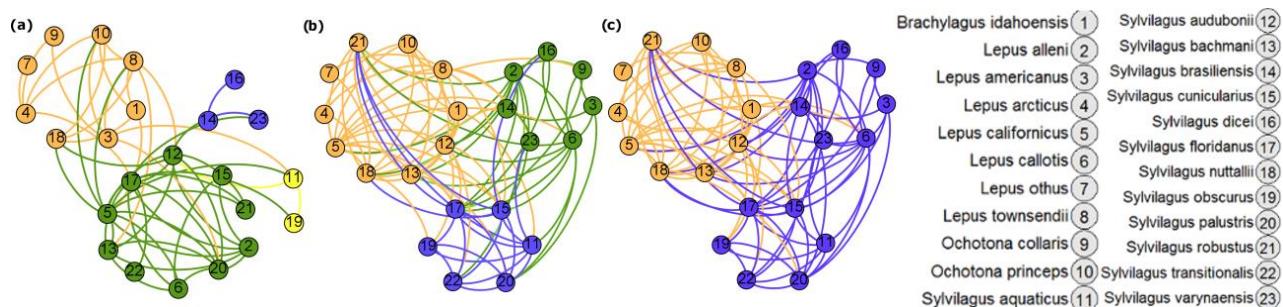


Fig. 7.3. Modularity in ecological association networks. Communities discovered in networks based on present distributions (a) and projected distributions in the 2050s (b) and 2070s (c). Distinct communities are coloured separately, but colours are not equivalent between time periods because composition changes substantially.

Communicability increases substantially under future climate scenarios, especially between cottontail rabbits i.e. *Sylvilagus* spp. due to the increased numbers of associations and pathways of connectedness (Fig. 7.4).

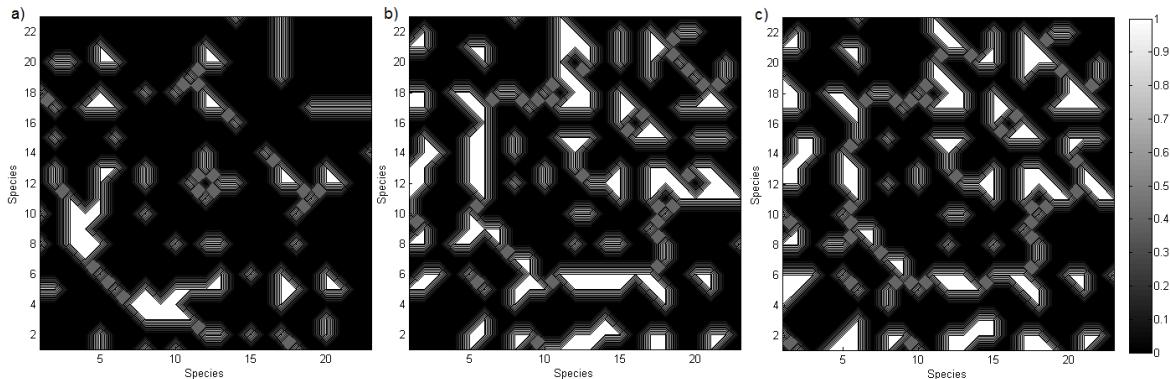


Fig. 7.4. Communicability in ecological association networks. These matrices show the communicability between each species based on present distributions (a), and projected distributions in the 2050s (b) and 2070s (c).

Ecological network betweenness centrality is predicted to decrease in the future i.e. become less important, with the same pattern observed when the order is split into the sub-groups of pikas, rabbits, hares and jackrabbits (Fig. 7.5). The decrease predicted in overall betweenness centrality seemed to be driven largely by the decrease for *S.s floridanus* (from 147 to 37) and *S. audubonii* (from 92 to 31; Appendix 4, Fig. 4.1), though some species (pygmy rabbit *Brachylagus idahoensis*, *L. callotis*, Mexican cottontail *S. cunicularius* and mountain cottontail *S. nuttallii*) exhibited marginal increases in betweenness centrality in the future. In terms of degree distribution, or number of connections to other species, there was a general increase under future conditions which was seen across all groups and was driven mostly by increased connections involving *B. idahoensis* (from 4 to 12 connections) and *S. cunicularius* (from 2 to 13; Appendix 4, Fig. 4.2).

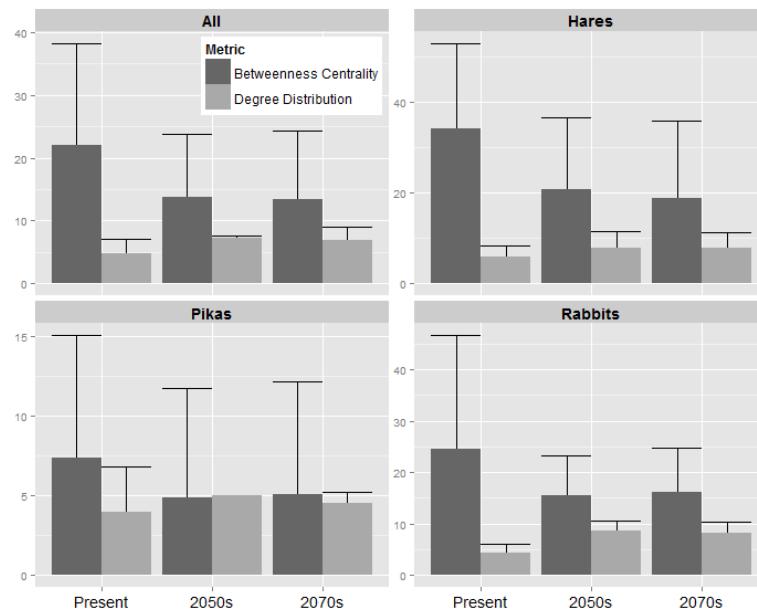


Fig. 7.5. Connectivity and centrality in lagomorphs from the present day to the 2070s. Degree distribution (number of connections to other nodes) and betweenness centrality (i.e. importance of the node) are averaged for each lagomorph group and shown with 95% confidence intervals.

Exploring possible species traits which may explain the changes in betweenness centrality and degree distribution, whilst accounting for phylogenetic relationships, suggested no significant influences (Table 7.2). Therefore, changes in ecological network structure for lagomorphs in North and South America do not appear to be linked to biological species traits, such as body mass.

Table 7.2. Bayesian Phylogenetic Mixed Model results for change in degree distribution and betweenness centrality between the present day (2008) and the 2070s. Asterisks indicate significance, i.e. where credible intervals do not cross zero.

Parameter	Degree distribution			Betweenness centrality		
	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI
(Intercept)	0.005	-0.454	0.433	0.002	-0.481	0.558
Body mass (g)	0.384	-0.496	1.203	0.012	-0.985	0.817
Activity cycle	0.178	-0.482	0.824	-0.276	-1.122	0.447
Diet breadth	-0.356	-0.916	0.190	-0.434	-1.018	0.144
Gestation length	-0.428	-1.431	0.506	-0.469	-1.514	0.587
Litter size	-0.004	-0.646	0.645	-0.056	-0.767	0.709
Litters per year	-0.281	-1.212	0.742	-0.663	-1.707	0.470

7.5 Discussion

The combination of SDMs and network analysis suggests that ecological association networks for North and South American lagomorph species are likely to alter substantially under projected, future climate change. Contrary to our hypothesis, we observe increased network stability in the future but with substantial variability between species in terms of importance and number of connections. Using rasterised IUCN geographic range polygons is particularly vulnerable to false positives (Murray *et al.* 2011), but in this study omission errors were more preferable to commission errors because only the associations we are most confident in are likely to be captured. The associations may not directly indicate species interactions, but they do indicate co-occurrence which increases the opportunity for potential interaction. Range maps are used because they are highly detailed for lagomorphs, and point occurrence data are extremely sparse; however, we suggest that when deciding what input data to be used, the purpose of the study and quality of the data available, are considered first.

High species turnover projected under future climatic conditions is frequently reported from SDM studies (e.g. Thuiller, 2004). This study projected notably higher species turnover in North and South American lagomorphs between the present day and the 2050s or 2070s than between the 2050s and 2070s. This supports a previous study which also projected large changes in lagomorph species richness throughout the Americas by 2050 (Leach *et al.* 2015a). We also project an increase in the number of pairwise species associations under future climate, but with substantial turnover in these associations. This may be explained by species becoming more widespread under future conditions, due to novel connections emerging (Gilman *et al.* 2010) and previous associations between co-occurring species no longer being possible (Schweiger *et al.* 2008). Albouy *et al.* (2014) found opposing patterns of change in marine networks reporting a decrease in the number of connections associated with declines in species richness and local extinctions. Albouy *et al.* (2014) ran their models at a spatial resolution of approximately 10km² grid cells, albeit restricted to the Mediterranean Sea and, thus, on a much smaller extent than the current study. It should be remembered that we excluded five highly range restricted species from our analysis (because their ≤50km² ranges were smaller than the spatial resolution of our models). If changes in these species had been included patterns may have been different. However, including these species, which requires finer resolution models, would have been prohibitive

computationally due to costs in terms of processing power and time required. INLA uses a large amount of memory and processing power to account for spatial autocorrelation in the iCAR error structure even when models are run at a resolution of 50km² grid cells across the Americas.

Under projected future climate, ecological association network complexity, clustering and nestedness of lagomorphs are predicted to increase. Increased clustering with more close links is likely due to the increased number of connections, creating more ‘normal’ ecological association networks, which could also result in structural network changes (Montoya *et al.* 2006). Increased complexity does not always go hand in hand with increased nestedness, especially in ecological network theory which suggests that complex networks are more fragile and less resilient, but in practice we know that species persist despite multiple real-world disturbances (Montoya *et al.* 2006); thus, increased complexity may have no effect on stability. However, increased nestedness and clustering predicted in lagomorph networks suggests they do increase in stability under future conditions (Memmott *et al.* 2004).

The structure of lagomorph ecological networks changed considerably, becoming more assortative, i.e. more associations between groups than within groups, and less modular under future climate scenarios. Divisions between lagomorph communities, from four to two by the 2070s, appear to be mainly due to high species turnover. The present day assemblage with four communities and a lower number of associations had a less nested, more modular network but by the 2070s, there may be two communities with more associations, and a more nested, less modular network. This is contrary to the findings of Fortuna *et al.* (2010) who found that highly nested networks with a low number of associations tended to be highly modular. The highly nested, low modular and high association networks for North and South American lagomorphs under future climate may be due to the increased ratio of range-restricted specialist species to widespread generalist species, but further investigations are needed to support this interpretation.

Communicability among cottontail *Sylvilagus* species was projected to increase under future conditions, reducing network vulnerability and increasing resilience as they create pathways to communicate between a larger number of nodes (Estrada, 2011). *Sylvilagus* are projected to have an increased number of connections in the future which is likely driving the increased network communicability. However, some widespread

Sylvilagus species including *S. audubonii* and *S. floridanus* become less important in the future, reducing communication and potentially impacting many co-occurring species (Freeman, 1979; Estrada, 2011). In contrast, some species, including *B. idahoensis* and *S. cunicularius*, are projected to become more important in the future, increasing the number of their connections and facilitating more communication between nodes.

Testing the link between species traits and changes in ecological network properties resulted in unexpected projections. Given that lagomorphs exhibit substantial trait variation, we expected that multiple species traits would influence network structure (Montoya *et al.* 2009), but none were associated with change. Since pikas, rabbits, hares and jackrabbits vary considerably in body size we expected some relationship between group or body mass and change in network properties. It may be that our inclusion of phylogenetic controls damped variability within groups absorbing variation due to their taxonomic group or body size (Leach *et al.* 2015a) or that interspecific interaction networks are in fact not influenced by species traits and cannot be predicted from their responses to environmental change.

In this study we examined ecological associations at one trophic level, but expanding network methods to include bottom-up and top-down processes such as herbivory or predation (by including plants and carnivores) would add additional insights for taxa such as lagomorphs. However, even exploring ecological networks at one trophic level for herbivorous mammals can provide great insight into the potential expected changes under future climatic conditions. Here, we project an increase in pairwise species associations concomitant with decreased individual species' importance and structure, but show increased communication and stability in networks under future conditions. Although biological traits are expected to have large impacts on network structure and properties, this is not the case for interspecific interactions in lagomorphs. Incorporating the SDM methodology of Chapter 5, which accounts for the presence of co-occurring, potentially competing species, would greatly advance the work in this chapter because interspecific interactions would be accounted for and distributions constrained prior to ecological network analysis and would allow improved projections of change.

CHAPTER 8

General Discussion

8.1 Overview

Climate change is predicted to have major impacts on the ecology and distribution of species and habitats (e.g. Warren *et al.* 2013). The processes which contribute to changes in distribution of species must be understood before potential impacts can be predicted with confidence and informed decisions made with regards to mitigation in, for example, conservation management. It is probably impossible to understand the macroecological processes affecting every living species, but selecting a group of species which are representative of a wide range of environmental conditions with varying levels of threat, enables broad interpretation of impacts which are potentially of general relevance. The order Lagomorpha was used here as the study system as they have an extremely widespread distribution and span a huge range of environmental conditions (Chapman & Flux, 2008). A quarter of lagomorph species are listed as threatened by the IUCN allowing the study of taxa with varying levels of imperilment from Least Concern to Critically Endangered. Moreover, there are now numerous studies presenting empirical data on the observable impacts of current and past climate change suggesting they may be a particularly vulnerable group (e.g. Calkins *et al.* 2012; Ge *et al.* 2012). Their responses may reflect wider changes in habitats; of which they occupy nearly the full terrestrial spectrum from Arctic tundra to tropical rainforest including agricultural pasture and cropland. Thus, it is likely that climate change will have large impacts on lagomorph ecology and distribution.

In this thesis, the processes which contribute to the global distribution of lagomorphs are examined using a combination of approaches, involving Species Distribution Modelling (SDM), bibliometric review and network analyses. Assessing the projected change in lagomorph distributions under future climatic conditions at a species-level across Earth revealed that two-thirds of species are likely to be affected. Larger leporid species (rabbits, hares and jackrabbits) are predicted to shift polewards with little overall change in range extent, but, smaller lagomorph species like pikas are predicted to shift upwards in elevation with dramatic declines in range (Leach *et al.* 2015a). However, this analysis did not account for potentially important interspecific drivers delineating species extent. Bibliometric analyses of data on lagomorph interspecific interactions revealed a large number of within-order competitive interactions documented in published literature. There appeared to be more interspecific interactions between closely related, large-bodied, similarly sized species occurring in

regions of human-modified landscapes, typically agricultural lands, or at high elevations. Consequently, capturing and incorporating interspecific interactions into SDM is vital to understand all potential factors determining species distributions and enables the effects of future climatic change to be fully projected with confidence (Leach *et al.* 2015b).

Quantifying the influence of environmental and interspecific interaction effects on lagomorph species distributions in Europe, which are documented to exhibit particularly strong competition, suggested that these factors are equal determinants of species ranges, but the effects are spatially heterogeneous. Regions of lagomorph species distributions strongly influenced by interspecific interactions are likely to be more vulnerable to future climatic change than areas strongly influenced by current environmental conditions; suggesting a disproportionate impact of global climate change on species interactions. However, it is imperative that scale is considered in continental and global analyses of this nature, especially in studies examining species interactions or climate which may only be captured in full at fine scale resolutions. Nevertheless, interspecific interactions and environmental effects are shown to be similar in terms of strength and direction in models run at coarser scales, but there was a trade-off between precision and processing power. Effects are more precise at finer resolutions, whilst co-occurrence patterns between lagomorph species show considerable differences between scales. Finally, extending this work to assess projected change in American lagomorph assemblages under future climatic conditions at a community-level, suggested high turnover and substantial changes in ecological network properties, including the homogenisation of species communities, with increased species associations conferring ecological stability and therefore presenting a challenge to future conservationists attempting to restore diversity. Surprisingly, no evidence was found that species traits, for example body mass or fecundity, influenced ecological network properties or their change under projected future climatic conditions.

8.2 Impacts of climate change

This thesis took two approaches to study the impacts of climate change on species distributions. Firstly, impacts were assessed on a species-level across the order, but only data for the distribution of 58 (out of 87) species, assessed with expert evaluation

and model statistics, were projected under future climatic conditions and used in further analysis. As only a low proportion of these 58 species are listed as threatened or Data Deficient by the IUCN and most have a greater number of records than the 29 ‘unmodellable’ species, present results (Chapter 3) are a conservative estimate of diversity in climate change responses. Species are very likely to be listed as threatened where data are deficient (Bland *et al.* 2015). Hence, there may be vast changes in results if more data were available for these species, allowing a model to be constructed for future climatic conditions. There is a particularly strong bias for Africa where there are simply insufficient data for many species.

Generally, where sufficient data are available to make useful inferences on the impact of future climatic change, the majority of lagomorph species will experience poleward movement, elevational increase and range loss; but, a third of species are predicted to exhibit movement away from the poles, elevational decreases and range expansions due to climatic changes. Although, global changes in predicted lagomorph species richness suggest that almost a third of the Earth’s terrestrial surface (31.5 million km²) currently occupied by lagomorphs may experience loss of species by the 2080s, lagomorph species richness is likely to remain similar or even increase across two-thirds of the Earth’s surface. The average poleward shift for the Order Lagomorpha was estimated at 1.1° with an elevational upward shift of 165m. These are much greater changes than those calculated in a meta-analysis collating information on a wide variety of taxonomic groups (Parmesan & Yohe, 2003): on average birds, butterflies and alpine herbs are predicted to shift by approximately 0.8° poleward and increase in elevation by about 90m by 2100. The vast array of environmental conditions occupied by lagomorphs, including islands and mountainous regions, may explain these larger changes in poleward and elevational shifts compared to other taxa.

Pikas showed substantial increases in elevation and range contraction. Kozlov’s pika *Ochotona koslowi* is predicted to become extinct by the 2080s and there may be substantial range contraction of the America pika *O. princeps*. The latter is congruent with other studies which report that nineteen of the 31 (49%) subspecies in the USA are predicted to lose >98% of their suitable habitat under a 7°C increase in the mean temperature of the warmest quarter of the year, and 88–95% of suitable habitat under a less dramatic 4°C increase (Calkins *et al.* 2012). This is also supported by empirical studies from Beever *et al.* (2013), who observe fewer pikas in the 2000s than in the

1990s at lower elevation boundaries, upslope contraction of lower elevation boundaries on southerly facing slopes and increases in elevation up to 120m from 1994 to 2008. However, pikas are known to exhibit behavioural plasticity, inhabiting thermally buffered habitats in the micro-climate of the talus (Henry *et al.* 2012) and altering diel patterns in activity (Bhattacharya *et al.* 2014), thus they can survive in conditions beyond the predicted bioclimatic niche and SDMs based solely on climatic factors may be overly conservative. Climatic factors, however, were not among the top predictors of *O. princeps* site occupancy in the Southern Rocky Mountains, USA where the diversity and relative cover of forbs (their main food source) are the best predictors (Erb *et al.* 2014) and this may be the case for many other lagomorphs too.

As well as pikas, other lagomorphs have already begun to exhibit phenotypic adaptation to changes in future climate; for example Mills *et al.* (2013) show plasticity in seasonal coat colour changes in the snowshoe hare *Lepus americanus* affecting white to brown moult in spring but not in autumn moults or initiation date of colour change. Given that some parts of the hare's range may lose up to 69 days a year of snow coverage by 2100, there will be increasing mismatch of coat colour unless rapid evolution occurs. Additionally, Zimova *et al.* (2014) found no behavioural modification in response to colour mismatch; for example, there is no increase in hiding behaviour, so plasticity affecting some characters, but not all, may be insufficient for adaptation to future climate change.

High species turnover was projected under future climatic conditions for North and South American species, consistent with earlier SDM studies (e.g. Thuiller *et al.* 2004), but the statistical approach taken is likely to be more reliable than commonly used techniques given that it explicitly accounted for spatial dependencies in the data i.e. spatial autocorrelation. It is expected that changes in climatic conditions will lead to declines in species ranges (e.g. Chen *et al.* 2011) and, therefore, fewer coexisting species, as shown by the decreased ecological network connections in Albouy *et al.* (2014). However, turnover in North and South American lagomorph assemblages resulted in an increased number of connections. This could be due to a large number of poleward shifts in American lagomorph distributions (Leach *et al.* 2015a); if the many endemic Mexican species shift their ranges poleward, they will coincide with the ranges of a large number of North American species, leading to more connections and consequent changes in community composition. Climatic effects on lagomorph

ecological communities, also include unexpected increases in stability, due to increased nestedness (Memmott *et al.* 2004), and equally unexpected decreases in structure and modularity, potentially due to large increases in the number of connections (Fortuna *et al.* 2010). As in Chapter 3, a number of range-restricted species were left out of the analysis because of data restraints and future inclusion of these species could impact predictions of ecological network properties substantially. Species-level and community-level impacts of climate change both indicate that future work, with adapted analytical techniques, should be directed at rare species especially with regards to enhanced distribution data.

8.3 Incorporating interspecific interactions into Species Distribution Models

Chapter 4 shows that there are at least thirty-three documented competitive interactions between species in the order Lagomorpha, involving at least thirty-three species. These interactions mostly involve hares (*Lepus* sp.) and tend to be located in specific places in North America and eastern Asia, around 30-50°N of the Equator. Although interspecific interactions are known to be key determinants of species distributions, they are rarely considered in SDM studies, and there only appears to have been one lagomorph study attempting to explore these factors alongside climate. The Iberian hare *L. granatensis* is predicted to be the beneficiary in competition with the European hare *L. europaeus* in their zone of contact in Northern Iberia, and interactions between the mountain hare *L. timidus* and *L. europaeus* are expected to contribute to the decline of the former in areas of co-occurrence in Northern Europe under future climate change (Acevedo *et al.* 2012a).

SDMs in Chapter 5 indicated competition between *L. europaeus* and *L. granatensis* (Gortázar *et al.* 2007), as well as competition between *L. europaeus* and *L. timidus* (Thulin, 2003; Reid, 2011). In addition, models from Chapter 5 hint at a potentially mutualistic relationship, as yet undocumented in the literature, between *L. granatensis* and *Oryctolagus cuniculus*, which is likely due to their highly coincidental ranges. A competitive interaction between *L. timidus* and *O. cuniculus* was also suggested even though it has not been reported in the literature. Their ranges show significant overlap and biotic interactions are both possible and probable, particularly at the southerly

range margin of *L. timidus*. Joint SDMs in Chapter 6 also captured competitive interactions between *L. granatensis* and *L. europaeus* and between *L. europaeus* and *L. timidus*, as well as competition between *L. europaeus* and *L. corsicanus* (Angelici *et al.* 2008) and mutualism between *O. cuniculus* and *L. europaeus* (Flux, 2008). In addition, interspecific interactions reported in the literature review in Chapter 4 for American species correspond to interactions also captured in the SDM and network analysis approach in Chapter 7 (11 out of 14 captured); the interactions between *Brachylagus idahoensis* and *S. audubonii*, *L. callotis* and *S. audubonii*, and *S. nuttallii* and *S. floridanus* were not captured. However, further investigation suggested that this appeared to be due to only slight overlap in the IUCN range maps for these species, resulting in difficulties for the model in capturing specific interactions.

Incorporating interspecific interactions into SDMs, therefore, appeared successful in Chapters 5-7, revealing many of the already known competitive interactions, as well as some suspected but as yet undocumented mutualistic interactions. SDMs including biotic factors were much improved upon those based on abiotic factors only, in terms of predictive ability for the majority of species tested. Moreover, both abiotic and biotic factors appeared equally influential in delineating distributions, albeit with spatial variability in the strength of their relative contribution. Nevertheless, further improvements could still be made, for example inclusion of bottom-up effects (plant distributions) and top-down effects (predator distributions) whilst also modelling the direct effects of climate change on the strength of species interactions.

8.4 Methodological review

This thesis incorporates a wide range of methods and analytical techniques, mostly centred on Species Distribution Modelling (SDM); a popular tool in macroecology. Three different SDM methods were used, with the first, MAXENT, selected to produce an initial basis for species responses to climate change; the second, Integrated Nested Laplace Approximation (INLA), is, a more sophisticated, Bayesian method for modelling species responses; and, the third, Joint SDM, selected to simultaneously model the distributions of multiple coexisting species.

Correlative SDM, as used in Chapter 3, has numerous limitations (Elith & Leathwick, 2009); in the present research, issues with sampling bias, resolution, future climate

models, model evaluation and rare species, were either corrected or accounted for. Expert validation of models, as used in Chapter 3, are strongly advocated for future SDM studies, given the relative ease in obtaining opinions through website interfaces, as opposed to holding lengthy stakeholder meetings (e.g. Kremen *et al.* 2008), and expert validation may provide a more critical view compared to model statistics, like Kappa values. However, problems remain with thresholds, multicollinearity, autocorrelation and unaccounted for biotic interactions (Table 8.1). Bayesian SDMs run using INLA, as opposed to using Markov Chain Monte Carlo (MCMC) methods, accounted for spatial autocorrelation, had credible intervals for outputs, used only non-collinear variables and had more biologically realistic response curves between predicted probabilities of occurrence and environmental variables. Sampling bias issues, however, were not addressed due to the use of IUCN range map data, and issues with collinearity remain in Chapter 5 by including the ranges of co-occurring species as additional covariates to models (Table 8.1). Joint SDMs (used in Chapter 6) successfully modelled coexisting species with credible intervals, but had very lengthy processing times, due to the MCMC methods, and did not account for sampling bias or spatial autocorrelation (Table 8.1).

Species traits have played a large role in the analytical techniques and interpretation in this thesis, providing meaningful insight into the drivers behind species distributions (Angert *et al.* 2011). Body mass and fecundity had large effects on species-level responses to climate change in Chapter 3, whilst interacting species pairs tended to be defined by a number of traits, such as body mass and phylogenetic relatedness (Chapter 4). Community-level analysis in the Americas, in Chapter 7, however, suggested no influence of species traits on changes in ecological network structure and properties under future climatic conditions. This may be due to the large variability within similar species traits, for example two species with very low body masses, i.e. pikas, may exhibit very different responses, in terms of number of interactions, under climate change. Or perhaps this indicates that environmental factors, as opposed to species biology, are important in explaining changes in ecological network structure.

Table 8.1. Comparison of advantages and disadvantages of the SDM approaches implemented in this thesis.

	Method	Advantages	Disadvantages
Chapter 3	Correlative species distribution models e.g. MAXENT	<ul style="list-style-type: none"> ▪ Accounted for sampling bias ▪ High resolution data used: ~1km² data ▪ Averaged projected future climatic data across multiple models ▪ Model validation framework including expert evaluation and model statistics ▪ Only 'modellable' species used 	<ul style="list-style-type: none"> ▪ One climate change scenario: A2 ▪ Did not account for biotic interactions ▪ Model outputs thresholded ▪ Invasive ranges not modelled ▪ Multicollinearity in parameters ▪ Unaccounted for spatial autocorrelation ▪ Used Kappa for evaluation
Chapters 5 & 7	Bayesian species distribution models e.g. INLA	<ul style="list-style-type: none"> ▪ Assessed using out of sample prediction which adjusts for overfitting: WAIC ▪ Flexible, unimodal and more biologically realistic response curves ▪ iCAR models accounted for spatial autocorrelation ▪ Short processing time ▪ Produced credible intervals ▪ Only non-collinear variables used 	<ul style="list-style-type: none"> ▪ Possible collinearity between co-occurring species included as covariates ▪ Unaccounted for sampling bias ▪ One climate change scenario in Chapter 7: RCP8.5
Chapter 6	Joint species distribution models	<ul style="list-style-type: none"> ▪ Simultaneously modelled coexisting species ▪ Produced credible intervals ▪ Only non-collinear variables used 	<ul style="list-style-type: none"> ▪ Lengthy processing times ▪ MCMC techniques too time-consuming to account for spatial autocorrelation ▪ Unaccounted for sampling bias

8.5 Limitations

The present research addresses many of the biases in modelling species distributions under future climate change. However, this area of research has unavoidable limitations. First, and foremost, the taxonomic accuracy of species occurrence data is questionable given that phylogenetic relationships are constantly changing. Therefore, the results of many chapters could be affected if taxonomy were to be altered. In particular, the Ochotonidae family (pikas) are understudied and as further information comes to light on their biology, their taxonomy changes. To account for this limitation the Ochotonidae taxonomic expertise of Dr Andrey Lissovsky, Zoological Museum of Moscow State University, was enlisted with several species being considered as colour

morphs of other species – see Chapter 2. Despite this, the taxonomy of the order is in constant flux, and this needs to be considered when interpreting results. The Lagomorph Genomics (LaGomiCs) project (created at an inaugural meeting in Zagreb, Croatia in May 2014) aims to sequence the genomes of all 87 lagomorph species and 3 extinct species within five years. If successful the Lagomorpha will be the first order to have its complete genome sequenced and such data will be instrumental in definitively resolving ongoing taxonomic difficulties. In terms of species trait data, there was significant individual variation in traits which was not captured in datasets such as PanTHERIA (Jones *et al.* 2009). Intraspecific variation can be calculated using the coefficient of variation among species estimates, but only when more than one data point is available for each species – as is available for 2,761 species in the PanTHERIA dataset – but not for all traits (see Gonzalez-Suarez & Revilla, 2013). Incorporating individual variation would likely alter results, with more flexible species perhaps being less vulnerable to changes in future climate (Forsman *et al.* 2012).

The majority of methodological limitations are addressed in section 8.4, but the issue of invasive species remains. Non-native ranges for invasive lagomorphs were not included in SDMs in this thesis because invasives are not at equilibrium with their environment and their niches cannot be transferred in space and time (Gallien *et al.* 2012). However, invasive lagomorphs are extremely important, and often destructive, in a number of countries, for example, Australia. Therefore, it is important that future research considers modelling invasive distributions under climate change. In addition, there are limitations with respect to capturing interspecific interactions and inclusion in SDMs. Information on interactions from the literature, used in Chapter 4, tends to be biased towards particular taxonomic groups and researchers' preference for reporting significant effects, whilst, many other interactions may be undocumented via field observations or experiments. Capturing interactions based on co-occurrence patterns and IUCN range map data, as in Chapters 5-7, may overestimate areas of interaction, due to functional separation of interacting species' habitats, and may capture species' associations and perhaps not interactions.

Finally, assessing the influence of scale using IUCN range map data (Chapter 6) limited the discovery of potential interspecific interactions, because using this type of data will always create ranges of the same extent, even though the resolution of the

input data is altered. Neither method, using range maps or point occurrence data is without error (Pineda & Lobo, 2012) and the relationship with scale may in fact be an artefact of coarse input data, regardless of resolution, but in this study omission errors were more preferable to commission errors because only the interactions with most confidence are likely to be captured by the models. However, for these types of studies the input data to be used, the purpose of the study and quality of the data available needs considering before implementation.

8.6 Impact and directions for future research

It is hoped that this research will be useful for both lagomorph researchers and ecological modellers. The projected impacts of climate change in Chapters 3 and 7 will help inform conservation practitioners in designing effective strategies to prevent lagomorph extinctions, for example the likely extinction of *Ochotona koslowi* by the 2080s. Whereas, the improvements suggested for SDM in Chapters 3, 4, 5 and 6, particularly the inclusion of biotic factors, will advance the development of realistic models of species distributions. In addition, the combination of SDM and network analysis used in Chapter 7 will bring together work from macroecology and community ecology, which, with further improvements, could be highly advantageous in informing future conservation management.

There are many potential directions for future research based on the work presented in this thesis, both in terms of lagomorph research and SDM research. It is suggested that future lagomorph behavioural observation studies focus on areas of sympatry, particularly those areas in which *Lepus* species co-occur in a narrow contact zone or in species-rich regions (most notably, the hotspots in southern Russia on the border of Mongolia and north western USA), to increase our knowledge of interspecific interactions in the order. In addition, collection of further lagomorph occurrence data, particularly of understudied Asian pikas and African hare species, would greatly aid studies aiming to guide future conservation management.

SDM research can be advanced in many ways; one of the most important advances is extending SDMs across whole ecosystems. Using a similar approach to that in Chapter 7, but incorporating plant-soil interactions, bottom-up herbivore-plant interactions and top-down predator-prey interactions into a single network would provide a more

holistic picture of the macroecology of an ecosystem and allow better understanding of potential threats, for example, global climate change and invasive species. *In-situ* field and experimental studies will be vital in order to verify identified interactions based on co-occurrence patterns and studying interactions in their natural environment is necessary to fully understand the patterns. Exploring the inclusion of physiological and experimental data in SDM and network analysis studies would be very interesting; mechanistic modelling is at the forefront of spatial ecology and allows information related to species biology to be used when modelling distributions (Kearney & Porter, 2009). Only when models include this level of information will they be able to accurately inform future conservation management to prevent extinctions and loss of species' ranges.

8.7 Conclusions

- Climate change is likely to impact more than two-thirds of lagomorph species, with leporids (rabbits, hares and jackrabbits) likely to undertake poleward shifts with little overall change in range extent, whilst pikas are likely to show extreme shifts to higher altitudes associated with marked range declines.
- Bibliometric data can provide insights into species interactions, which along with abiotic determinants, are known to limit species' distributions. Closely related, large-bodied, similarly sized species occurring in regions of human-modified, typically agricultural landscapes, or at high elevations are significantly more likely to have reported competitive interactions than other lagomorph species.
- Environmental and interspecific effects appeared equally important as determinants of lagomorph ranges, and inclusion of both increased the predictive ability of models, but the influences of environmental and interspecific interactions were spatially heterogeneous.
- Spatial scale is a major concern inherent in SDM and strongly influenced lagomorph co-occurrence patterns estimated from Joint SDMs. These multi-species distribution models produced very precise estimates of environmental and interspecific interaction effects on a continental and fine scale resolution, but required a considerable amount of time and processing power to run and produced similar results to models run at coarser resolutions.
- Projected future climate change will likely have tremendous impacts on lagomorph ecological communities, including potentially advantageous effects such as increased stability and adverse effects such as substantial changes in species composition.
- Studying the impacts of climate change at a species-level can be very informative, but identifying community-level responses, whilst accounting for interspecific interactions, are likely to provide more reliable estimates of the impacts of projected future climate change.

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Appendices

Appendix 1. Species accounts

Species accounts (#1-89)

Key for response curves

Abbreviation	Description
HII	Human Influence index
Hilliness	Surface Roughness index
MaxPrec	Maximum precipitation
MaxTemp	Maximum temperature
MinPrec	Minimum precipitation
MinTemp	Minimum temperature
PrecSea	Precipitation seasonality
RealMAR	Mean annual precipitation
RealMAT	Mean annual temperature
TempSea	Temperature seasonality
etpsum	Annual evapotranspiration
ndvi	Normalised difference vegetation index
radiation	Solar radiation
wbann	Annual water balance
wbpos	Number of months with a positive water balance

The past and current occurrence records underlying these species accounts can be viewed on <http://lagomorphclimatechange.wordpress.com/>.

#1 - Pygmy rabbit (*Brachylagus idahoensis*)

n = 39

Expert: Penny Becker, Washington Dept. of Fish & Wildlife, USA

Expert evaluation: Medium

Data: Modern and historic

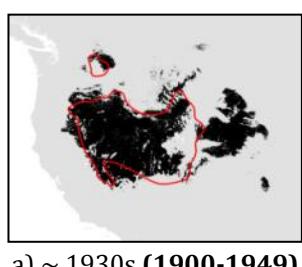
Envelope: Climatic and habitat

Dispersal distance: 15km/year (Expert)

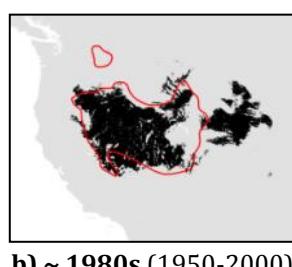
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.90
Specificity	1.00
Proportion correct	1.00
Kappa	0.75
True Skill Statistic	0.90

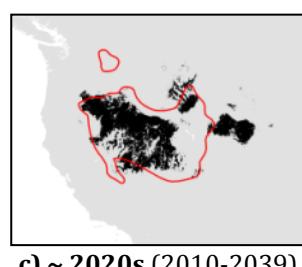
Summary: The Pygmy rabbit's bioclimatic envelope is predicted to decline by 87% with a 1° mean latitudinal poleward shift and mean increase in elevation of ~300m driven predominately by an increase in mean minimum elevation (>600m) with little change in mean maximum elevation (~50m). 95% of the permutation importance of the model was contributed to by mean annual temperature (64.5%), maximum temperature (25.2%) and annual water balance (5.9%).



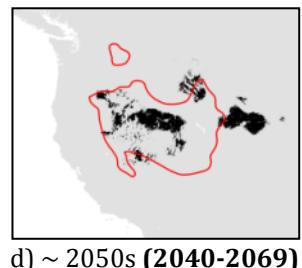
a) ~1930s (1900-1949)



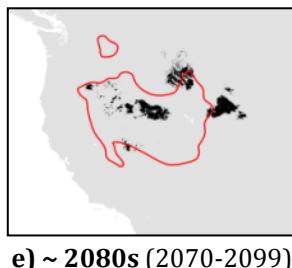
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



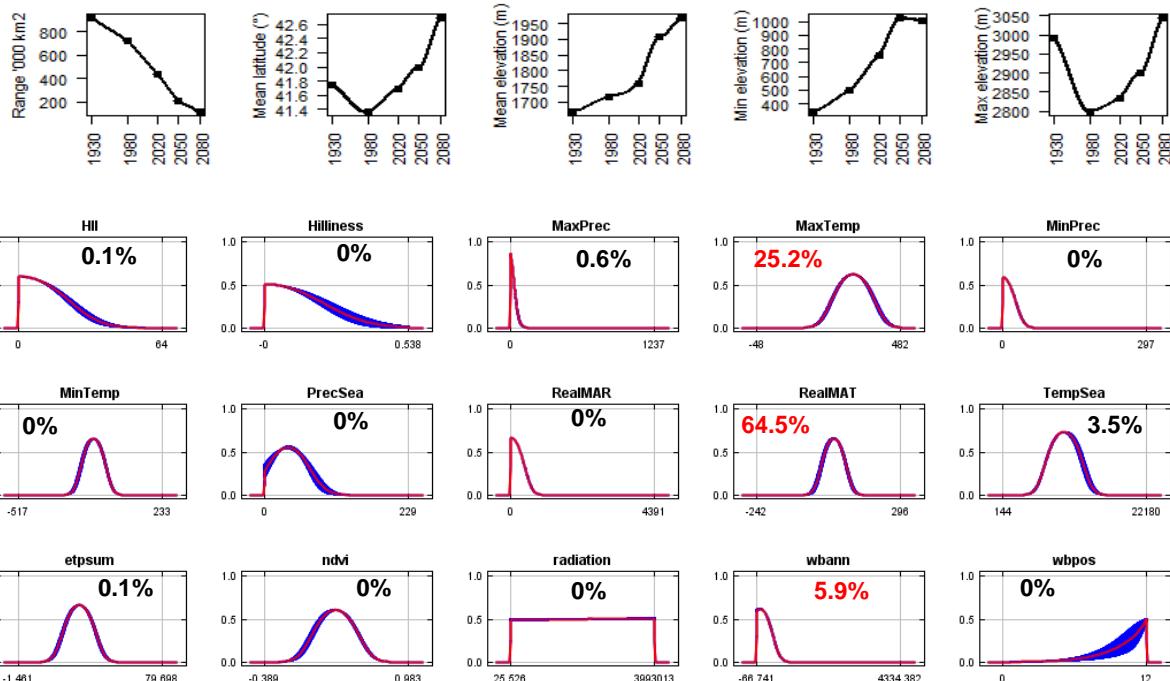
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Beauvais GP, et al. 2008)



#2 - Riverine rabbit (*Bunolagus monticularis*)

n = 109

Status: Kai Collins, University of Pretoria, South Africa

Expert evaluation: Good

Data: Modern and historic

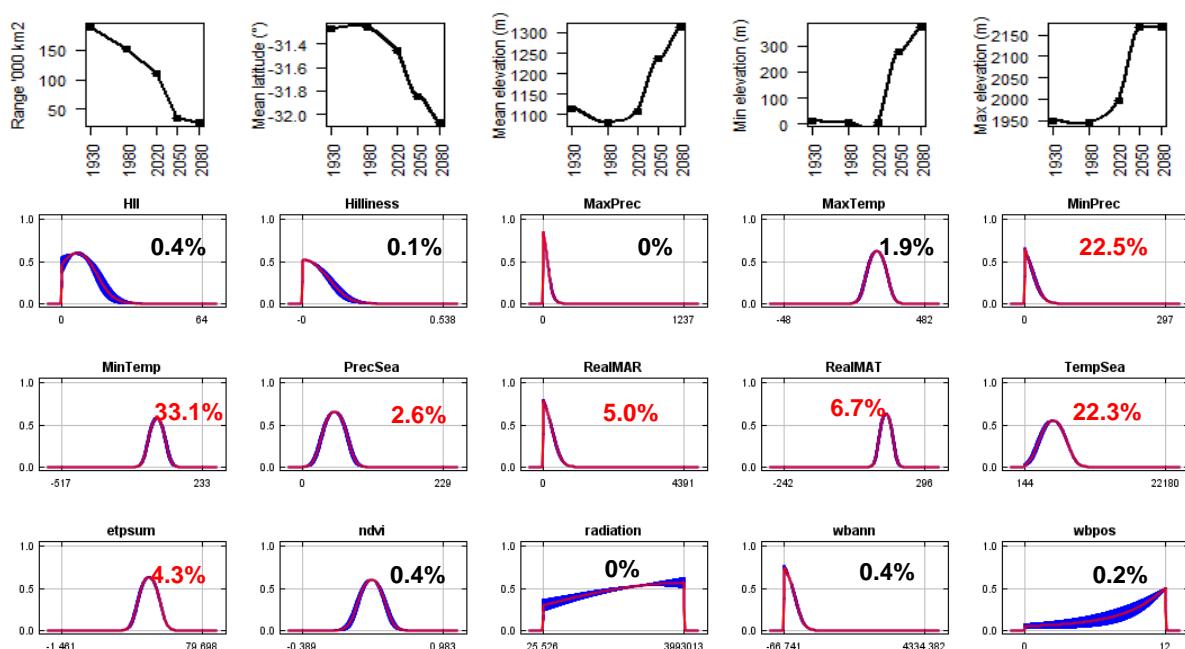
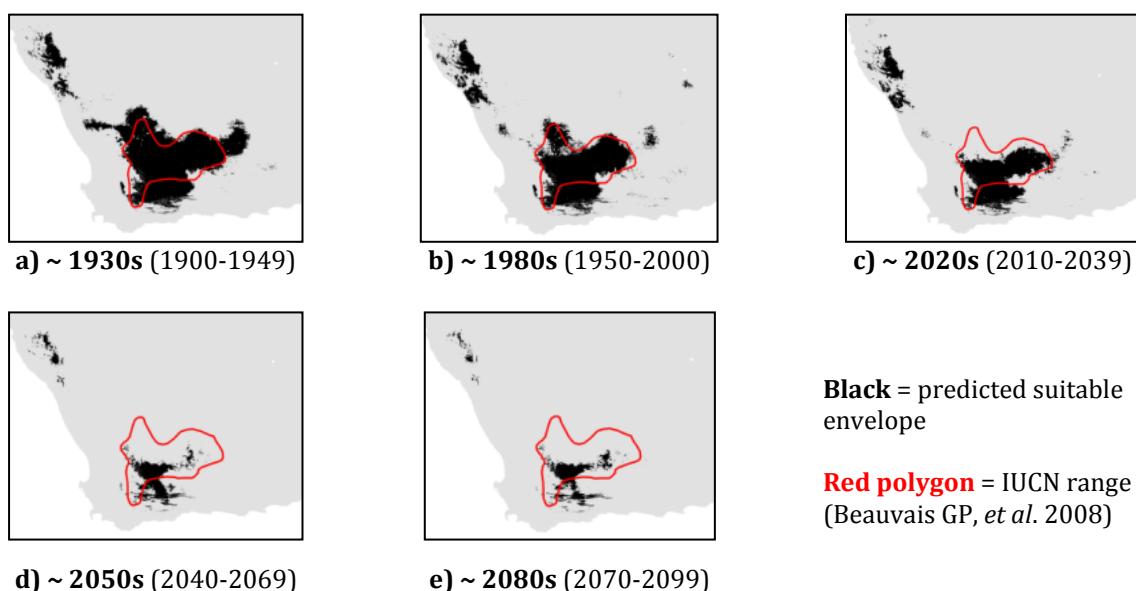
Envelope: Climatic and habitat

Dispersal distance: 7.5km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.98
Omission rate	0.03
Sensitivity	0.97
Specificity	1.00
Proportion correct	1.00
Kappa	0.85
True Skill Statistic	0.97

Summary: The Riverine rabbit's bioclimatic envelope is predicted to decline by 85% with a ~1° mean latitudinal poleward shift and mean increase in elevation of ~200m driven by similar increases in both minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by minimum temperature (33.1%) and precipitation (22.5%), temperature seasonality (22.3%), mean annual temperature (6.7%) and precipitation (5.0%), annual evapotranspiration (4.3%) and precipitation seasonality (2.6%).



#3 - Hispid hare (*Caprolagus hispidus*)

n = 18

Expert: Gopinathan Maheswaran, Zoological Survey India

Expert evaluation: Medium

Data: Modern and historic

Envelope: Climatic and habitat

Dispersal distance: 5km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.97
Omission rate	0.06
Sensitivity	0.94
Specificity	0.99
Proportion correct	0.99
Kappa	0.81
True Skill Statistic	0.94

Summary: The Hispid hare's bioclimatic envelope is predicted to increase by 21% with a ~1.5° mean latitudinal poleward shift and mean increase in elevation of ~70m driven by increases in maximum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (52.7%), precipitation seasonality (29.0%), annual evapotranspiration (6.6%), number of months with a positive water balance (2.9%), maximum precipitation (2.2%) and minimum temperature (1.7%).



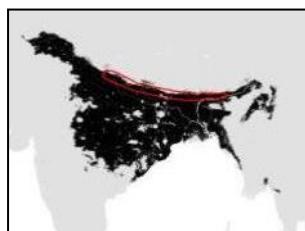
a) ~1930s (1900-1949)



b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



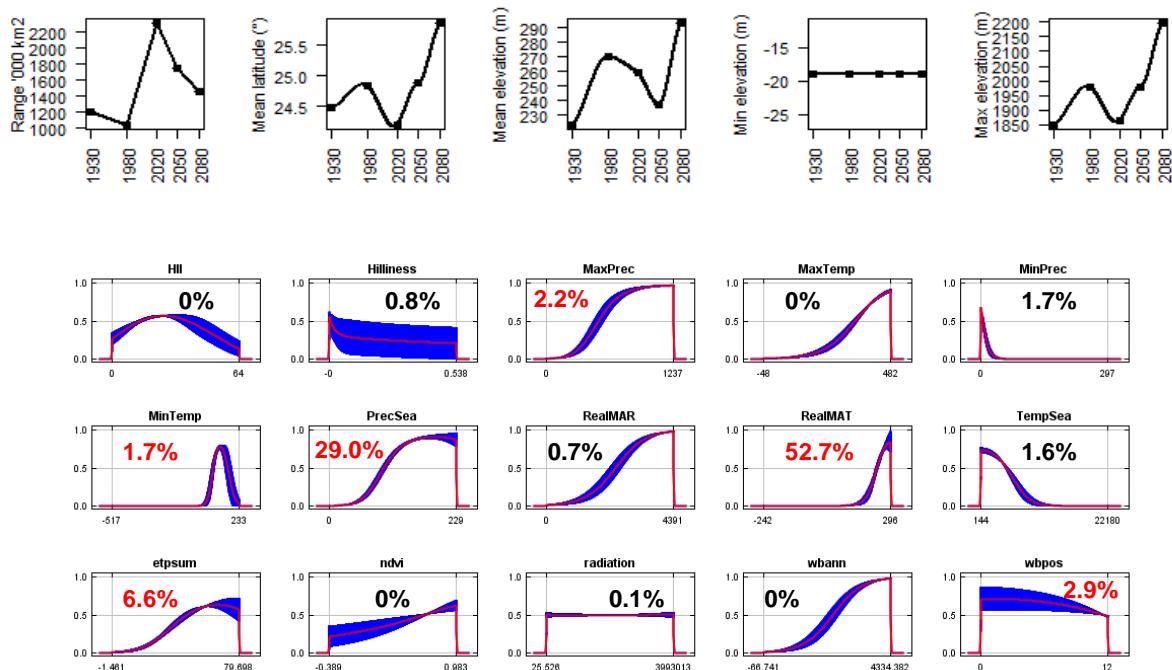
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Maheswaran, G. & Smith, A.T. 2008)



#4 – Antelope jackrabbit (*Lepus alleni*)

n = 32

Expert: Paul Krausman , University of Montana

Expert evaluation: Medium

Data: Modern and historic

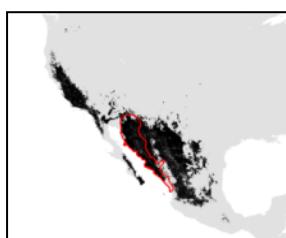
Envelope: Climatic and habitat

Dispersal distance: 25km/year (Expert)

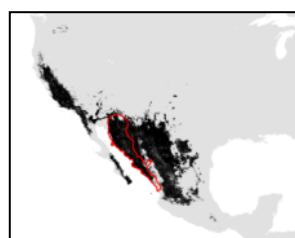
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.91
Omission rate	0.16
Sensitivity	0.84
Specificity	0.99
Proportion correct	0.98
Kappa	0.26
True Skill Statistic	0.83

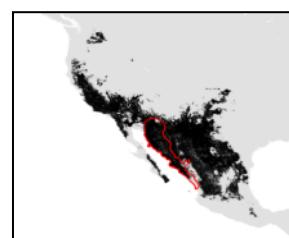
Summary: The Antelope jackrabbit's bioclimatic envelope is predicted to increase by 172% with a ~3° mean latitudinal poleward shift and mean increase in elevation of ~20m driven by increases in maximum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (24.8%), minimum precipitation (21.1%), annual water balance (16.3%), minimum temperature (13.0%), temperature seasonality (7.3%), normalised difference vegetation index (5.8%), annual evapotranspiration (5.2%) and human influence index (3.7%).



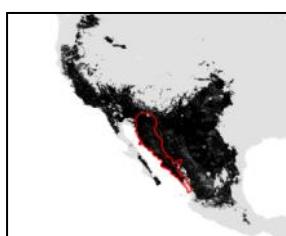
a) ~1930s (1900-1949)



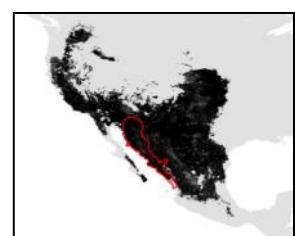
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



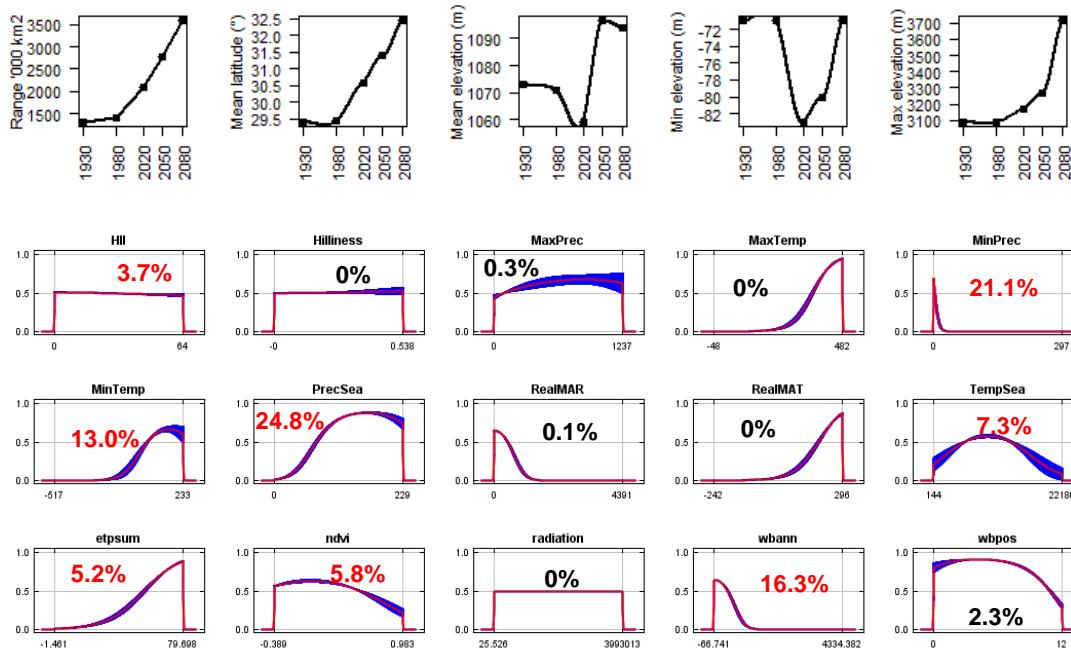
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range (Malpica, F.J. & Rangel Cordero, H. 2008)



#5 – Snowshoe hare (*Lepus americanus*)

n = 506

Expert: Charles Krebs, University of British Columbia & Rudy Boonstra, University of Toronto Scarborough

Expert evaluation: Good

Data: Only modern

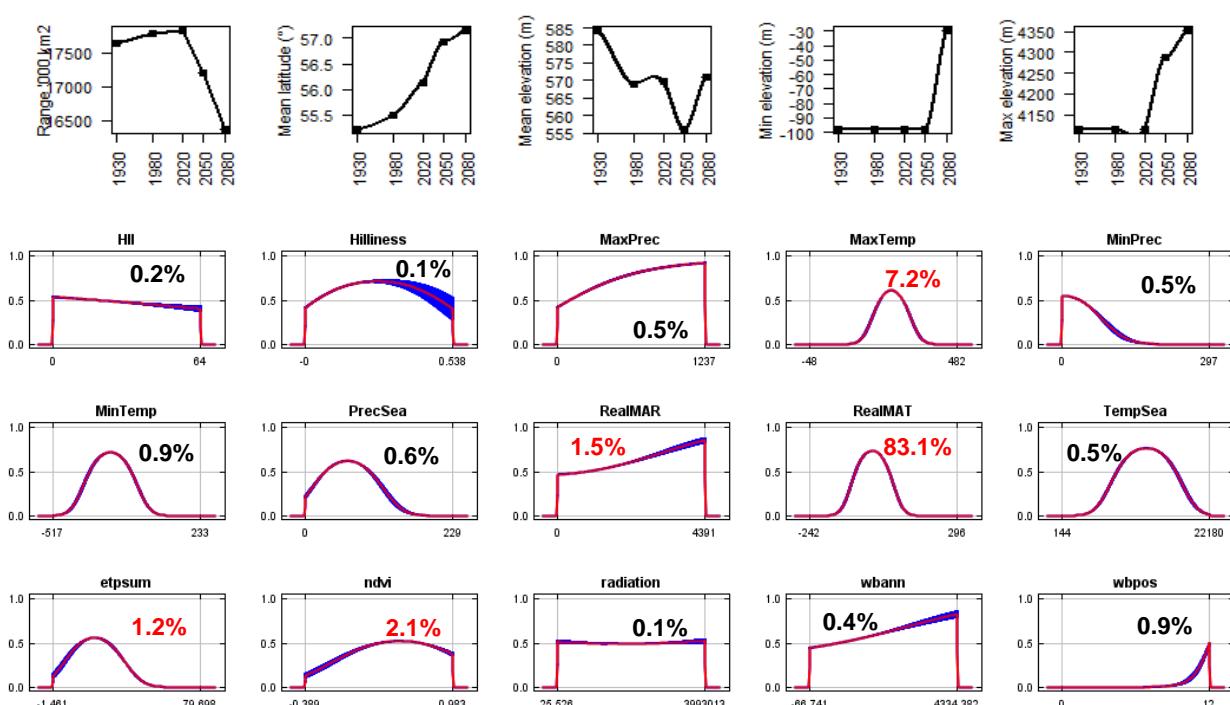
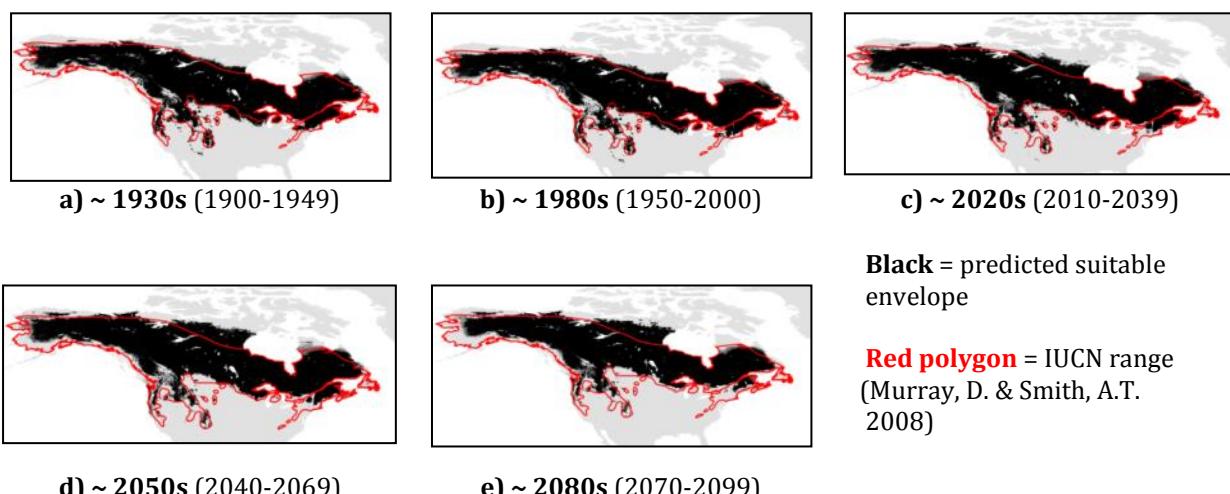
Envelope: Climatic and habitat

Dispersal distance: 24km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.95
Omission rate	0.07
Sensitivity	0.93
Specificity	0.97
Proportion correct	0.97
Kappa	0.72
True Skill Statistic	0.90

Summary: The Snowshoe hare's bioclimatic envelope is predicted to decline by 7% with a ~2° mean latitudinal poleward shift and mean decrease in elevation of ~10m, but with increases in both minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (83.1%), maximum temperature (7.2%), normalised difference vegetation index (2.1%), mean annual precipitation (1.5%) and annual evapotranspiration (1.2%).



#6 – Arctic hare (*Lepus arcticus*)

n = 18

Expert: David Gray, Grayhound Information Services

Expert evaluation: Poor

Data: Modern and historic

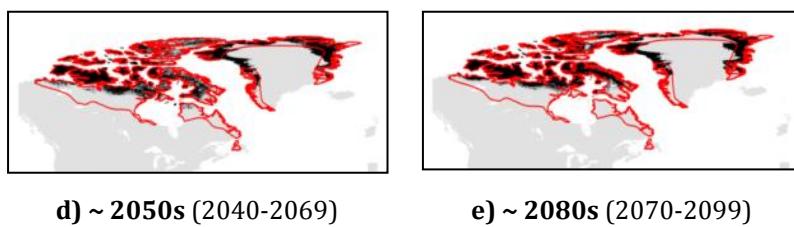
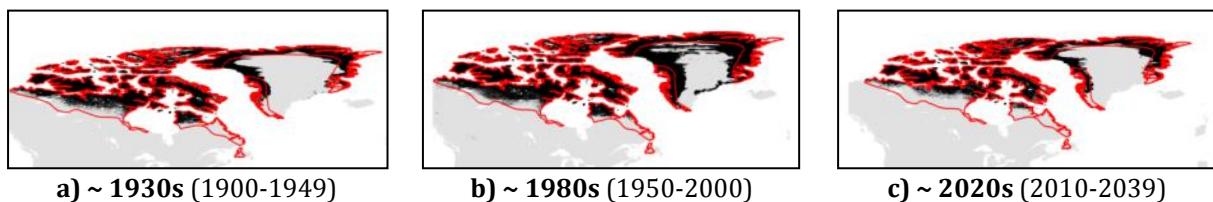
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Chapman & Flux, 1990)

Status: UNMODELLABLE; Included in final analysis: X

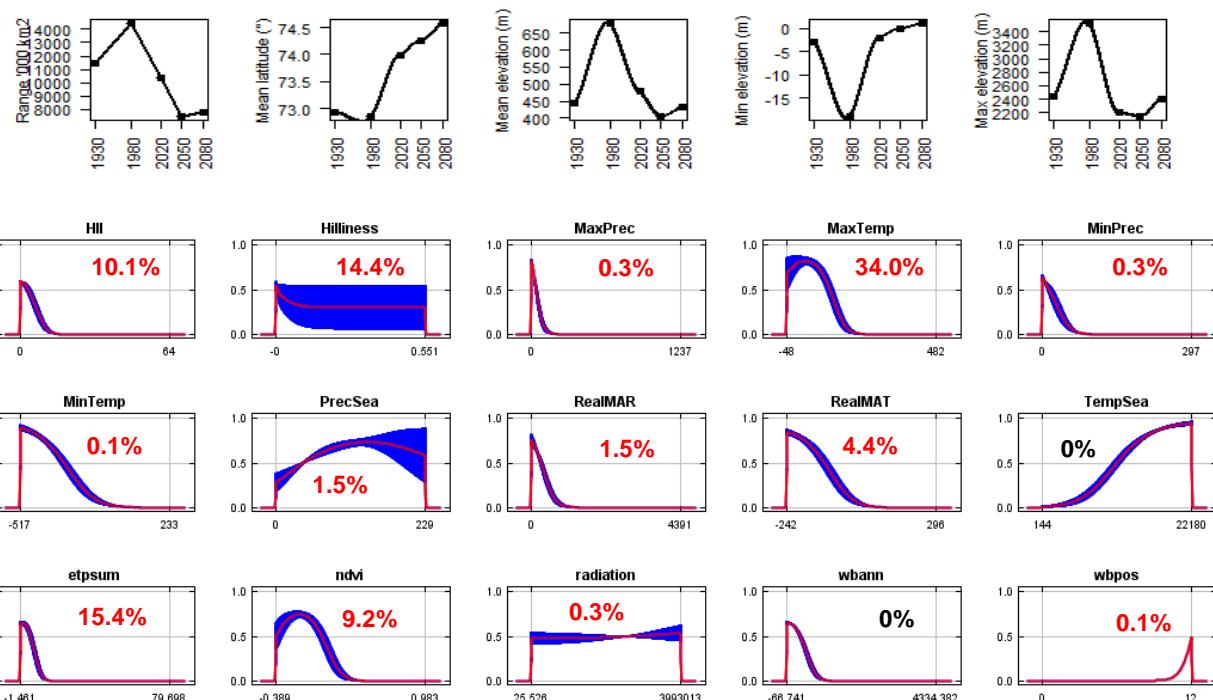
Model evaluation metric	
AUC	0.97
Omission rate	0.06
Sensitivity	0.94
Specificity	0.99
Proportion correct	0.99
Kappa	0.36
True Skill Statistic	0.94

Summary: The Arctic hare's bioclimatic envelope is predicted to decline by 30% with a ~2° mean latitudinal poleward shift and mean decrease in elevation of ~10m driven by decreases in maximum elevation. 95% of the permutation importance of the model was contributed to by maximum temperature (34.0%), annual evapotranspiration (15.4%), surface roughness index (14.4%), human influence index (10.1%), normalised difference vegetation index (9.2%), mean annual temperature (4.4%), precipitation seasonality (1.5%), mean annual precipitation (1.5%), maximum precipitation (0.3%), minimum precipitation (0.3%), solar radiation (0.3%), minimum temperature (0.1%) and number of months with a positive water balance (0.1%).



Black = predicted suitable envelope

Red polygon = IUCN range
(Murray, D. & Smith, A.T. 2008)



#7 – Japanese hare (*Lepus brachyurus*)

n = 9

Expert: Koji Shimano, Shinshu University, Japan

Expert evaluation: Medium

Data: Modern and historic

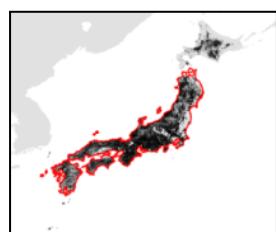
Envelope: Climatic and habitat

Dispersal distance: 1km/year (Expert)

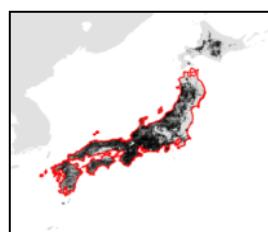
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.43
True Skill Statistic	0.99

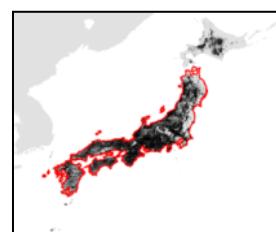
Summary: The Japanese hare's bioclimatic envelope is predicted to increase by 9% with no latitudinal poleward shift and a mean increase in elevation of ~10m driven by a decrease in minimum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (31.8%), annual water balance (20.6%), human influence index (13.5%), mean annual precipitation (8.9%), maximum precipitation (6.2%), precipitation seasonality (5.4%) and minimum precipitation (4.4%).



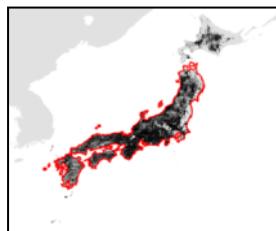
a) ~1930s (1900-1949)



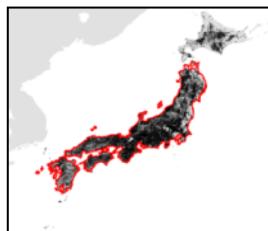
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



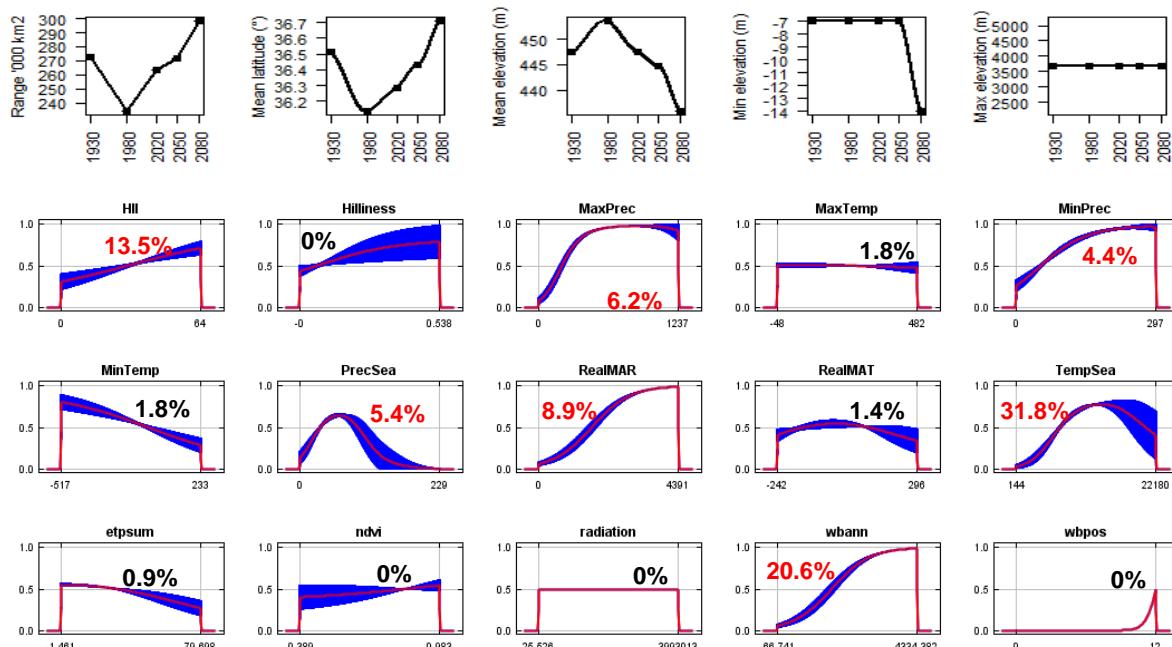
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Yamada, F. & Smith, A.T.
2008)



#8 – Black-tailed jackrabbit (*Lepus californicus*)

n = 970

Expert: Alejandro Velasquez, UNAM-Canada

Expert evaluation: Medium

Data: Modern and historic

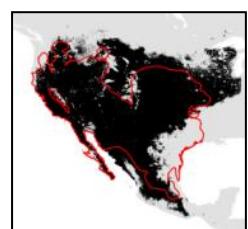
Envelope: Climatic and habitat

Dispersal distance: 18.9km/year (N.Am. leporids, range 2-25)

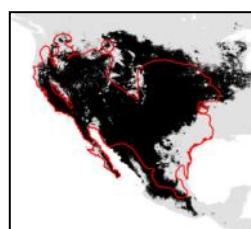
Status: MODELLABLE; **Included in final analysis:** ✓

Model evaluation metric	
AUC	0.93
Omission rate	0.07
Sensitivity	0.93
Specificity	0.94
Proportion correct	0.94
Kappa	0.69
True Skill Statistic	0.87

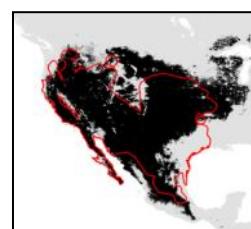
Summary: The Black-tailed jackrabbit's bioclimatic envelope is predicted to decline by 25% with a ~2° mean latitudinal poleward shift and mean decrease in elevation of ~75m, but with increases in both minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (31.8%), annual evapotranspiration (18.5%), maximum temperature (17.0%), mean annual temperature (8.9%), minimum temperature (8.0%), minimum precipitation (4.0%), human influence index (3.9%) and temperature seasonality (3.5%).



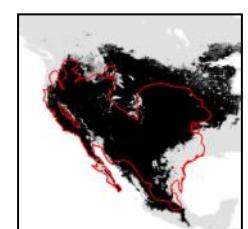
a) ~ 1930s (1900-1949)



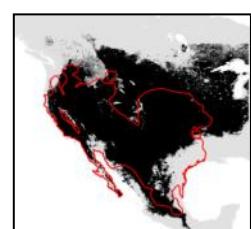
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



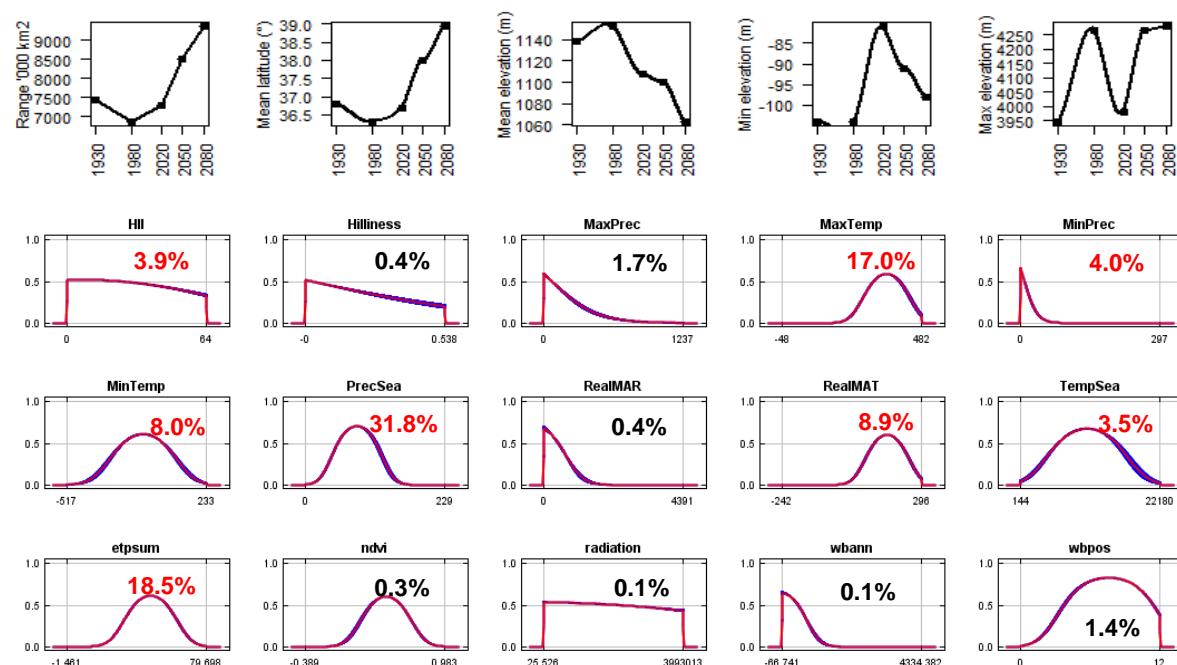
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Romero Malpica, F.J. & Rangel Cordero, H. 2008)



#9 – White-sided jackrabbit (*Lepus callotis*)

n = 37

Expert: Jennifer Frey, New Mexico State University

Expert evaluation: Medium

Data: Modern and historic

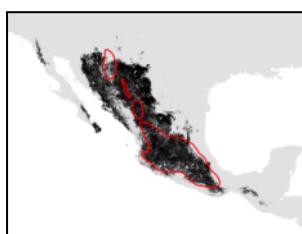
Envelope: Climatic and habitat

Dispersal distance: 18.9km/year (N.Am. leporids, range 2-25)

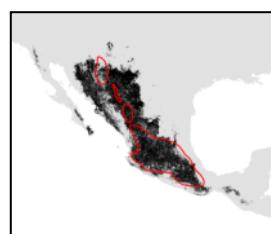
Status: UNMODELLABLE; **Included in final analysis:** X

Model evaluation metric	
AUC	0.97
Omission rate	0.05
Sensitivity	0.95
Specificity	0.99
Proportion correct	0.99
Kappa	0.36
True Skill Statistic	0.93

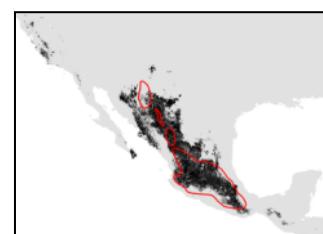
Summary: The White-sided jackrabbit's bioclimatic envelope is predicted to increase by 3% with a ~1° mean latitudinal poleward shift and a mean increase in elevation of ~150m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (35.4%), annual evapotranspiration (22.3%), minimum temperature (17.0%), mean annual temperature (10.5%), minimum precipitation (6.5%), maximum precipitation (6.5%), surface roughness index (3.0%) and number of months with a positive water balance (2.7%).



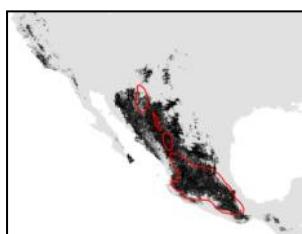
a) ~ 1930s (1900-1949)



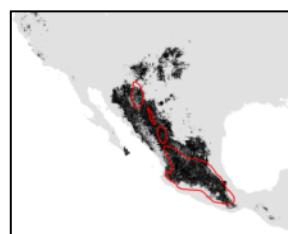
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



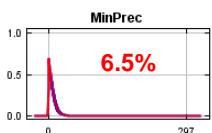
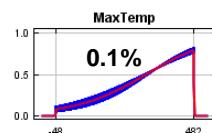
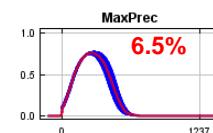
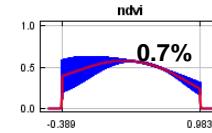
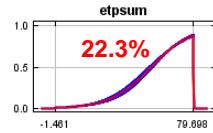
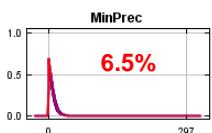
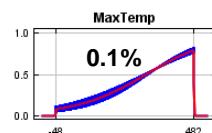
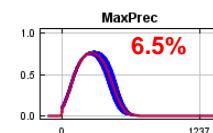
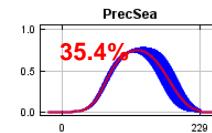
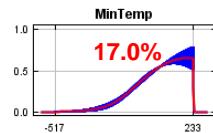
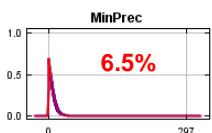
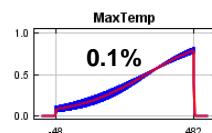
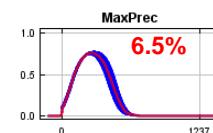
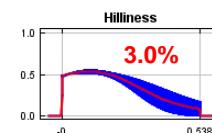
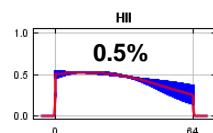
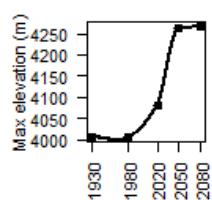
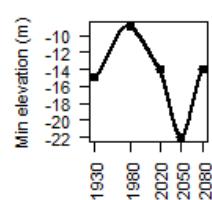
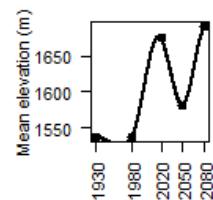
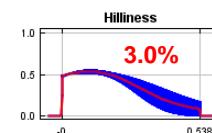
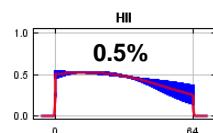
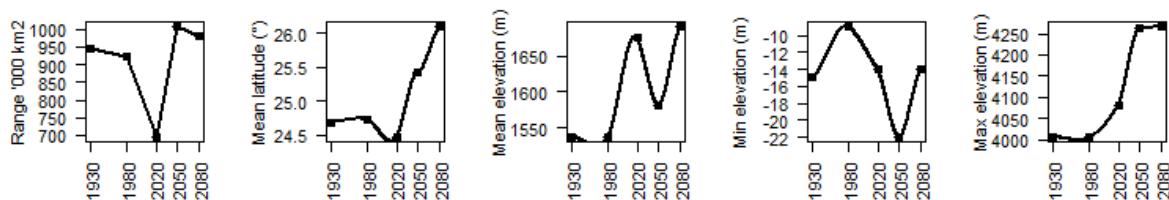
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Romero Malpica, F.J. & Rangel Cordero, H. 2008)



#10 – Cape hare (*Lepus capensis*)

n = 231

Expert: John Flux, IUCN Lagomorph Specialist Group

Expert evaluation: Poor

Data: Modern and historic

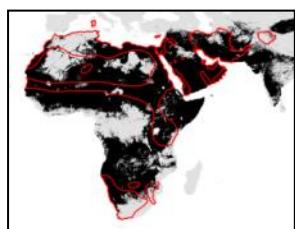
Envelope: Climatic and habitat

Dispersal distance: 35km/year (Expert)

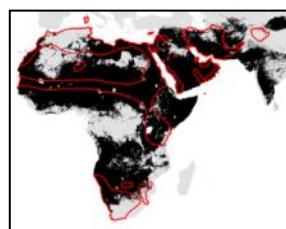
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.93
Omission rate	0.10
Sensitivity	0.90
Specificity	0.97
Proportion correct	0.97
Kappa	0.56
True Skill Statistic	0.87

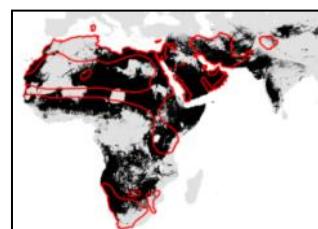
Summary: The Cape hare's bioclimatic envelope is predicted to decrease by 45% with ~2° mean latitudinal shift towards the Equator and a mean increase in elevation of ~330m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (33.1%), minimum precipitation (29.6%), maximum temperature (9.7%), human influence index (7.2%), normalised difference vegetation index (4.6%), minimum temperature (3.2%), number of months with a positive water balance (2.9%), maximum precipitation (2.2%), mean annual precipitation (2.1%) and precipitation seasonality (2.0%).



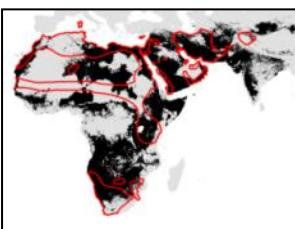
a) ~1930s (1900-1949)



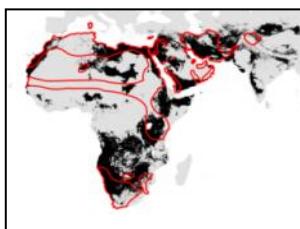
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



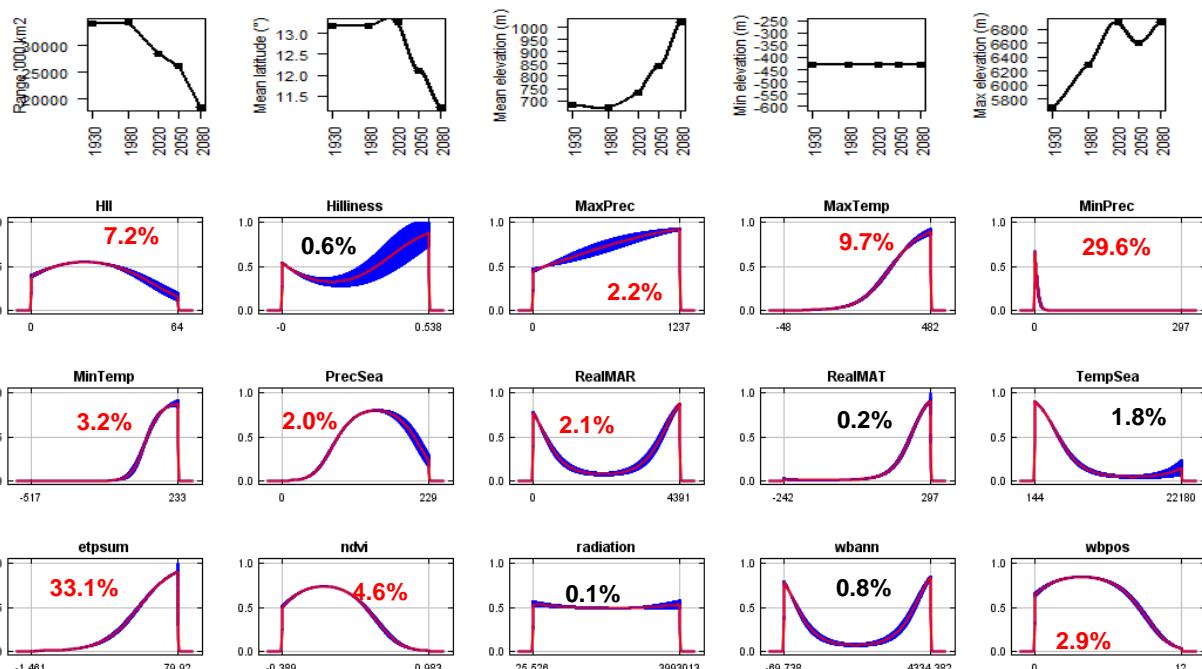
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range (Drew, C., et al. 2008)



#11 – Broom hare (*Lepus castroviejoi*)

n = 164

Expert: Pelayo Acevedo, University of Porto

Expert evaluation: Medium

Data: Only modern

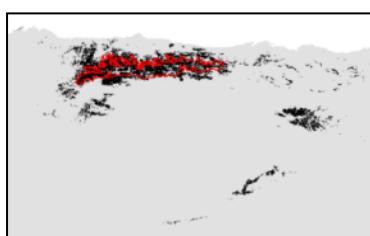
Envelope: Climatic and habitat

Dispersal distance: 1km/year (Expert)

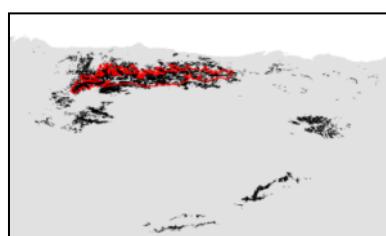
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.94
Omission rate	0.11
Sensitivity	0.89
Specificity	0.99
Proportion correct	0.99
Kappa	0.80
True Skill Statistic	0.89

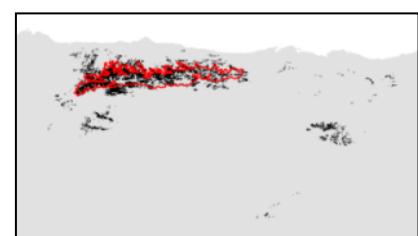
Summary: The Broom hare's bioclimatic envelope is predicted to decrease by 90% with a ~0.2° mean latitudinal poleward shift and a mean increase in elevation of ~450m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (62.0%), maximum temperature (20.6%), temperature seasonality (10.9%) and surface roughness index (3.8%).



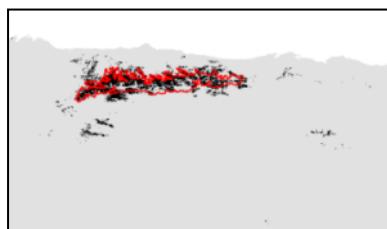
a) ~1930s (1900-1949)



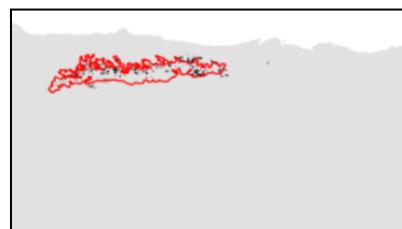
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



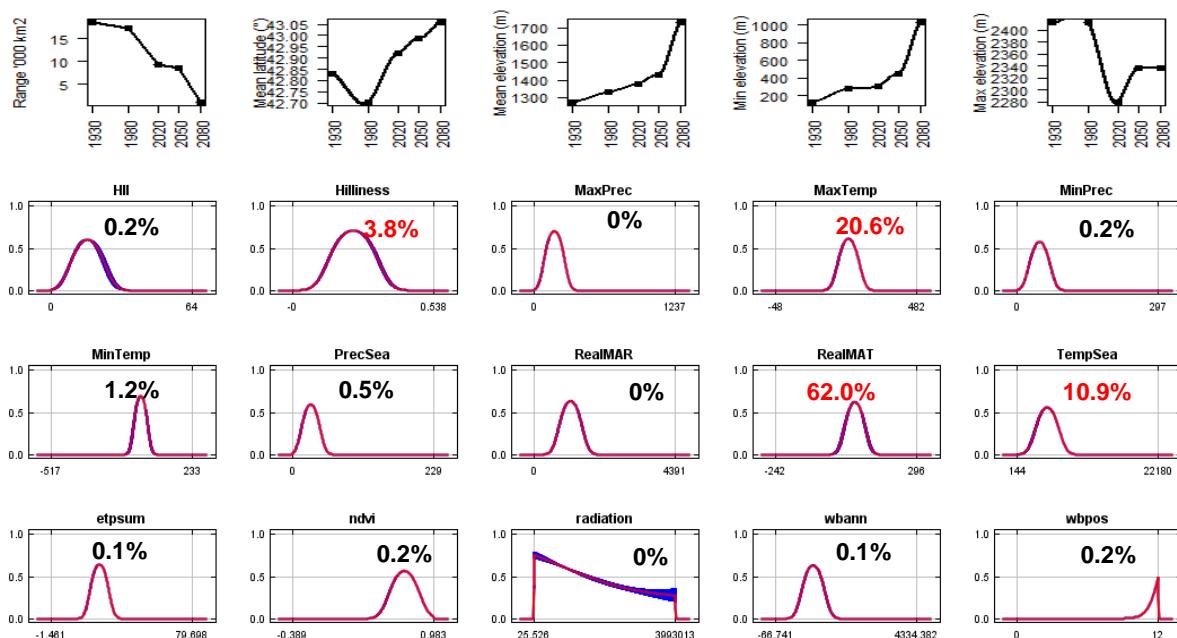
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#12 – Yunnan hare (*Lepus comus*)

n = 59

Expert: Weihe Yang, Institute of Zoology, Chinese Academy of Sciences

Expert evaluation: Medium

Data: Modern and historic

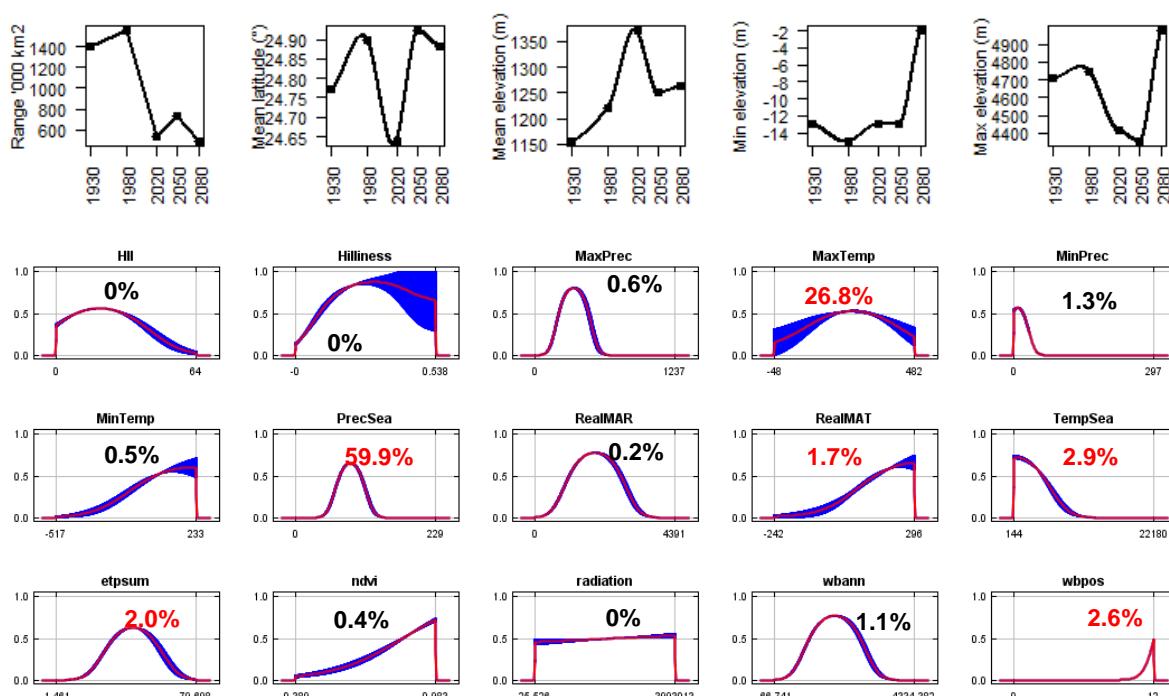
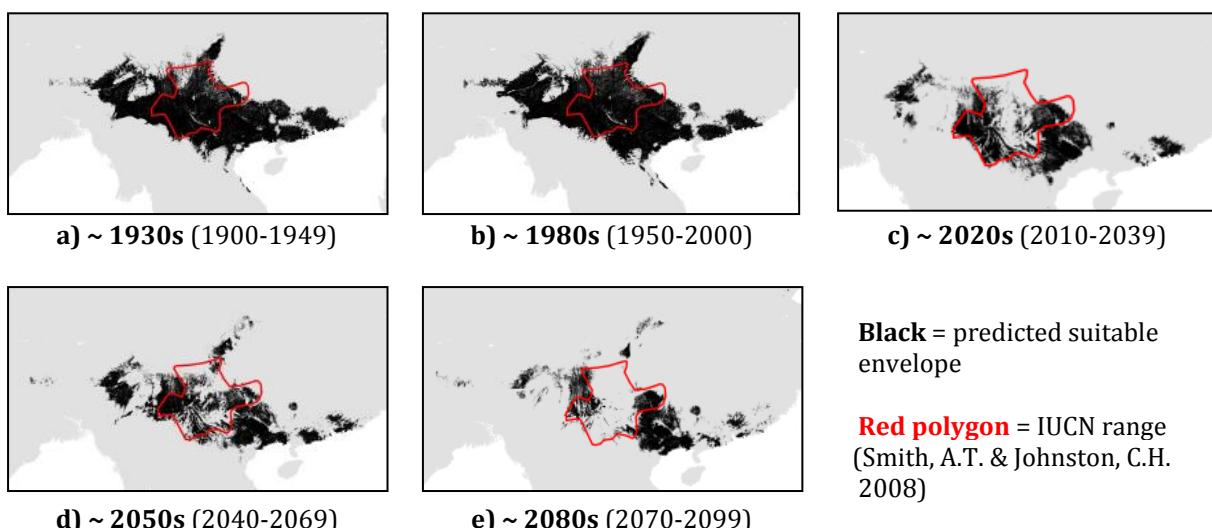
Envelope: Climatic and habitat

Dispersal distance: 2.5km/year (Asian leporids, range 1-35)

Status: MODELLABLE; **Included in final analysis:** ✓

Model evaluation metric	
AUC	0.92
Omission rate	0.15
Sensitivity	0.85
Specificity	0.99
Proportion correct	0.99
Kappa	0.67
True Skill Statistic	0.84

Summary: The Yunnan hare's bioclimatic envelope is predicted to decrease by 65% with a ~0.1° mean latitudinal poleward shift and a mean increase in elevation of ~100m driven by both increases in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (59.9%), maximum temperature (26.8%), temperature seasonality (2.9%), number of months with a positive water balance (2.6%), annual evapotranspiration (2.0%) and mean annual temperature (1.7%).



#13 – Korean hare (*Lepus coreanus*)

n = 6

Expert: Weihe Yang, Institute of Zoology, Chinese Academy of Sciences

Expert evaluation: Medium

Data: Modern and historic

Envelope: Climatic and habitat

Dispersal distance: 2.5km/year (Asian leporids, range 1-35)

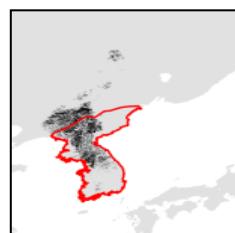
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.86
True Skill Statistic	0.99

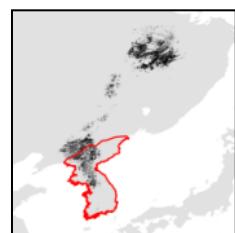
Summary: The Korean hare's bioclimatic envelope is predicted to increase by 500% with a ~8° mean latitudinal poleward shift and a mean increase in elevation of ~70m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (27.2%), mean annual precipitation (25.6%), minimum temperature (17.7%), annual water balance (13.1%), normalised difference vegetation index (4.7%) and precipitation seasonality (4.5%) and human influence index (2.4%).



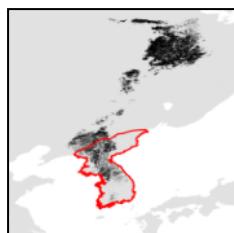
a) ~ 1930s (1900-1949)



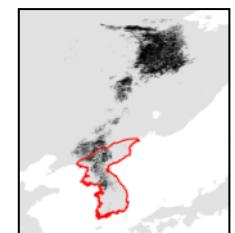
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



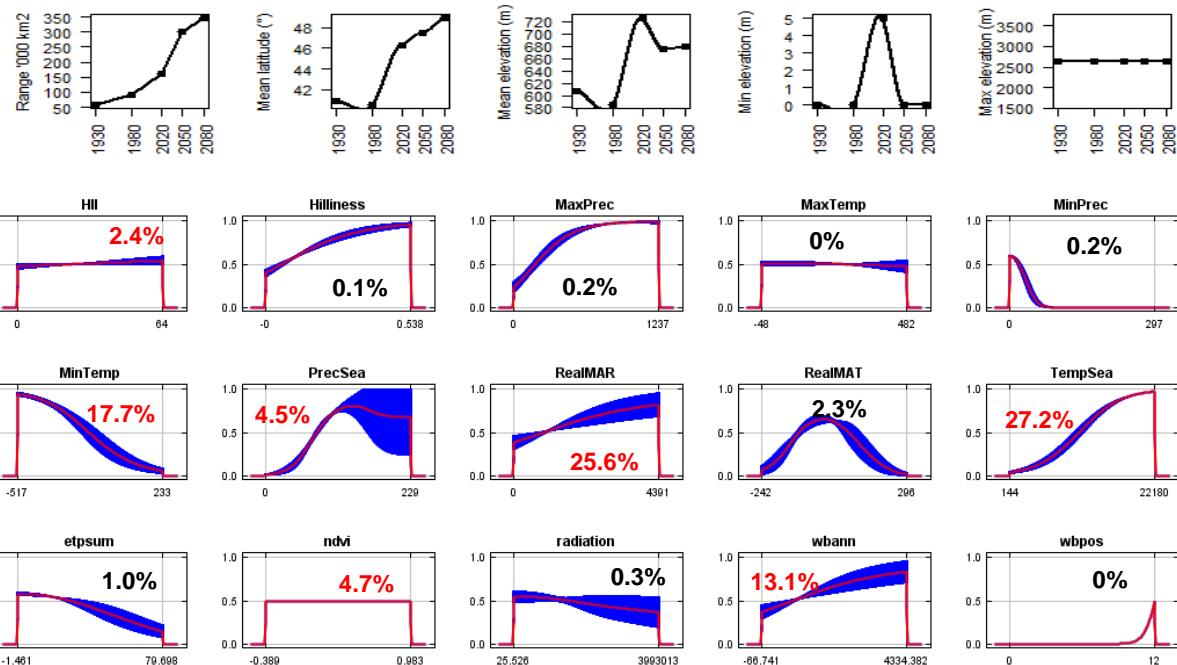
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#14 – Apennine hare (*Lepus corsicanus*)

n = 59

Expert: Francesco Angelici, Italian Foundation of Vertebrate Zoology

Expert evaluation: Medium

Data: Only modern

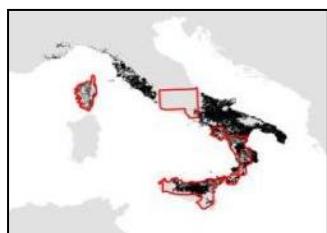
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Expert)

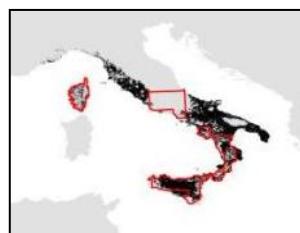
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.53
True Skill Statistic	0.99

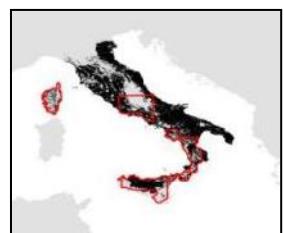
Summary: The Apennine hare's bioclimatic envelope is predicted to increase by 125% with a ~2° mean latitudinal poleward shift and a mean decrease in elevation of ~60m. 95% of the permutation importance of the model was contributed to by minimum temperature (37.9%), annual evapotranspiration (34.3%), temperature seasonality (11.4%), minimum precipitation (11.1%) and maximum temperature (2.8%).



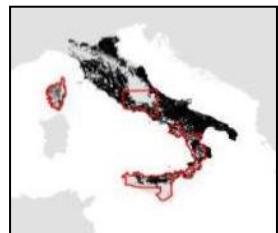
a) ~ 1930s (1900-1949)



b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



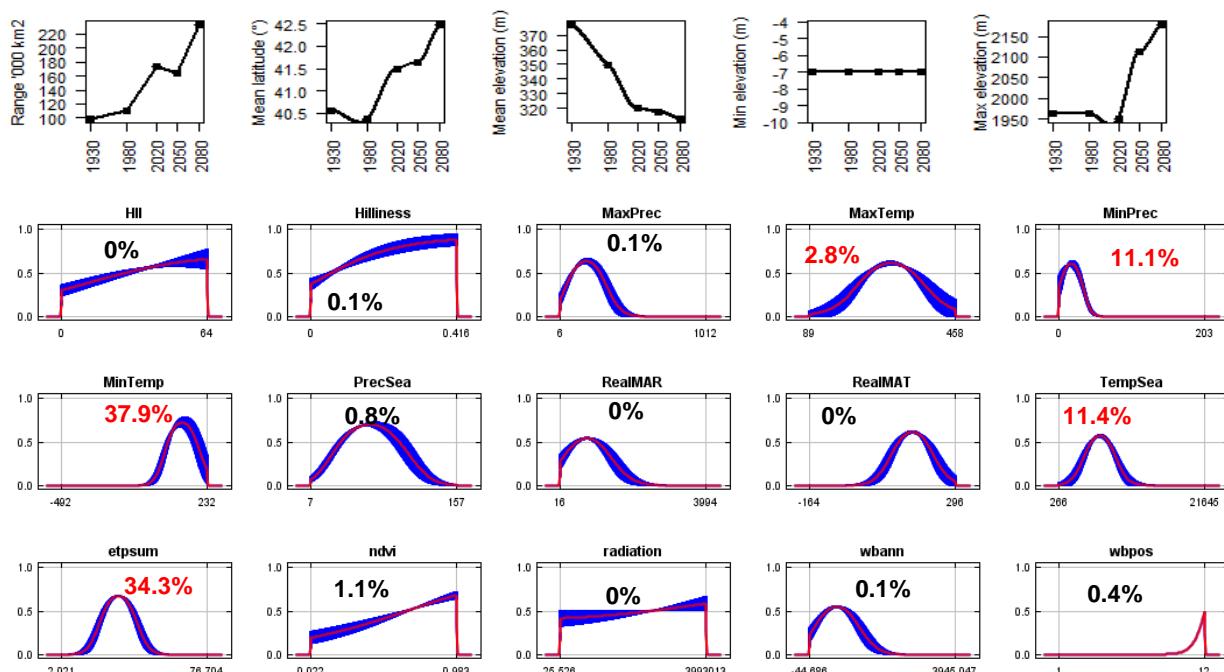
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Angelici, F.M., Randi, E., Riga, F. & Trocchi, V. 2008)



#15 – European hare (*Lepus europaeus*)-native range only

n = 6,186

Expert: Neil Reid, Queen's University Belfast

Expert evaluation: Medium

Data: Only modern

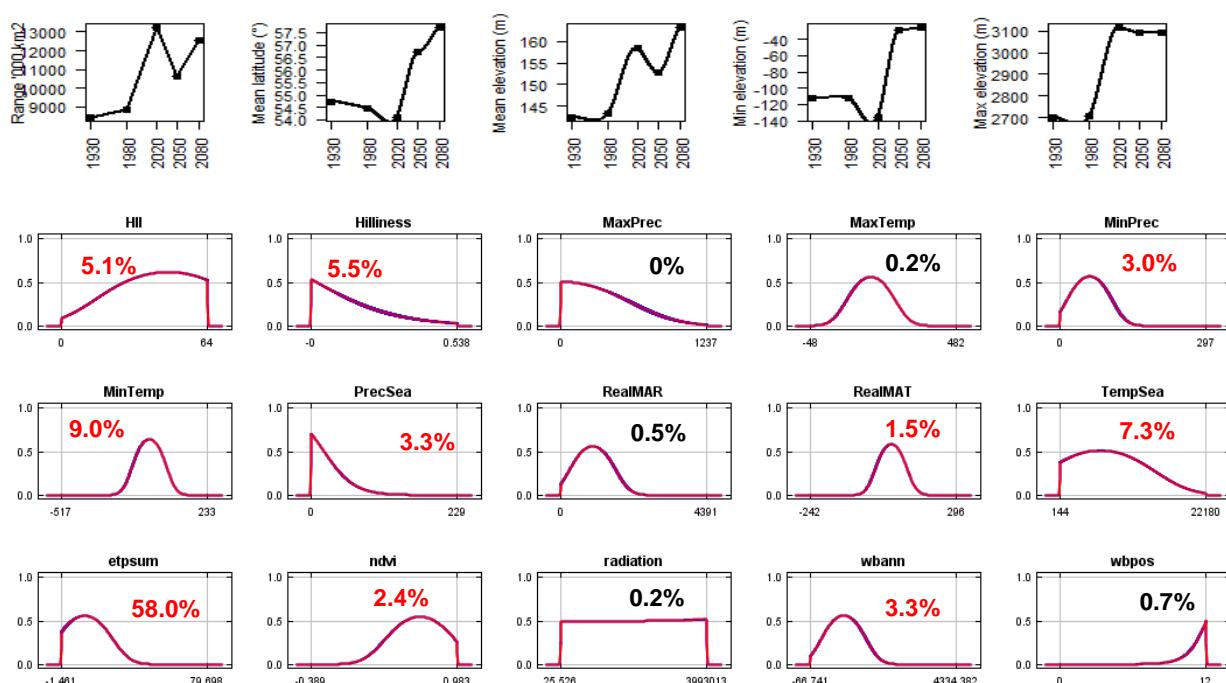
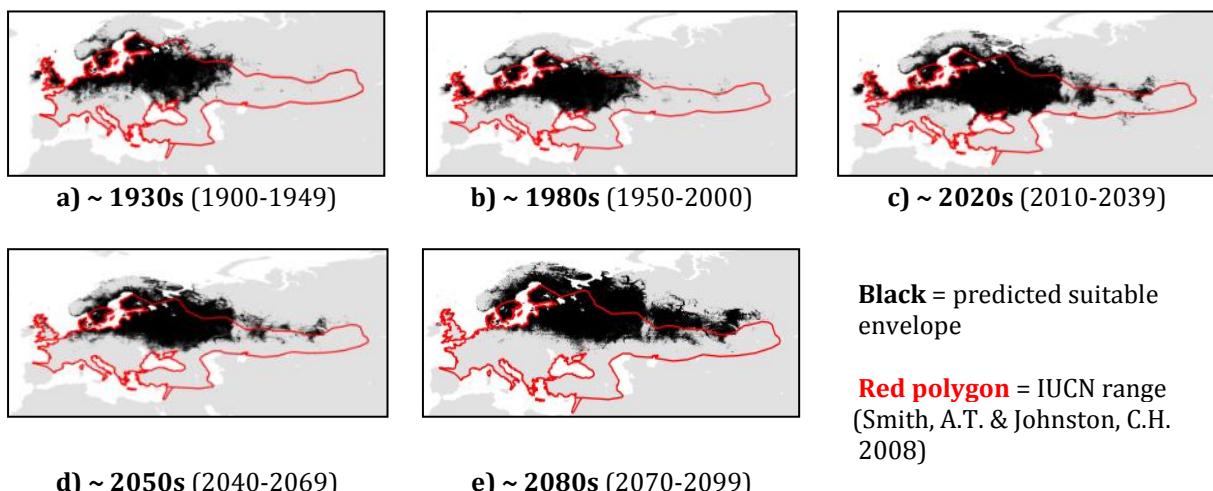
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Chapman & Flux, 1990)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.81
Omission rate	0.07
Sensitivity	0.93
Specificity	0.69
Proportion correct	0.78
Kappa	0.57
True Skill Statistic	0.62

Summary: The European hare's bioclimatic envelope is predicted to increase by 50% with a ~3° mean latitudinal poleward shift and a mean increase in elevation of ~20m driven by an increase in both maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (58.0%), minimum temperature (9.0%), temperature seasonality (7.3%), surface roughness index (5.5%), human influence index (5.1%), precipitation seasonality (3.3%), annual water balance (3.3%), minimum precipitation (3.0%), normalised difference vegetation index (2.4%) and mean annual temperature (1.5%).



#16 – Ethiopian hare (*Lepus fagani*)

n = 9

Expert: Zelalem Tolesa, Addis Ababa University

Expert evaluation: Poor

Data: Modern and historic

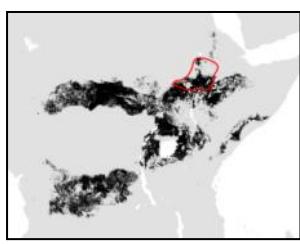
Envelope: Climatic and habitat

Dispersal distance: 25km/year (African leporids, range 15-35)

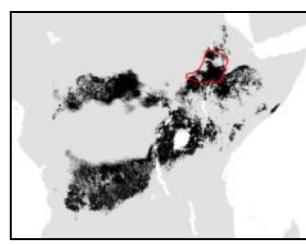
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.56
True Skill Statistic	0.99

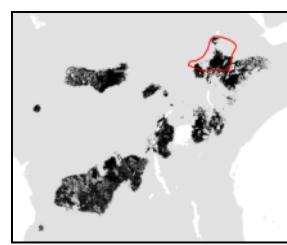
Summary: The Ethiopian hare's bioclimatic envelope is predicted to decrease by 15% with no latitudinal poleward shift and a mean increase in elevation of ~200m driven by an increase in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (92.7%) and annual evapotranspiration (5.3%).



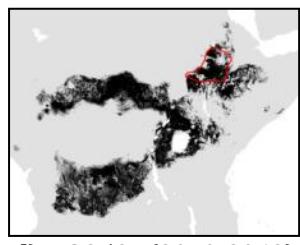
a) ~1930s (1900-1949)



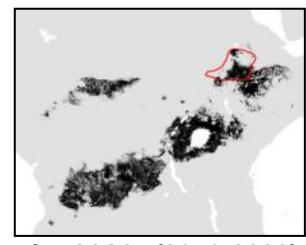
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



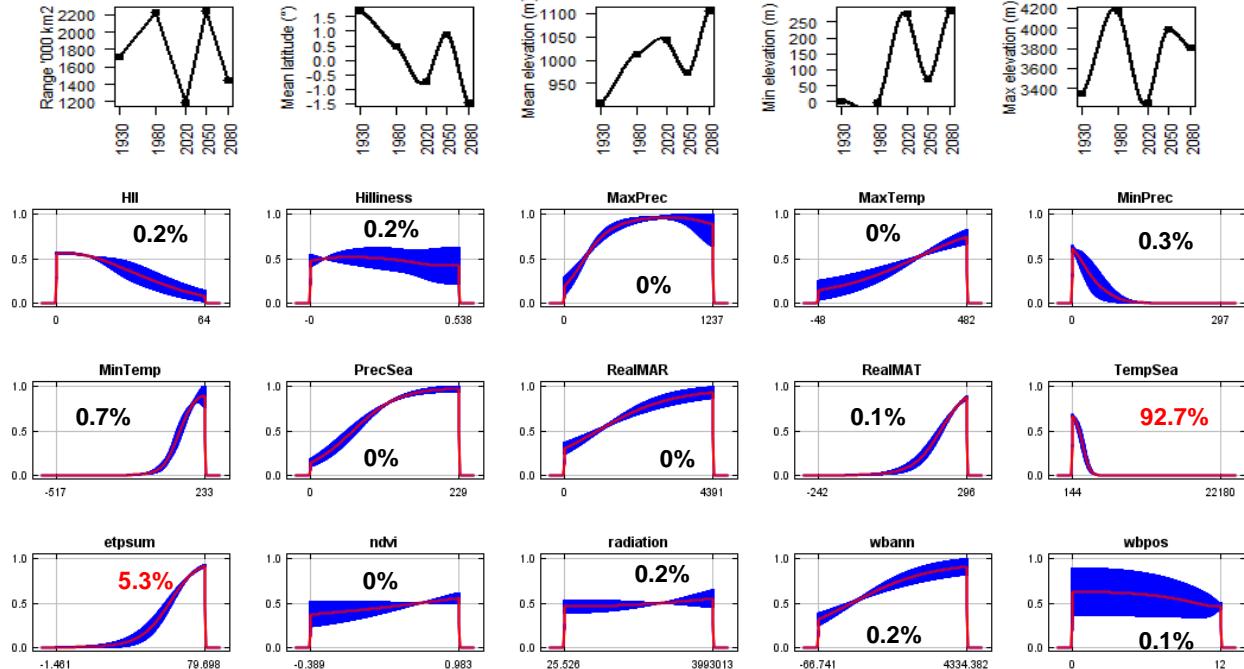
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#17 – Tehuantepec jackrabbit (*Lepus flavigularis*)

n = 8

Expert: Arturo Carillo-Reyes, Universidad de Ciencias y Artes de Chiapas

Expert evaluation: Poor

Data: Modern and historic

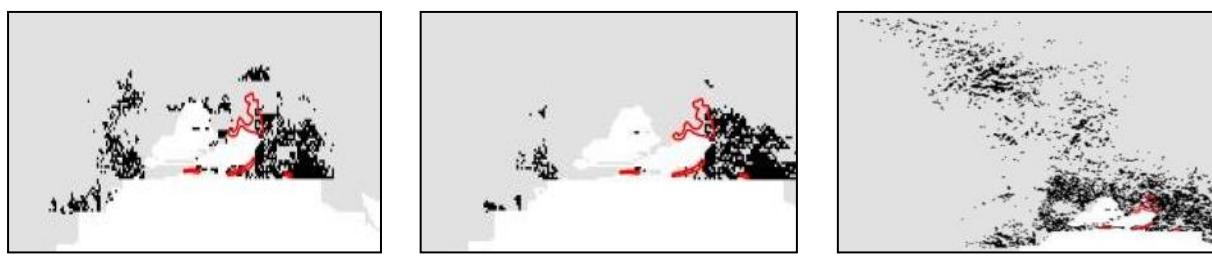
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Expert)

Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.95
True Skill Statistic	0.99

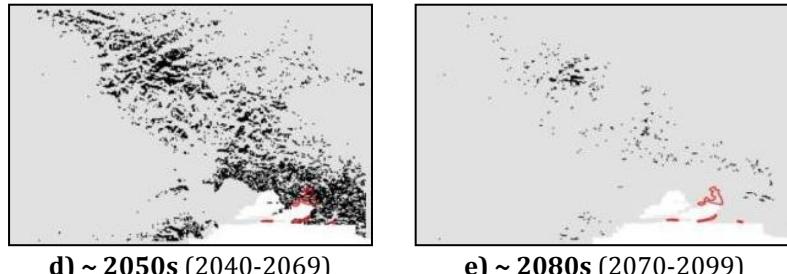
Summary: The Tehuantepec jackrabbit's bioclimatic envelope is predicted to decrease by 45% with a ~1° mean latitudinal poleward shift and a mean increase in elevation of ~450m driven by an increase in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (81.7%), mean annual temperature (2.7%) and normalised difference vegetation index (1.7%).



a) ~1930s (1900-1949)

b) ~1980s (1950-2000)

c) ~2020s (2010-2039)

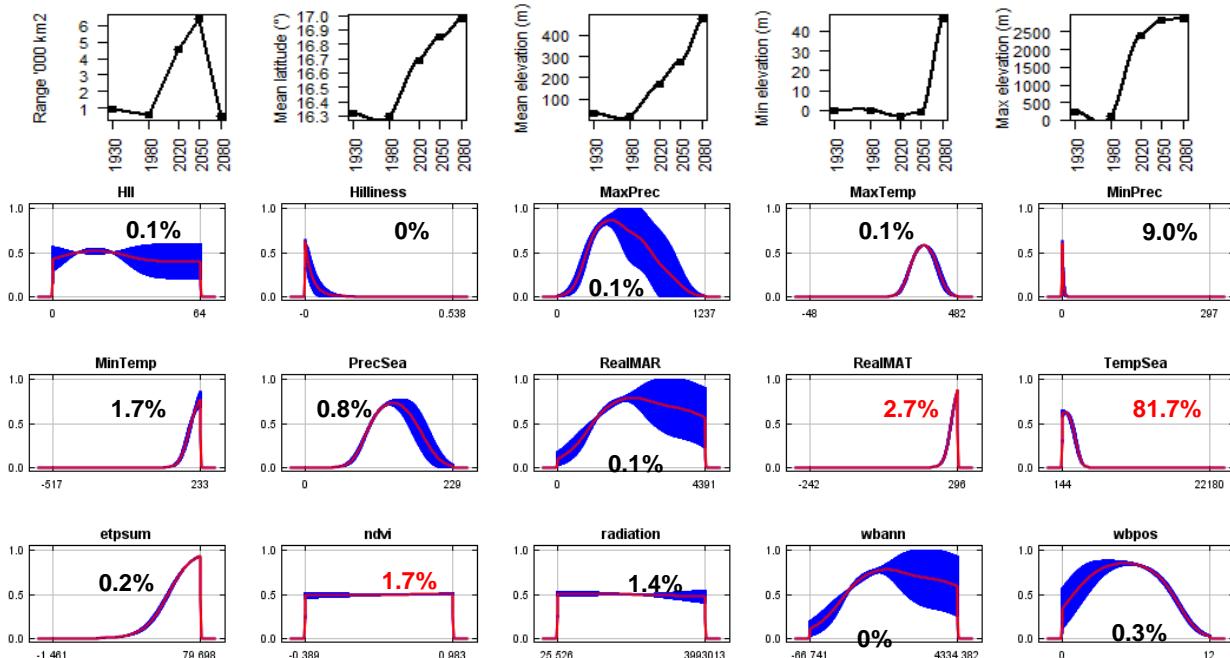


d) ~2050s (2040-2069)

e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Cervantes, F.A., et al. 2008)



#18 – Iberian hare (*Lepus granatensis*)

n = 1675

Expert: Pelayo Acevedo, University of Porto

Expert evaluation: Medium

Data: Modern and historic

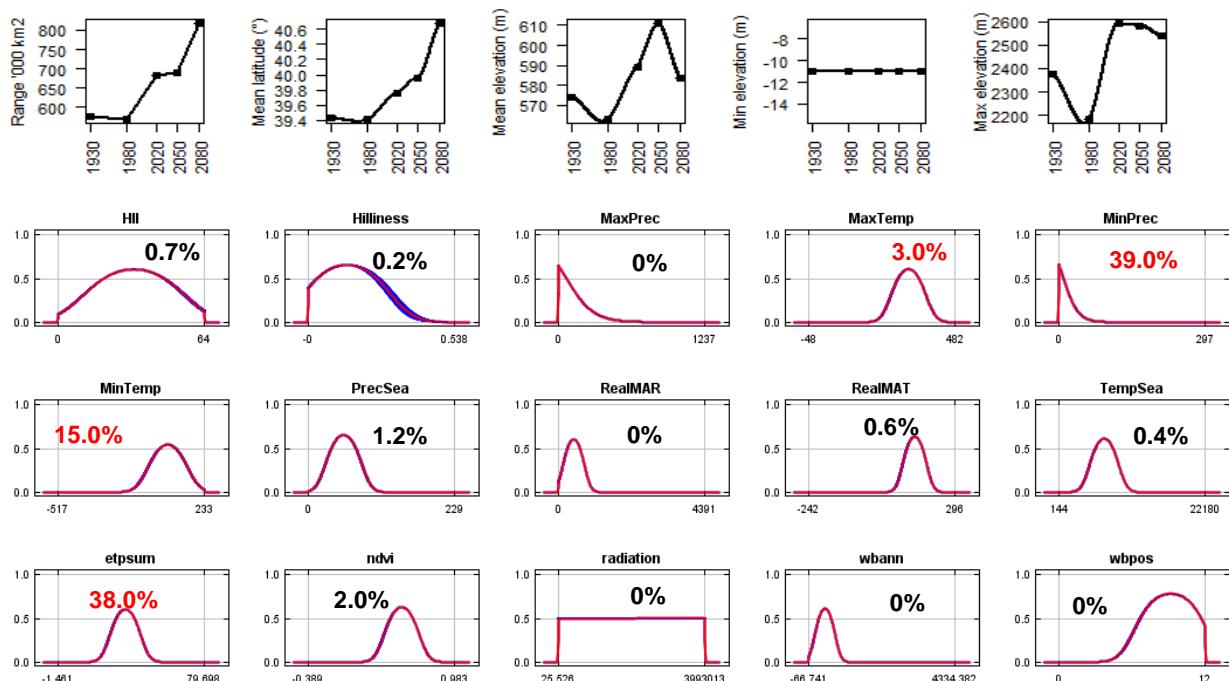
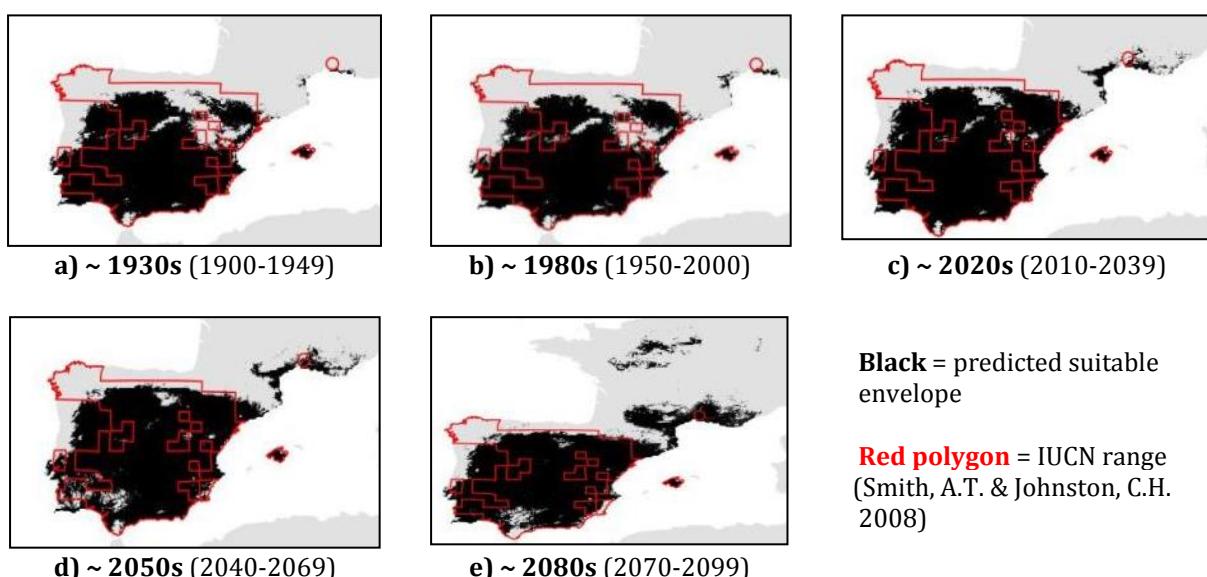
Envelope: Climatic and habitat

Dispersal distance: 7km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.94
Omission rate	0.08
Sensitivity	0.92
Specificity	0.95
Proportion correct	0.95
Kappa	0.81
True Skill Statistic	0.87

Summary: The Iberian hare's bioclimatic envelope is predicted to increase by 40% with a ~1° mean latitudinal poleward shift and a mean increase in elevation of ~10m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by maximum precipitation (39.0%), annual evapotranspiration (38.0%), minimum temperature (15.0%) and maximum temperature (3.0%).



#19 – Abyssinian hare (*Lepus habessinicus*)

n = 7

Expert: Zelalem Tolesa, Addis Ababa University

Expert evaluation: Medium

Data: Modern and historic

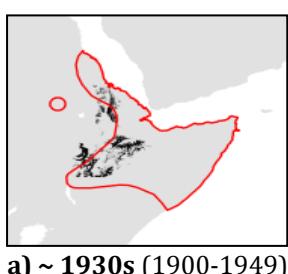
Envelope: Climatic and habitat

Dispersal distance: 25km/year (African leporids, range 15-35)

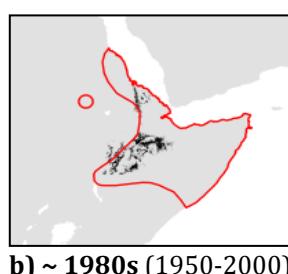
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.82
True Skill Statistic	0.99

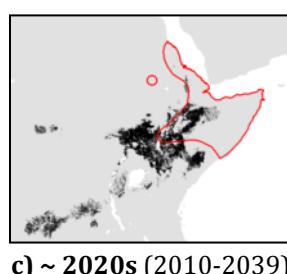
Summary: The Abyssinian hare's bioclimatic envelope is predicted to decrease by 4% with a ~4° mean latitudinal shift towards the Equator and a mean decrease in elevation of ~200m driven by an decrease in maximum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (87.6%), annual evapotranspiration (4.9%) and minimum precipitation (4.1%).



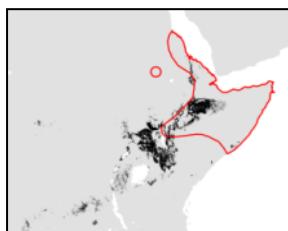
a) ~ 1930s (1900-1949)



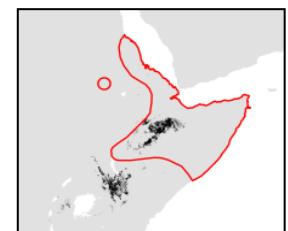
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



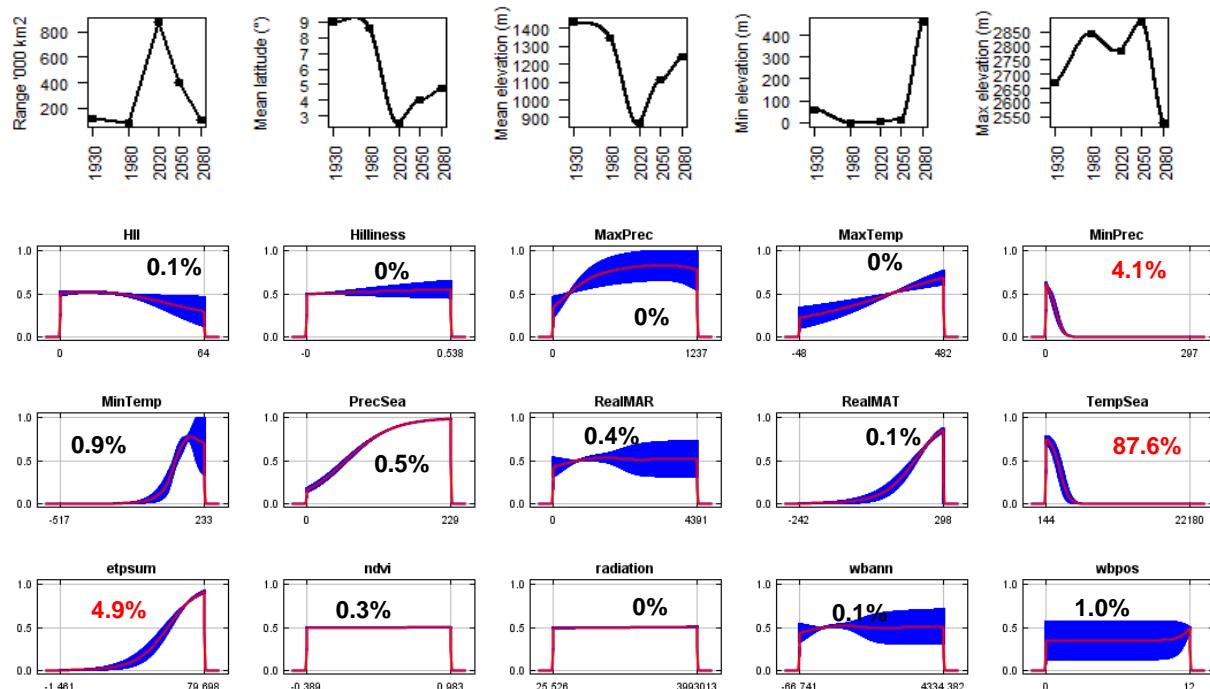
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range (Smith, A.T. & Johnston, C.H. 2008)



#20 – Hainan hare (*Lepus hainanus*)

n = 9

Expert: Youhua Chen, Wuhan University, China

Expert evaluation: Good

Data: Modern and historic

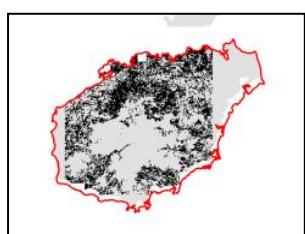
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Island species, range 0.01-0.01)

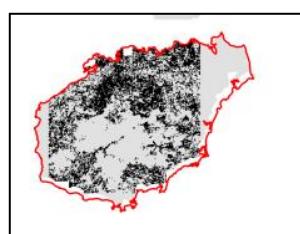
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.86
True Skill Statistic	0.99

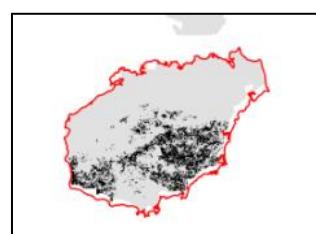
Summary: The Hainan hare's bioclimatic envelope is predicted to increase by 4% with no latitudinal poleward shift and a mean increase in elevation of ~20m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by minimum temperature (71.0%), mean annual temperature (22.8%) and temperature seasonality (5.4%).



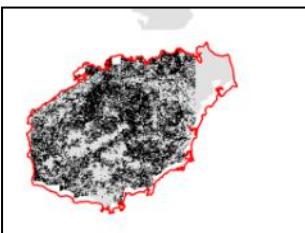
a) ~ 1930s (1900-1949)



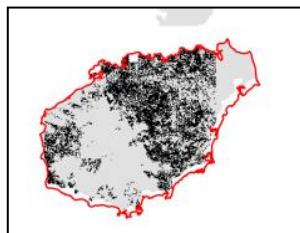
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



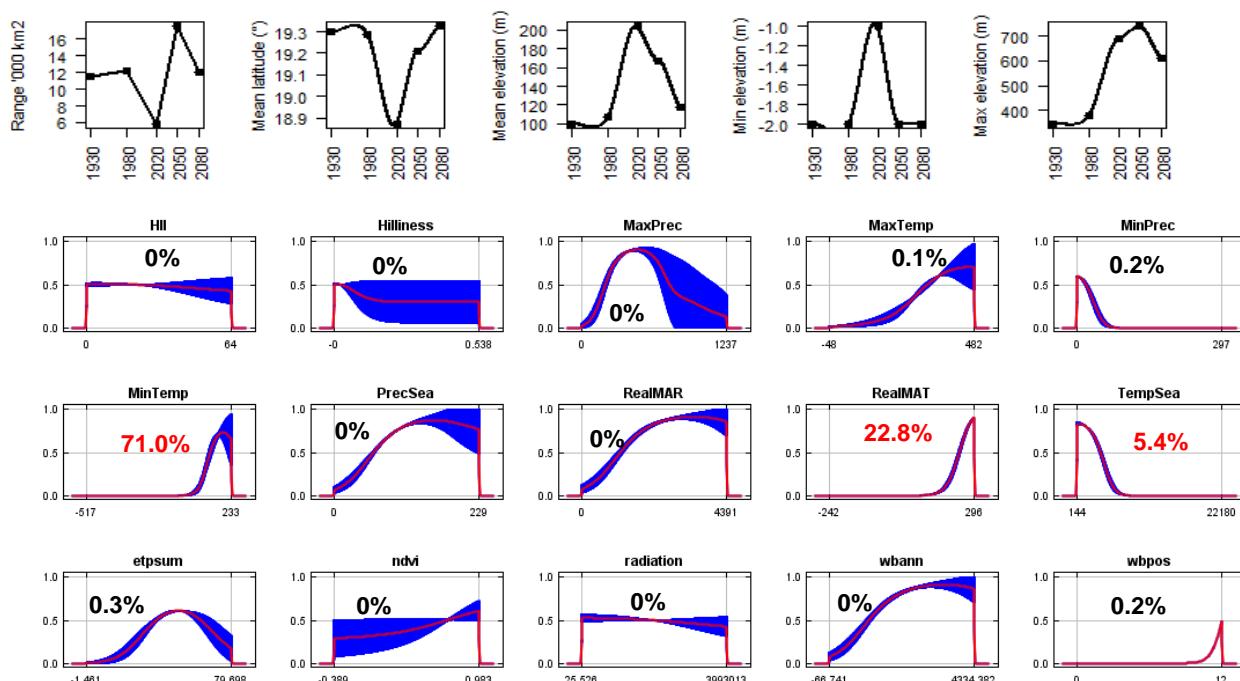
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Lazell, J., et al. 2008)



#21 – Black jackrabbit (*Lepus insularis*)

n = 3

Expert: Tamara Rioja Pardela, Universidad de Ciencias y Artes de Chiapas, Mexico

Expert evaluation: Good

Data: Modern and historic

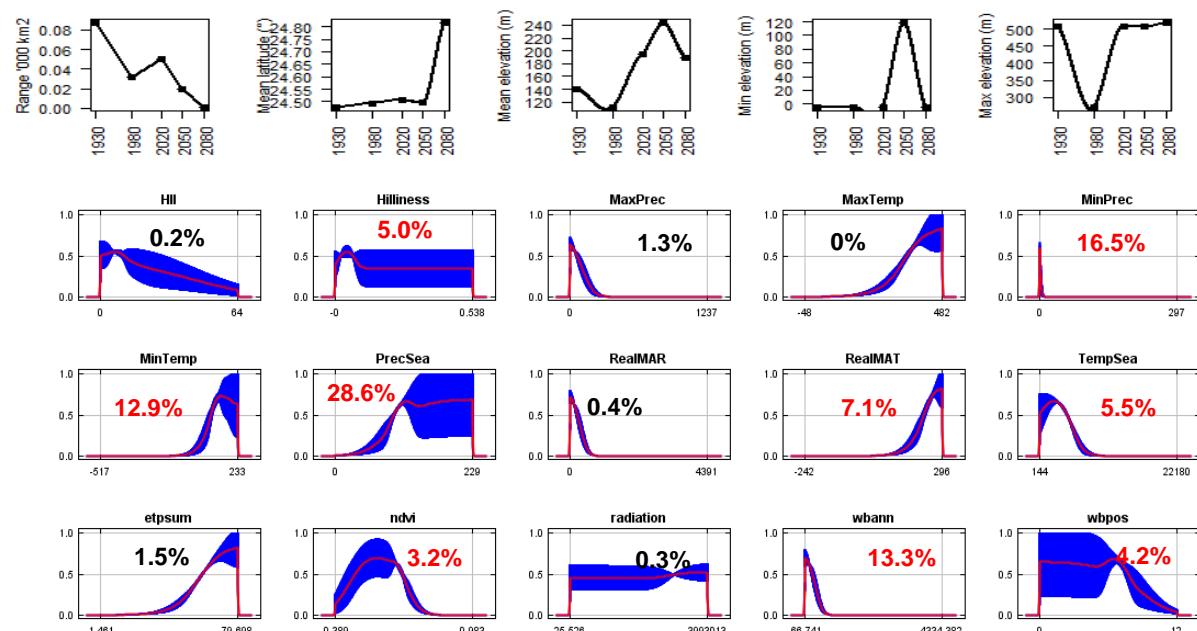
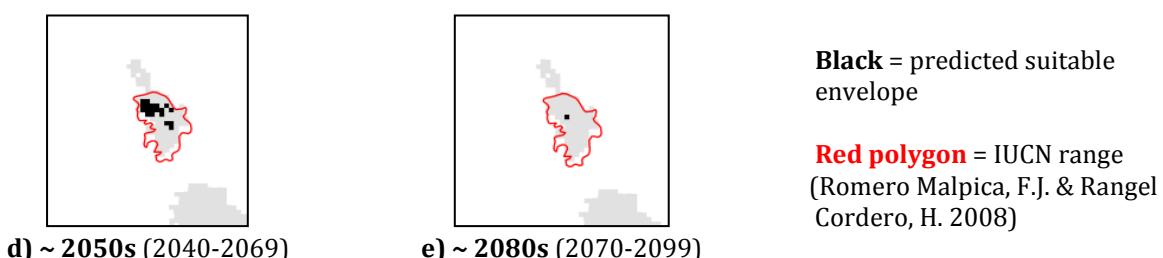
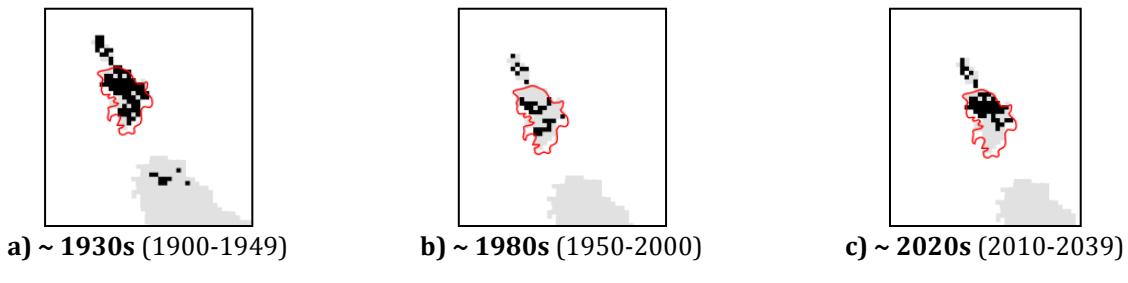
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Island species, range 0.01-0.01)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	1.00
Omission rate	0.00
Sensitivity	1.00
Specificity	1.00
Proportion correct	1.00
Kappa	1.00
True Skill Statistic	1.00

Summary: The Black jackrabbit's bioclimatic envelope is predicted to decrease by 100% with a ~0.3° mean latitudinal polewards shift and a mean increase in elevation of ~50m driven by an increase in both minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (28.6%), minimum precipitation (16.5%), annual water balance (13.3%), minimum temperature (12.9%), mean annual temperature (7.1%), temperature seasonality (5.5%), surface roughness index (5.0%) and normalised difference vegetation index (3.2%).



#22 – Manchurian hare (*Lepus mandshuricus*)

n = 36

Expert: Deyan Ge, Institute of Zoology, Chinese Academy of Sciences

Expert evaluation: Medium

Data: Modern and historic

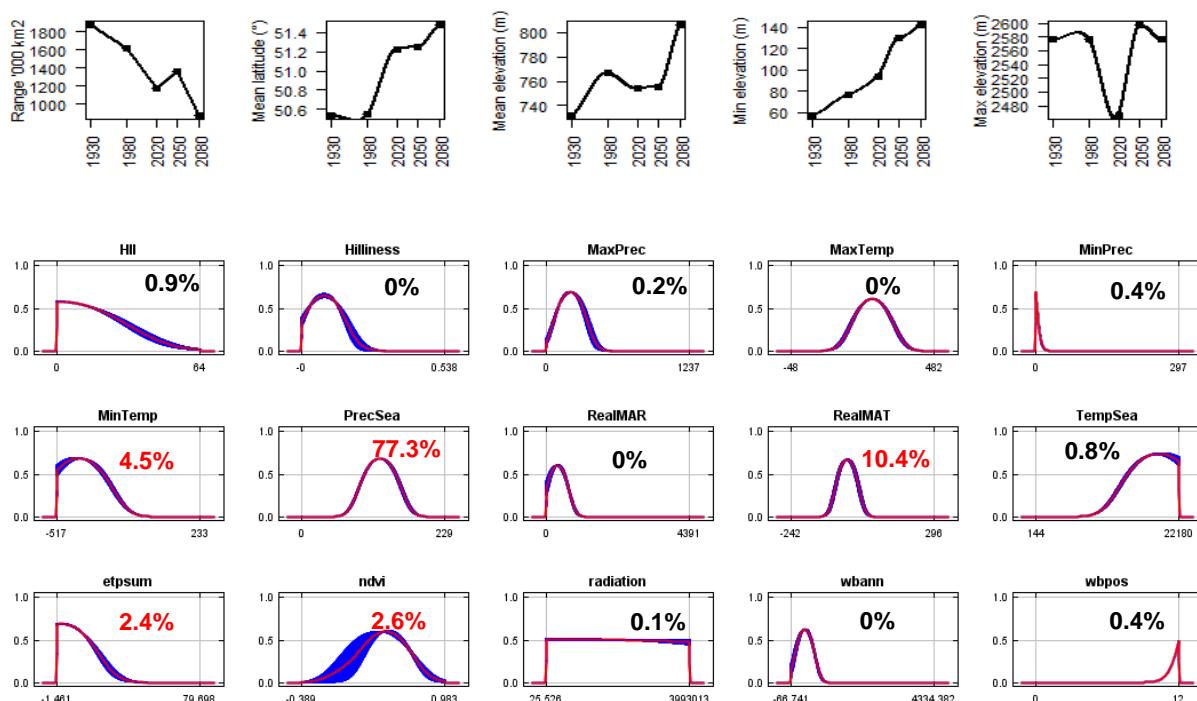
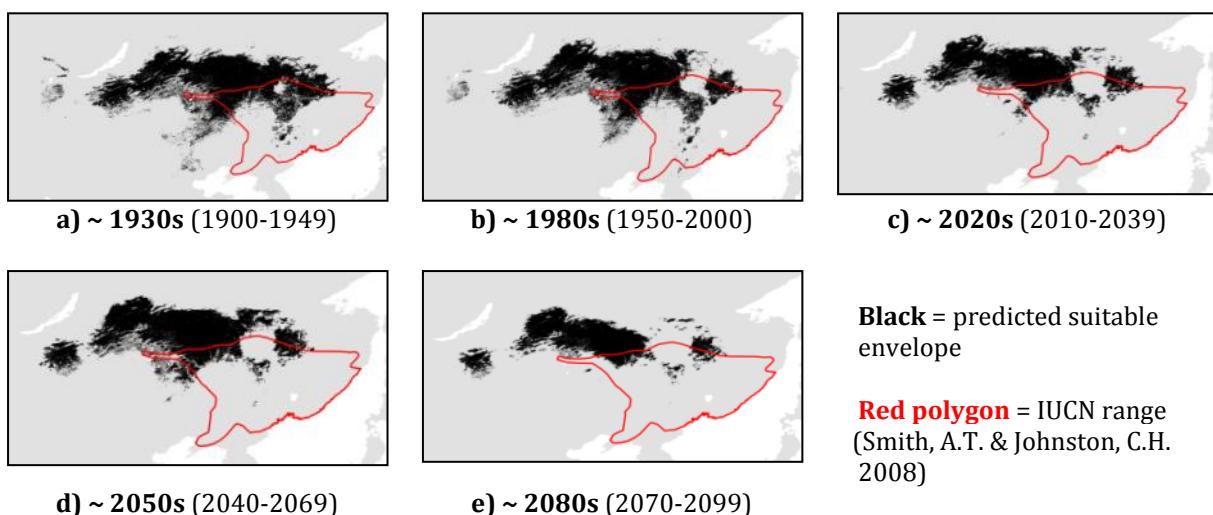
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Sokolov, V.E. et al., 2009)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.96
Omission rate	0.08
Sensitivity	0.92
Specificity	0.99
Proportion correct	0.99
Kappa	0.78
True Skill Statistic	0.92

Summary: The Manchurian hare's bioclimatic envelope is predicted to decrease by 50% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~70m driven by an increase in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (77.3%), mean annual temperature (10.4%), minimum temperature (4.5%), normalised difference vegetation index (2.6%) and annual evapotranspiration (2.4%).



#23 – African savannah hare (*Lepus microtis*)

n = 82

Expert: John Flux, IUCN Lagomorph Specialist Group

Expert evaluation: Medium

Data: Modern and historic

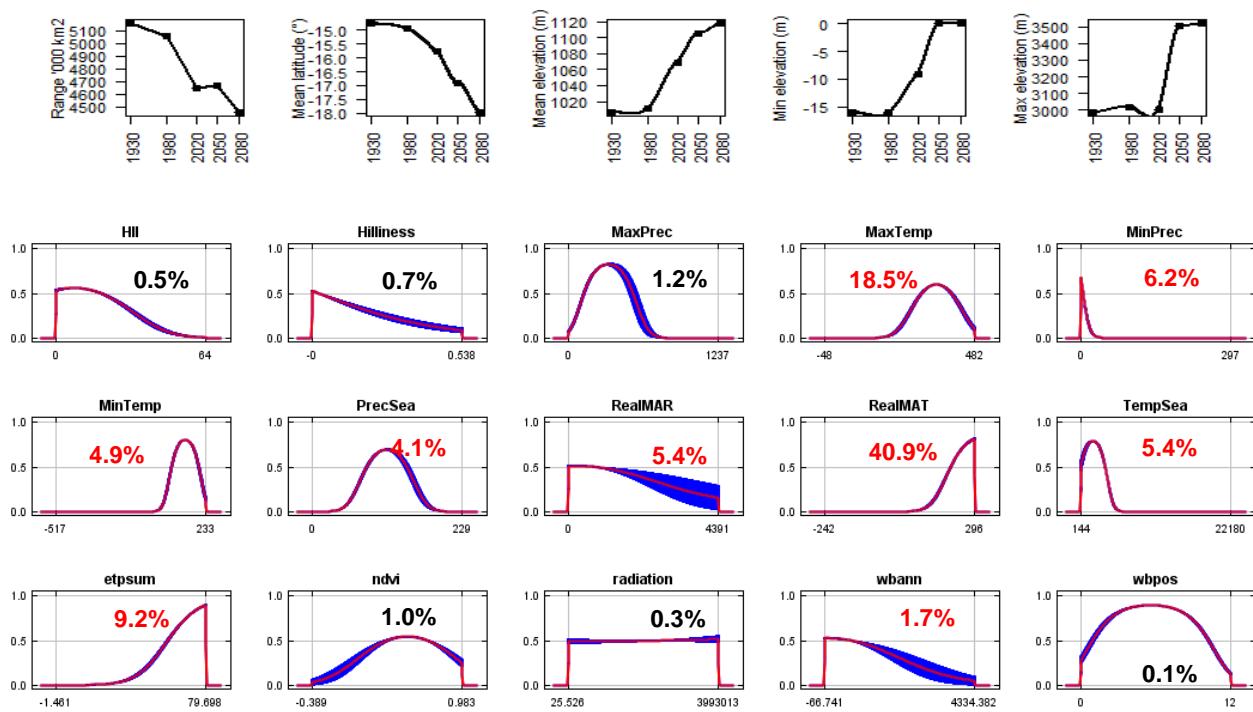
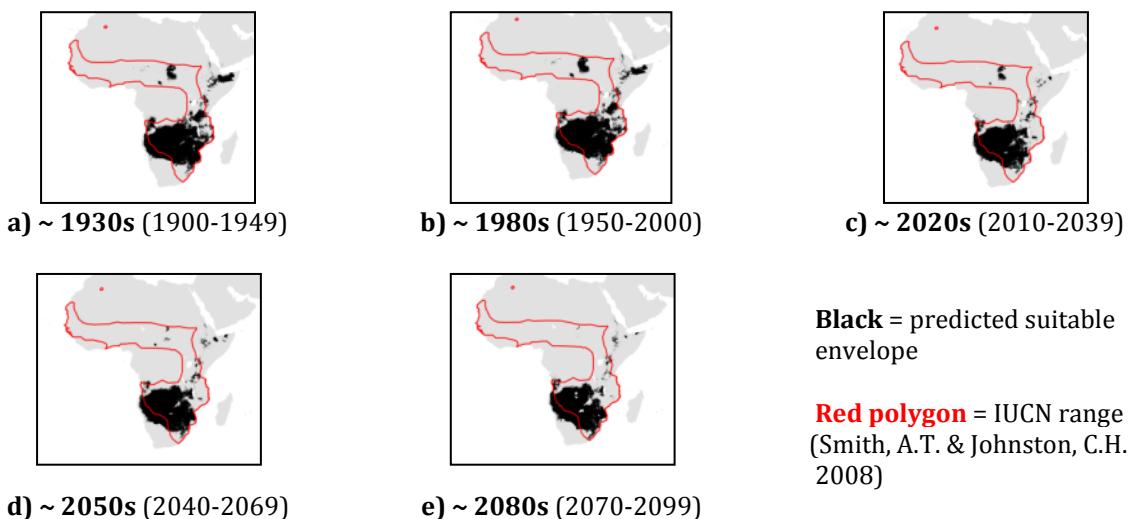
Envelope: Climatic only

Dispersal distance: 15km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.93
Omission rate	0.13
Sensitivity	0.87
Specificity	0.99
Proportion correct	0.99
Kappa	0.62
True Skill Statistic	0.86

Summary: The African savannah hare's bioclimatic envelope is predicted to decrease by 15% with a ~3° mean latitudinal polewards shift and a mean increase in elevation of ~100m driven by an increase in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (40.9%), maximum temperature (18.5%), annual evapotranspiration (9.2%), minimum precipitation (6.2%), temperature seasonality (5.4%), mean annual precipitation (5.4%), minimum temperature (4.9%), precipitation seasonality (4.1%) and annual water balance (1.7%).



#24 – Indian hare (*Lepus nigricollis*)

n = 17

Expert: Gopinathan Maheswaran , Zoological Survey of India

Expert evaluation: Good

Data: Modern and historic

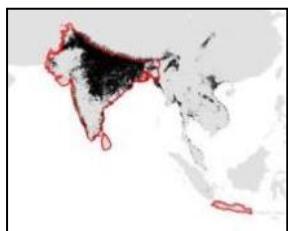
Envelope: Climatic and habitat

Dispersal distance: 6km/year (Expert)

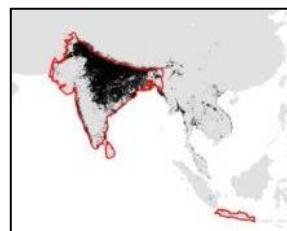
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.59
True Skill Statistic	0.99

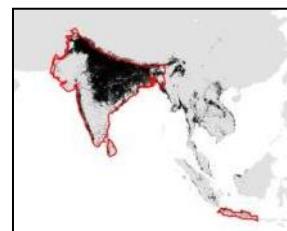
Summary: The Indian hare's bioclimatic envelope is predicted to decrease by 10% with a ~2° mean latitudinal polewards shift and a mean increase in elevation of ~80m driven by an increase in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (48.0%), mean annual temperature (14.9%), human influence index (11.9%), minimum temperature (10.3%), temperature seasonality (7.0%), number of months with a positive water balance (2.8%) and minimum precipitation (1.5%).



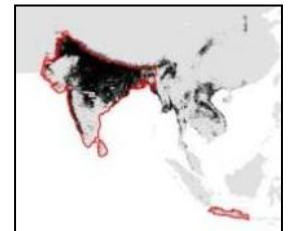
a) ~ 1930s (1900-1949)



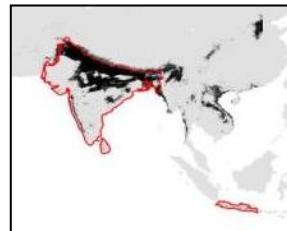
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



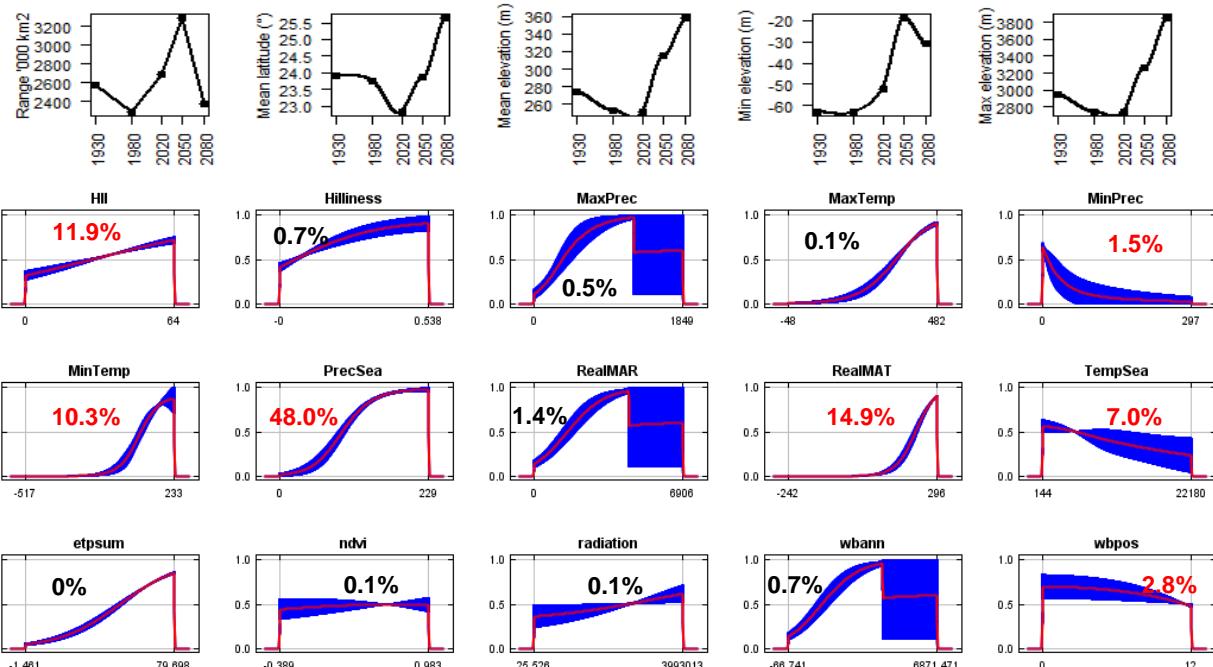
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Maheswaran, G. & Jordan, M. 2008)



#25 – Woolly hare (*Lepus oiostolus*)

n = 84

Expert: Weihe Yang , Institute of Zoology, Chinese Academy of Sciences

Expert evaluation: Medium

Data: Only modern

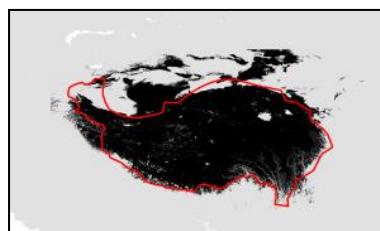
Envelope: Climatic and habitat

Dispersal distance: 2.5km/year (Asian leporids, range 1-35)

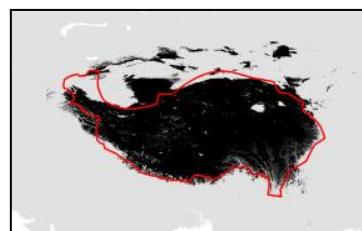
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.94
Omission rate	0.11
Sensitivity	0.89
Specificity	0.99
Proportion correct	0.99
Kappa	0.63
True Skill Statistic	0.89

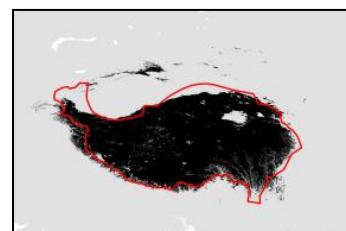
Summary: The Woolly hare's bioclimatic envelope is predicted to decrease by 25% with a ~1° mean latitudinal shift towards the Equator and a mean increase in elevation of ~680m driven by an increase in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (82.1%), maximum temperature (5.0%), minimum temperature (4.6%) and annual evapotranspiration (3.8%).



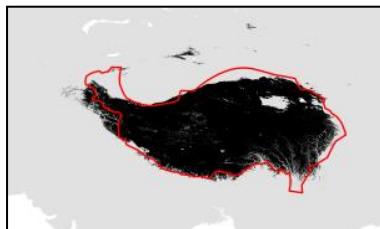
a) ~ 1930s (1900-1949)



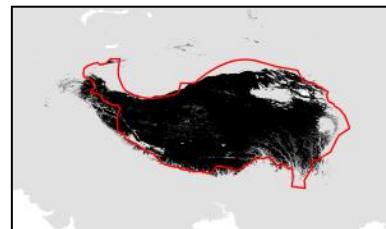
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



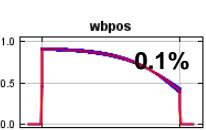
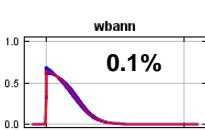
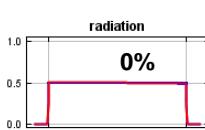
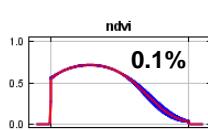
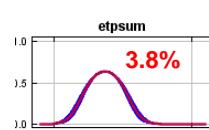
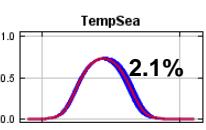
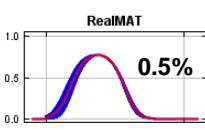
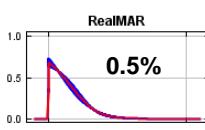
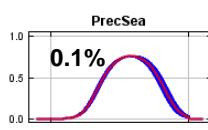
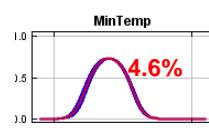
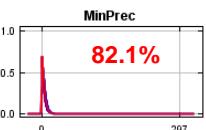
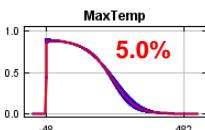
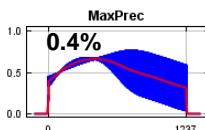
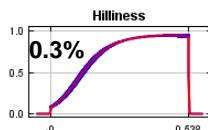
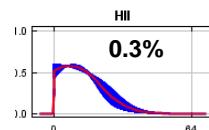
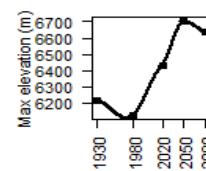
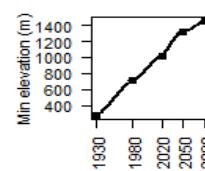
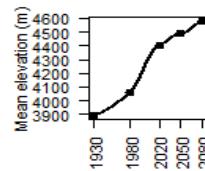
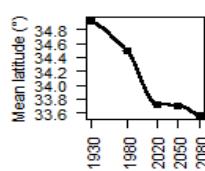
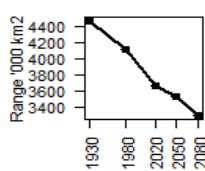
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Indian CAMP Workshop & Johnston, C.H. 2008)



#26 – Alaskan hare (*Lepus othus*)

n = 8

Expert: Eric Waltari, City University of New York

Expert evaluation: Medium

Data: Modern and historic

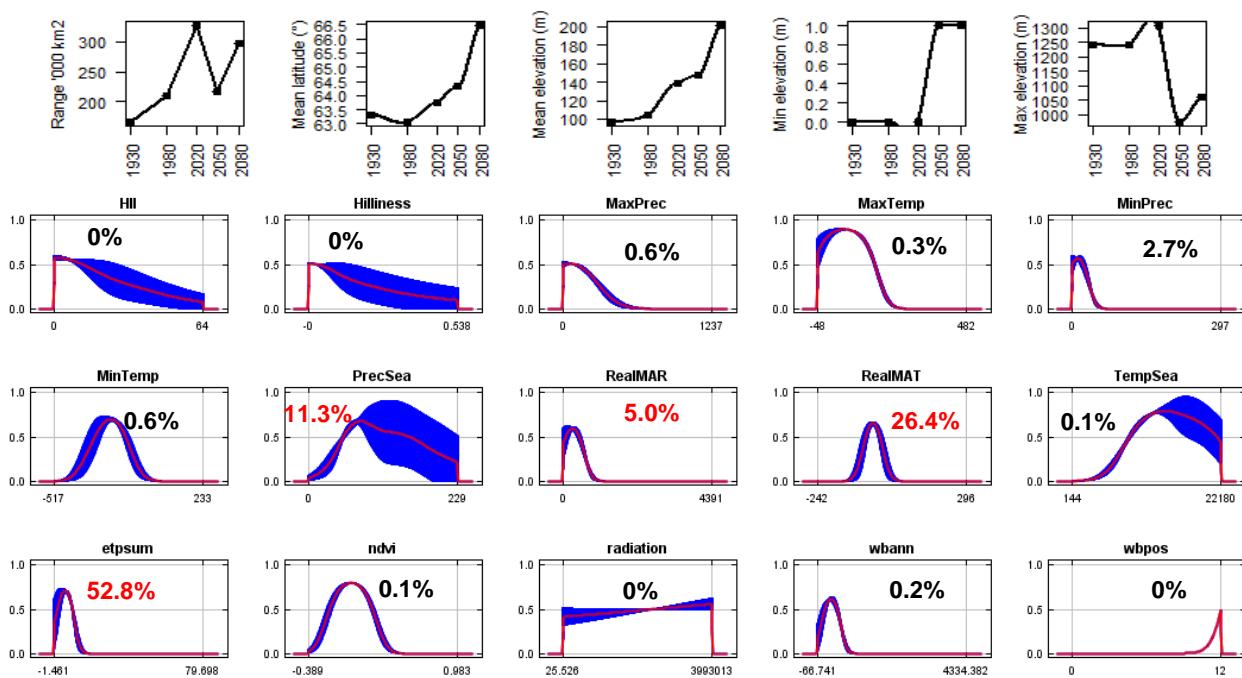
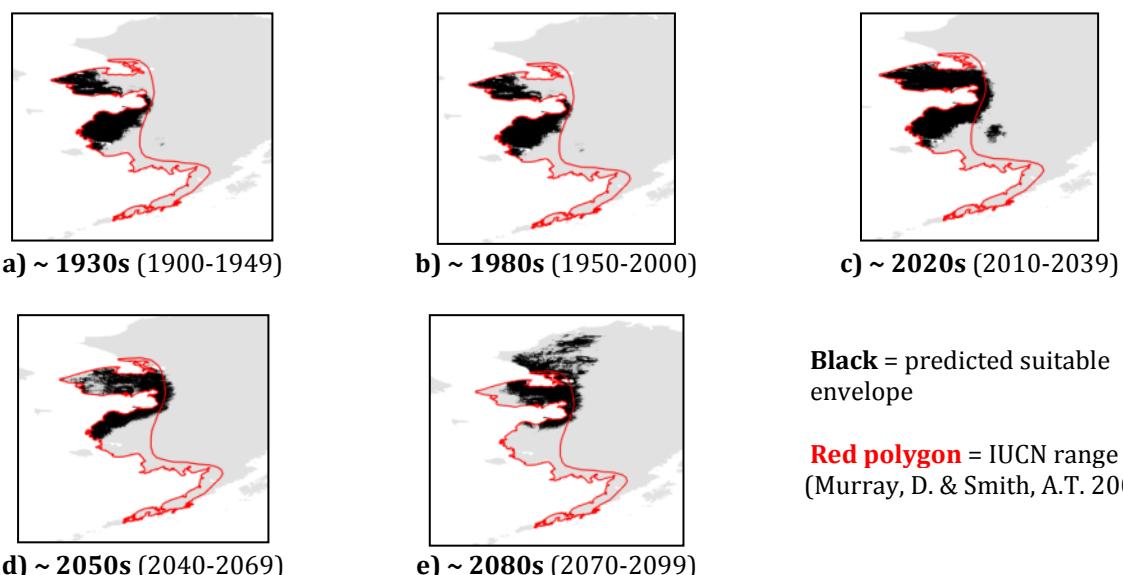
Envelope: Climatic only

Dispersal distance: 2km/year (similar to Arctic hare)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.89
True Skill Statistic	0.99

Summary: The Alaskan hare's bioclimatic envelope is predicted to increase by 80% with a ~3° mean latitudinal polewards shift and a mean increase in elevation of ~100m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (52.8%), mean annual temperature (26.4%), precipitation seasonality (11.3%) and mean annual precipitation (5.0%).



#27 – Burmese hare (*Lepus peguensis*)

n = 7

Expert: Thomas Gray, WWF Greater Mekong

Expert evaluation: Medium

Data: Modern and historic

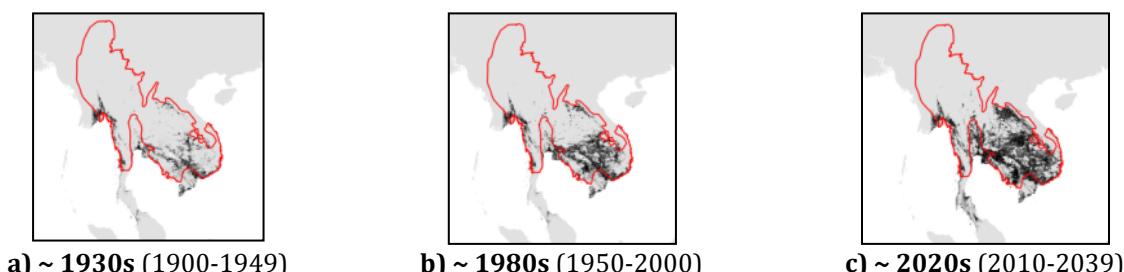
Envelope: Climatic and habitat

Dispersal distance: 2.5km/year (Asian leporids, range 1-35)

Status: MODELLABLE; Included in final analysis: ✓

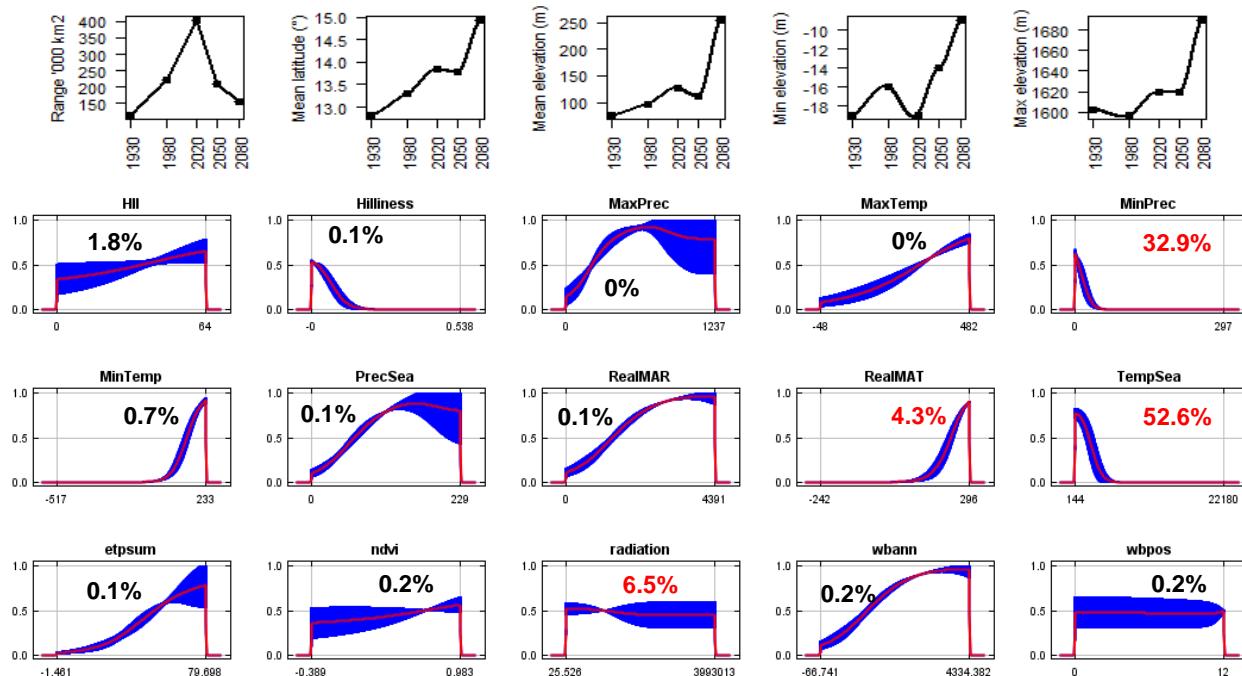
Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.58
True Skill Statistic	0.99

Summary: The Burmese hare's bioclimatic envelope is predicted to increase by 40% with a ~2° mean latitudinal polewards shift and a mean increase in elevation of ~180m driven by an increase in minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (52.6%), minimum precipitation (32.9%), solar radiation (6.5%) and mean annual temperature (4.3%).



Black = predicted suitable envelope

Red polygon = IUCN range
(Duckworth, J.W., et al. 2008)



#28 – Scrub hare (*Lepus saxatilis*)

n = 39

Expert: Kai Collins, University of Pretoria

Expert evaluation: Poor

Data: Only modern

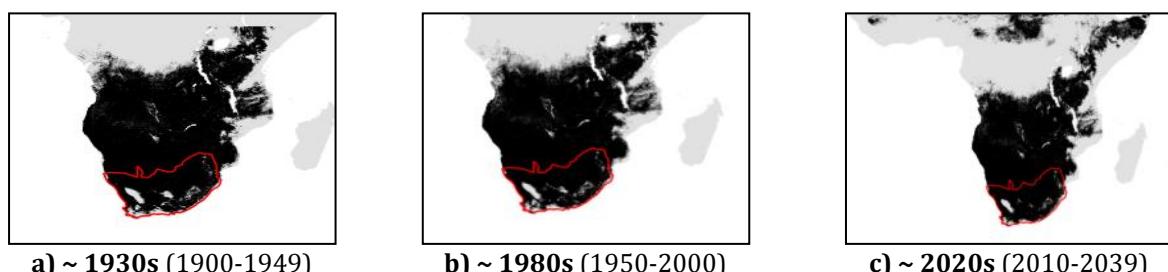
Envelope: Climatic and habitat

Dispersal distance: 25km/year (African leporids, range 15-35)

Status: UNMODELLABLE; **Included in final analysis:** X

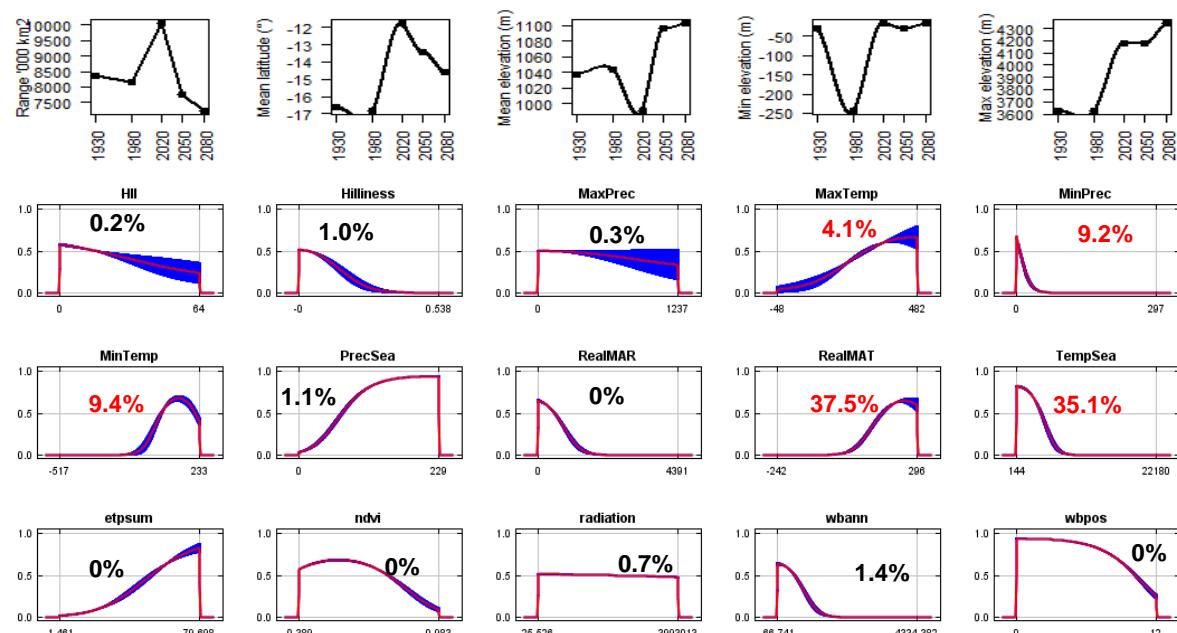
Model evaluation metric	
AUC	0.95
Omission rate	0.08
Sensitivity	0.92
Specificity	0.97
Proportion correct	0.97
Kappa	0.18
True Skill Statistic	0.89

Summary: The Scrub hare's bioclimatic envelope is predicted to decrease by 15% with a ~2° mean latitudinal shift towards the Equator and a mean increase in elevation of ~65m driven by an increase in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (52.8%), mean annual temperature (26.4%), precipitation seasonality (11.3%) and mean annual precipitation (5.0%).



Black = predicted suitable envelope

Red polygon = IUCN range
(Collins, K., et al, 2008)



#29 – Chinese hare (*Lepus sinensis*)

n = 141

Expert: Weihe Yang, Institute of Zoology, Chinese Academy of Sciences

Expert evaluation: Medium

Data: Modern and historic

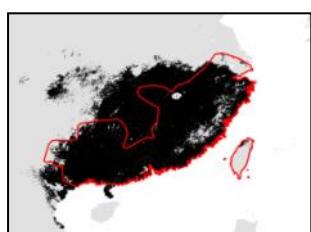
Envelope: Climatic and habitat

Dispersal distance: 2.5km/year (Asian leporids, range 1-35)

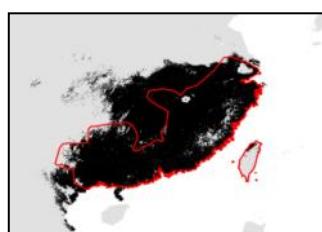
Status: MODELLABLE; **Included in final analysis:** ✓

Model evaluation metric	
AUC	0.94
Omission rate	0.11
Sensitivity	0.89
Specificity	0.99
Proportion correct	0.99
Kappa	0.81
True Skill Statistic	0.89

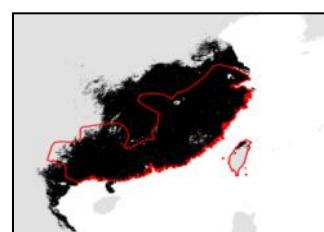
Summary: The Chinese hare's bioclimatic envelope is predicted to increase by 60% with a ~2° mean latitudinal polewards shift and a mean increase in elevation of ~25m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (56.5%), temperature seasonality (22.9%), precipitation seasonality (8.0%), mean annual precipitation (5.4%) and annual evapotranspiration (3.5%).



a) ~ 1930s (1900-1949)



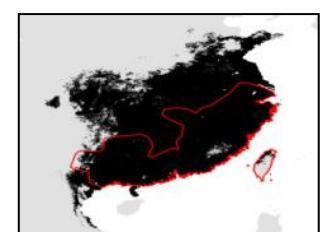
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



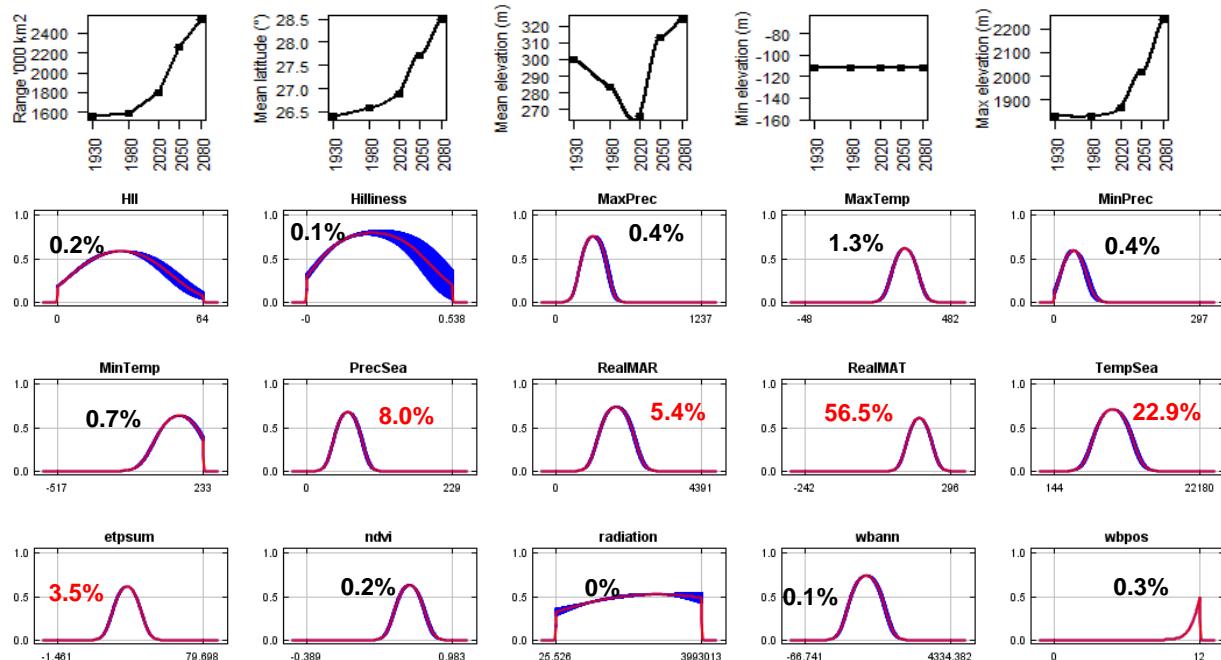
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range (Smith, A.T. & Johnston, C.H. 2008)



#30 – Ethiopian highland hare (*Lepus starcki*)

n = 13

Expert: Zelalem Tolesa, Addis Ababa University

Expert evaluation: Medium

Data: Modern and historic

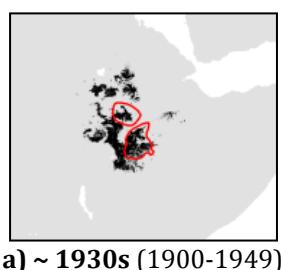
Envelope: Climatic and habitat

Dispersal distance: 25km/year (African leporids, range 15-35)

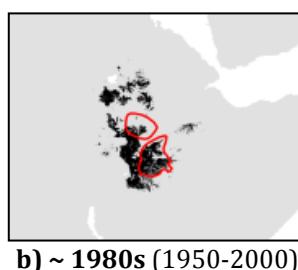
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.96
Omission rate	0.08
Sensitivity	0.92
Specificity	0.99
Proportion correct	0.99
Kappa	0.86
True Skill Statistic	0.92

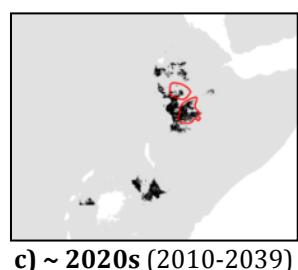
Summary: The Ethiopian highland hare's bioclimatic envelope is predicted to decrease by 90% with a ~7° mean latitudinal shift towards the Equator and a mean decrease in elevation of ~140m driven by a decrease in maximum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (80.6%) and minimum temperature (18.5%).



a) ~1930s (1900-1949)



b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



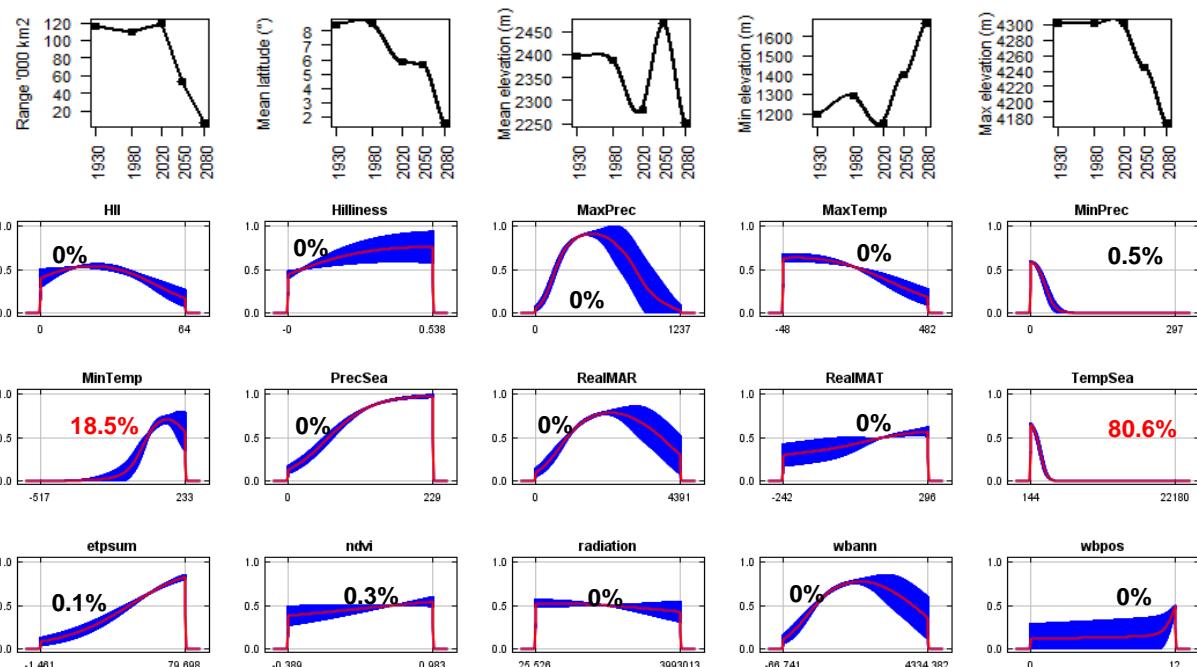
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#31 – Desert hare (*Lepus tibetanus*)

n = 55

Expert: Chelmala Srinivasulu, Osmania University, India

Expert evaluation: Medium

Data: Only modern

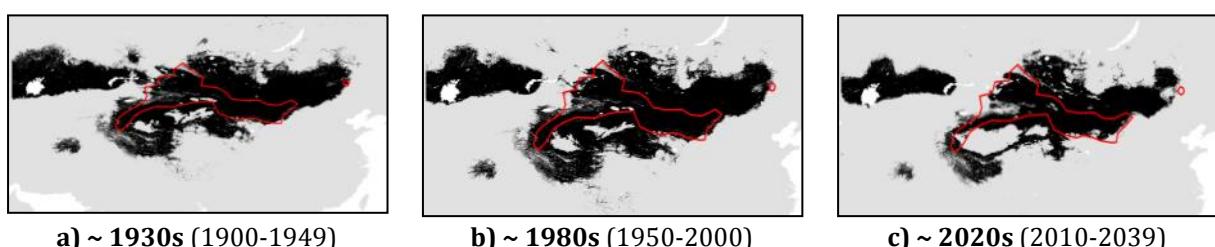
Envelope: Climatic and habitat

Dispersal distance: 2.5km/year (Asian leporids, range 1-35)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.92
Omission rate	0.15
Sensitivity	0.85
Specificity	0.99
Proportion correct	0.99
Kappa	0.57
True Skill Statistic	0.85

Summary: The Desert hare's bioclimatic envelope is predicted to decrease by 50% with no latitudinal shift towards the Equator, but a mean increase in elevation of ~320m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (54.5%), minimum temperature (19.3%), maximum precipitation (17.3%), annual evapotranspiration (2.8%) and human influence index (1.7%).



a) ~ 1930s (1900-1949)

b) ~ 1980s (1950-2000)

c) ~ 2020s (2010-2039)

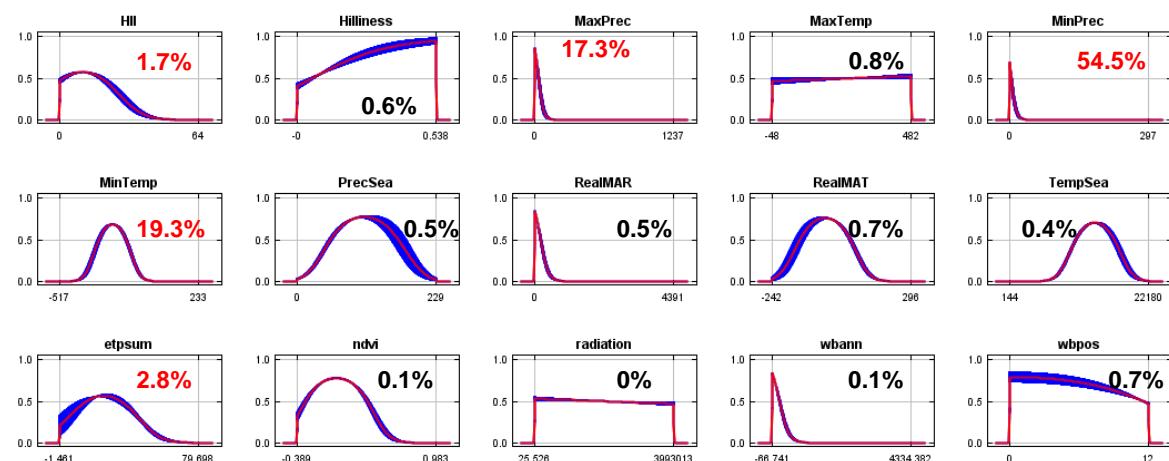
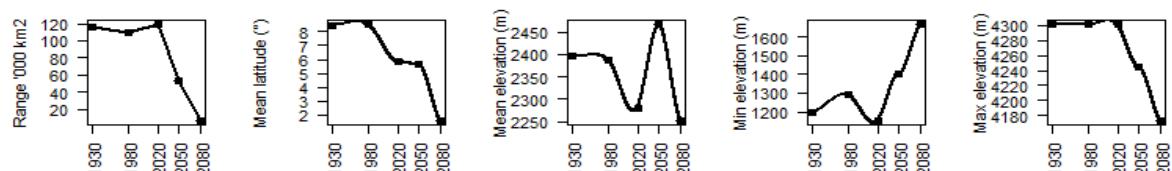


d) ~ 2050s (2040-2069)

e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(China Red List & Johnston, C.H. 2008)



#32 – Mountain hare (*Lepus timidus*) – Eurasian populations

n = 2,460

Expert: Neil Reid, Queen's University Belfast

Expert evaluation: Medium

Data: Only modern

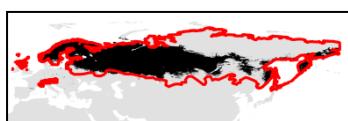
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Expert)

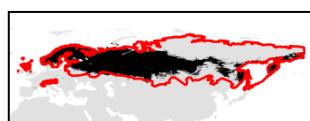
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.91
Omission rate	0.08
Sensitivity	0.92
Specificity	0.90
Proportion correct	0.91
Kappa	0.74
True Skill Statistic	0.82

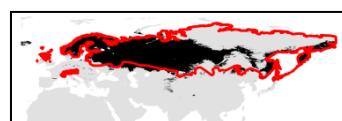
Summary: The Mountain hare's bioclimatic envelope is predicted to decrease by 10% with a ~4° mean latitudinal polewards shift and a mean decrease in elevation of ~10m driven by a decrease in maximum elevation. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (87.9%), temperature seasonality (3.9%), minimum precipitation (2.1%) and minimum temperature (1.6%).



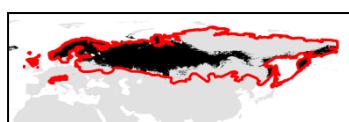
a) ~1930s (1900-1949)



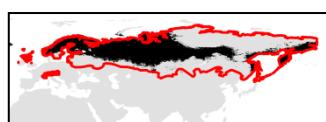
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



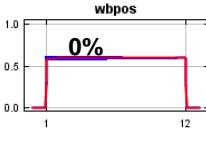
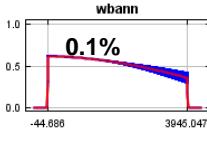
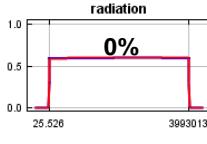
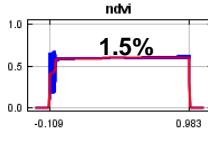
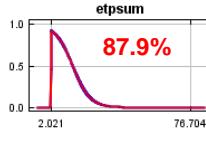
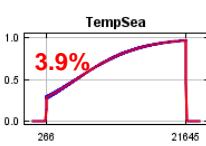
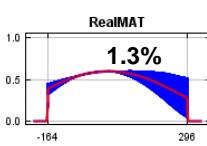
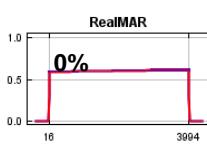
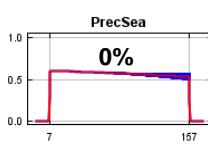
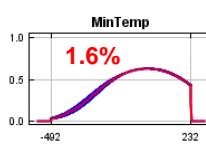
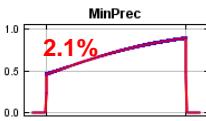
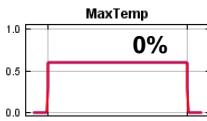
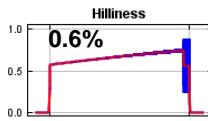
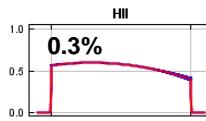
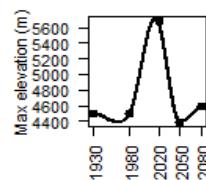
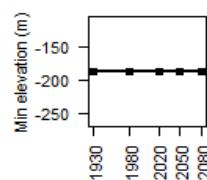
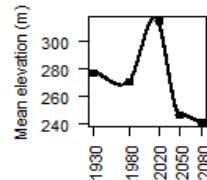
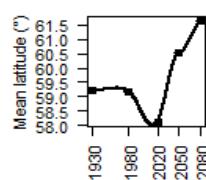
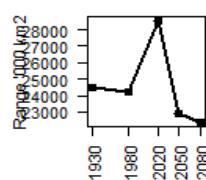
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#33 – Irish hare (*Lepus timidus hibernicus*)

n = 706

Expert: Neil Reid, Queen's University Belfast

Expert evaluation: Medium

Data: Only modern

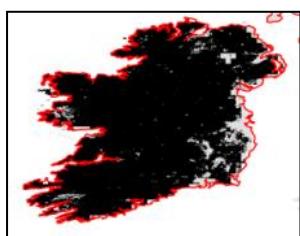
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Expert)

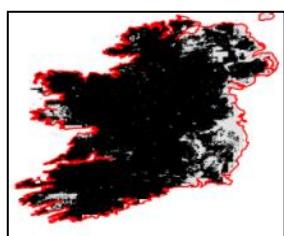
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.94
Omission rate	0.08
Sensitivity	0.92
Specificity	0.97
Proportion correct	0.96
Kappa	0.75
True Skill Statistic	0.88

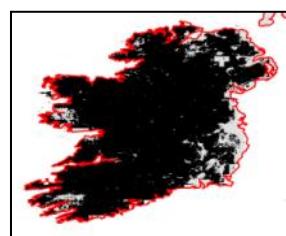
Summary: The Irish hare's bioclimatic envelope is predicted to decrease by 50% with a ~0.5° mean latitudinal polewards shift and a mean decrease in elevation of ~10m driven by a decrease in maximum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (44.6%), annual evapotranspiration (41.5%), normalised difference vegetation index (6.4%) and precipitation seasonality (3.6%) and maximum precipitation (2.5%).



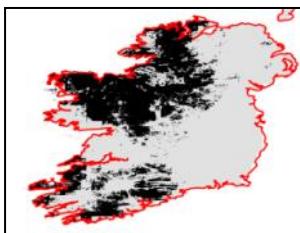
a) ~1930s (1900-1949)



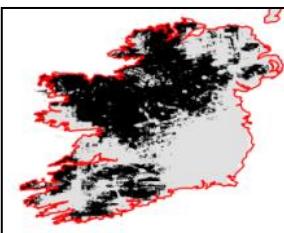
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



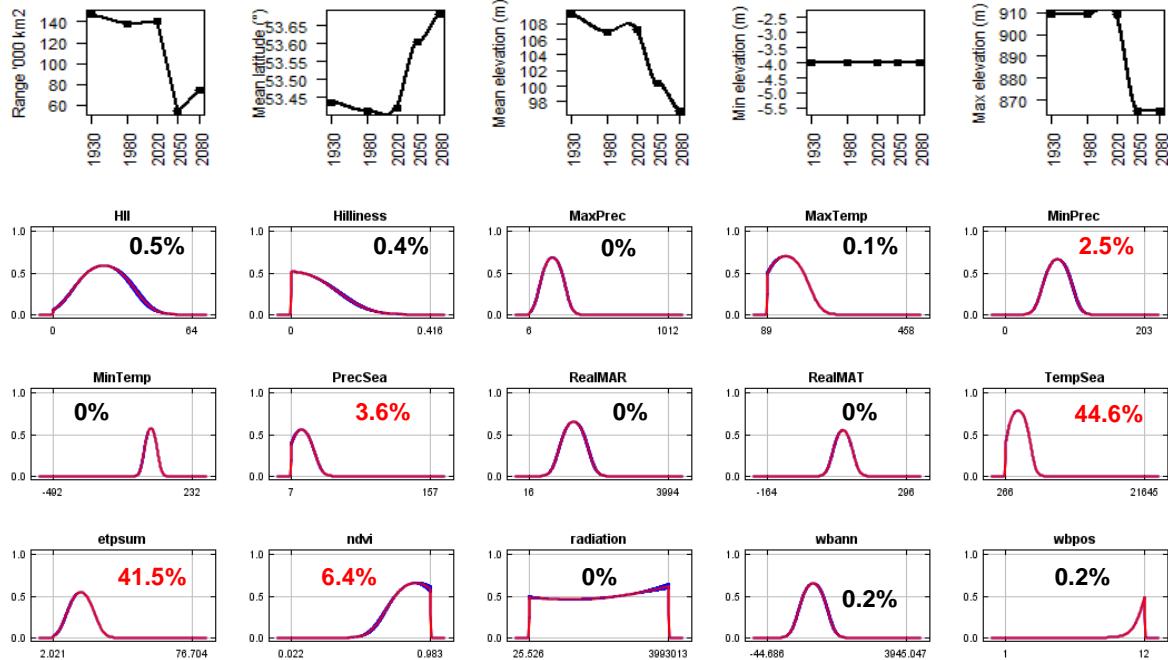
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#34 – Mountain hare (*Lepus timidus*)
– Eurasian & Irish populations combined
n = 3,166

Expert: Neil Reid, Queen's University Belfast

Expert evaluation: Medium

Data: Only modern

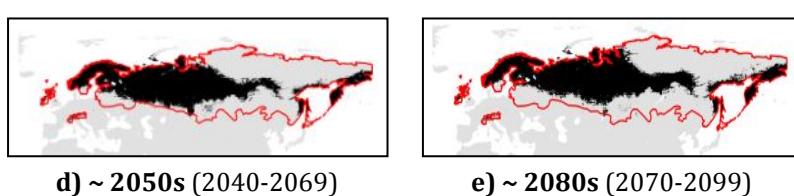
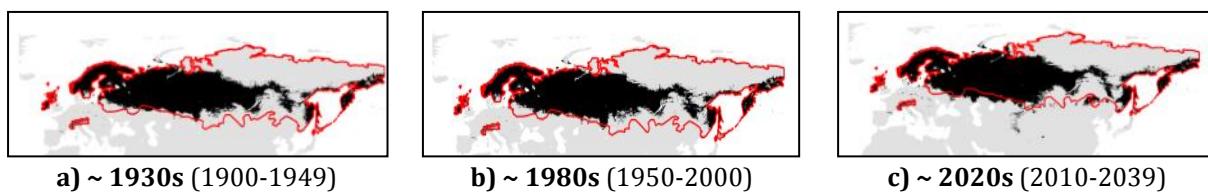
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

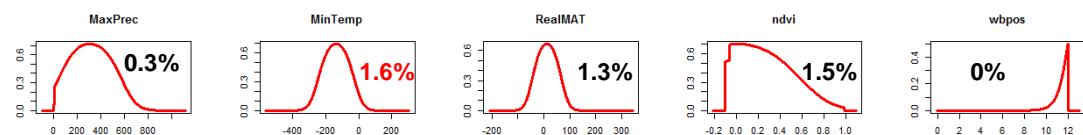
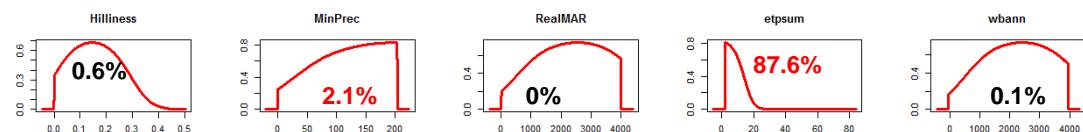
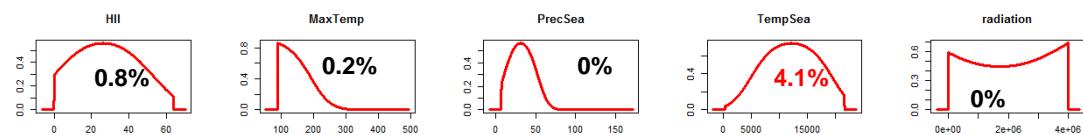
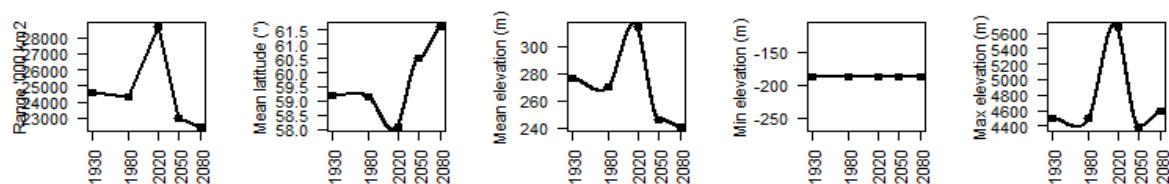
Model evaluation metric	
AUC	0.92
Omission rate	0.07
Sensitivity	0.93
Specificity	0.91
Proportion correct	0.91
Kappa	0.78
True Skill Statistic	0.84

Summary: The Mountain hare's bioclimatic envelope is predicted to decrease by 10% with a ~2° mean latitudinal polewards shift and a mean decrease in elevation of ~40m driven by a decrease in maximum elevation. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (87.6%), temperature seasonality (4.1%), minimum precipitation (2.1%) and minimum temperature (1.6%).



Black = predicted suitable envelope

Red polygon = IUCN range (Smith, A.T. & Johnston, C.H. 2008)



#35 – Tolai hare (*Lepus tolai*)

n = 316

Expert: Chelmala Srinivasulu, Osmania University, India

Expert evaluation: Medium

Data: Only modern

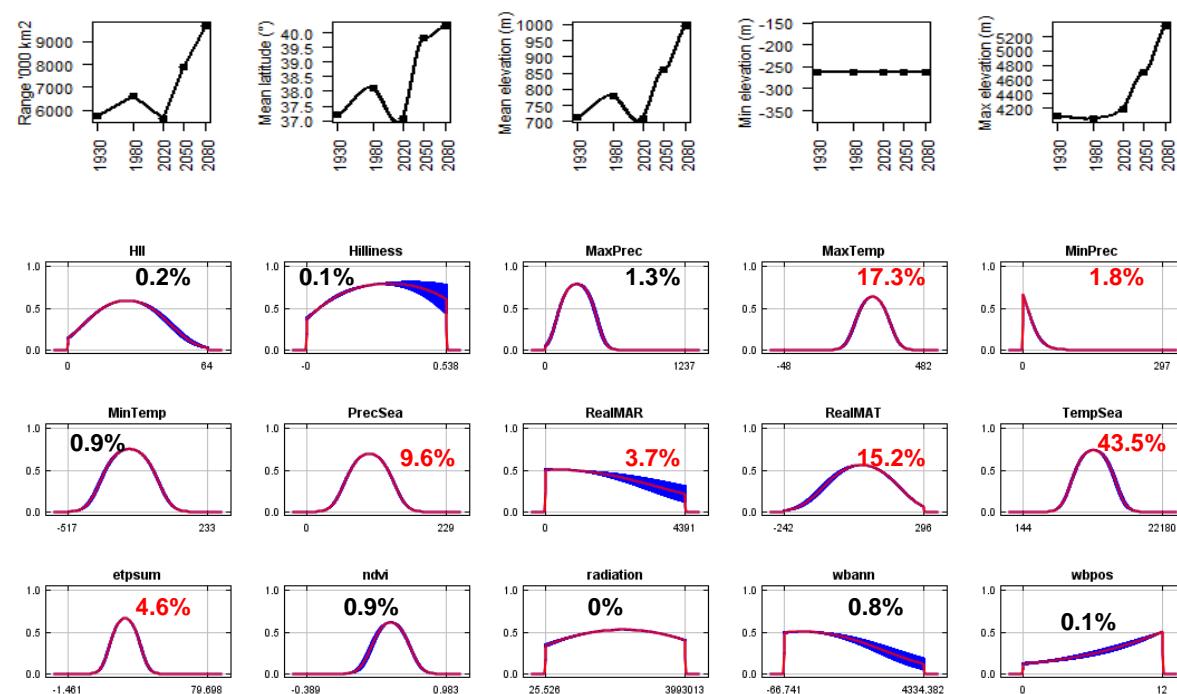
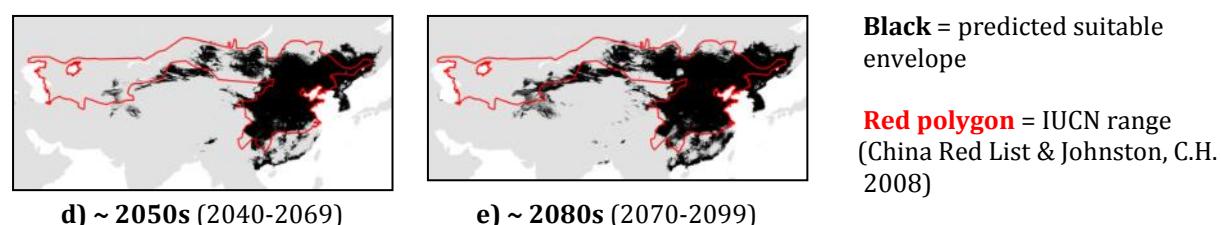
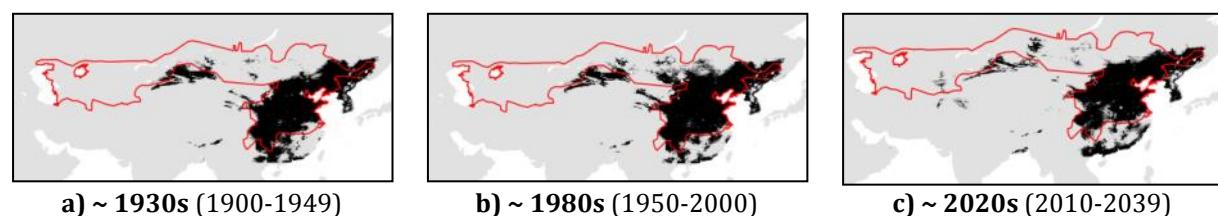
Envelope: Climatic and habitat

Dispersal distance: 2.5km/year (Asian leporids, range 1-35)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.94
Omission rate	0.11
Sensitivity	0.89
Specificity	0.99
Proportion correct	0.98
Kappa	0.76
True Skill Statistic	0.88

Summary: The Tolai hare's bioclimatic envelope is predicted to increase by 70% with a ~3° mean latitudinal polewards shift and a mean increase in elevation of ~280m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (43.5%), maximum temperature (17.3%), mean annual temperature (15.2%), precipitation seasonality (9.6%), annual evapotranspiration (4.6%), mean annual precipitation (3.7%) and minimum precipitation (1.8%).



#36 – White-tailed jackrabbit (*Lepus townsendii*)

n = 275

Expert: Eric Waltari, City University of New York

Expert evaluation: Medium

Data: Only modern

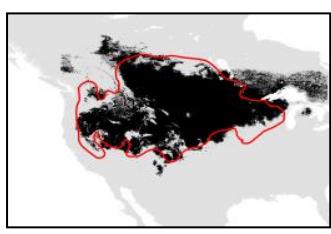
Envelope: Climatic and habitat

Dispersal distance: 18.9km/year (N.Am. leporids, range 2-25)

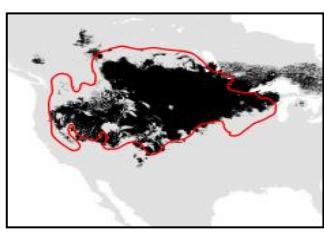
Status: MODELLABLE; **Included in final analysis:** ✓

Model evaluation metric	
AUC	0.94
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.76
True Skill Statistic	0.89

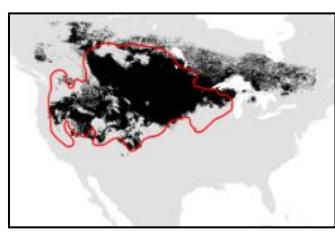
Summary: The White-tailed jackrabbit's bioclimatic envelope is predicted to decrease by 10% with a ~4° mean latitudinal polewards shift and a mean increase in elevation of ~200m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (62.5%), maximum temperature (28.5%), temperature seasonality (3.4%) and annual evapotranspiration (1.6%).



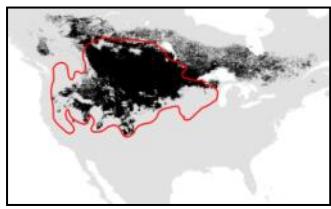
a) ~1930s (1900-1949)



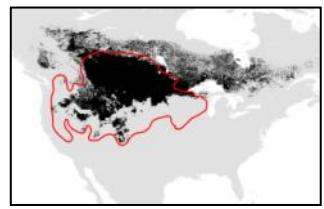
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



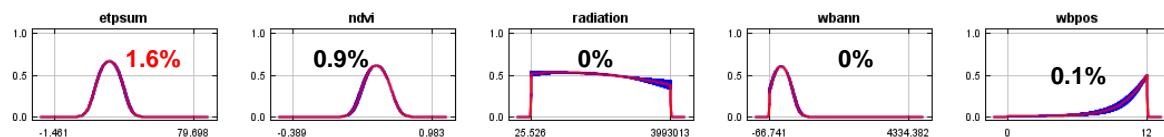
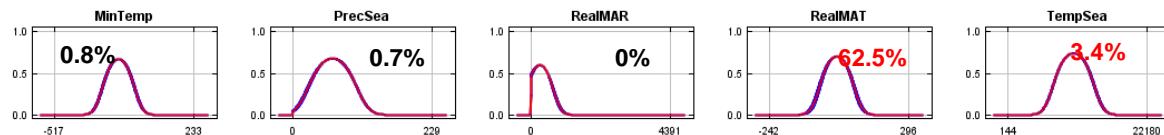
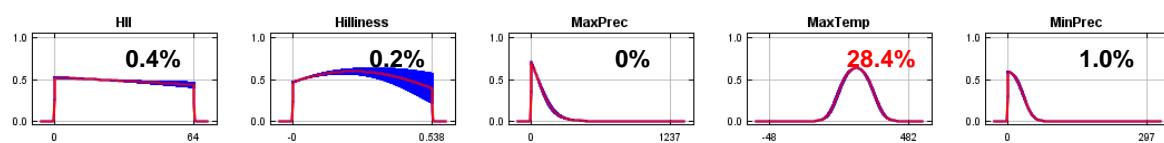
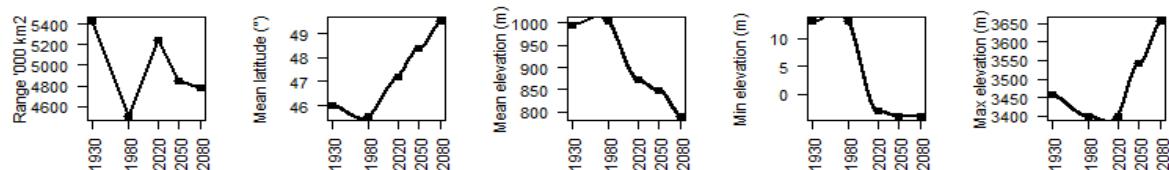
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#37 – Yarkand hare (*Lepus yarkandensis*)

n = 49

Expert: Weihe Yang, Institute of Zoology, Chinese Academy of Sciences

Expert evaluation: Medium

Data: Modern and historic

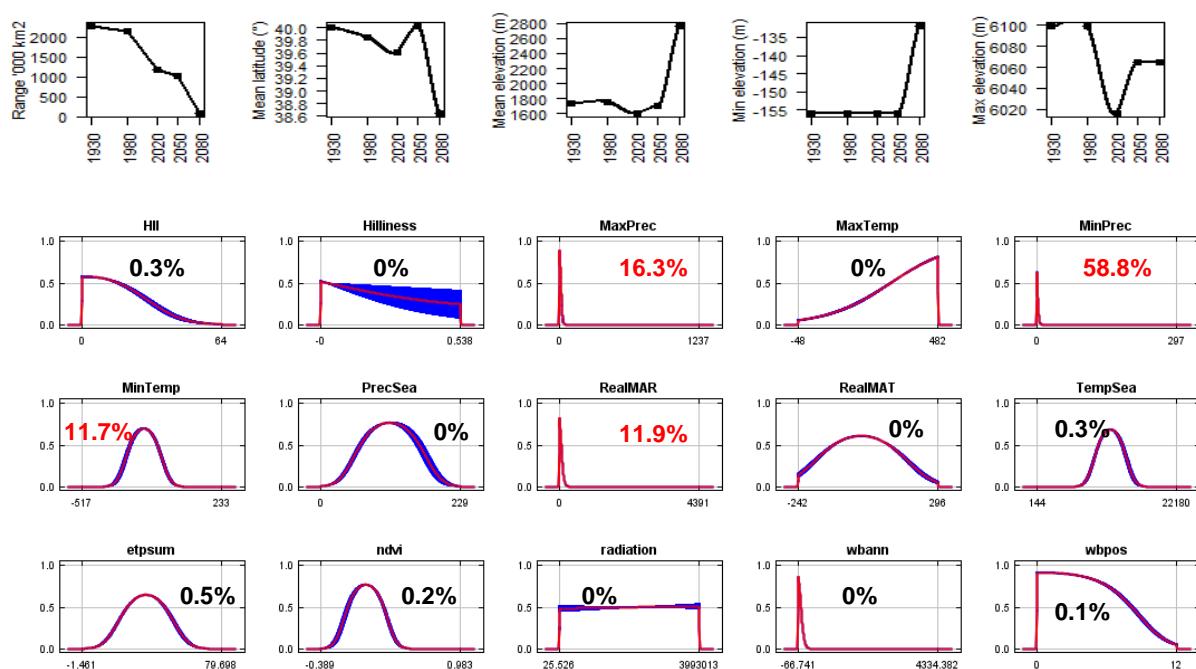
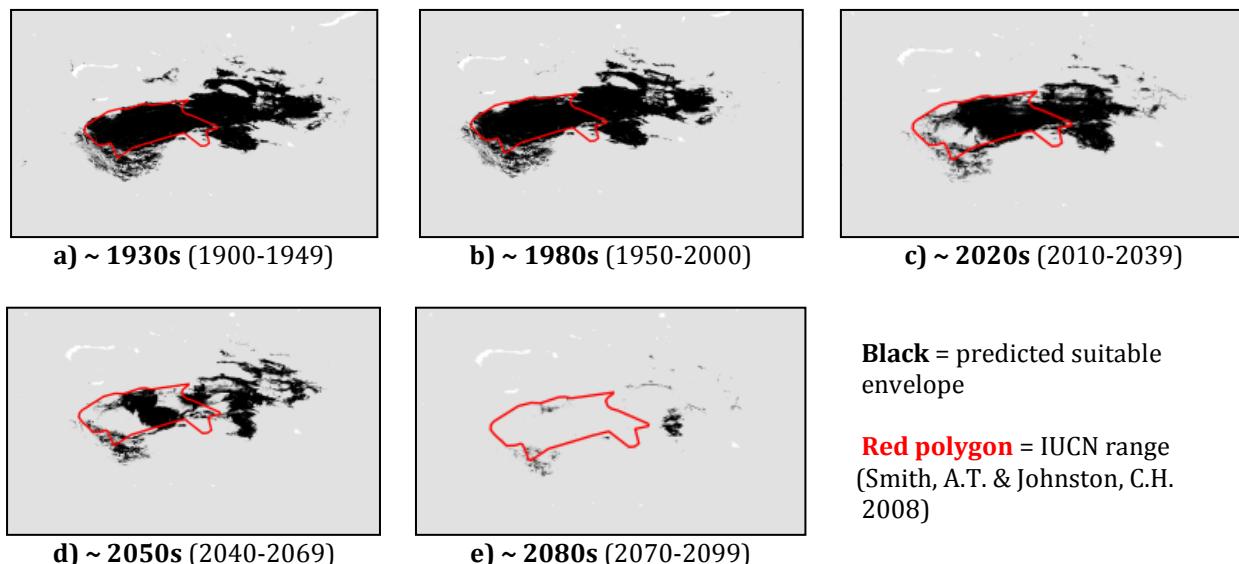
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Smith & Xie, 2008)

Status: MODELLABLE; **Included in final analysis:** ✓

Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.74
True Skill Statistic	0.90

Summary: The Yarkand hare's bioclimatic envelope is predicted to decrease by 100% with a ~1° mean latitudinal shift towards the Equator and a mean increase in elevation of ~1000m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (58.8%), maximum precipitation (16.3%), mean annual precipitation (11.9%) and minimum temperature (11.7%).



#38 – Sumatran striped rabbit (*Nesolagus netscheri*)

n = 11

Expert: Hariyo Wibisono, Wildlife Conservation Society, Indonesia

Expert evaluation: Poor

Data: Modern and historic

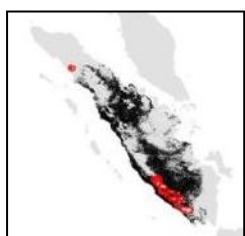
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Expert)

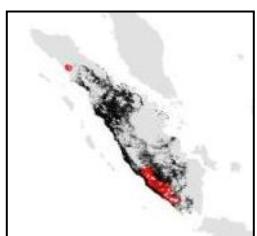
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.95
True Skill Statistic	0.99

Summary: The Sumatran striped rabbit's bioclimatic envelope is predicted to decrease by 91% with a ~1° mean latitudinal shift towards the Equator and a mean increase in elevation of ~330m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (99.3%).



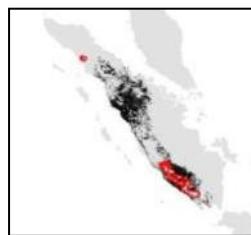
a) ~1930s (1900-1949)



b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



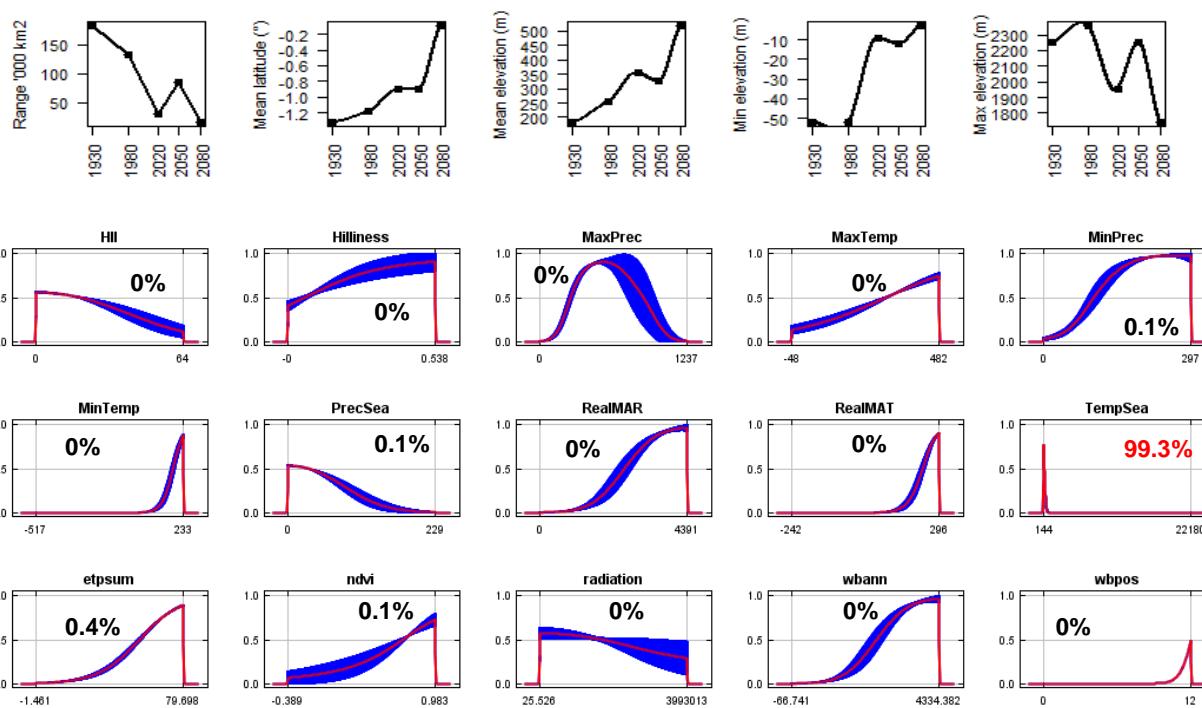
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Meijaard, E. & Sugardjito, J. 2008)



#39 – Annamite striped rabbit (*Nesolagus timminsi*)

n = 4

Expert: Thomas Gray, WWF Greater Mekong & Andrew Tilker, University of Texas Austin

Expert evaluation: Poor

Data: Only modern

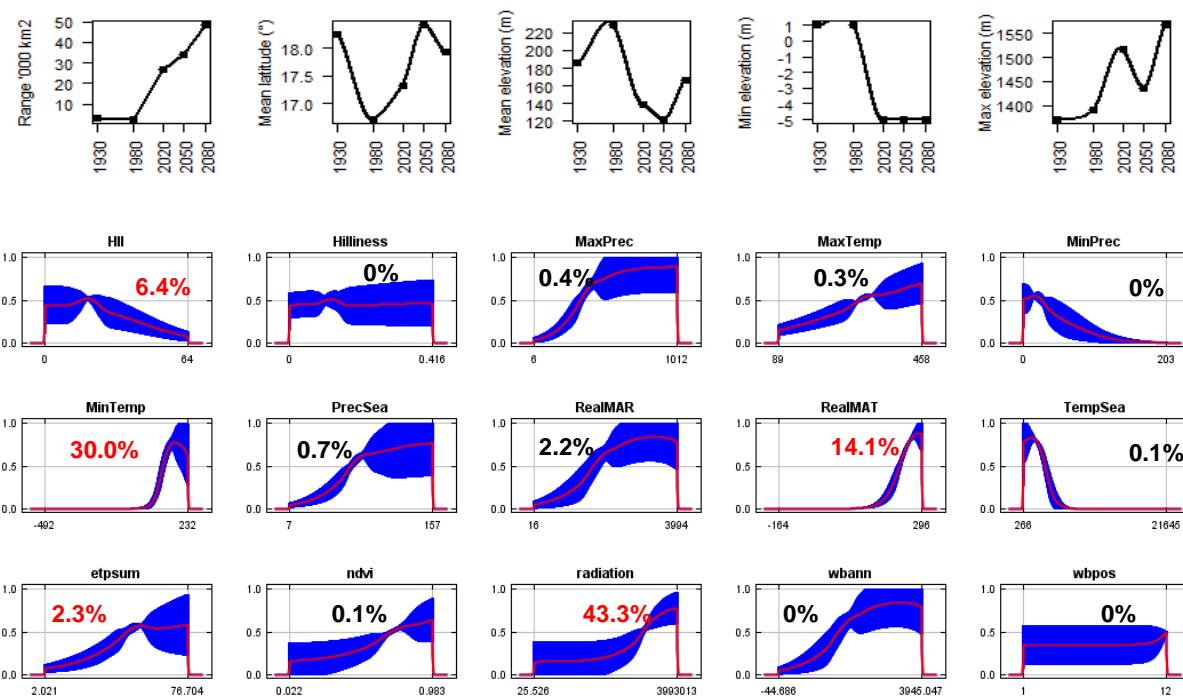
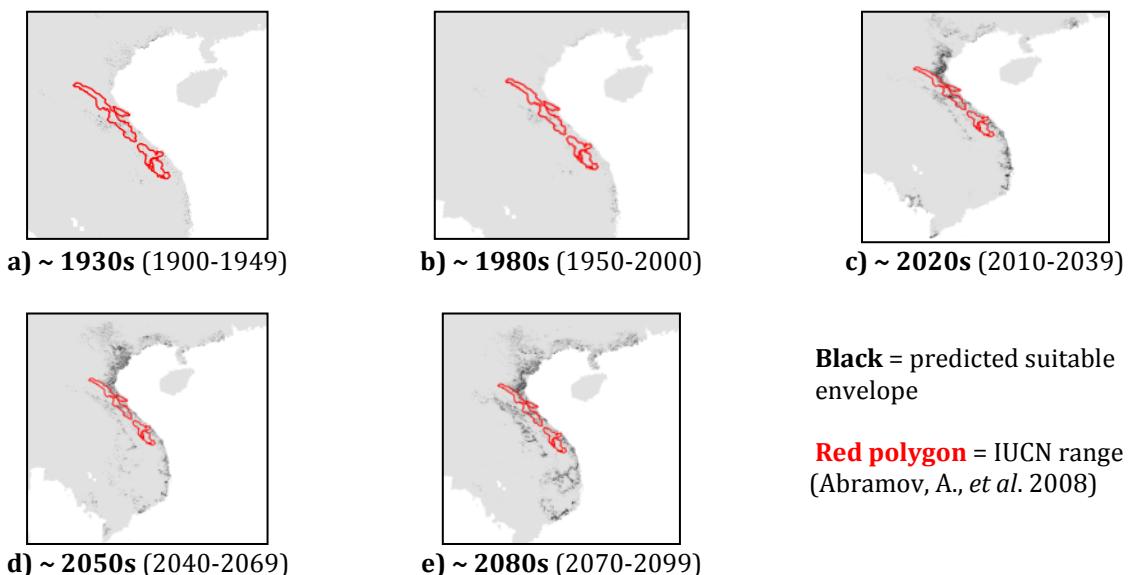
Envelope: Climatic and habitat

Dispersal distance: 10km/year (Expert)

Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.50
True Skill Statistic	0.99

Summary: The Annamite striped rabbit's bioclimatic envelope is predicted to decrease by 1500% with a ~0.3° mean latitudinal shift towards the Equator and a mean decrease in elevation of ~20m driven by an decrease in minimum elevation. 95% of the permutation importance of the model was contributed to by solar radiation (43.3%), minimum temperature (30.0%), mean annual temperature (14.1%), human influence index (6.4%) and annual evapotranspiration (2.3%).



#40 – Alpine pika (*Ochotona alpina*)

n = 16

Expert: Sumiya Ganzorig, Hokkaido University

Expert evaluation: Poor

Data: Modern and historic

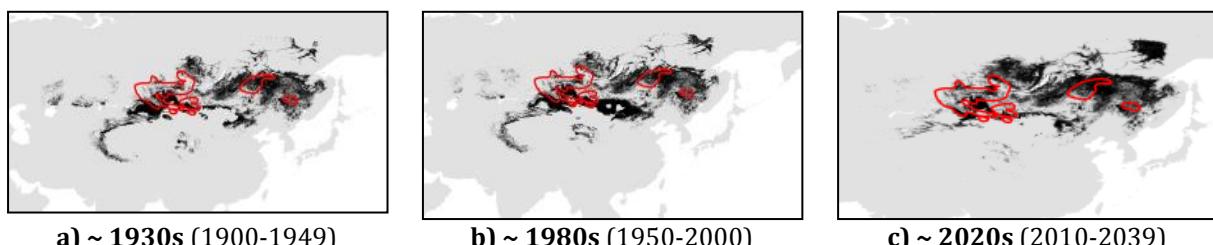
Envelope: Climatic and habitat

Dispersal distance: 10km/year (Similar ecology to *O.pallasii*)

Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.29
True Skill Statistic	0.99

Summary: The Alpine pika's bioclimatic envelope is predicted to decrease by 10% with a ~4° mean latitudinal polewards shift and a mean decrease in elevation of ~80m. 95% of the permutation importance of the model was contributed to by minimum precipitation (50.1%), mean annual temperature (31.1%), number of months with a positive water balance (10.9%), minimum temperature (2.3%) and annual evapotranspiration (1.3%).



a) ~1930s (1900-1949)

b) ~1980s (1950-2000)

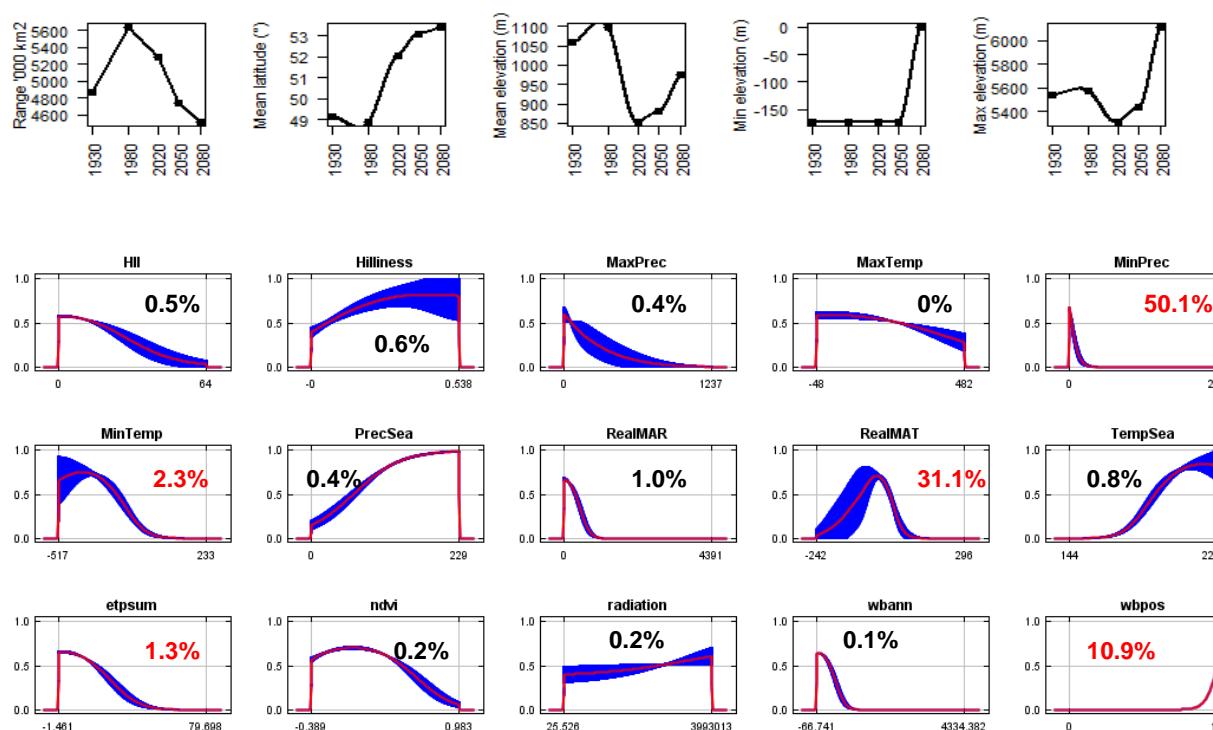
c) ~2020s (2010-2039)

d) ~2050s (2040-2069)

e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#41 – Silver pika (*Ochotona argentata*)

n = 4

Expert: Andrew Smith, Arizona State University

Expert evaluation: Poor

Data: Only modern

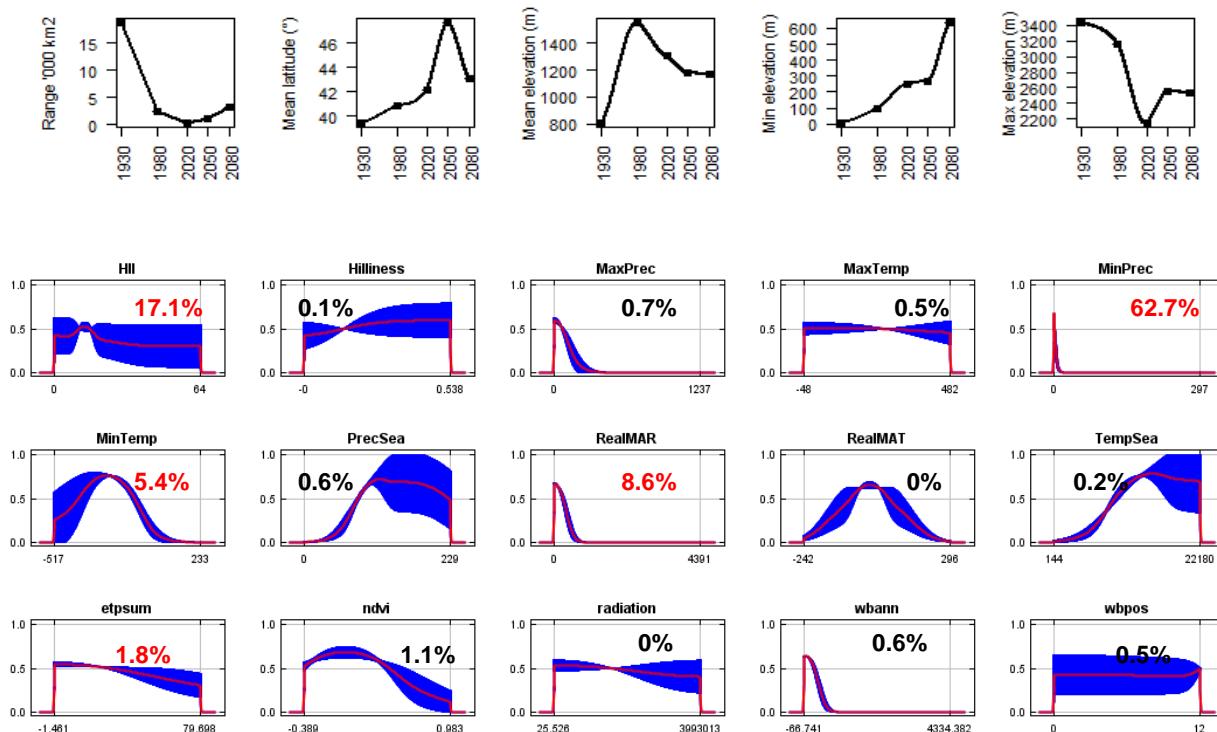
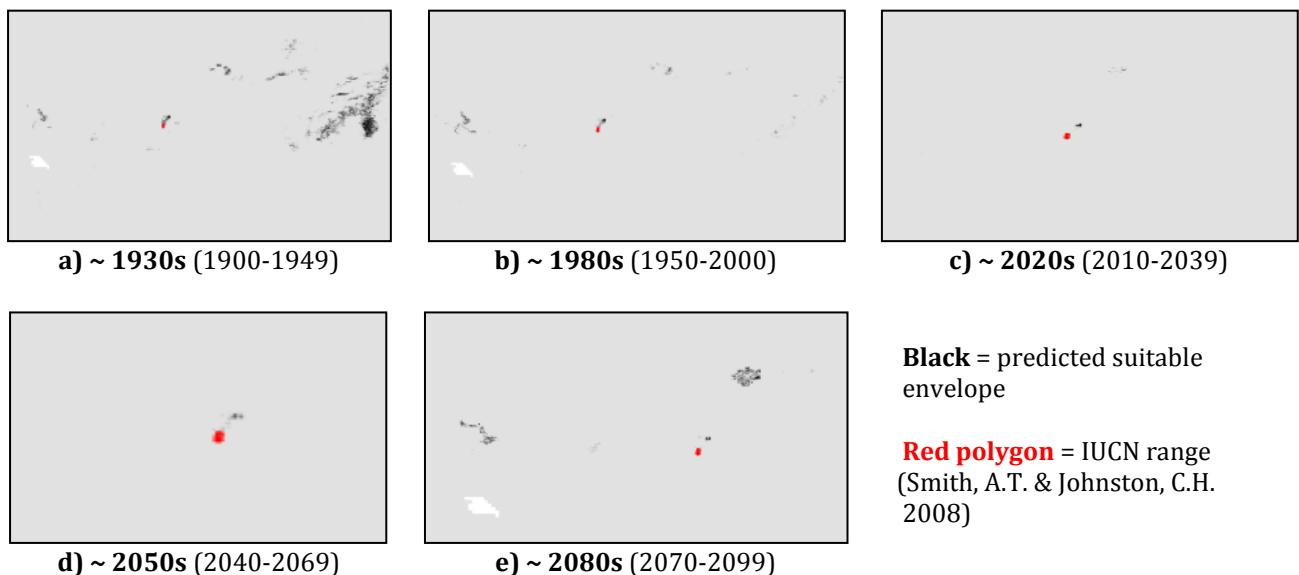
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Asian pikas, range 1-15)

Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	1.00
Omission rate	0.00
Sensitivity	1.00
Specificity	1.00
Proportion correct	1.00
Kappa	1.00
True Skill Statistic	1.00

Summary: The Silver pika's bioclimatic envelope is predicted to decrease by 80% with a ~4° mean latitudinal polewards shift and a mean increase in elevation of ~360m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (62.7%), human influence index (17.1%), mean annual precipitation (8.6%), minimum temperature (5.4%) and annual evapotranspiration (1.8%).



#42 – Gansu pika (*Ochotona cansus*)

n = 38

Expert: Andrew Smith, Arizona State University

Expert evaluation: Medium

Data: Modern and historic

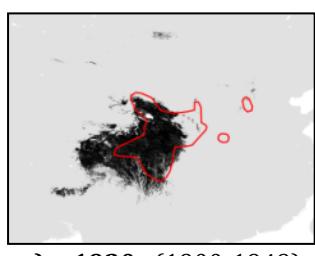
Envelope: Climatic and habitat

Dispersal distance: 1.5km/year (Similar ecology to *O.roylei*)

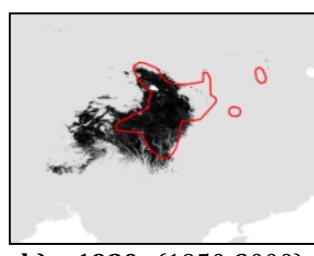
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.95
Omission rate	0.11
Sensitivity	0.89
Specificity	0.99
Proportion correct	0.99
Kappa	0.61
True Skill Statistic	0.89

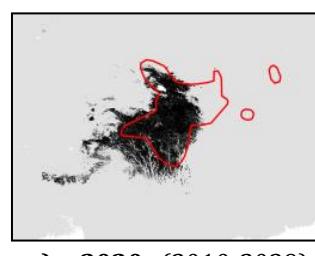
Summary: The Gansu pika's bioclimatic envelope is predicted to decrease by 60% with a ~0.4° mean latitudinal shift towards the Equator and a mean increase in elevation of ~230m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (89.8%) and minimum temperature (6.9%).



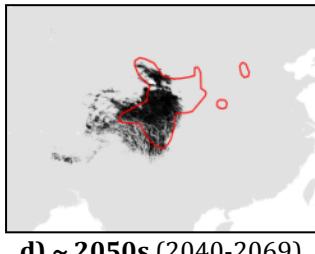
a) ~ 1930s (1900-1949)



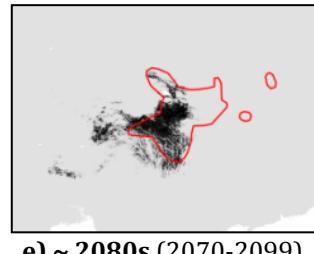
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



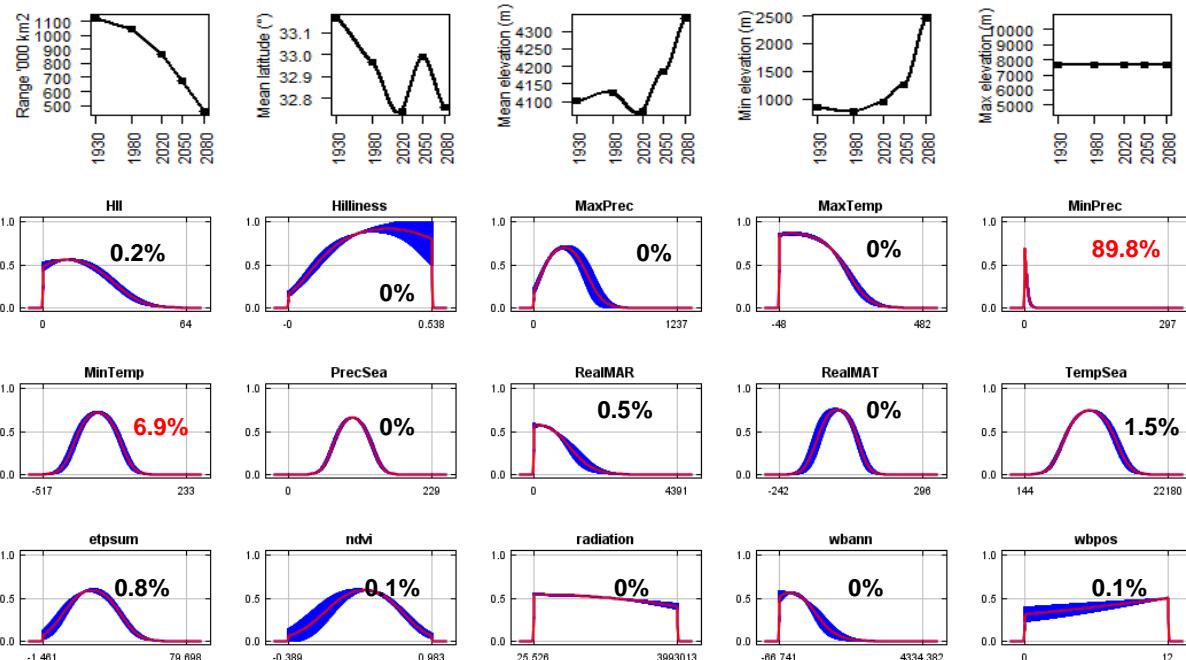
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range (Smith, A.T. & Johnston, C.H. 2008)



#43 – Collared pika (*Ochotona collaris*)

n = 193

Expert: Hayley Lanier, University of Michigan & David Hik, University of Alberta

Expert evaluation: Poor

Data: Modern and historic

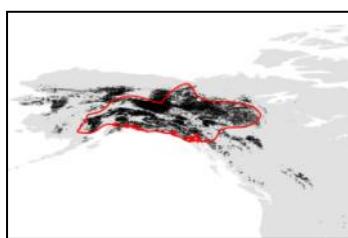
Envelope: Climatic and habitat

Dispersal distance: 1km/year (Expert)

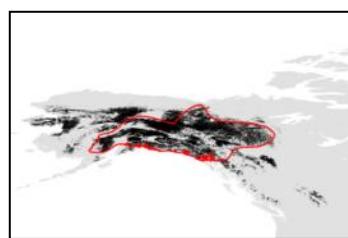
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.86
True Skill Statistic	0.90

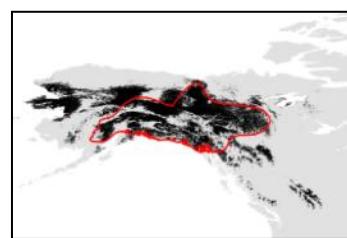
Summary: The Collared pika's bioclimatic envelope is predicted to increase by 20% with a ~2° mean latitudinal polewards shift and a mean decrease in elevation of ~140m. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (86.7%), mean annual temperature (3.3%), normalised difference vegetation index (3.2%) and maximum temperature (2.0%).



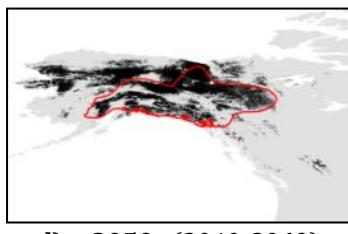
a) ~1930s (1900-1949)



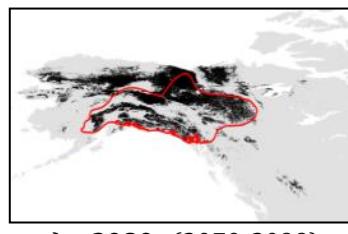
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



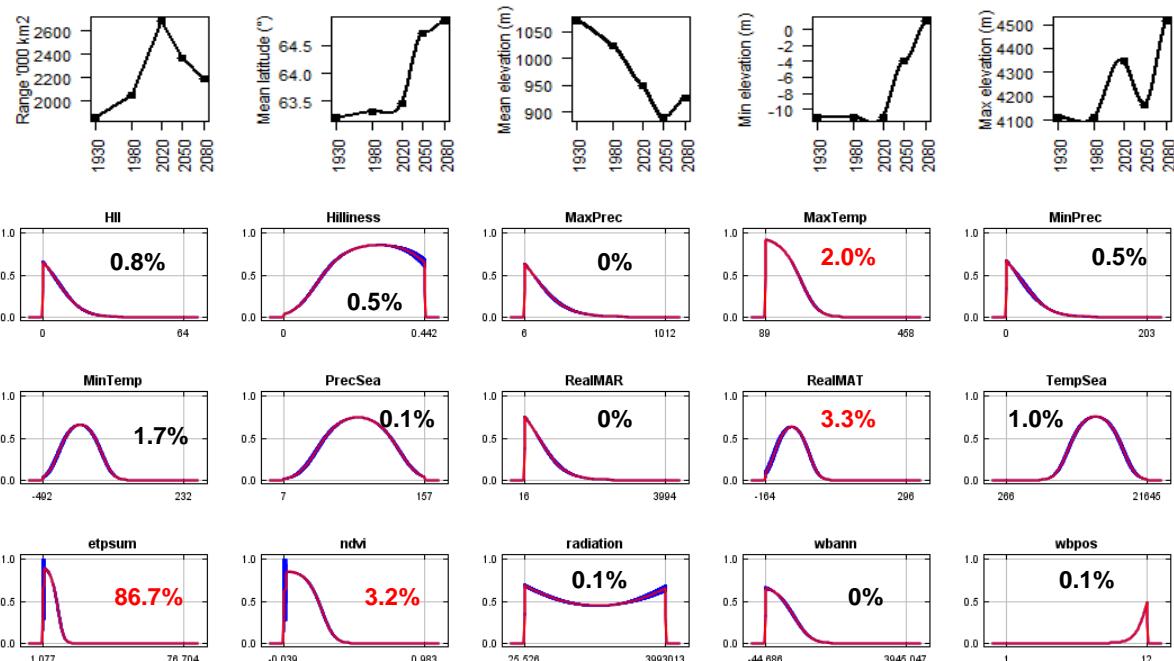
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range (Smith, A.T. & Johnston, C.H. 2008)



#44 – Plateau pika (*Ochotona curzoniae*)

n = 131

Expert: Andrew Smith, Arizona State University

Expert evaluation: Good

Data: Only modern

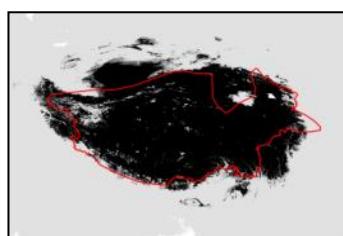
Envelope: Climatic and habitat

Dispersal distance: 0.1km/year (Expert)

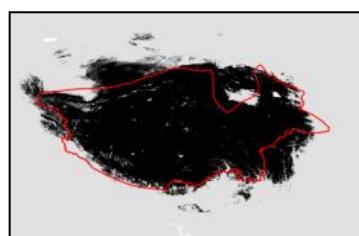
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.94
Omission rate	0.11
Sensitivity	0.89
Specificity	0.99
Proportion correct	0.99
Kappa	0.76
True Skill Statistic	0.88

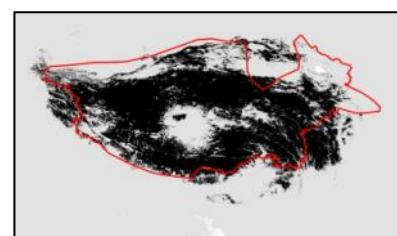
Summary: The Plateau pika's bioclimatic envelope is predicted to decrease by 30% with a ~1° mean latitudinal shift towards the Equator and a mean increase in elevation of ~700m driven by an increase in minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (48.0%), maximum temperature (42.0%) and annual evapotranspiration (6.8%).



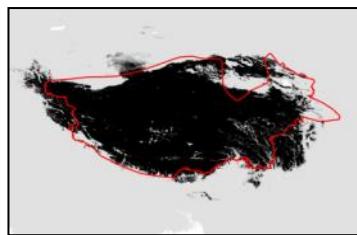
a) ~1930s (1900-1949)



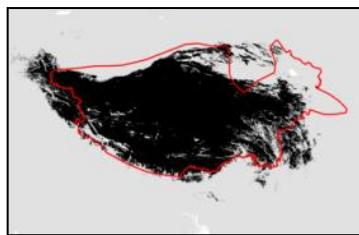
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



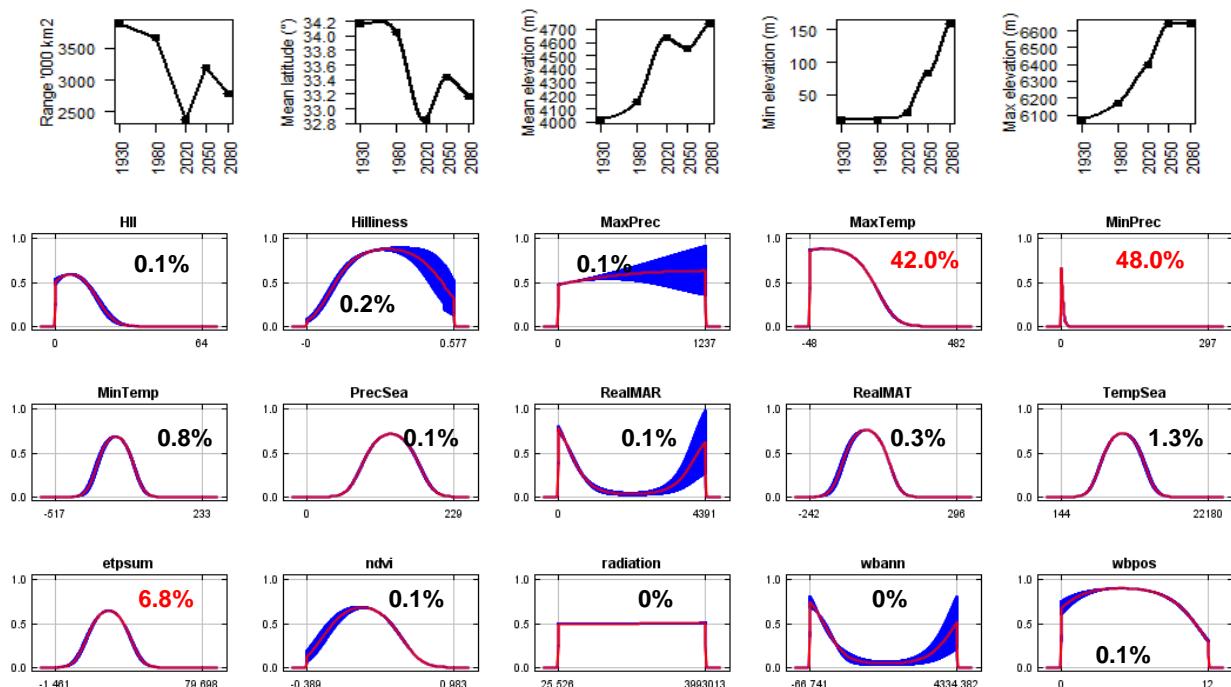
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#45 – Daurian pika (*Ochotona daurica*)

n = 131

Expert: Andrew Smith, Arizona State University

Expert evaluation: Medium

Data: Only modern

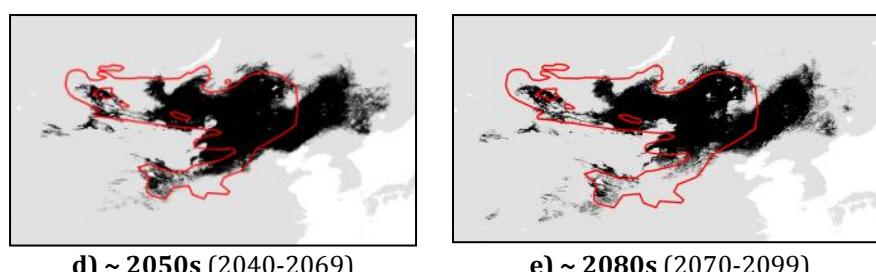
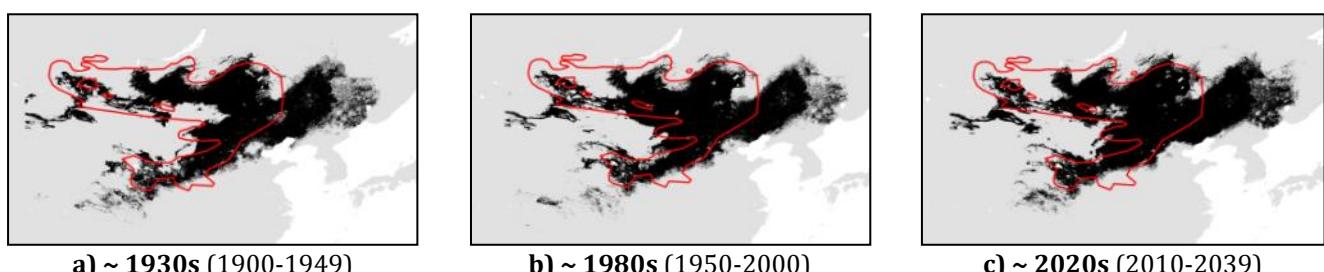
Envelope: Climatic and habitat

Dispersal distance: 0.1km/year (Similar ecology to *O. curzoniae*)

Status: MODELLABLE; Included in final analysis: ✓

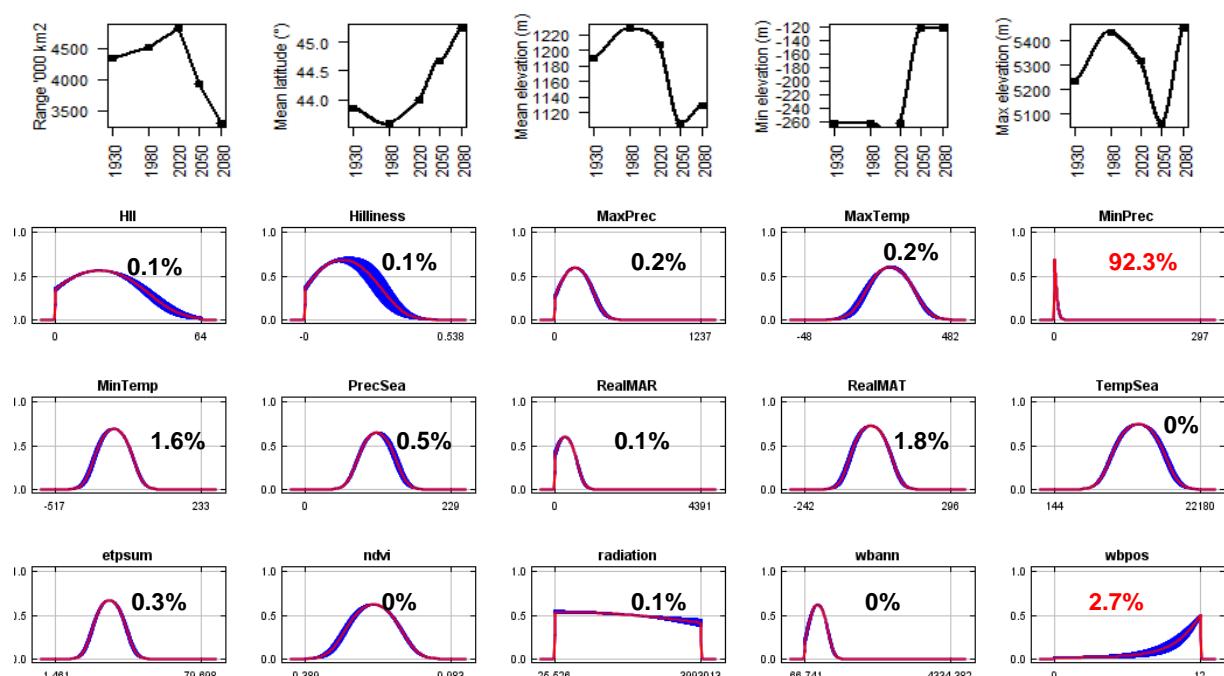
Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.66
True Skill Statistic	0.89

Summary: The Daurian pika's bioclimatic envelope is predicted to decrease by 25% with a ~1° mean latitudinal polewards shift and a mean decrease in elevation of ~60m. 95% of the permutation importance of the model was contributed to by minimum precipitation (92.3%) and number of months with a positive water balance (2.7%).



Black = predicted suitable envelope

Red polygon = IUCN range (Smith, A.T. & Johnston, C.H. 2008)



#46 – Chinese red pika (*Ochotona erythrotis*)

n = 39

Expert: Andrew Smith, Arizona State University

Expert evaluation: Poor

Data: Modern and historic

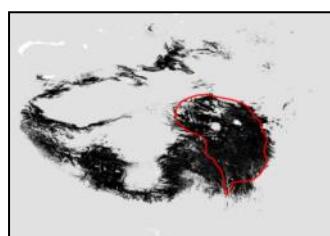
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Asian pikas, range 1-15)

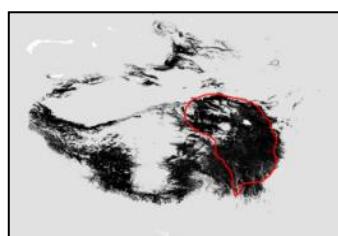
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.53
True Skill Statistic	0.89

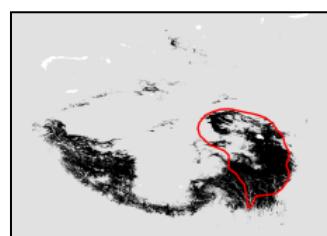
Summary: The Chinese red pika's bioclimatic envelope is predicted to decrease by 20% with a ~3° mean latitudinal polewards shift and a mean decrease in elevation of ~2400m driven by a decrease in minimum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (87.2%), minimum temperature (7.2%) and mean annual temperature (2.9%).



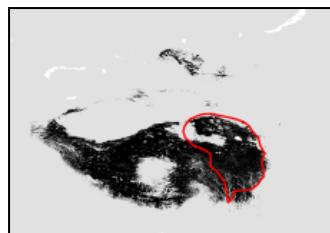
a) ~ 1930s (1900-1949)



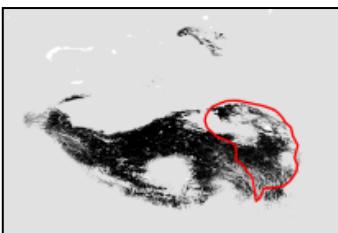
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



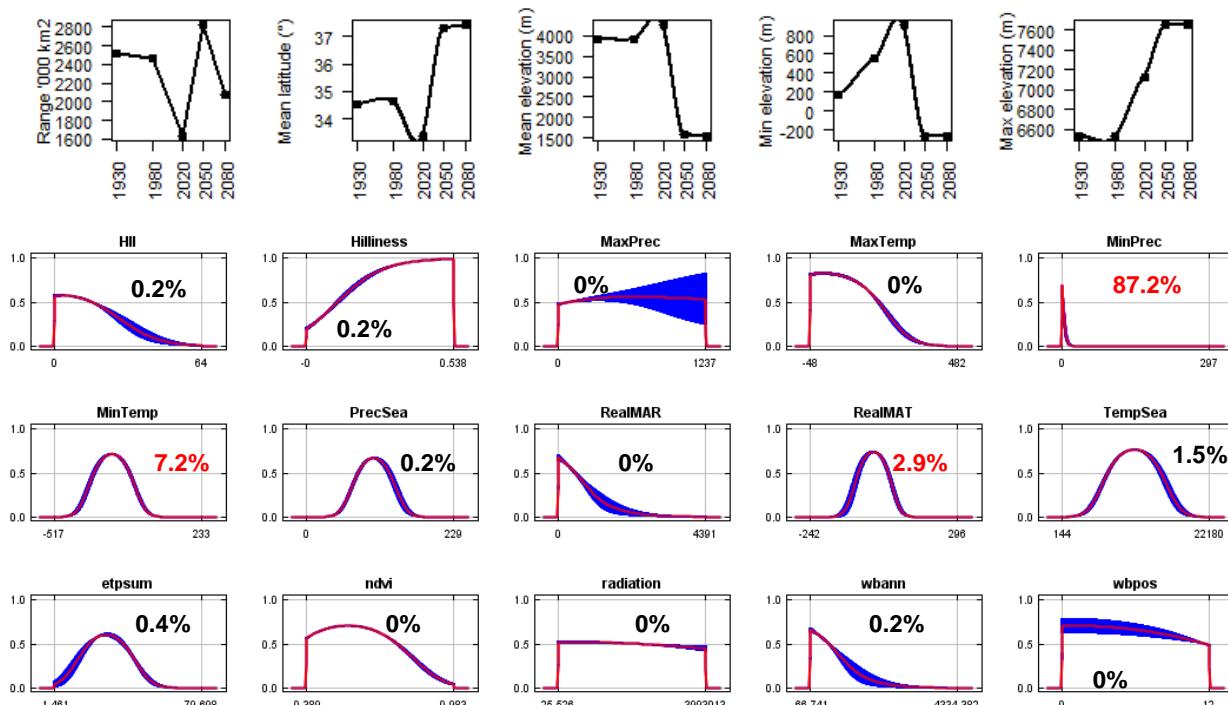
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#47 – Forrest's pika (*Ochotona forresti*)

n = 9

Expert: Andrew Smith, Arizona State University

Expert evaluation: Poor

Data: Only modern

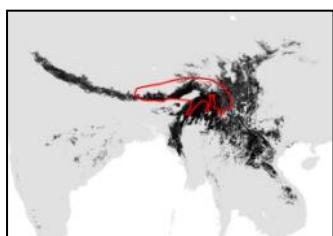
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Asian pikas, range 1-15)

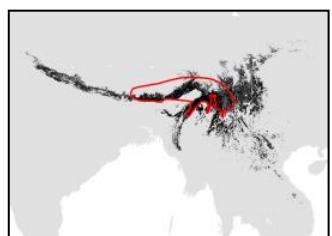
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.53
True Skill Statistic	0.89

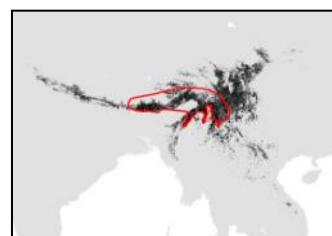
Summary: The Forrest's pika's bioclimatic envelope is predicted to decrease by 40% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~600m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (36.8%), temperature seasonality (20.6%), normalised difference vegetation index (12.1%), maximum temperature (9.3%), precipitation seasonality (7.6%), human influence index (6.2%) and surface roughness index (4.2%).



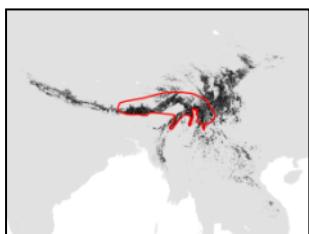
a) ~ 1930s (1900-1949)



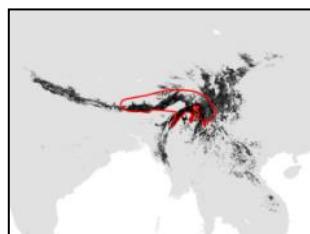
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



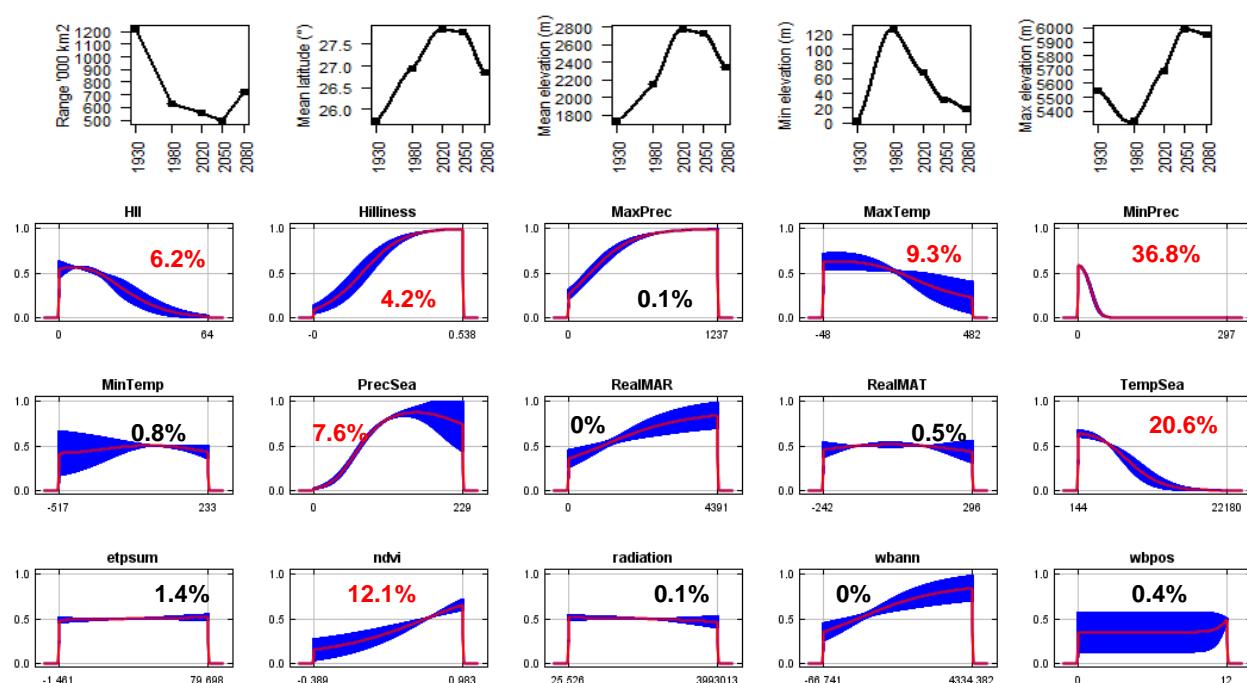
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#48 – Glover's pika (*Ochotona gloveri*)

n = 22

Expert: Andrew Smith, Arizona State University

Expert evaluation: Medium

Data: Only modern

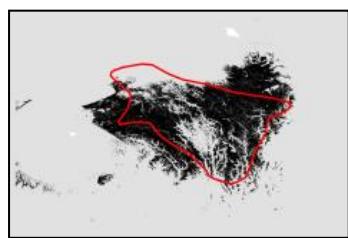
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Asian pikas, range 1-15)

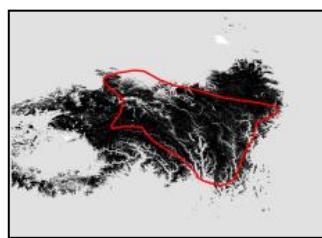
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.65
True Skill Statistic	0.99

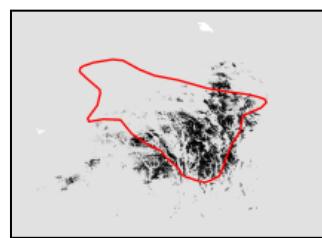
Summary: The Glover's pika's bioclimatic envelope is predicted to decrease by 50% with a ~0.5° mean latitudinal polewards shift and a mean increase in elevation of ~270m driven by an increase in minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (46.3%), minimum temperature (28.8%), mean annual temperature (12.7%), human influence index (3.8%), temperature seasonality (3.1%) and precipitation seasonality (1.8%).



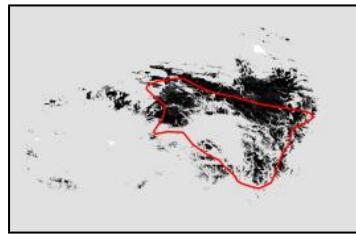
a) ~ 1930s (1900-1949)



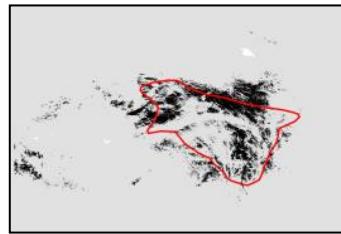
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



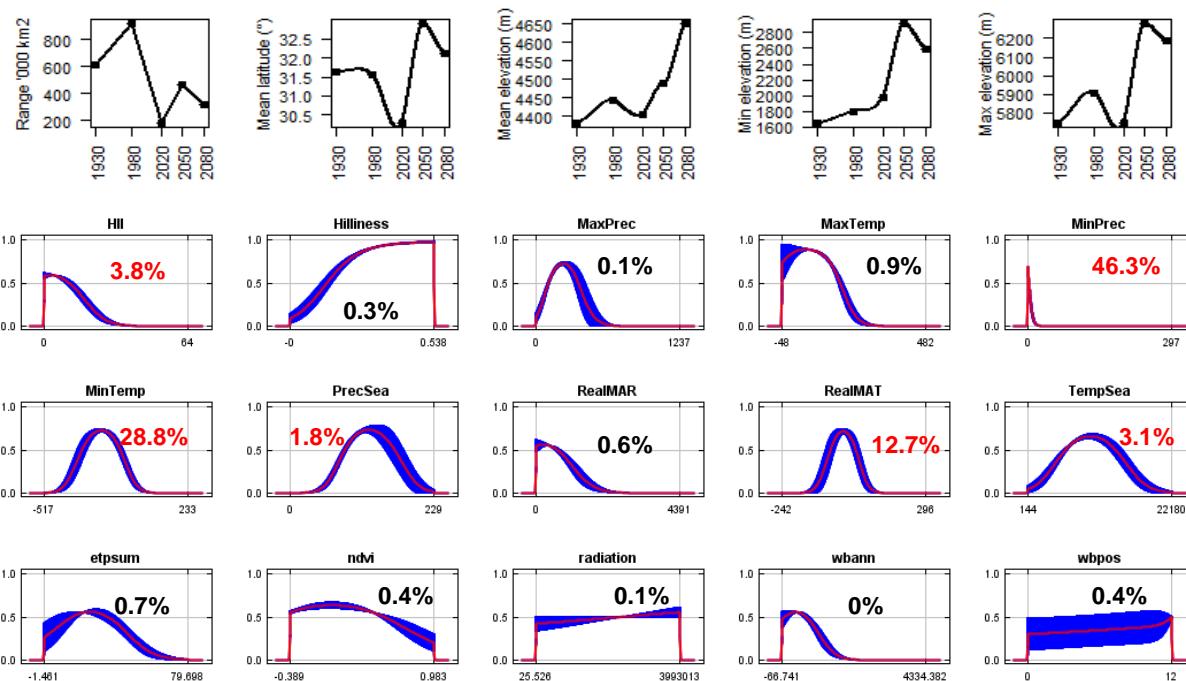
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#49 – Hoffmann's pika (*Ochotona hoffmanni*)

n = 5

Expert: Andrey Lissovsky, Zoological Museum of Moscow State University

Expert evaluation: Medium

Data: Modern and historic

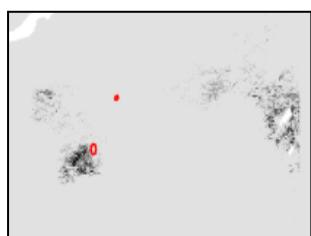
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Asian pikas, range 1-15)

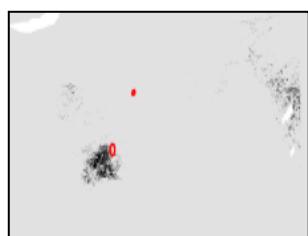
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.91
True Skill Statistic	0.99

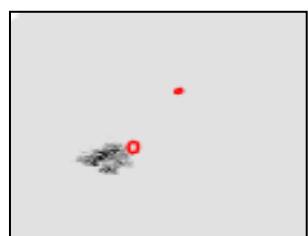
Summary: The Hoffmann's pika's bioclimatic envelope is predicted to decrease by 90% with a ~1° mean latitudinal shift towards the Equator and a mean increase in elevation of ~470m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (73.2%), mean annual temperature (12.6%), minimum temperature (6.5%) and minimum precipitation (5.3%).



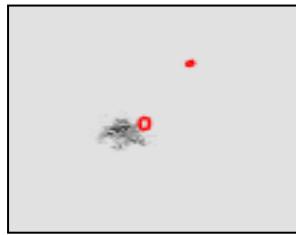
a) ~1930s (1900-1949)



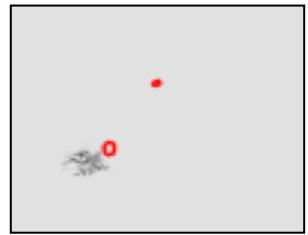
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



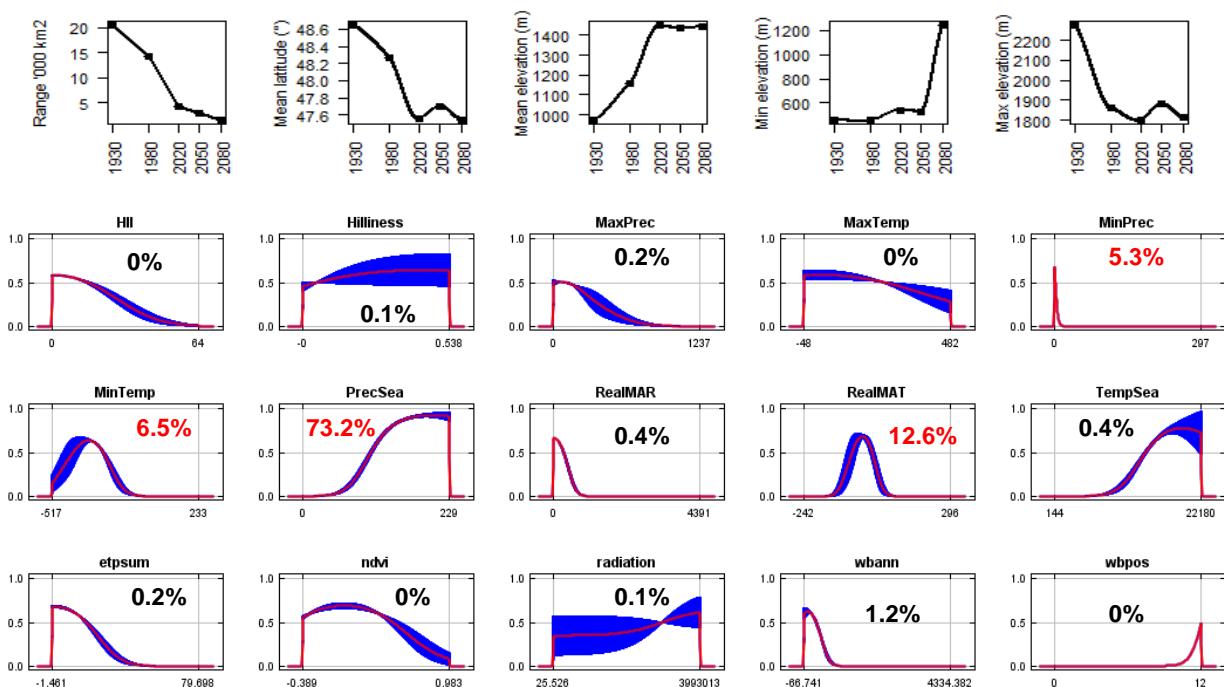
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#50 – Siberian pika (*Ochotona hyperborea*)

n = 16

Expert: Julia Witczuk, Warsaw Agricultural University, Poland

Expert evaluation: Poor

Data: Modern and historic

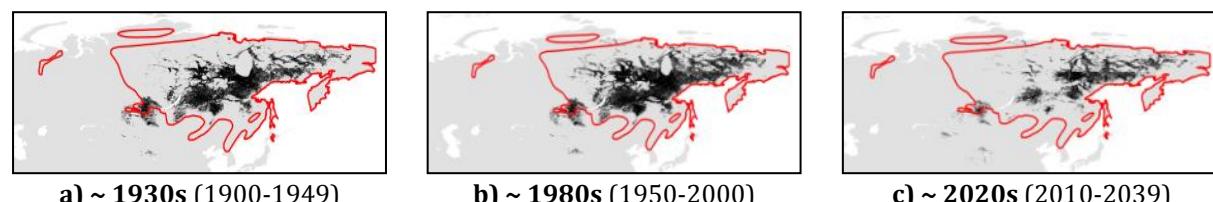
Envelope: Climatic and habitat

Dispersal distance: 10km/year (Similar ecology to *O.alpina*)

Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.97
Omission rate	0.06
Sensitivity	0.94
Specificity	0.99
Proportion correct	0.99
Kappa	0.40
True Skill Statistic	0.93

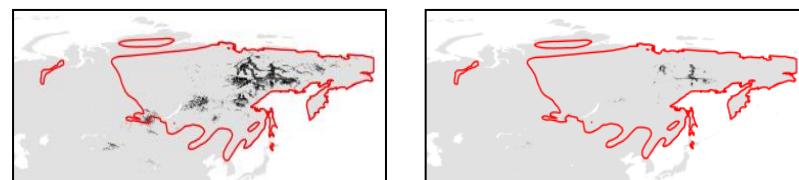
Summary: The Siberian pika's bioclimatic envelope is predicted to decrease by 100% with a ~5° mean latitudinal polewards shift and a mean increase in elevation of ~200m driven by an increase in minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (72.5%), annual evapotranspiration (10.4%), minimum precipitation (6.4%), human influence index (2.8%), normalised difference vegetation index (2.6%) and annual water balance (1.8%).



a) ~ 1930s (1900-1949)

b) ~ 1980s (1950-2000)

c) ~ 2020s (2010-2039)

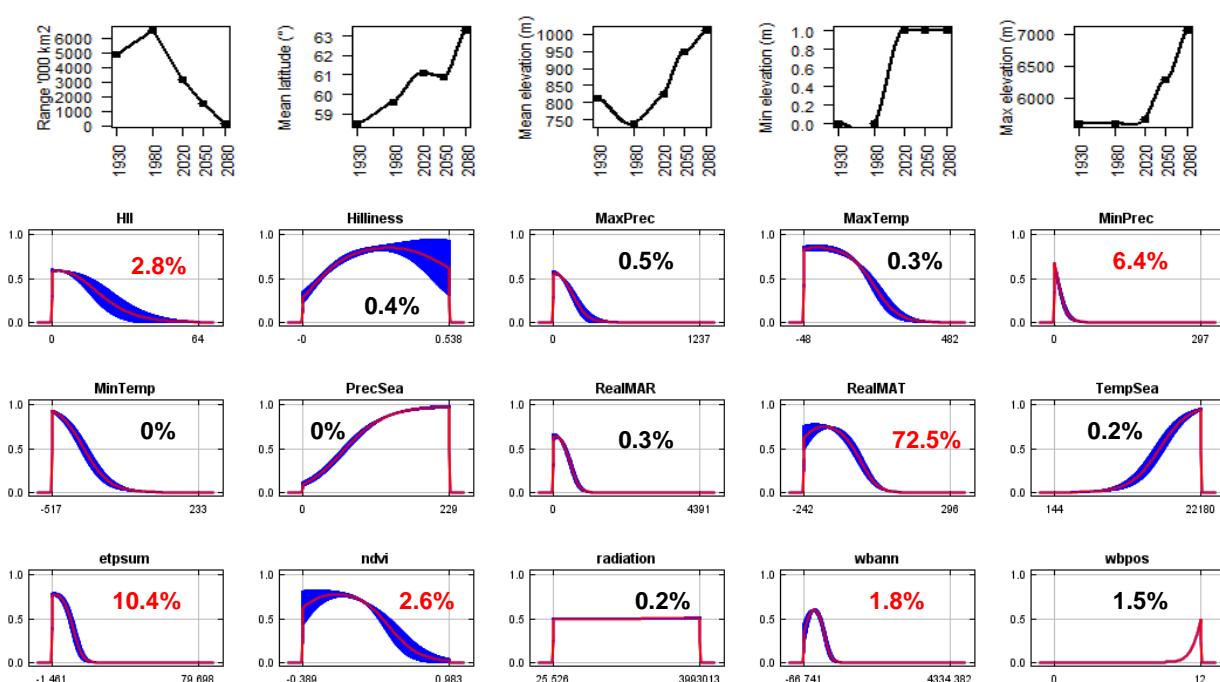


d) ~ 2050s (2040-2069)

e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range (Smith, A.T. & Johnston, C.H. 2008)



#51– Ili pika (*Ochotona iliensis*)

n = 11

Expert: Andrew Smith, Arizona State University

Expert evaluation: Poor

Data: Only modern

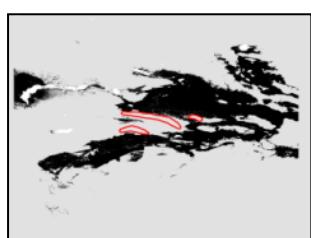
Envelope: Climatic and habitat

Dispersal distance: 1km/year (Similar ecology to *O.koslowi*)

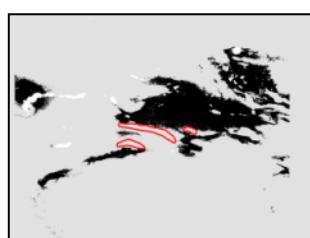
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.55
True Skill Statistic	0.99

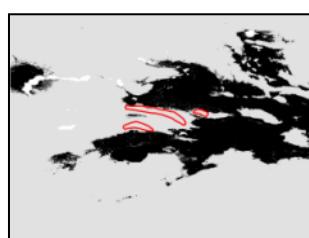
Summary: The Ili pika's bioclimatic envelope is predicted to decrease by 20% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~80m. 95% of the permutation importance of the model was contributed to by minimum precipitation (52.7%), minimum temperature (22.2%), mean annual temperature (8.8%), maximum precipitation (6.5%), temperature seasonality (3.0%) and human influence index (2.2%).



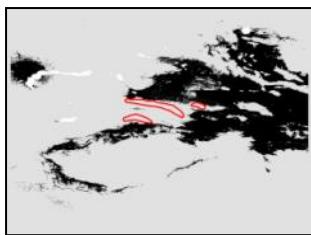
a) ~ 1930s (1900-1949)



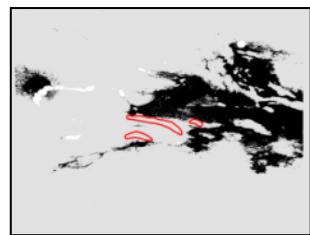
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



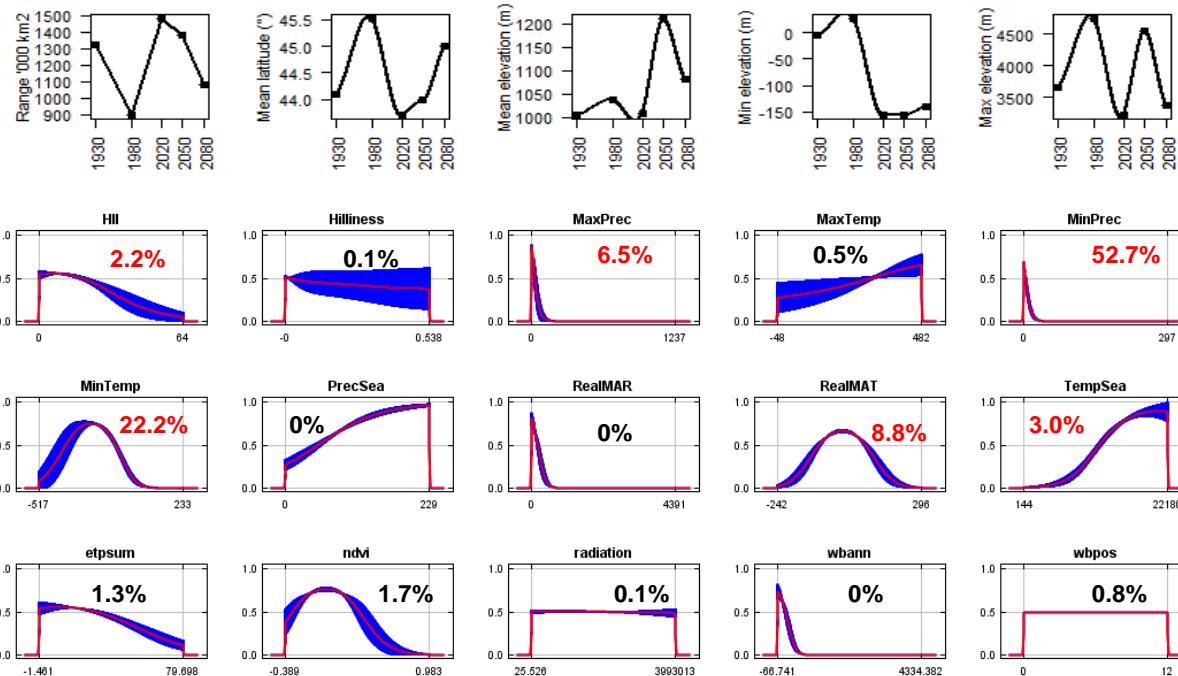
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#52 – Kozlov's pika (*Ochotona koslowi*)

n = 5

Expert: Andrew Smith, Arizona State University

Expert evaluation: Medium

Data: Only modern

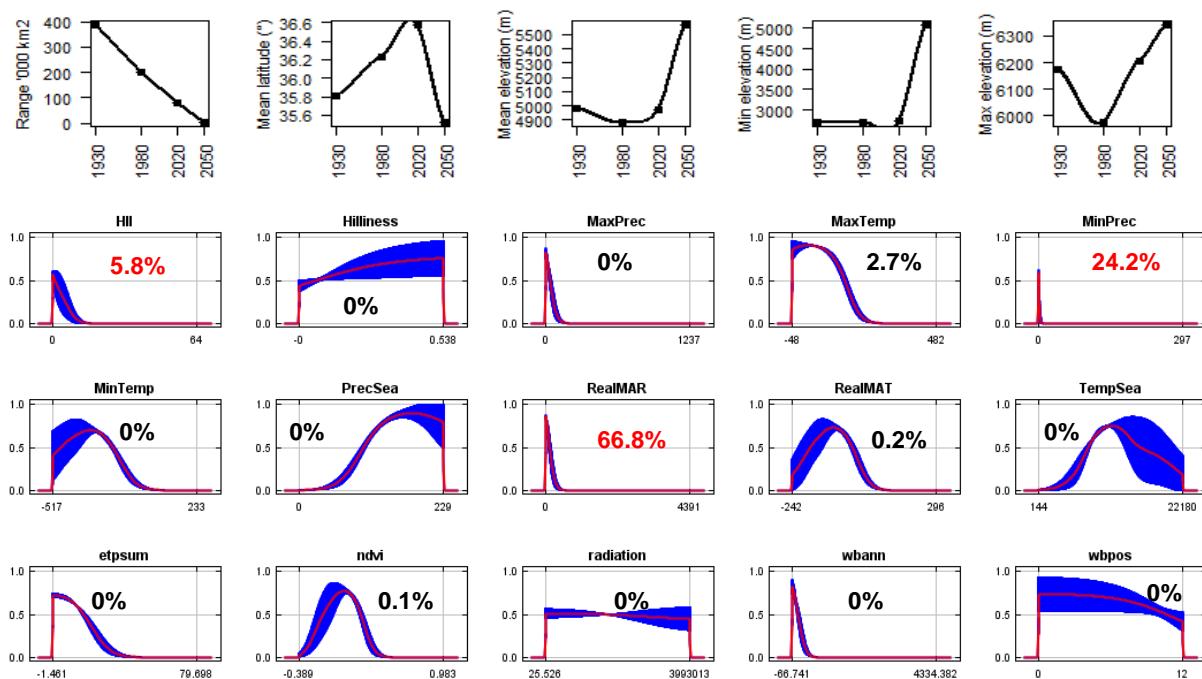
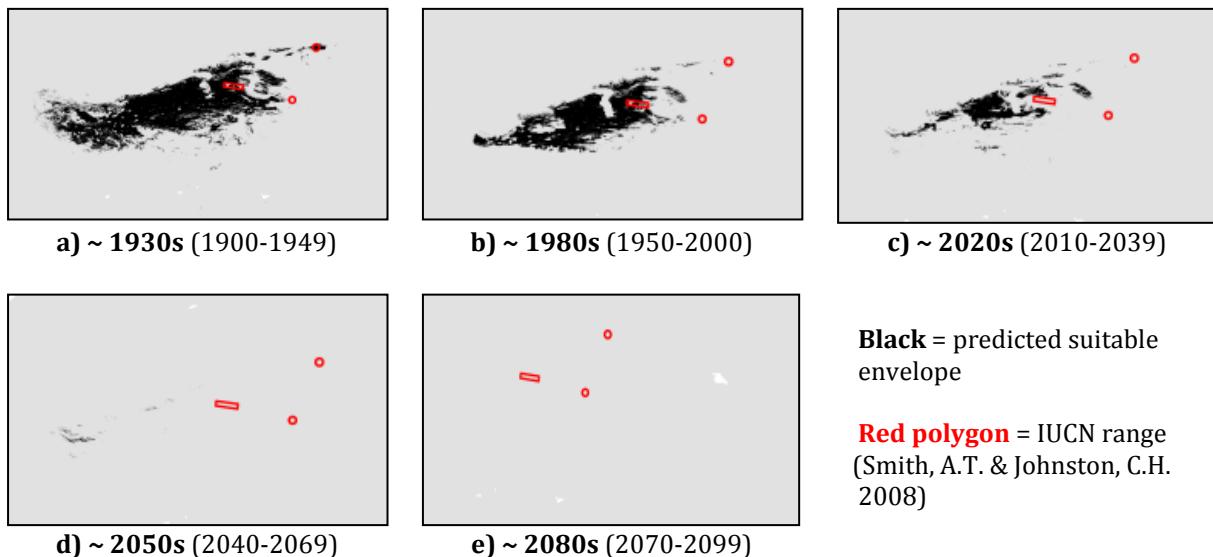
Envelope: Climatic and habitat

Dispersal distance: 1km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.86
True Skill Statistic	0.99

Summary: The Kozlov's pika's bioclimatic envelope is predicted to decrease by 100% (**total extinction**). 95% of the permutation importance of the model was contributed to by mean annual precipitation (66.8%), minimum precipitation (24.2%) and human influence index (5.8%).



#53 – Ladak pika (*Ochotona ladacensis*)

n = 18

Expert: Andrew Smith, Arizona State University

Expert evaluation: Medium

Data: Modern and historic

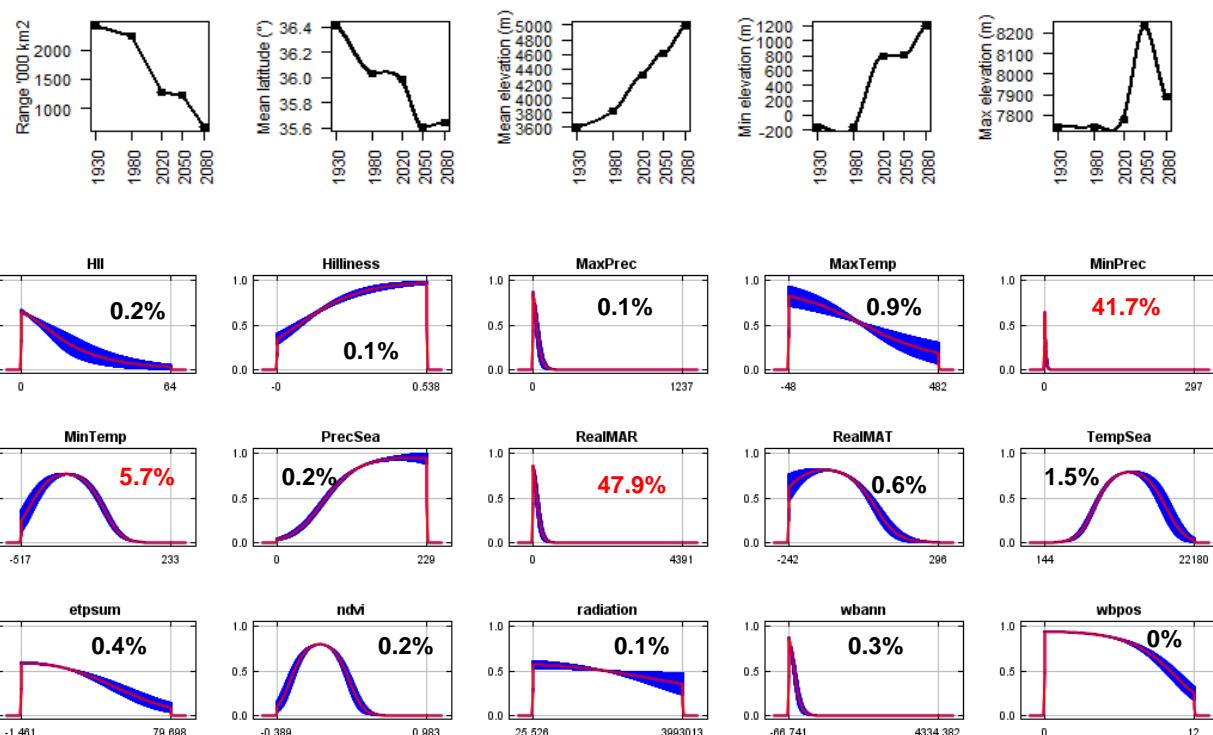
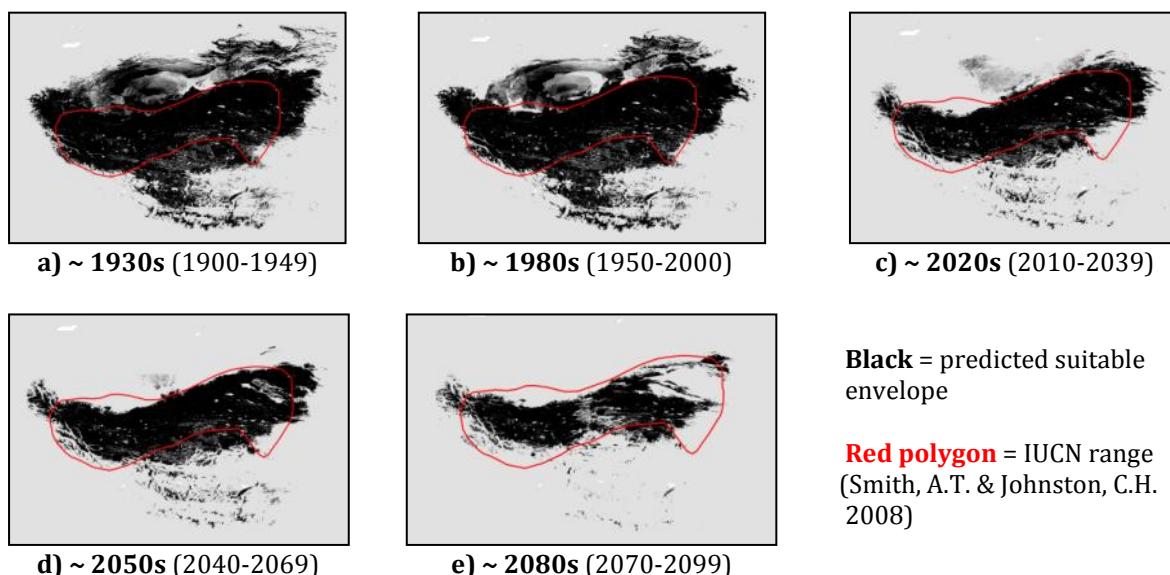
Envelope: Climatic and habitat

Dispersal distance: 0.05km/year (Similar ecology to *O. curzoniae*)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.63
True Skill Statistic	0.99

Summary: The Ladak pika's bioclimatic envelope is predicted to decrease by 70% with a ~1° mean latitudinal shift towards the Equator and a mean increase in elevation of ~1400m driven by an increase in minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by mean annual precipitation (47.9%), minimum precipitation (41.7%) and minimum temperature (5.7%).



#54 – Large-eared pika (*Ochotona macrotis*)

n = 49

Expert: Nishma Dahal, National Centre for Biological Sciences, India

Expert evaluation: Medium

Data: Modern and historic

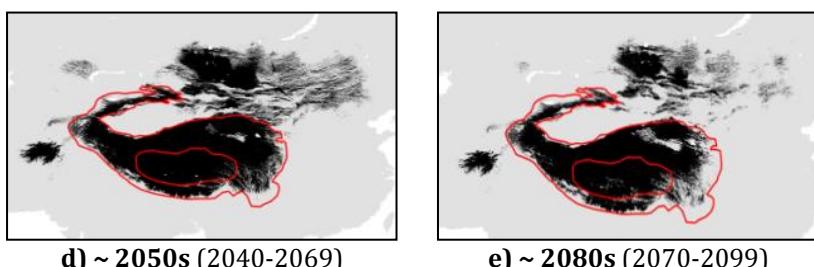
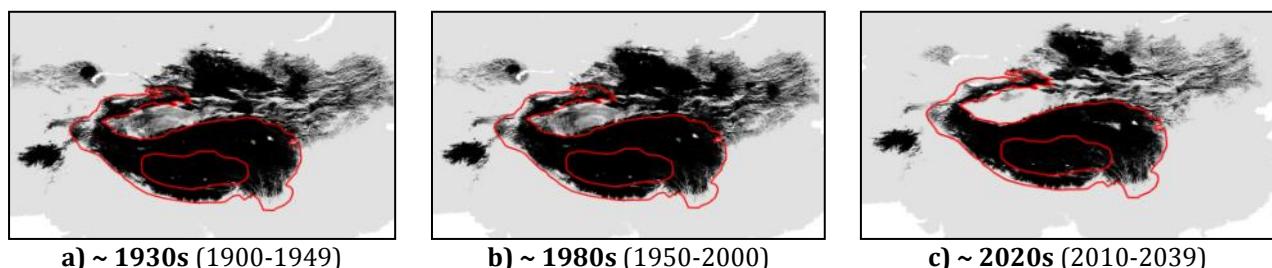
Envelope: Climatic and habitat

Dispersal distance: 1km/year (Similar ecology to *O.roylei*)

Status: MODELLABLE; Included in final analysis: ✓

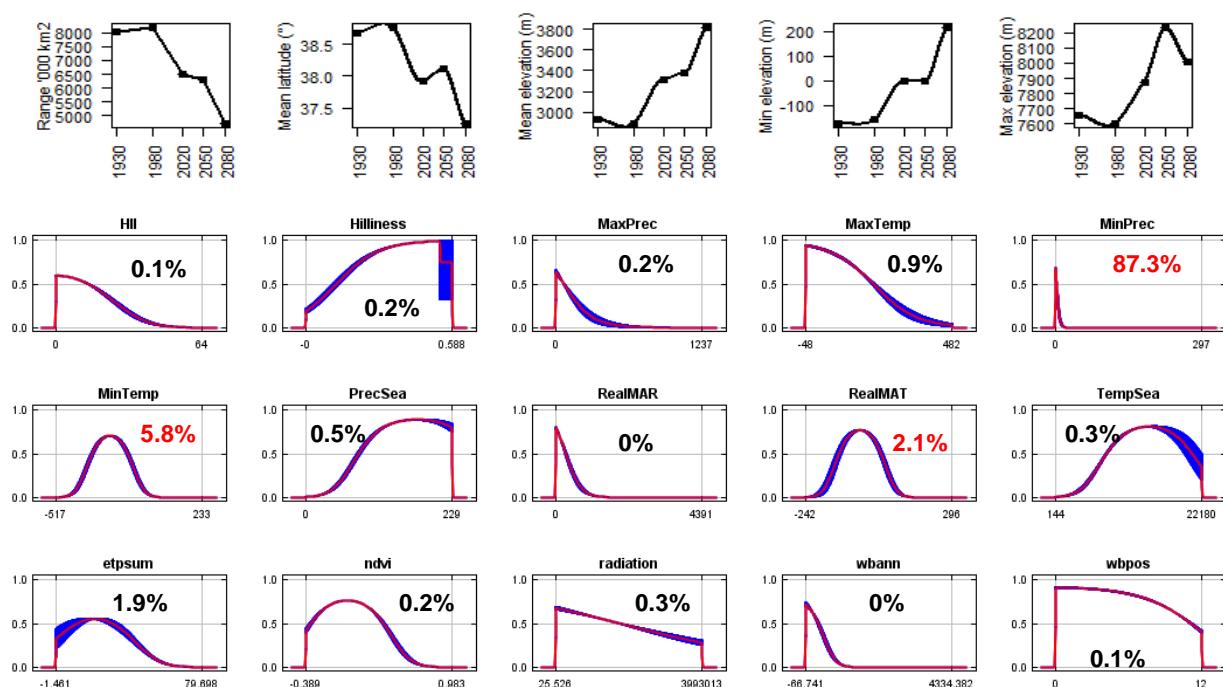
Model evaluation metric	
AUC	0.94
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.43
True Skill Statistic	0.89

Summary: The Large-eared pika's bioclimatic envelope is predicted to decrease by 40% with a ~1° mean latitudinal shift towards the Equator and a mean increase in elevation of ~880m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (87.3%), minimum temperature (5.8%) and mean annual temperature (2.1%).



Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#55 – Nubra's pika (*Ochotona nubrica*)

n = 13

Expert: Nishma Dahal, National Centre for Biological Sciences, India

Expert evaluation: Medium

Data: Only modern

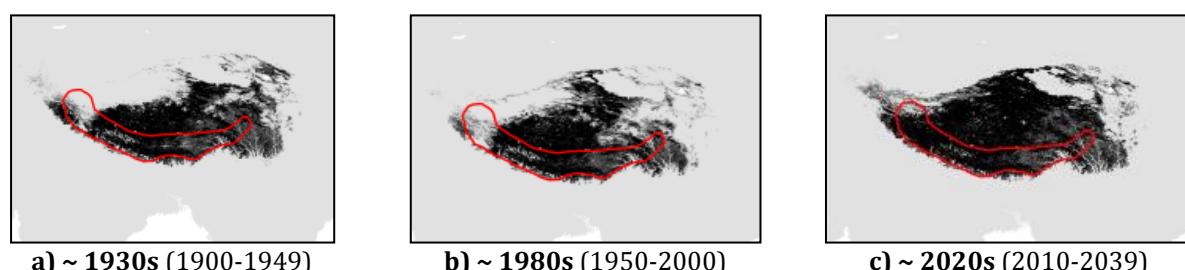
Envelope: Climatic and habitat

Dispersal distance: 0.05km/year (Similar ecology to *O.curzoniae*)

Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.35
True Skill Statistic	0.99

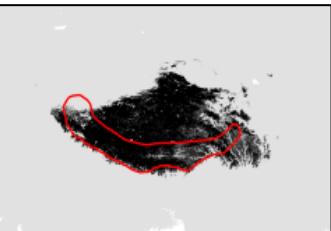
Summary: The Nubra's pika's bioclimatic envelope is predicted to increase by 1% with no latitudinal polewards shift, but a mean increase in elevation of ~200m driven by an increase in minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (76.1%) and mean annual temperature (20.9%).



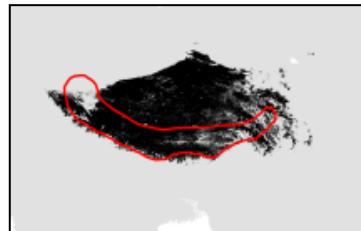
a) ~1930s (1900-1949)

b) ~1980s (1950-2000)

c) ~2020s (2010-2039)



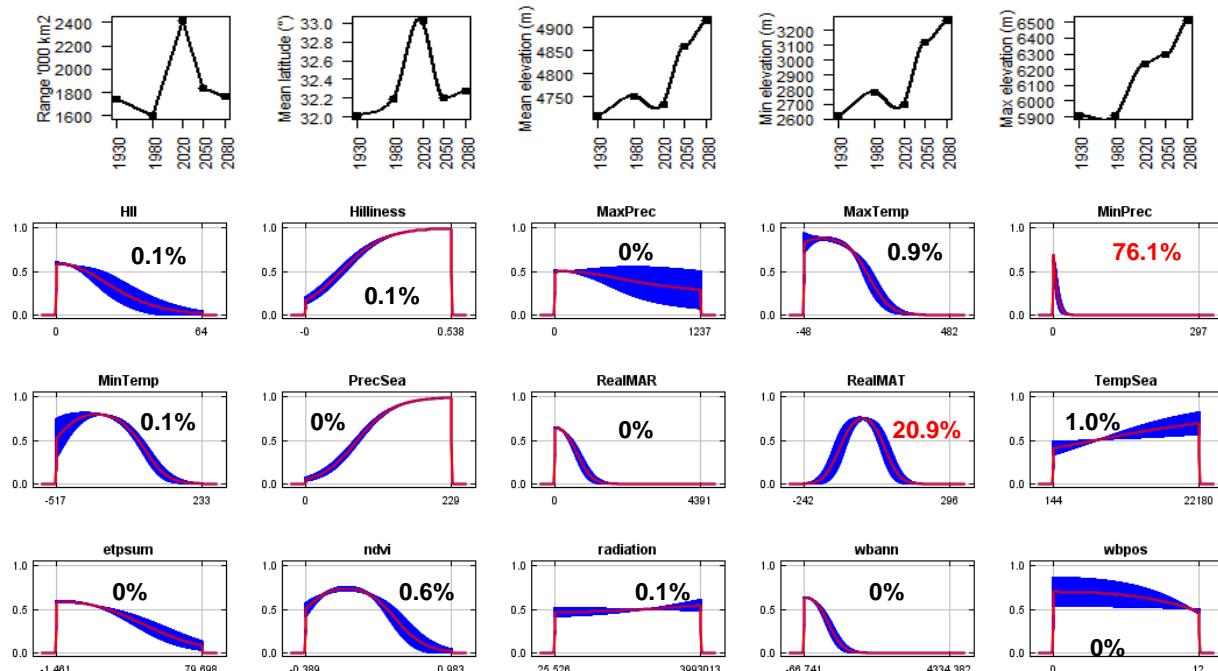
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Boyer, A. F. 2008)



#56 – Pallas's pika (*Ochotona pallasi*)

n = 19

Expert: Andrew Smith, Arizona State University

Expert evaluation: Medium

Data: Only modern

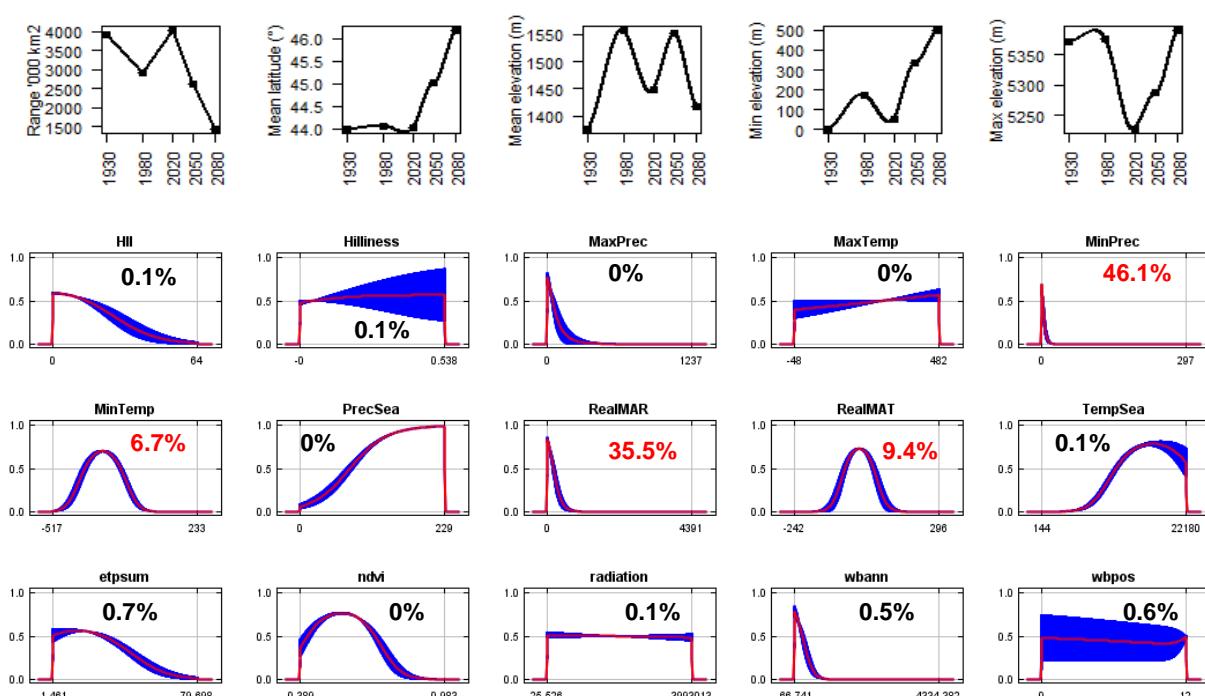
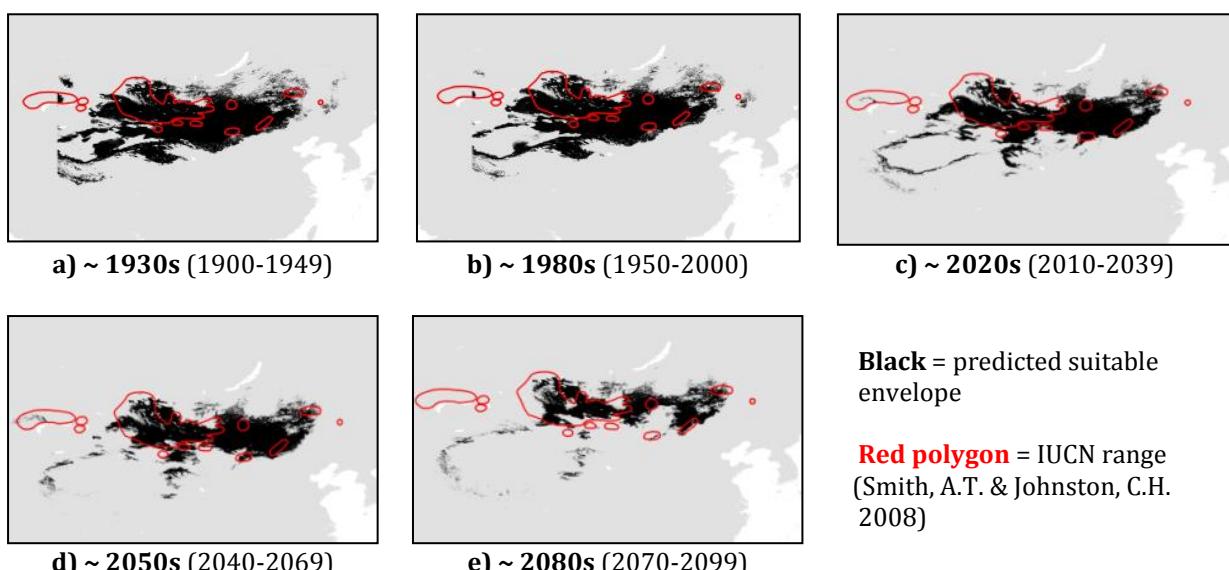
Envelope: Climatic and habitat

Dispersal distance: 10km/year (Sokolov, V.E. et al., 2009)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.46
True Skill Statistic	0.99

Summary: The Pallas's pika's bioclimatic envelope is predicted to decrease by 60% with a ~2° mean latitudinal polewards shift and a mean increase in elevation of ~40m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (46.1%), mean annual precipitation (35.5%), mean annual temperature (9.4%) and minimum temperature (6.7%).



#57 – American pika (*Ochotona princeps*)

n = 670

Expert: Andrew Smith, Arizona State University

Expert evaluation: Medium

Data: Only modern

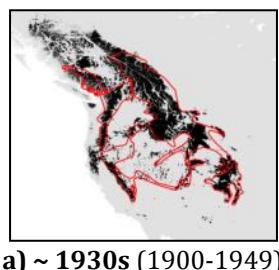
Envelope: Climatic and habitat

Dispersal distance: 16.1km/year (Expert)

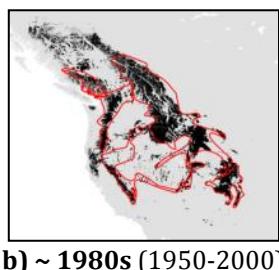
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.9
Specificity	0.99
Proportion correct	0.98
Kappa	0.87
True Skill Statistic	0.89

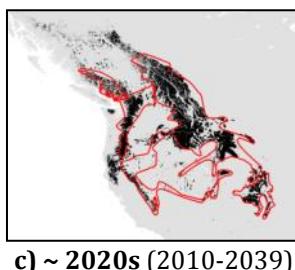
Summary: The American pika's bioclimatic envelope is predicted to decrease by 25% with a ~1° mean latitudinal polewards shift and a mean decrease in elevation of ~10m driven by a decrease in minimum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (88.1%), annual evapotranspiration (5.0%) and maximum temperature (2.8%).



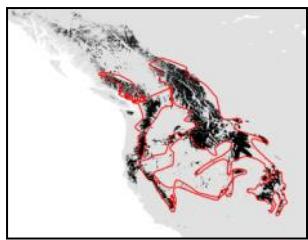
a) ~1930s (1900-1949)



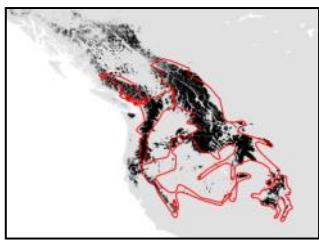
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



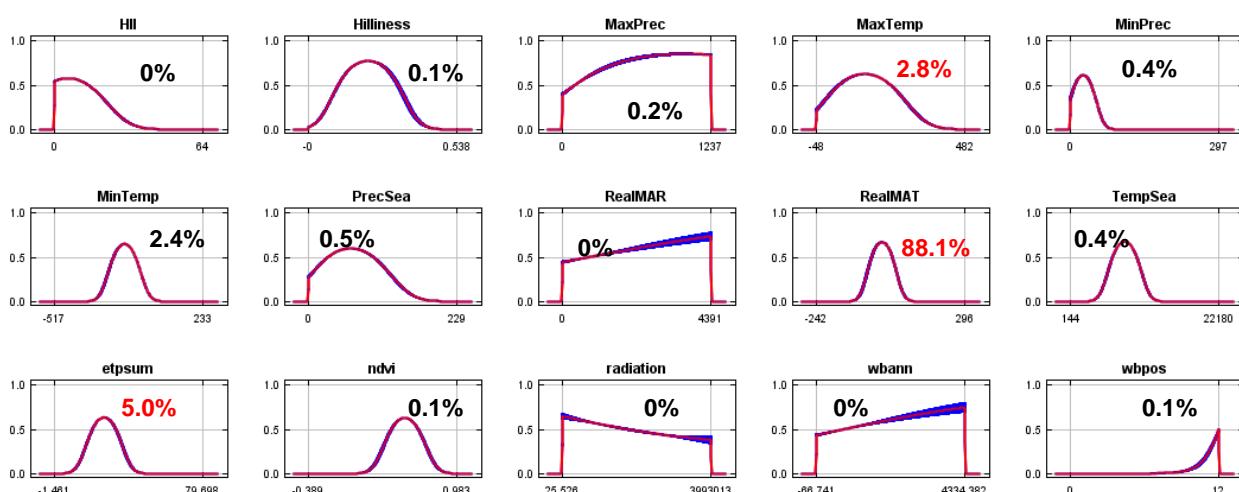
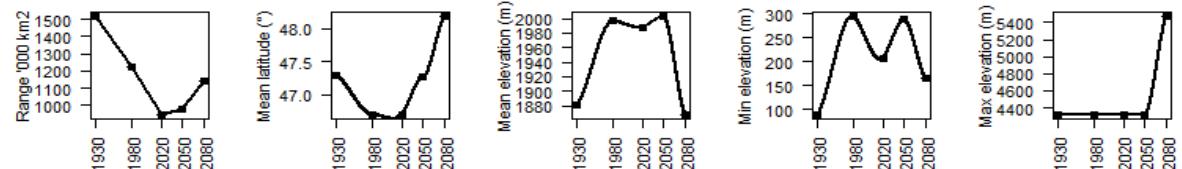
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Beever, E. & Smith, A.T. 2011)



#58 – Little pika (*Ochotona pusilla*)

n = 30

Expert: Andrew Smith, Arizona State University

Expert evaluation: Medium

Data: Modern and historic

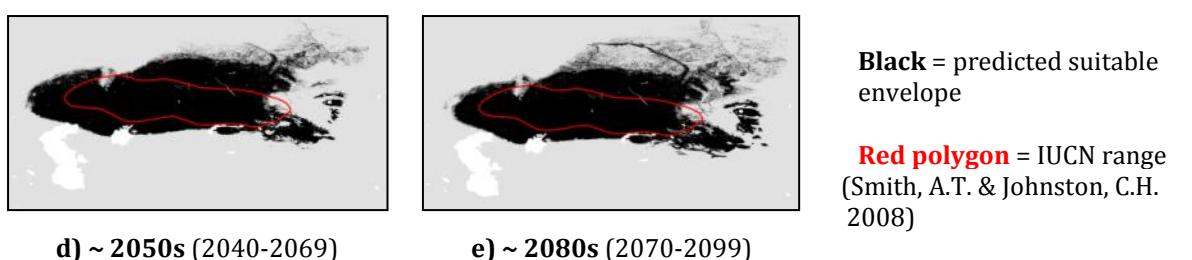
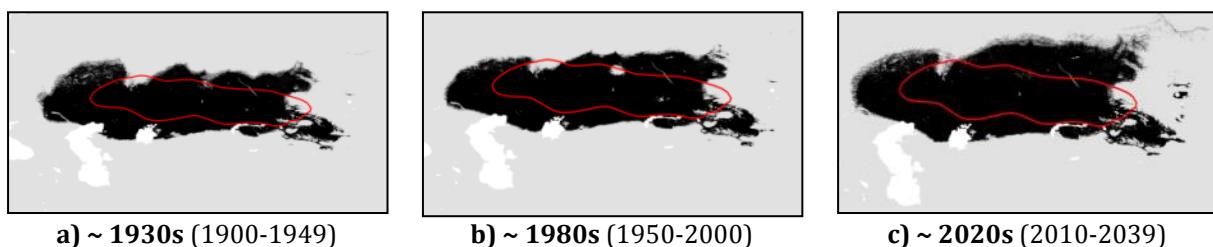
Envelope: Climatic and habitat

Dispersal distance: 4km/year (Sokolov, V.E. et al., 2009)

Status: MODELLABLE; Included in final analysis: ✓

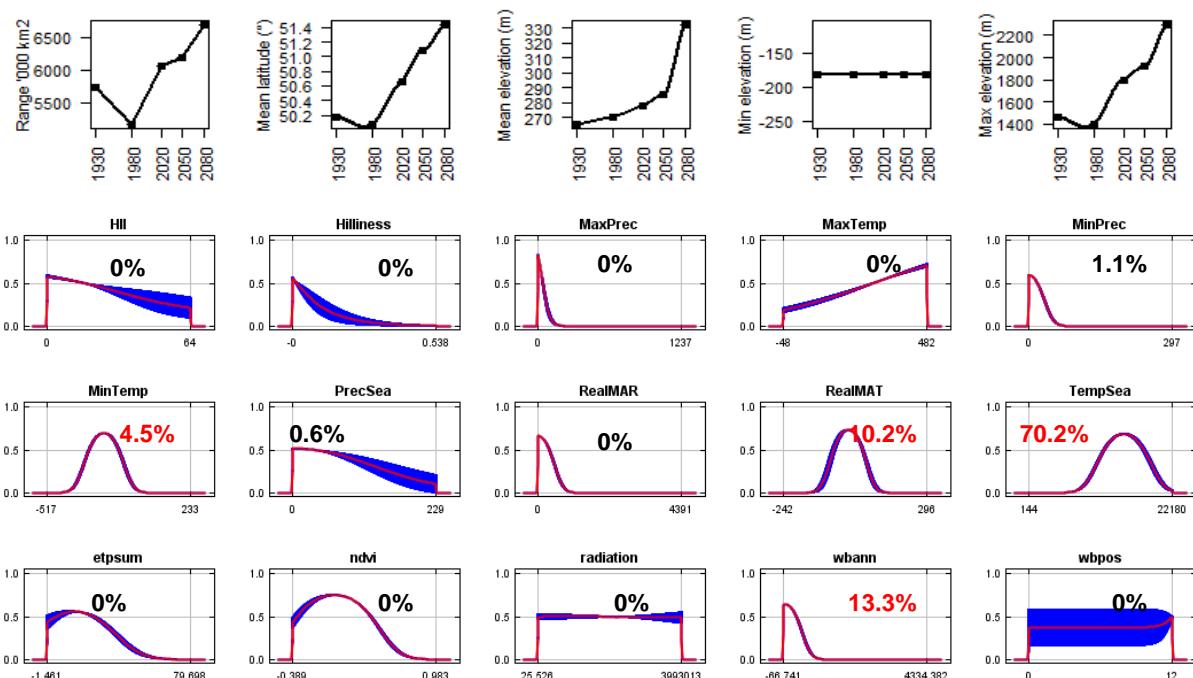
Model evaluation metric	
AUC	0.93
Omission rate	0.13
Sensitivity	0.87
Specificity	0.99
Proportion correct	0.99
Kappa	0.58
True Skill Statistic	0.86

Summary: The Little pika's bioclimatic envelope is predicted to increase by 20% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~70m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (70.2%), annual water balance (13.3%), mean annual temperature (10.2%) and minimum temperature (4.5%).



Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#59 – Royle's pika (*Ochotona roylei*)

n = 22

Expert: Sabuj Bhattacharya, Wildlife Institute of India

Expert evaluation: Medium

Data: Modern and historic

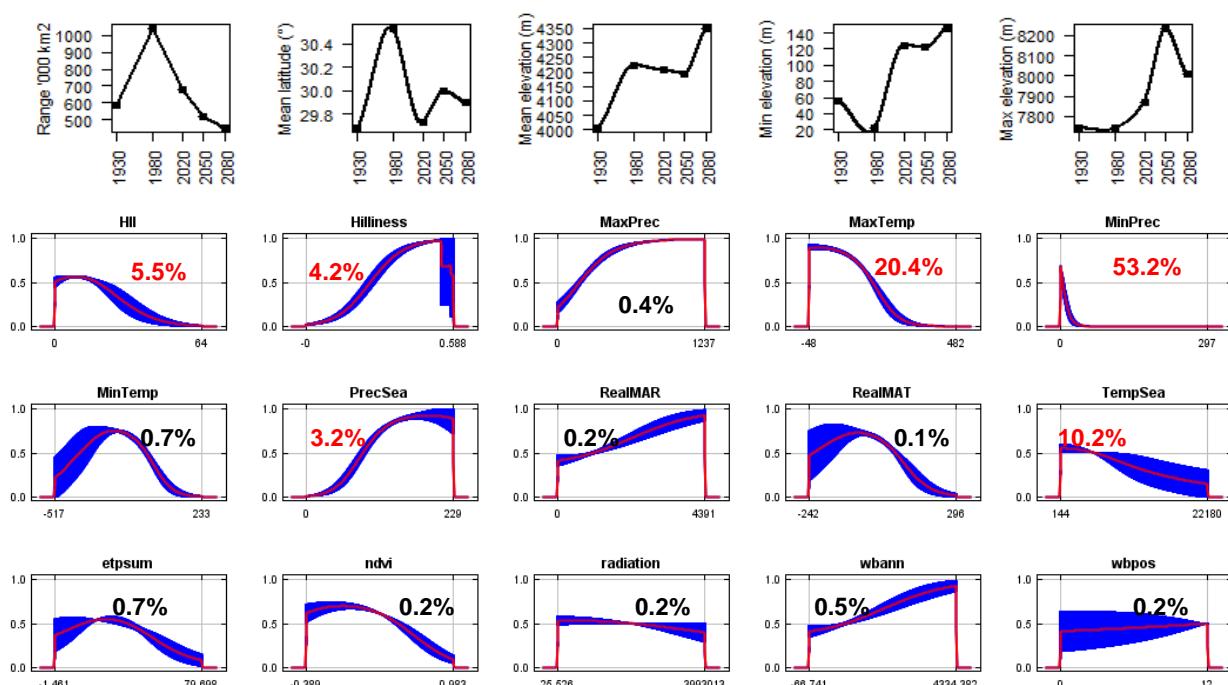
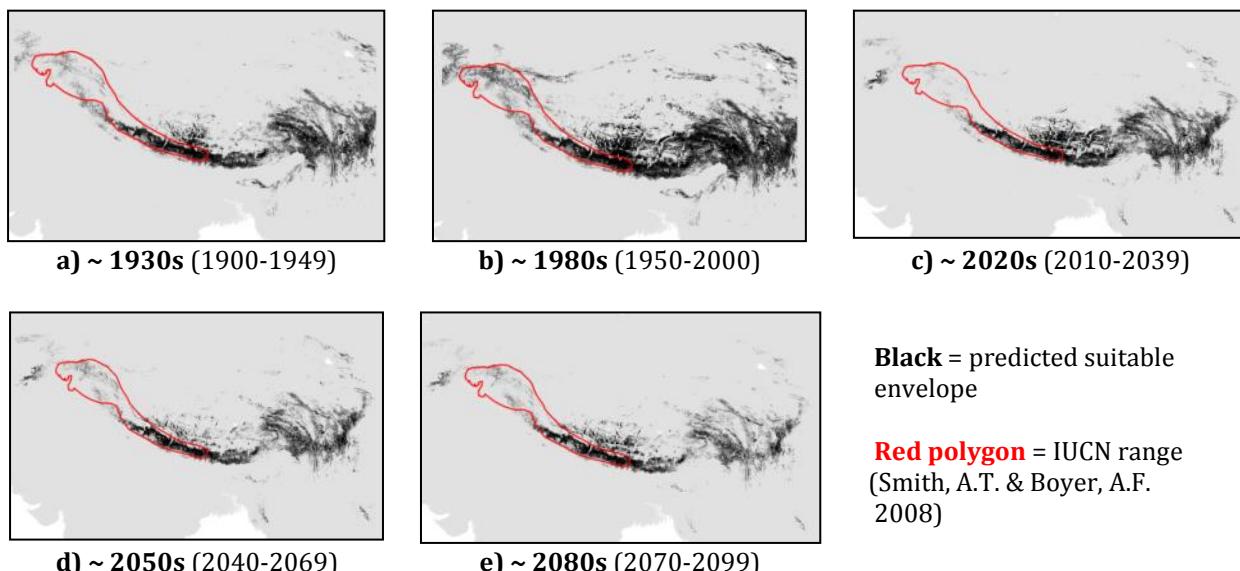
Envelope: Climatic and habitat

Dispersal distance: 1km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.98
Omission rate	0.05
Sensitivity	0.95
Specificity	0.99
Proportion correct	0.99
Kappa	0.76
True Skill Statistic	0.95

Summary: The Royle's pika's bioclimatic envelope is predicted to decrease by 20% with no latitudinal polewards shift and a mean increase in elevation of ~340m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (53.2%), maximum temperature (20.4%), temperature seasonality (10.2%), human influence index (5.5%), surface roughness index (4.2%) and precipitation seasonality (3.2%).



#60 – Afghan pika (*Ochotona rufescens*)

n = 17

Expert: Chelmala Srinivasulu, Osmania University, India

Expert evaluation: Medium

Data: Modern and historic

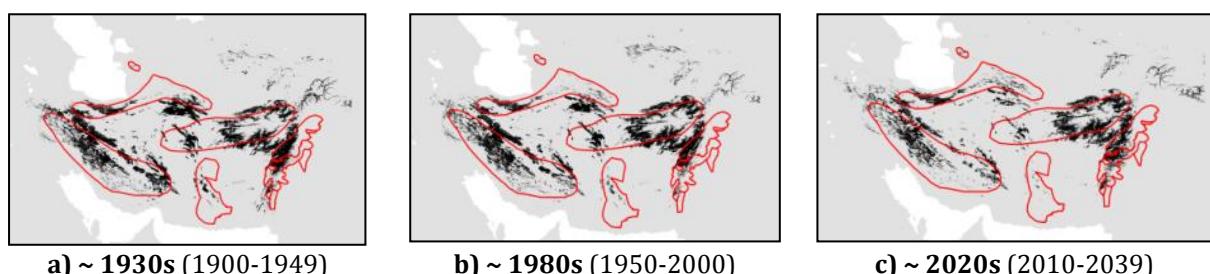
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Asian pikas, range 1-15)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.74
True Skill Statistic	0.99

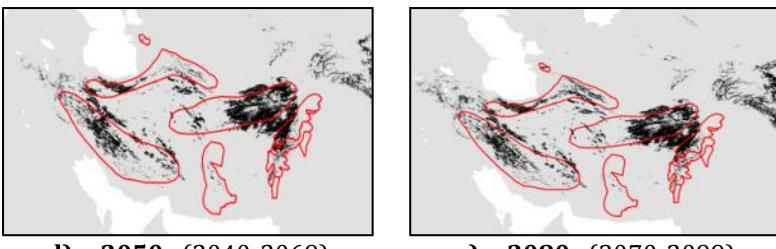
Summary: The Afghan pika's bioclimatic envelope is predicted to increase by 5% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~380m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (89.2%), minimum temperature (5.5%) and normalised difference vegetation index (2.3%).



a) ~1930s (1900-1949)

b) ~1980s (1950-2000)

c) ~2020s (2010-2039)

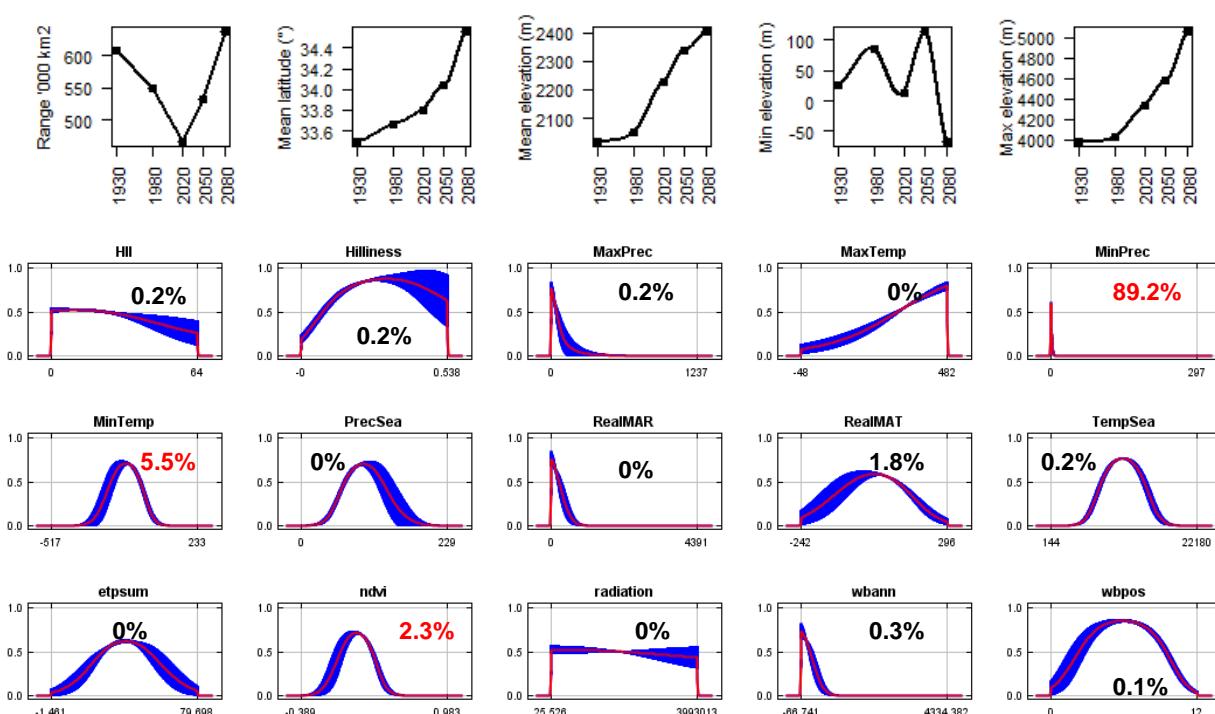


d) ~2050s (2040-2069)

e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Boyer, A.F. 2008)



#61 – Turkestan red pika (*Ochotona rutila*)

n = 13

Expert: Andrey Lissovsky, Zoological Museum of Moscow State University

Expert evaluation: Poor

Data: Modern and historic

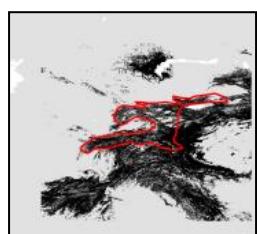
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Asian pikas, range 1-15)

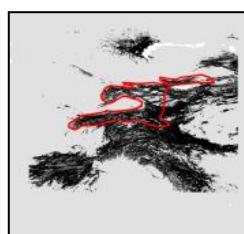
Status: UNMODELLABLE; **Included in final analysis:** X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.25
True Skill Statistic	0.99

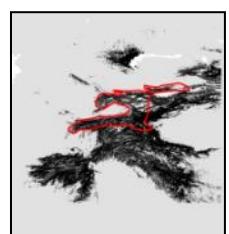
Summary: The Turkestan red pika's bioclimatic envelope is predicted to decrease by 10% with a ~1° mean latitudinal shift towards the Equator and a mean increase in elevation of ~630m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (82.5%), minimum temperature (5.9%), human influence index (3.0%), precipitation seasonality (2.5%) and surface roughness index (1.7%).



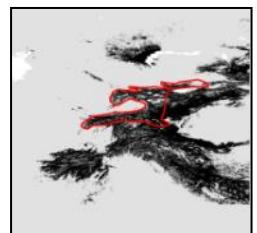
a) ~ 1930s (1900-1949)



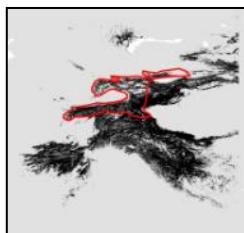
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



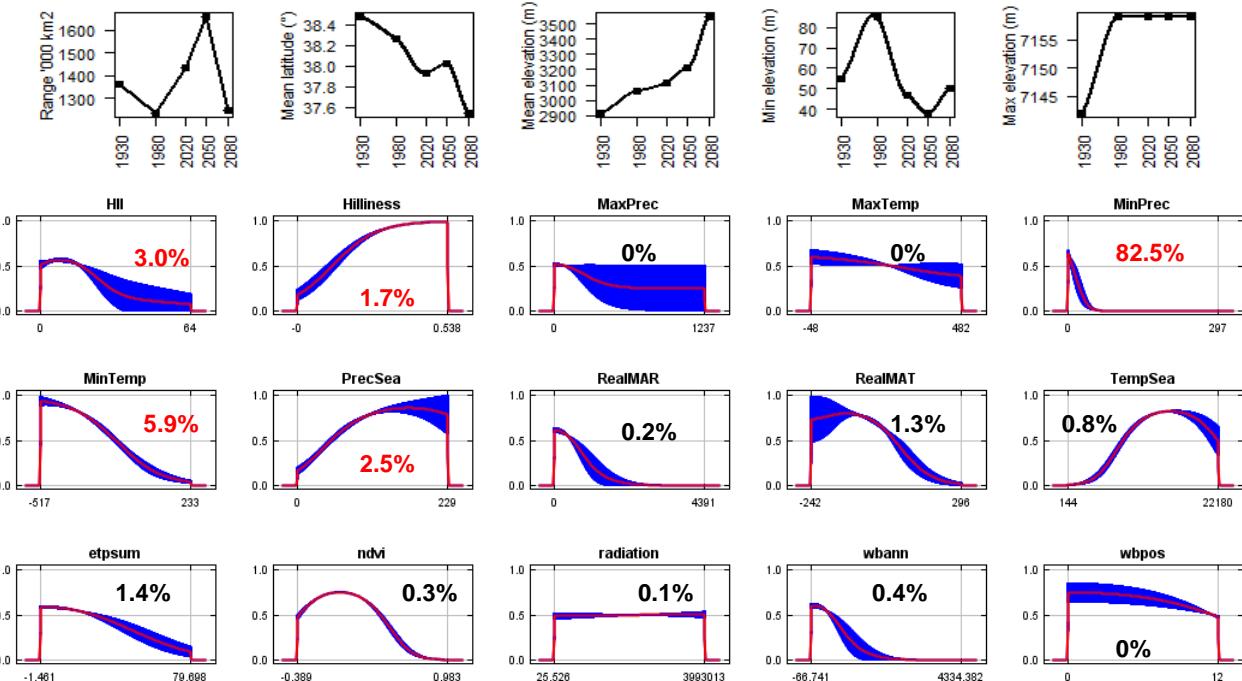
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Boyer, A.F. 2008)



#62 – Moupin pika (*Ochotona thibetana*)

n = 95

Expert: Deyan Ge, Institute of Zoology, Chinese Academy of Sciences

Expert evaluation: Poor

Data: Modern and historic

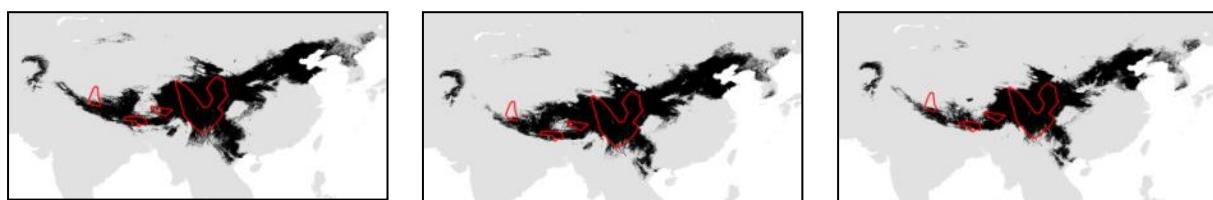
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Similar ecology to *O.roylei*)

Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.93
Omission rate	0.13
Sensitivity	0.87
Specificity	0.99
Proportion correct	0.99
Kappa	0.52
True Skill Statistic	0.86

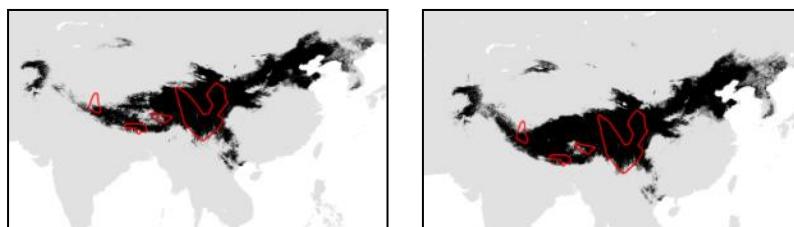
Summary: The Moupin pika's bioclimatic envelope is predicted to increase by 10% with a ~2° mean latitudinal polewards shift and a mean increase in elevation of ~370m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (43.5%), maximum temperature (38.5%), temperature seasonality (7.7%), annual evapotranspiration (3.7%) and mean annual precipitation (3.1%).



a) ~1930s (1900-1949)

b) ~1980s (1950-2000)

c) ~2020s (2010-2039)

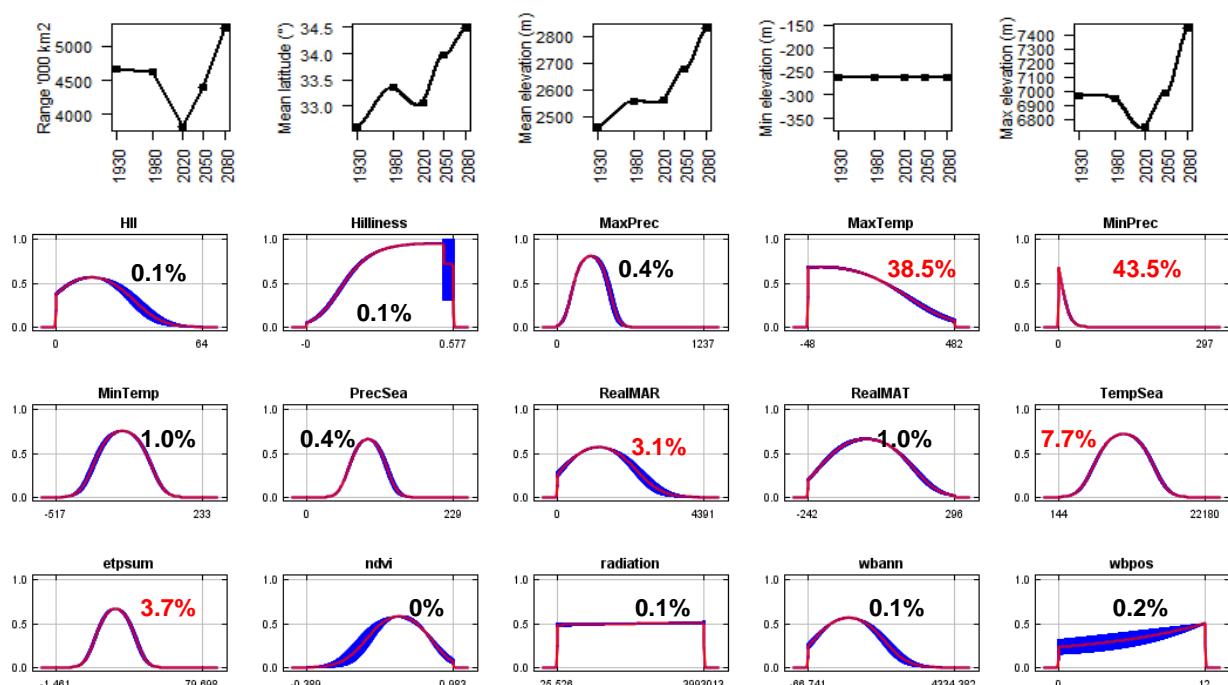


d) ~2050s (2040-2069)

e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Boyer, A.F. 2008)



#63 – Thomas's pika (*Ochotona thomasi*)

n = 16

Expert: Andrew Smith, Arizona State University

Expert evaluation: Good

Data: Modern and historic

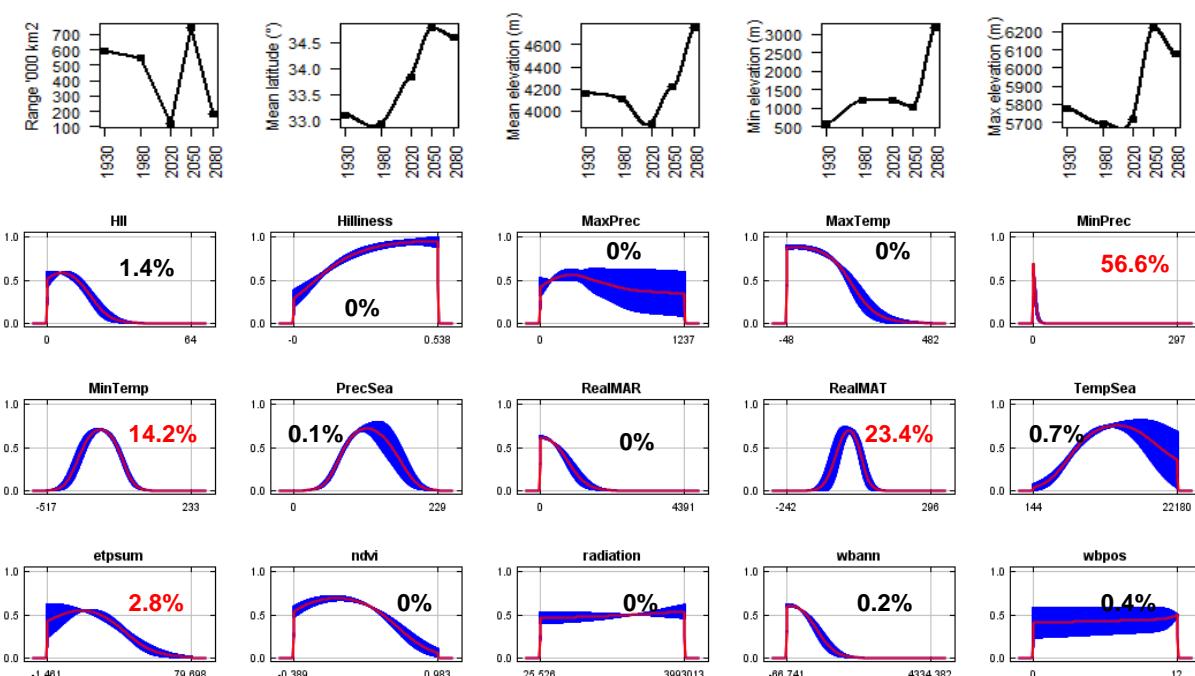
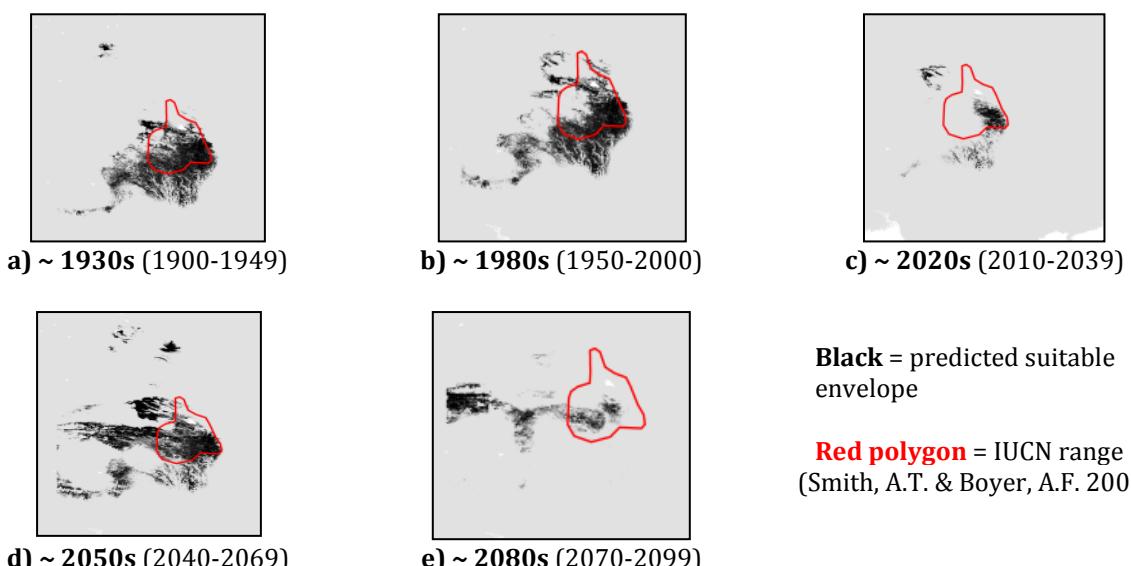
Envelope: Climatic and habitat

Dispersal distance: 1km/year (Similar ecology to *O.koslowi*)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.58
True Skill Statistic	0.99

Summary: The Thomas's pika's bioclimatic envelope is predicted to decrease by 70% with a ~1.5° mean latitudinal polewards shift and a mean increase in elevation of ~590m driven by an increase in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by minimum precipitation (56.6%), mean annual temperature (23.4%), minimum temperature (14.2%) and evapotranspiration (2.8%).



#64 – Turuchan pika (*Ochotona turuchanensis*)

n = 30

Expert: Andrey Lissovsky, Zoological Museum of Moscow State University

Expert evaluation: Medium

Data: Modern and historic

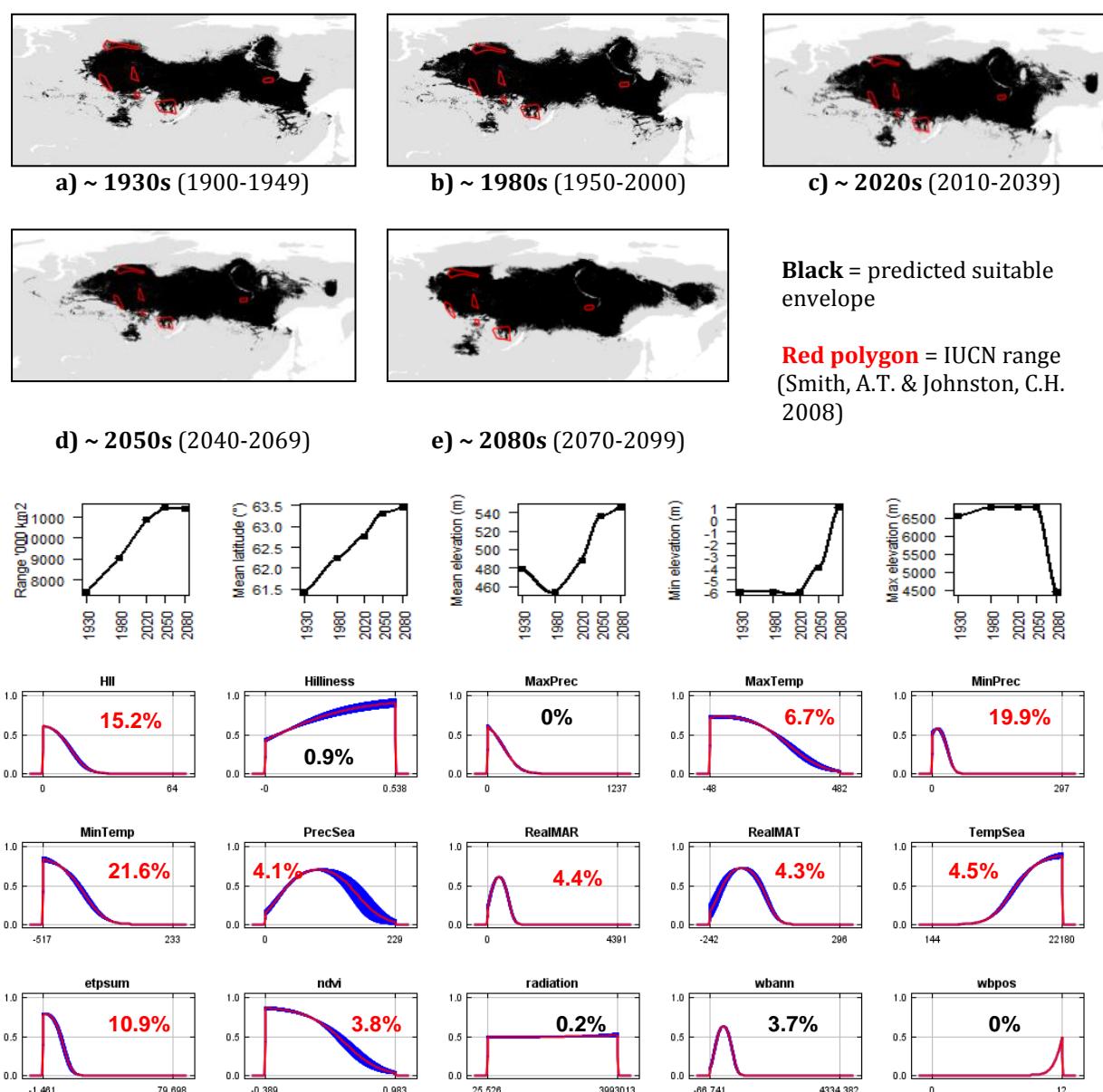
Envelope: Climatic and habitat

Dispersal distance: 15km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.93
Omission rate	0.13
Sensitivity	0.87
Specificity	0.99
Proportion correct	0.99
Kappa	0.50
True Skill Statistic	0.86

Summary: The Turuchan pika's bioclimatic envelope is predicted to increase by 50% with a ~2° mean latitudinal polewards shift and a mean increase in elevation of ~70m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by minimum temperature (21.6%), minimum precipitation (19.9%), human influence index (15.2%), annual evapotranspiration (10.9%).



#65 – European rabbit (*Oryctolagus cuniculus*)

n = 22,712

Expert: Neil Reid, Queen's University Belfast

Expert evaluation: Medium

Data: Modern and historic

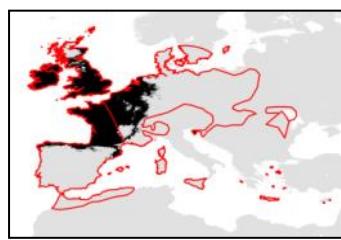
Envelope: Climatic and habitat

Dispersal distance: 1km/year (Expert)

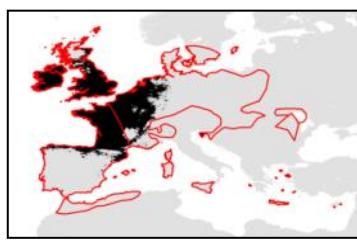
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.62
Omission rate	0.16
Sensitivity	0.84
Specificity	0.39
Proportion correct	0.62
Kappa	0.23
True Skill Statistic	0.23

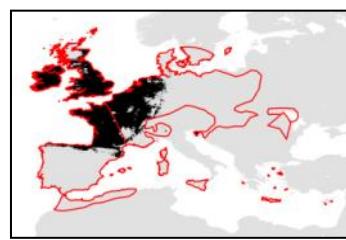
Summary: The European rabbit's bioclimatic envelope is predicted to increase by 30% with a ~2° mean latitudinal polewards shift and a mean decrease in elevation of ~10m. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (21.1%), mean annual temperature (19.0%), minimum temperature (13.9%), annual water balance (12.3%), mean annual precipitation (11.2%), human influence index (9.8%), precipitation seasonality (7.6%) and normalised difference vegetation index (2.9%).



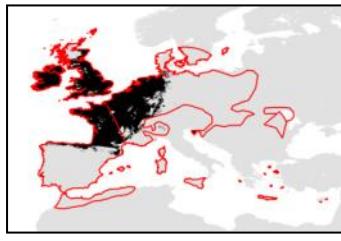
a) ~ 1930s (1900-1949)



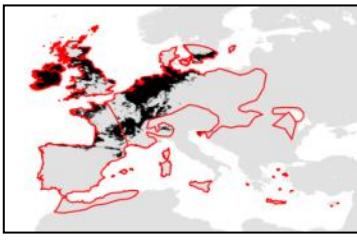
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



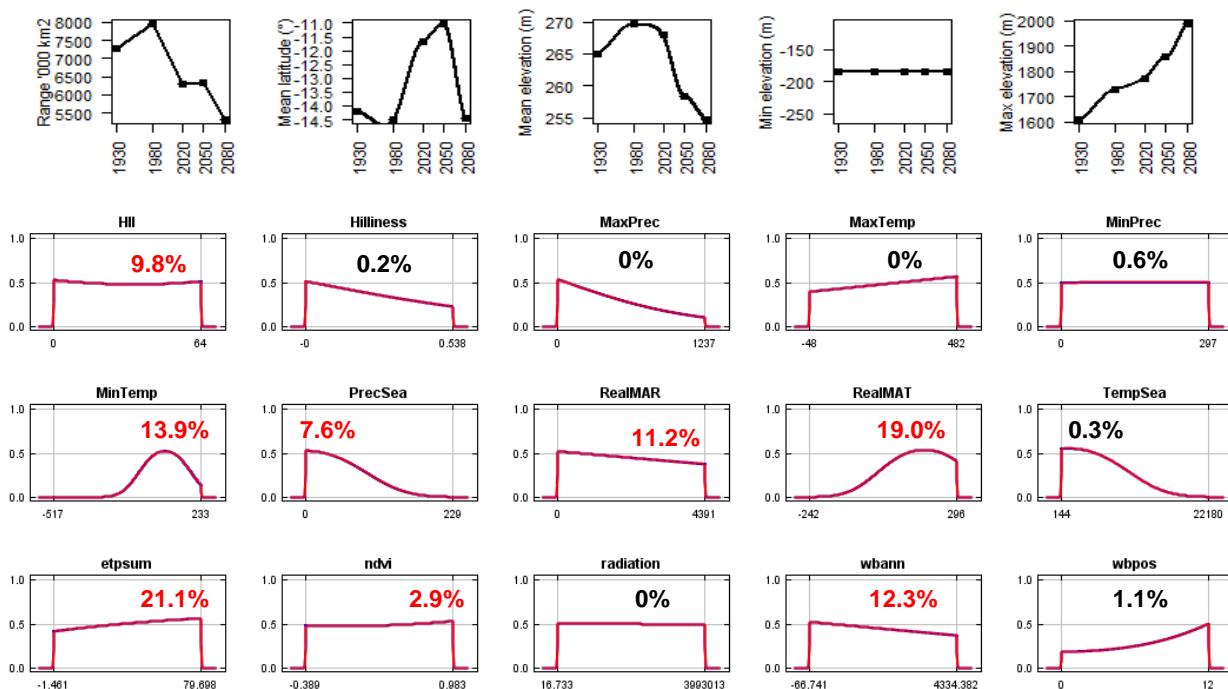
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Boyer, A.F. 2008)



#66 – Amami rabbit (*Pentalagus furnessi*)

n = 9

Expert: Fumio Yamada, Forestry and Forest Products Research Institute, Japan

Expert evaluation: Good

Data: Modern and historic

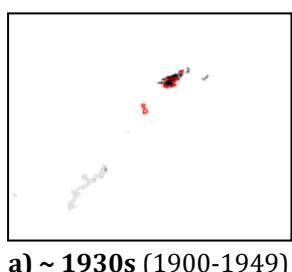
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Expert)

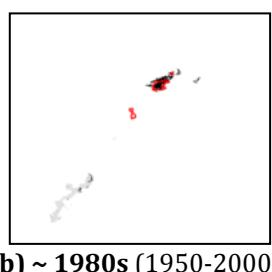
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	0.99
Specificity	0.99
Proportion correct	0.99
Kappa	0.95
True Skill Statistic	0.99

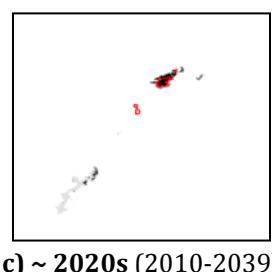
Summary: The Amami rabbit's bioclimatic envelope is predicted to increase by 150% with a ~1° mean latitudinal shift towards the Equator and a mean decrease in elevation of ~25m. 95% of the permutation importance of the model was contributed to by minimum temperature (97.3%), temperature seasonality (1.7%) and annual evapotranspiration (0.8%).



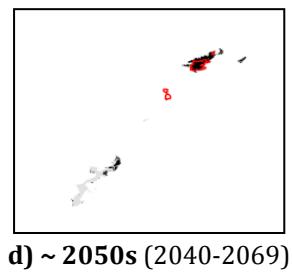
a) ~1930s (1900-1949)



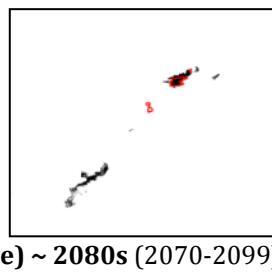
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



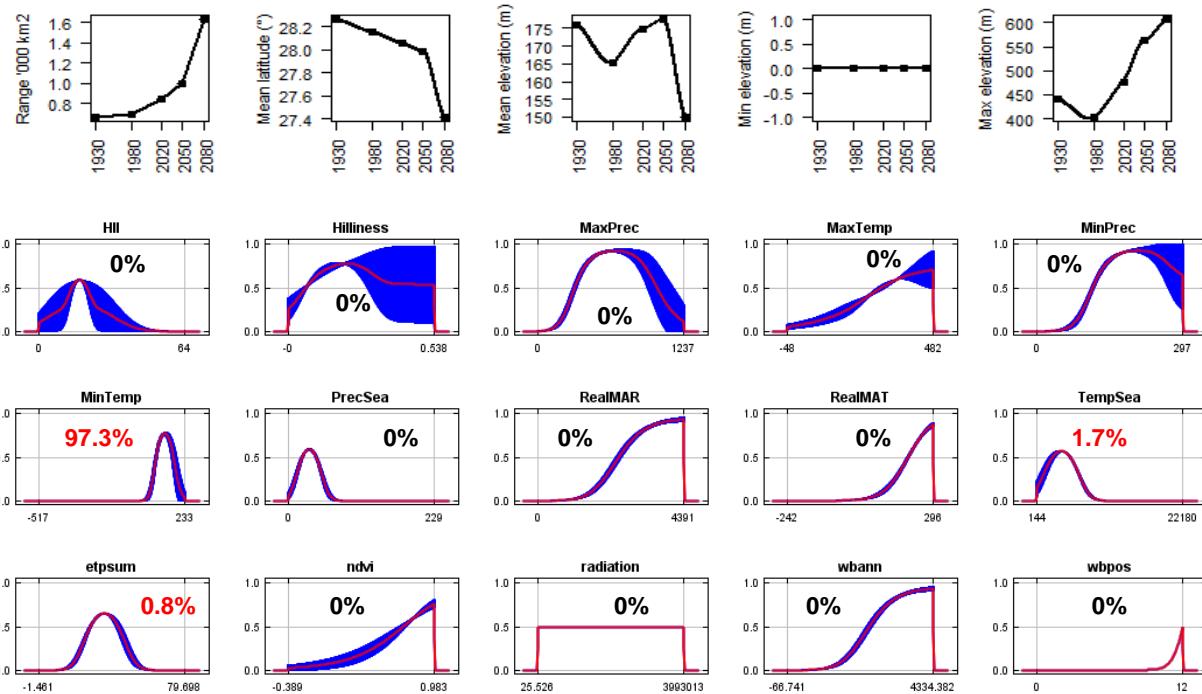
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range (Yamada, F & Sugimura, K. 2008)



#67 – Bunyoro rabbit (*Poelagus marjorita*)

n = 8

Expert: David Happold, Australian National University

Expert evaluation: Poor

Data: Only modern

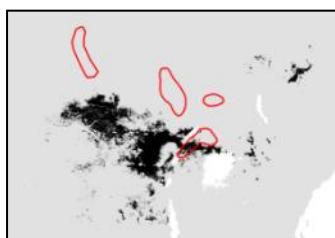
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Similar ecology to *Pronolagus* sp.)

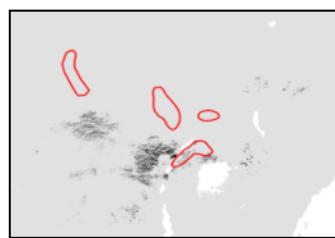
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.89
True Skill Statistic	0.99

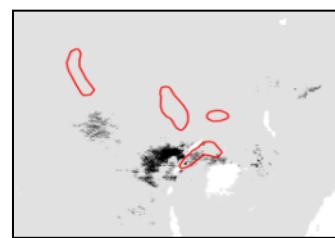
Summary: The Bunyoro rabbit's bioclimatic envelope is predicted to decrease by 90% with a ~1° mean latitudinal shift towards the Equator and a mean increase in elevation of ~200m driven by an increase in minimum elevation.. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (61.7%), temperature seasonality (31.4%) and number of months with a positive water balance (6.3%).



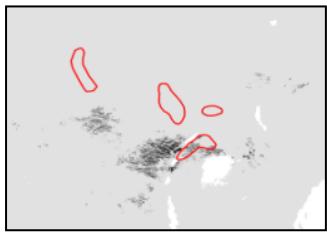
a) ~ 1930s (1900-1949)



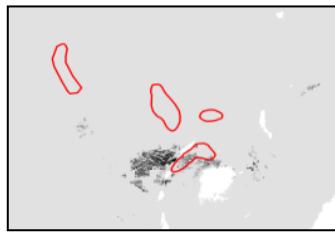
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



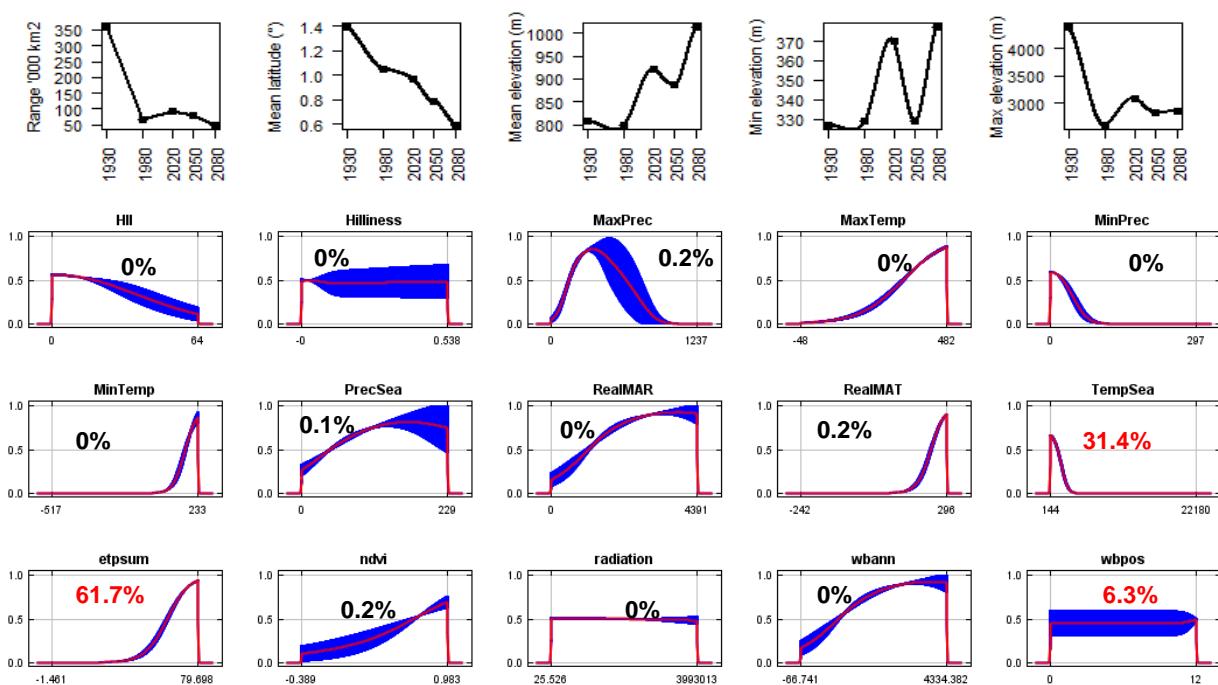
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Collins, K. & Smith, A.T. 2008)



#68 – Greater red rock hare (*Pronolagus crassicaudatus*)

n = 7

Expert: Kai Collins, University of Pretoria

Expert evaluation: Poor

Data: Only modern

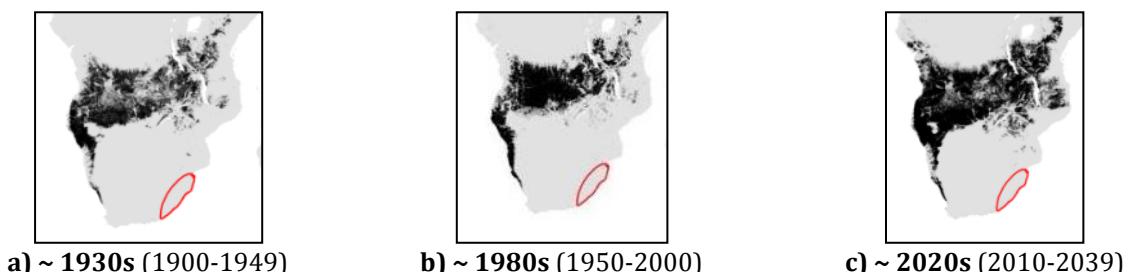
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Similar ecology to *P.randensis*)

Status: UNMODELLABLE; Included in final analysis: X

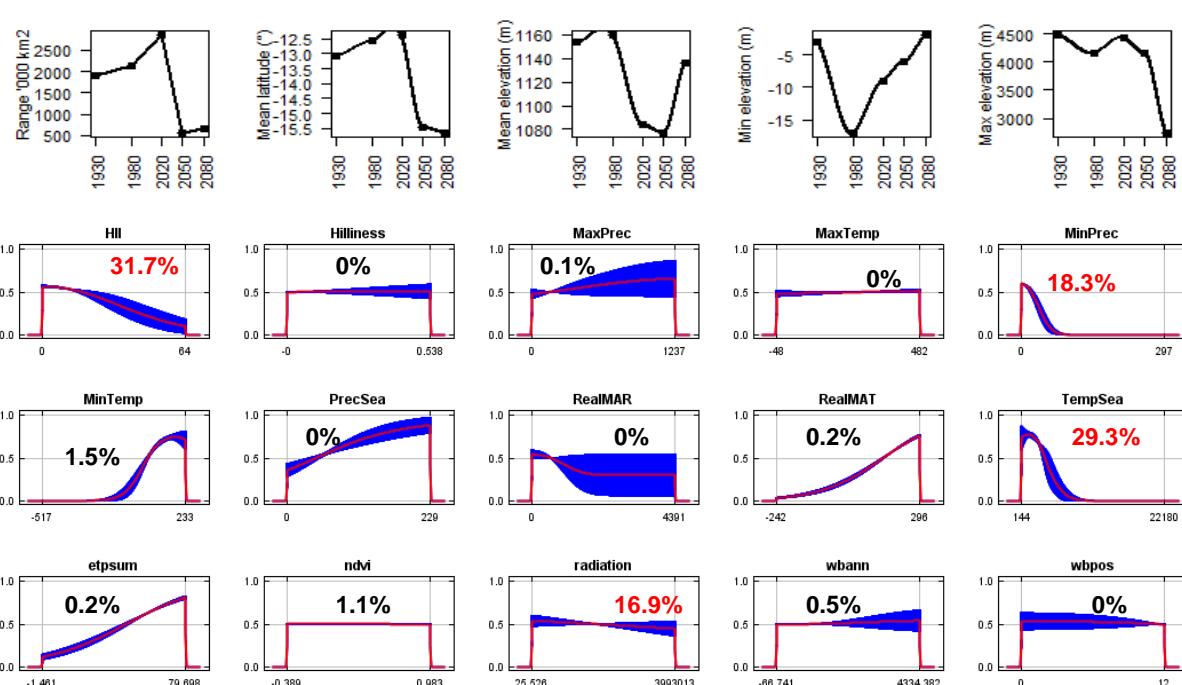
Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.98
Proportion correct	0.98
Kappa	0.06
True Skill Statistic	0.98

Summary: The Greater red rock hare's bioclimatic envelope is predicted to decrease by 65% with a ~3° mean latitudinal polewards shift and a mean decrease in elevation of ~20m driven by a decrease in maximum elevation. 95% of the permutation importance of the model was contributed to by human influence index (31.7%), temperature seasonality (29.3%) solar radiation (16.9%) and minimum precipitation (18.3%).



Black = predicted suitable envelope

Red polygon = IUCN range
(Matthee, C., et al. 2008)



#69 – Jameson's red rock hare (*Pronolagus randensis*)

n = 27

Expert: Kai Collins, University of Pretoria

Expert evaluation: Poor

Data: Modern and historic

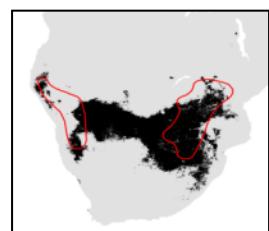
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Expert)

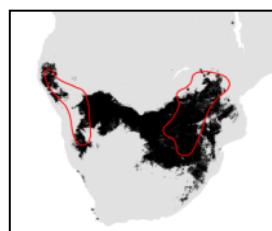
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.98
Omission rate	0.04
Sensitivity	0.96
Specificity	0.99
Proportion correct	0.99
Kappa	0.55
True Skill Statistic	0.96

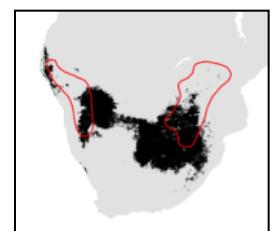
Summary: The Jameson's red rock hare's bioclimatic envelope is predicted to decrease by 70% with a ~5° mean latitudinal polewards shift and a mean increase in elevation of ~325m driven by an increase in maximum and minimum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (46.2%), maximum temperature (23.3%), minimum precipitation (16.3%), minimum temperature (7.0%) and temperature seasonality (1.4%).



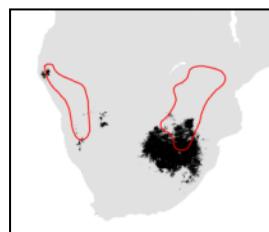
a) ~1930s (1900-1949)



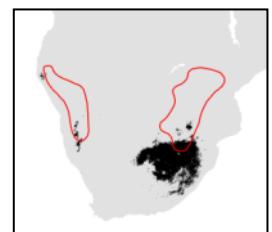
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



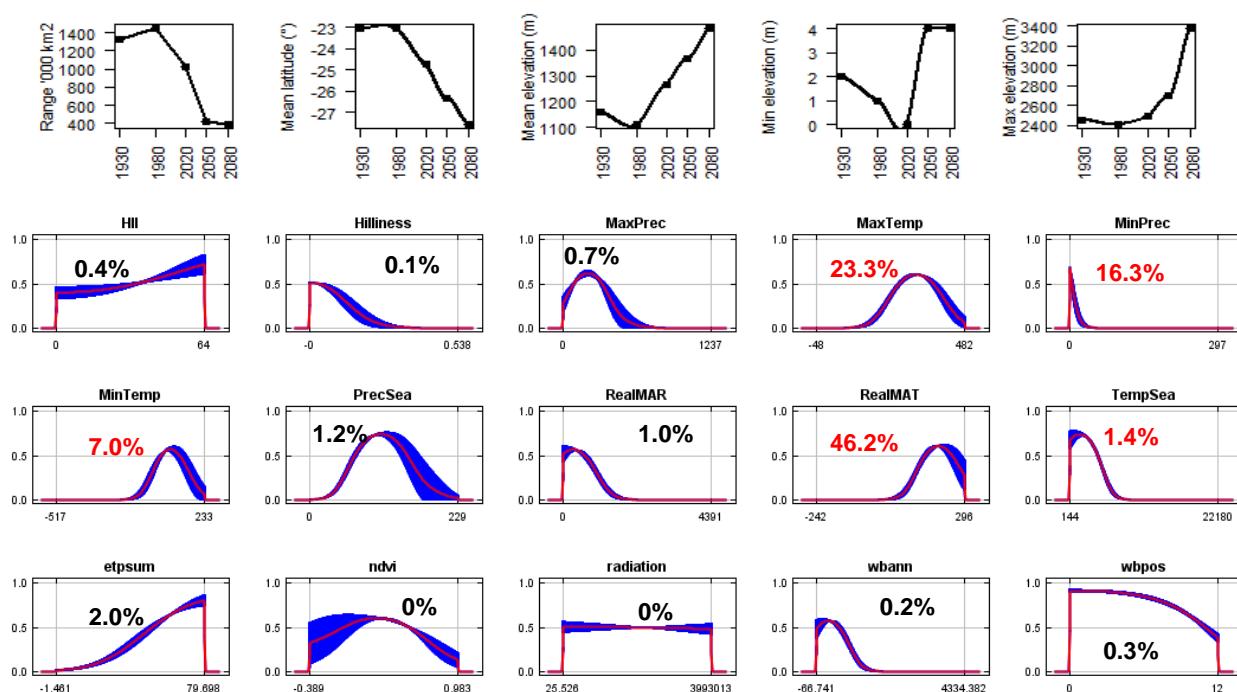
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Matthee, C., et al. 2008)



#70 – Smith's red rock hare (*Pronolagus rupestris*)

n = 9

Expert: Kai Collins, University of Pretoria

Expert evaluation: Poor

Data: Modern and historic

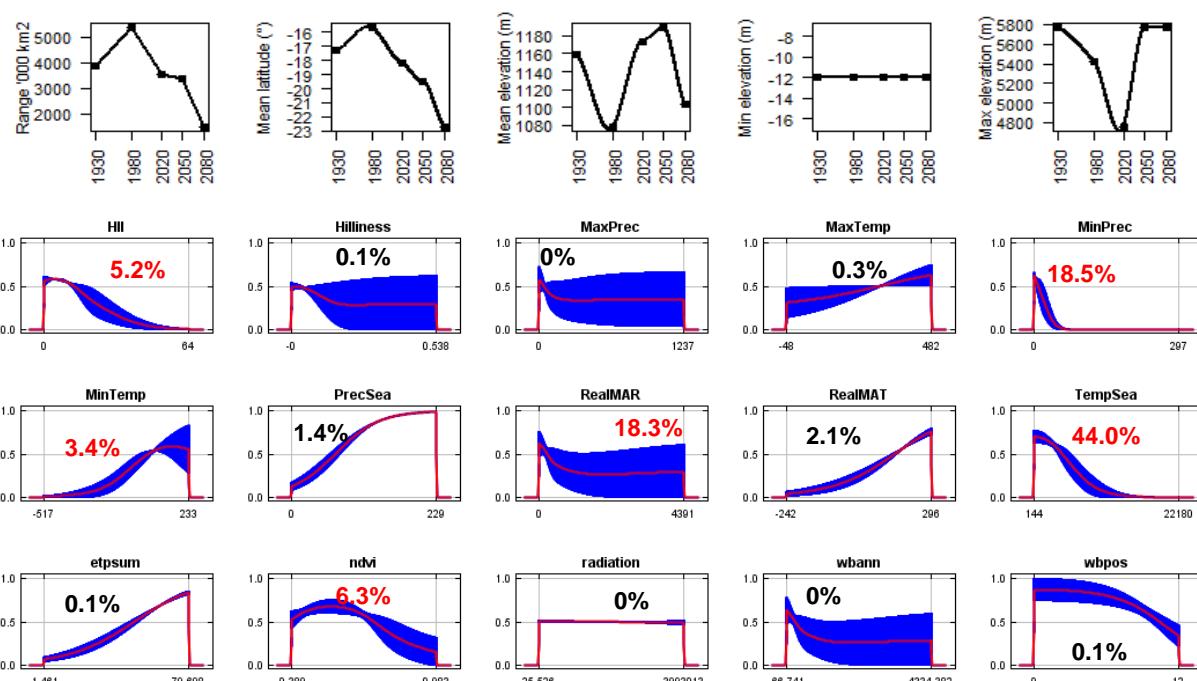
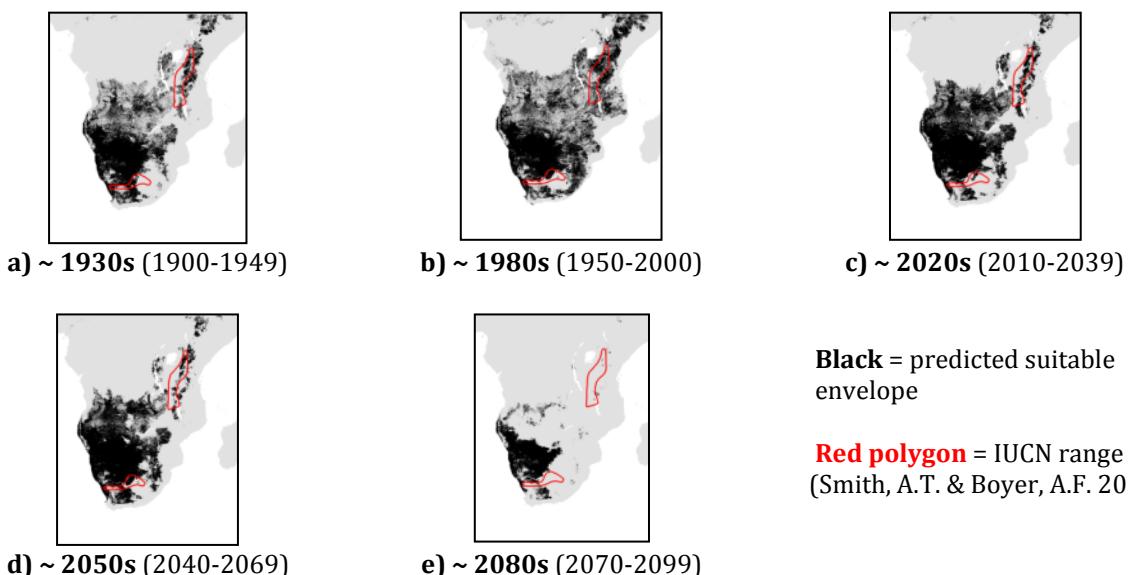
Envelope: Climatic and habitat

Dispersal distance: 2km/year (Similar ecology to *P.randensis*)

Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.98
Proportion correct	0.98
Kappa	0.07
True Skill Statistic	0.98

Summary: The Smith's red rock hare's bioclimatic envelope is predicted to decrease by 60% with a ~5° mean latitudinal polewards shift and a mean decrease in elevation of ~60m. 95% of the permutation importance of the model was contributed to by temperature seasonality (44.0%), minimum precipitation (18.5%), mean annual precipitation (18.3%), normalised difference vegetation index (6.3%), human influence index (5.2%) and minimum temperature (3.4%).



#71 – Hewitt's red rock hare (*Pronolagus saundersiae*)

n = 9

Expert: Kai Collins, University of Pretoria

Expert evaluation: Poor

Data: Modern and historic

Envelope: Climatic and habitat

Dispersal distance: 2km/year (Similar ecology to *P.randensis*)

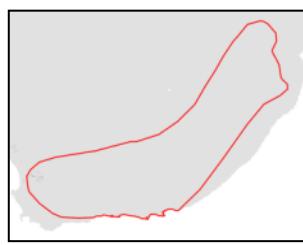
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	1.00
Omission rate	0.00
Sensitivity	1.00
Specificity	1.00
Proportion correct	1.00
Kappa	1.00
True Skill Statistic	1.00

Summary: The Hewitt's red rock hare's bioclimatic envelope is predicted to decrease by 100% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~15m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (28.7%), precipitation seasonality (24.3%), maximum temperature (18.0%), annual evapotranspiration (16.0%), human influence index (5.6%), minimum temperature (1.9%) and minimum precipitation (1.6%).



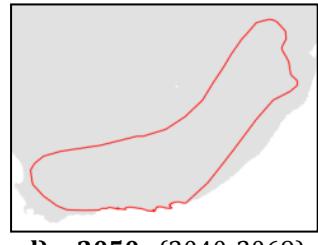
a) ~1930s (1900-1949)



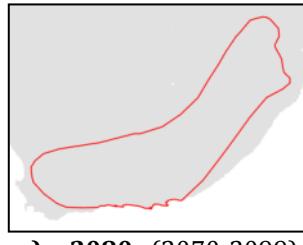
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



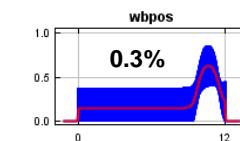
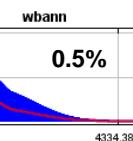
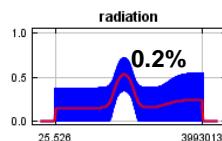
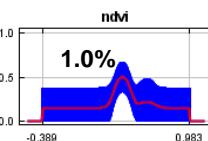
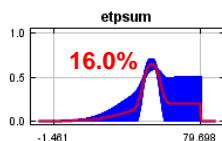
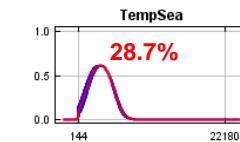
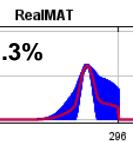
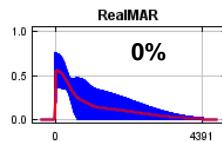
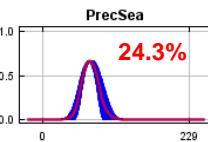
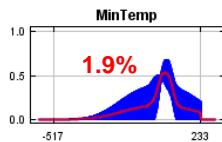
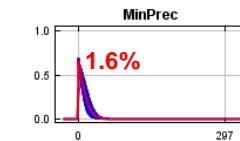
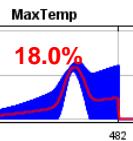
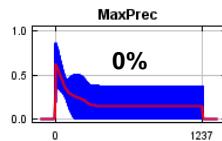
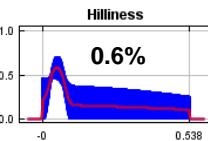
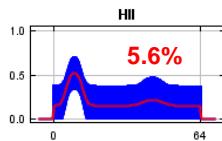
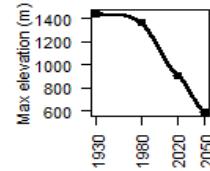
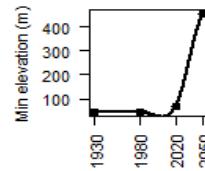
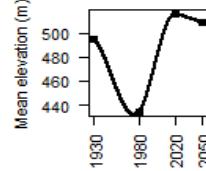
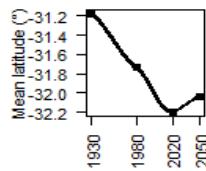
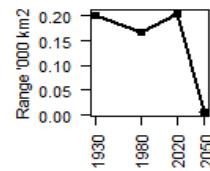
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Johnston, C.H. 2008)



#72 – Volcano rabbit (*Romerolagus diazi*)

n = 31

Expert: Jose Antonio Martinez-Garcia, Universidad Autónoma Metropolitana, Mexico

Expert evaluation: Poor

Data: Only modern

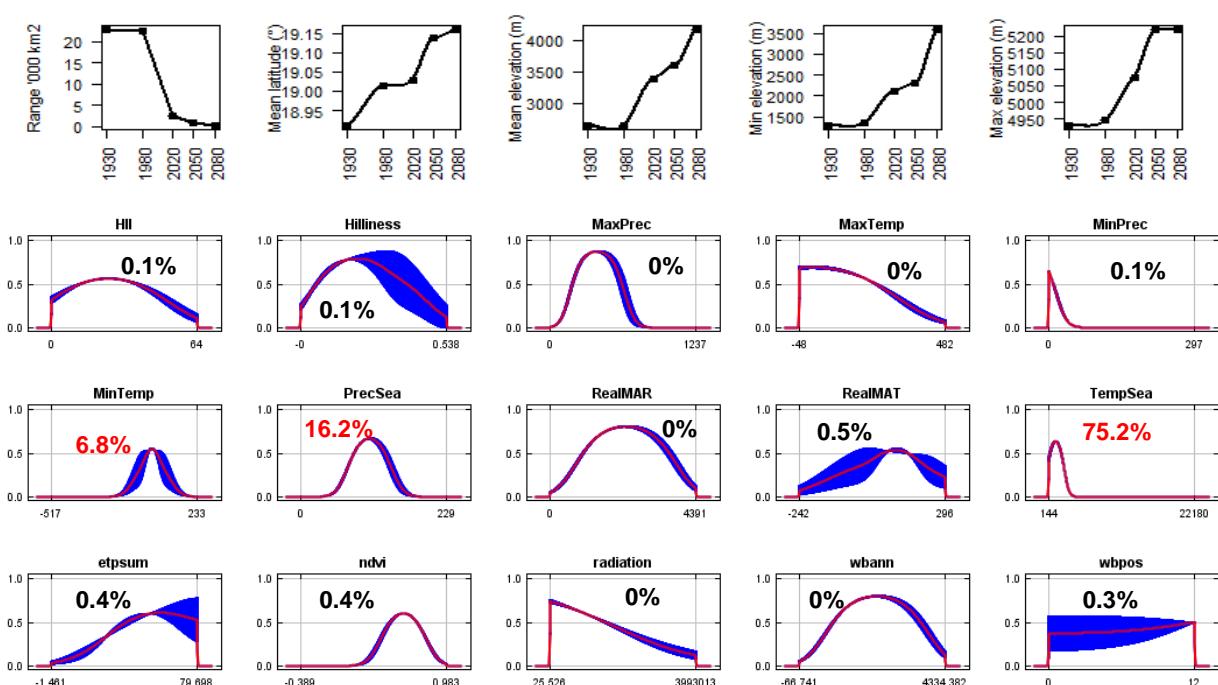
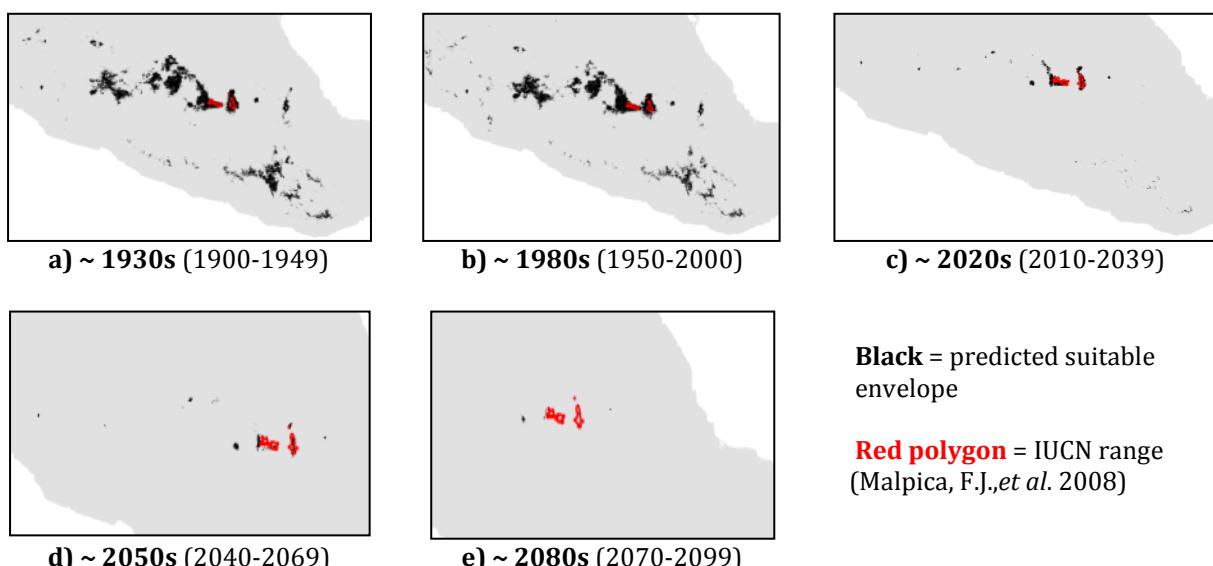
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Island species, range 0.01-0.01)

Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.79
True Skill Statistic	0.90

Summary: The Volcano rabbit's bioclimatic envelope is predicted to decrease by 100% with a ~0.2° mean latitudinal polewards shift and a mean increase in elevation of ~1500m driven by increases in minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (75.2%), precipitation seasonality (16.2%) and minimum temperature (6.8%).



#73 – Swamp rabbit (*Sylvilagus aquaticus*)

n = 66

Expert: Robert Kissell, Memphis State University

Expert evaluation: Medium

Data: Modern and historic

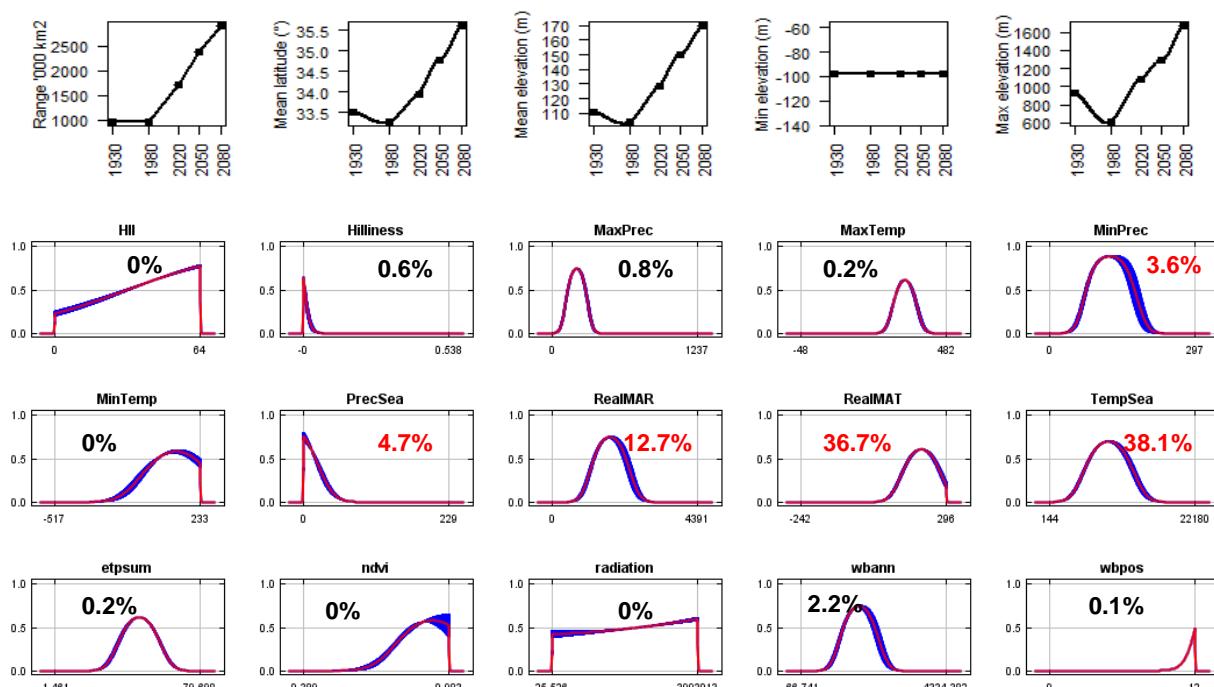
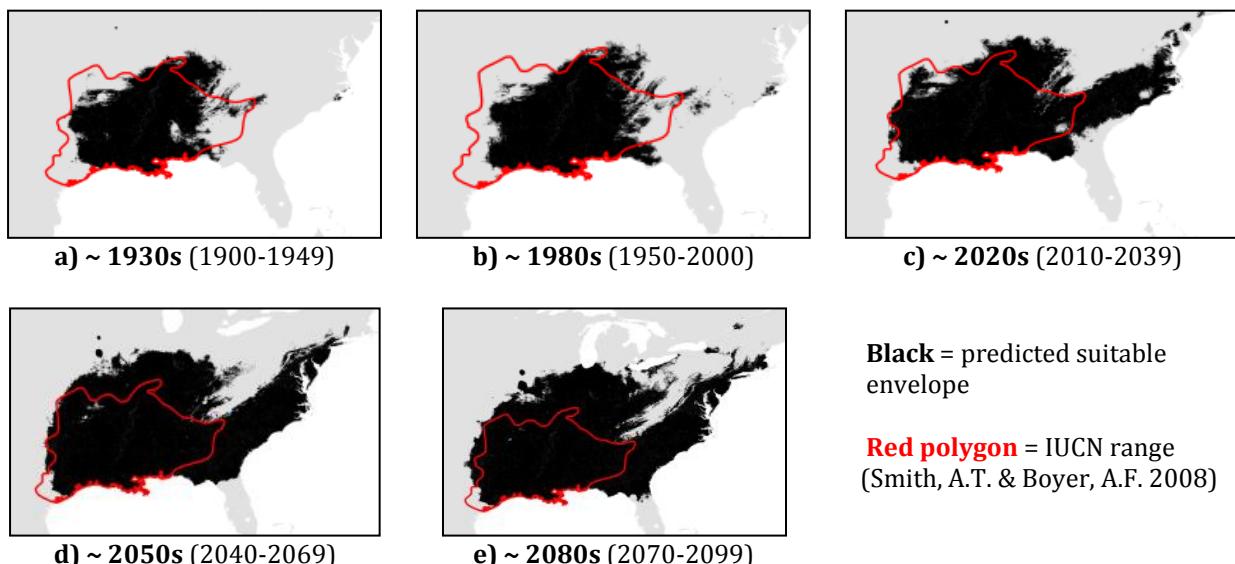
Envelope: Climatic and habitat

Dispersal distance: 25km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.95
Omission rate	0.09
Sensitivity	0.91
Specificity	0.99
Proportion correct	0.99
Kappa	0.76
True Skill Statistic	0.91

Summary: The Swamp rabbit's bioclimatic envelope is predicted to increase by 200% with a ~2° mean latitudinal polewards shift and a mean increase in elevation of ~60m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (38.1%), mean annual temperature (36.7%), mean annual precipitation (12.7%), precipitation seasonality (4.7%) and minimum precipitation (3.6%).



#74 – Desert cottontail (*Sylvilagus audubonii*)

n = 1040

Expert: Consuelo Lorenzo, Departamento Conservación de la Biodiversidad, Chiapas

Expert evaluation: Medium

Data: Modern and historic

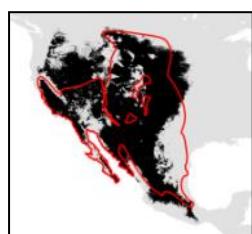
Envelope: Climatic and habitat

Dispersal distance: 7.5km/year (Similar ecology to *S.palustris*)

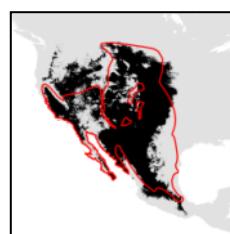
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.94
Omission rate	0.08
Sensitivity	0.92
Specificity	0.96
Proportion correct	0.96
Kappa	0.78
True Skill Statistic	0.88

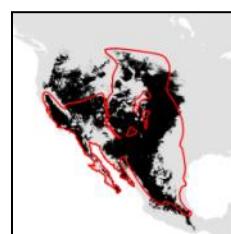
Summary: The Desert cottontail's bioclimatic envelope is predicted to increase by 5% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~30m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (36.6%), annual evapotranspiration (27.1%), mean annual temperature (13.6%), minimum temperature (9.1%), maximum temperature (3.0%), annual water balance (2.1%), minimum precipitation (1.9%) and human influence index (1.7%).



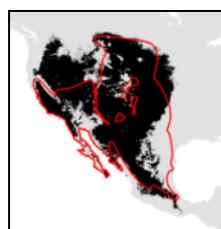
a) ~ 1930s (1900-1949)



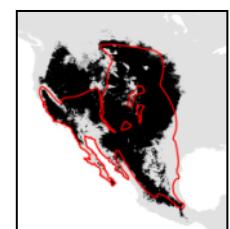
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



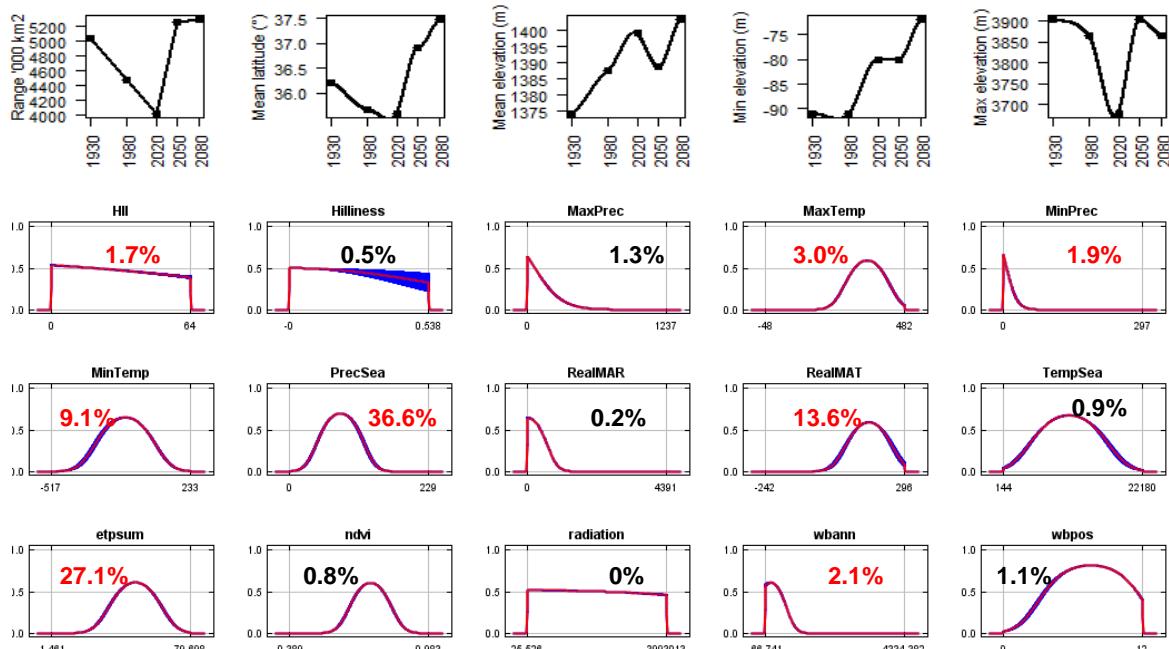
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Romero Malpica, F.J. & Rangel Cordero, H. 2008)



#75 – Brush rabbit (*Sylvilagus bachmani*)

n = 263

Expert: Consuelo Lorenzo, Departamento Conservación de la Biodiversidad, Chiapas

Expert evaluation: Medium

Data: Modern and historic

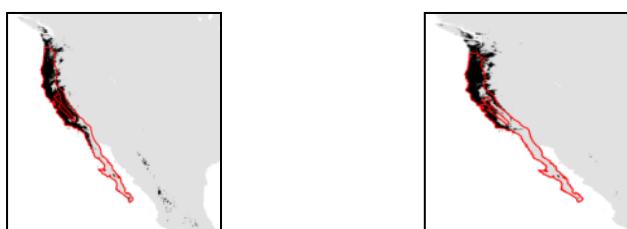
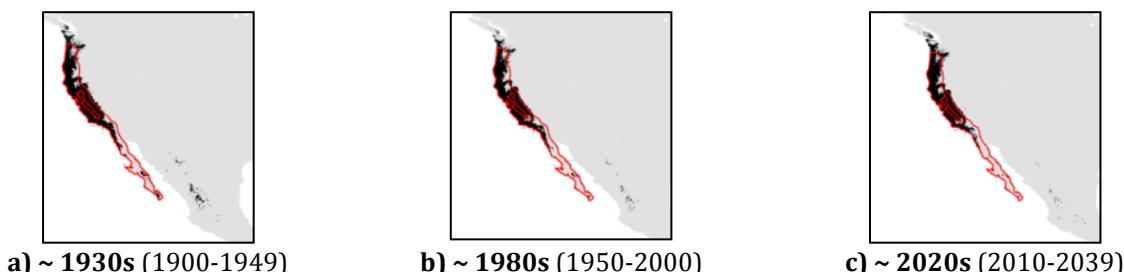
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Similar ecology to *S.transitionalis*)

Status: MODELLABLE; Included in final analysis: ✓

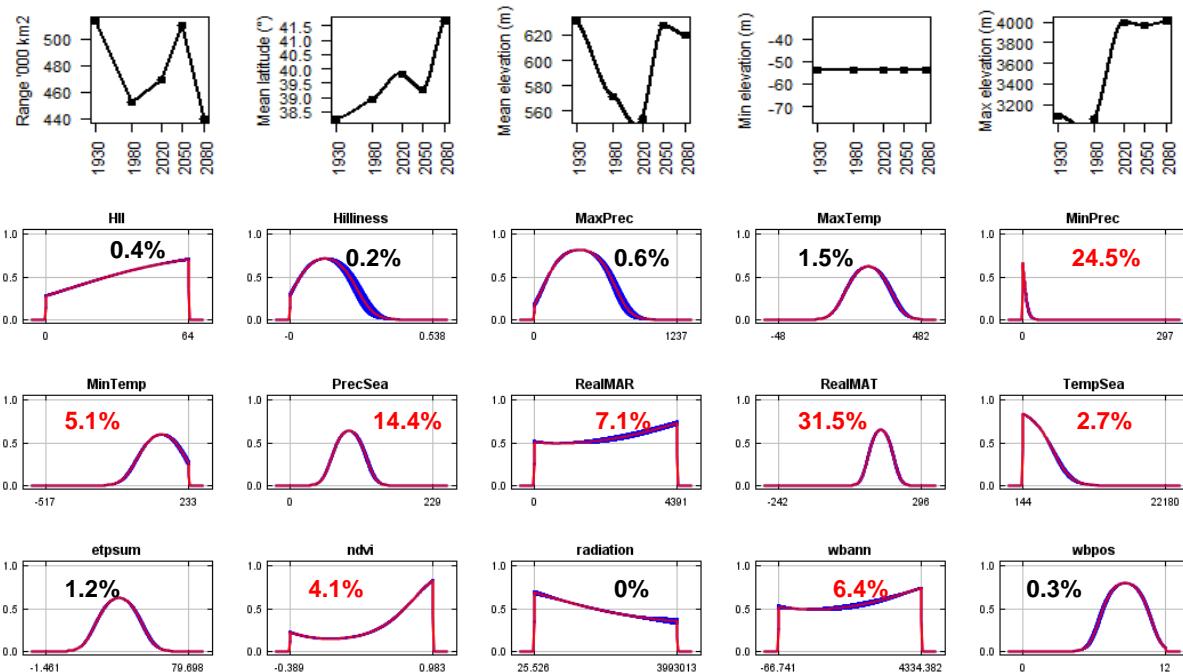
Model evaluation metric	
AUC	0.96
Omission rate	0.08
Sensitivity	0.92
Specificity	0.99
Proportion correct	0.99
Kappa	0.89
True Skill Statistic	0.91

Summary: The Brush rabbit's bioclimatic envelope is predicted to decrease by 15% with a ~3° mean latitudinal polewards shift and a mean decrease in elevation of ~10m. 95% of the permutation importance of the model was contributed to by mean annual temperature (31.5%), minimum precipitation (24.5%), precipitation seasonality (14.4%), mean annual precipitation (7.1%), annual water balance (6.4%), minimum temperature (5.1%), normalised difference vegetation index (4.1%) and temperature seasonality (2.7%).



Black = predicted suitable envelope

Red polygon = IUCN range
(Romero Malpica, F.J.*et al.* 2008)



#76 – Forest rabbit (*Sylvilagus brasiliensis*)

n = 181

Expert: Jorge Salazar-Bravo, Texas Tech University

Expert evaluation: Medium

Data: Modern and historic

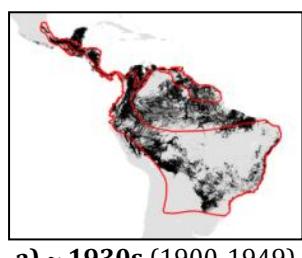
Envelope: Climatic and habitat

Dispersal distance: 7.5km/year (Similar ecology to *S.palustris*)

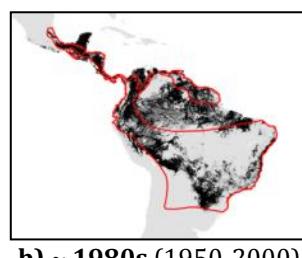
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.73
True Skill Statistic	0.89

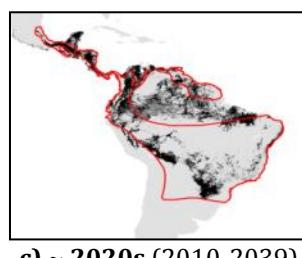
Summary: The Forest rabbit's bioclimatic envelope is predicted to decrease by 50% with a ~6° mean latitudinal polewards shift and a mean increase in elevation of ~210m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (71.4%), temperature seasonality (11.6%), normalised difference vegetation index (4.9%) and minimum temperature (4.6%).



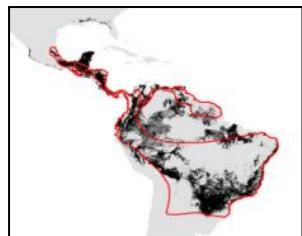
a) ~ 1930s (1900-1949)



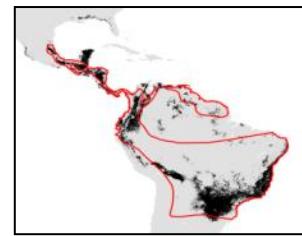
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



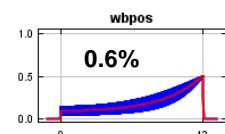
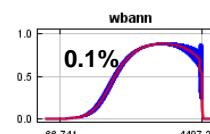
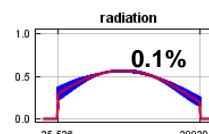
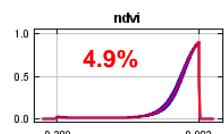
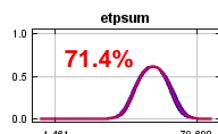
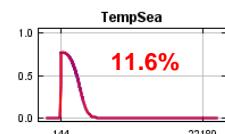
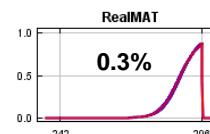
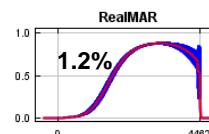
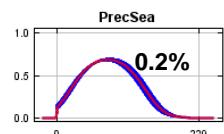
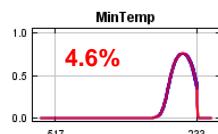
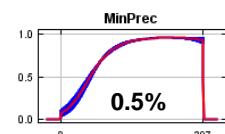
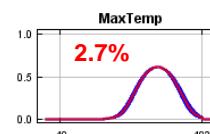
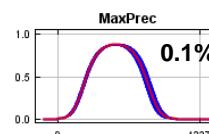
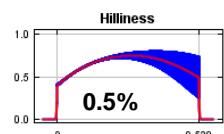
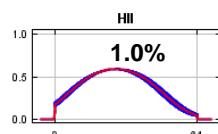
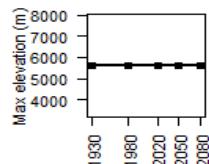
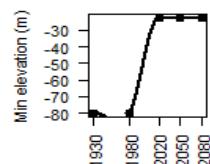
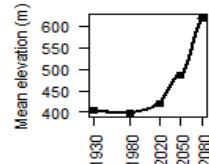
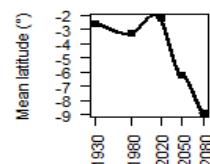
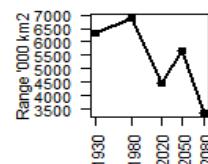
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Romero Malpica, F.J. & Rangel Cordero, H. 2008)



#77 – Manzano mountain cottontail (*Sylvilagus cognatus*)

n = 7

Expert: Jennifer Frey, New Mexico State University

Expert evaluation: Medium

Data: Modern and historic

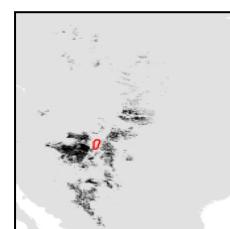
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Similar ecology to *R.diazi*)

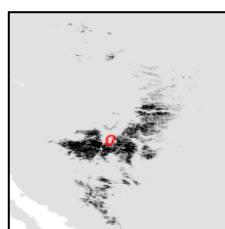
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.52
True Skill Statistic	0.99

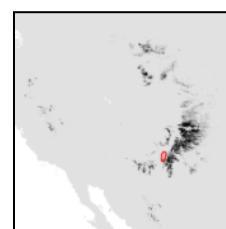
Summary: The Manzano mountain cottontail's bioclimatic envelope is predicted to decrease by 90% with a ~2° mean latitudinal polewards shift and a mean increase in elevation of ~230m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by annual water balance (40.8%), minimum temperature (21.7%), precipitation seasonality (11.3%), mean annual temperature (8.2%), temperature seasonality (6.1%), minimum precipitation (4.3%) and mean annual precipitation (2.6%).



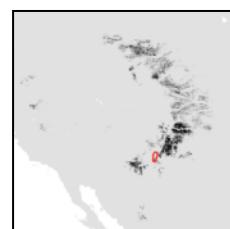
a) ~ 1930s (1900-1949)



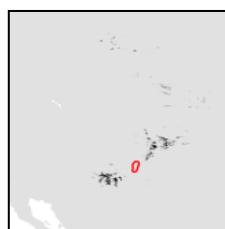
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



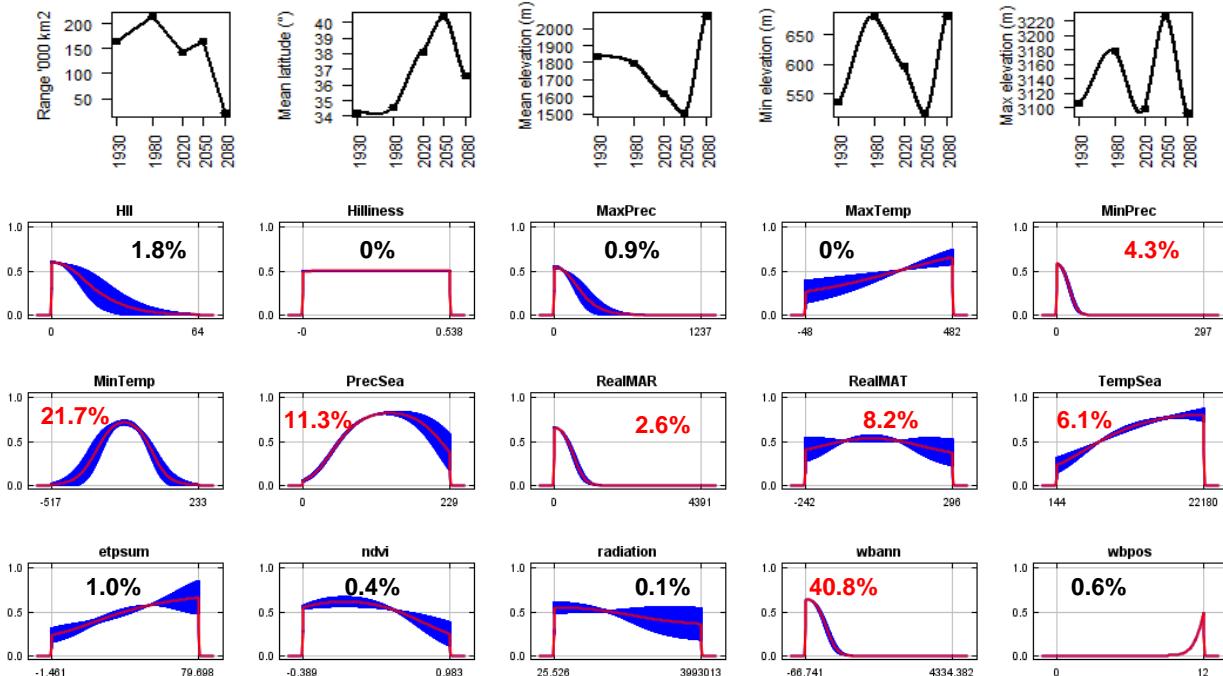
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Boyer, A. F. 2008)



#78 – Mexican cottontail (*Sylvilagus cunicularius*)

n = 76

Expert: Jorge Vazquez, Laboratorio de Ecología del Comportamiento, UAT-UNAM

Expert evaluation: Medium

Data: Only modern

Envelope: Climatic and habitat

Dispersal distance: 7.5km/year (Similar ecology to *S.palustris*)

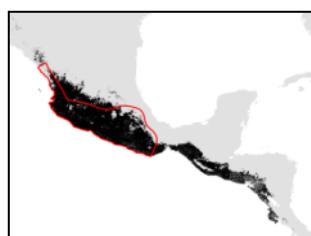
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.95
Omission rate	0.10
Sensitivity	0.90
Specificity	0.99
Proportion correct	0.99
Kappa	0.73
True Skill Statistic	0.89

Summary: The Mexican cottontail's bioclimatic envelope is predicted to decrease by 15% with a ~0.5° mean latitudinal polewards shift and a mean increase in elevation of ~200m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (48.3%), precipitation seasonality (42.8%), normalised difference vegetation index (3.5%) and minimum temperature (2.2%).



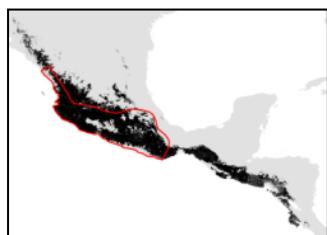
a) ~ 1930s (1900-1949)



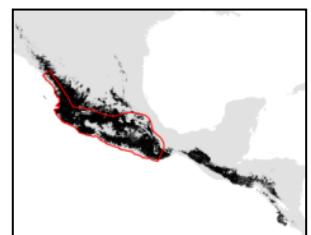
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



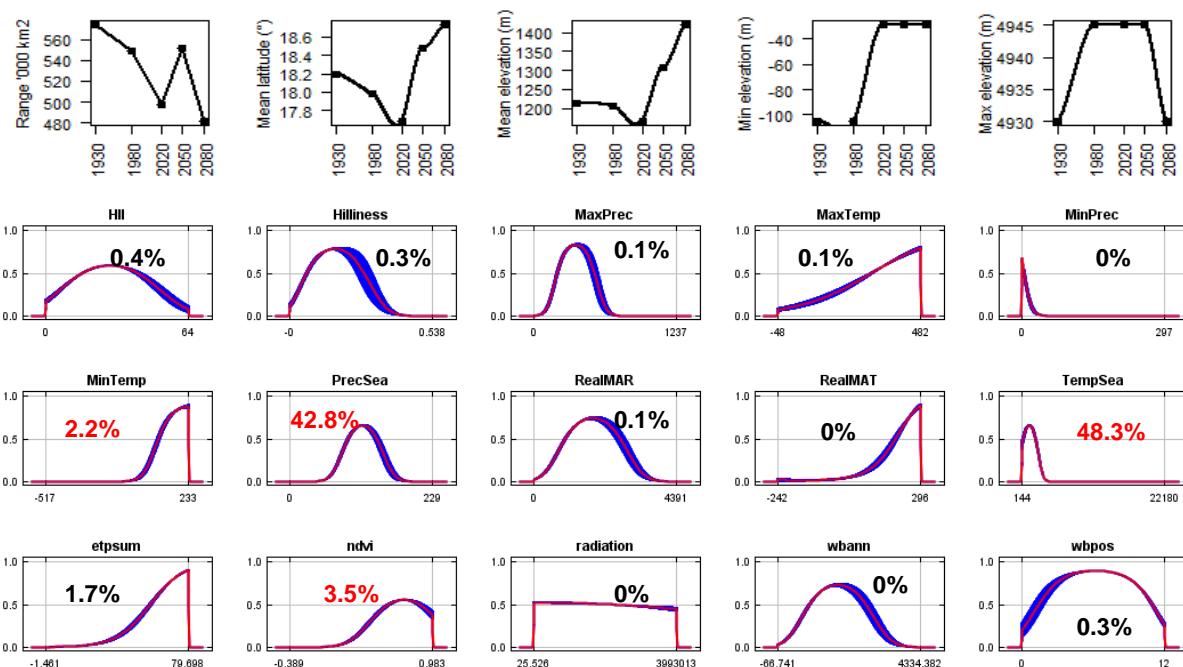
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Romero Malpica, F.J. & Rangel Cordero, H. 2008)



#79 – Dice's cottontail (*Sylvilagus dicei*)

n = 8

Expert: Jan Schipper, Arizona State University

Expert evaluation: Poor

Data: Only modern

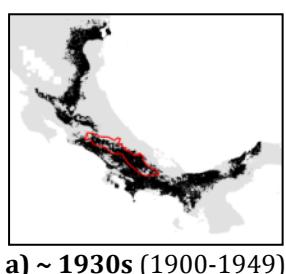
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Similar ecology to *S. cognatus*)

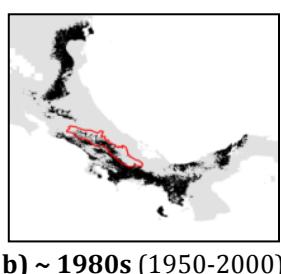
Status: UNMODELLABLE; Included in final analysis: X

Model evaluation metric	
AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.73
True Skill Statistic	0.99

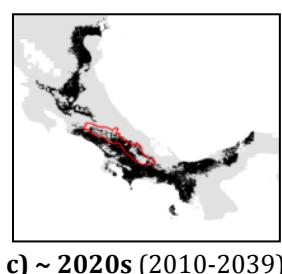
Summary: The Dice's cottontail's bioclimatic envelope is predicted to decrease by 50% with a ~1° mean latitudinal shift towards the Equator and a mean decrease in elevation of ~50m driven by a decrease in maximum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (93.7%) and annual water balance (2.6%).



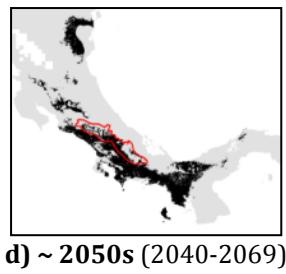
a) ~1930s (1900-1949)



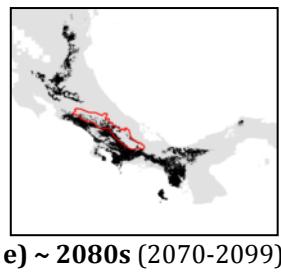
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



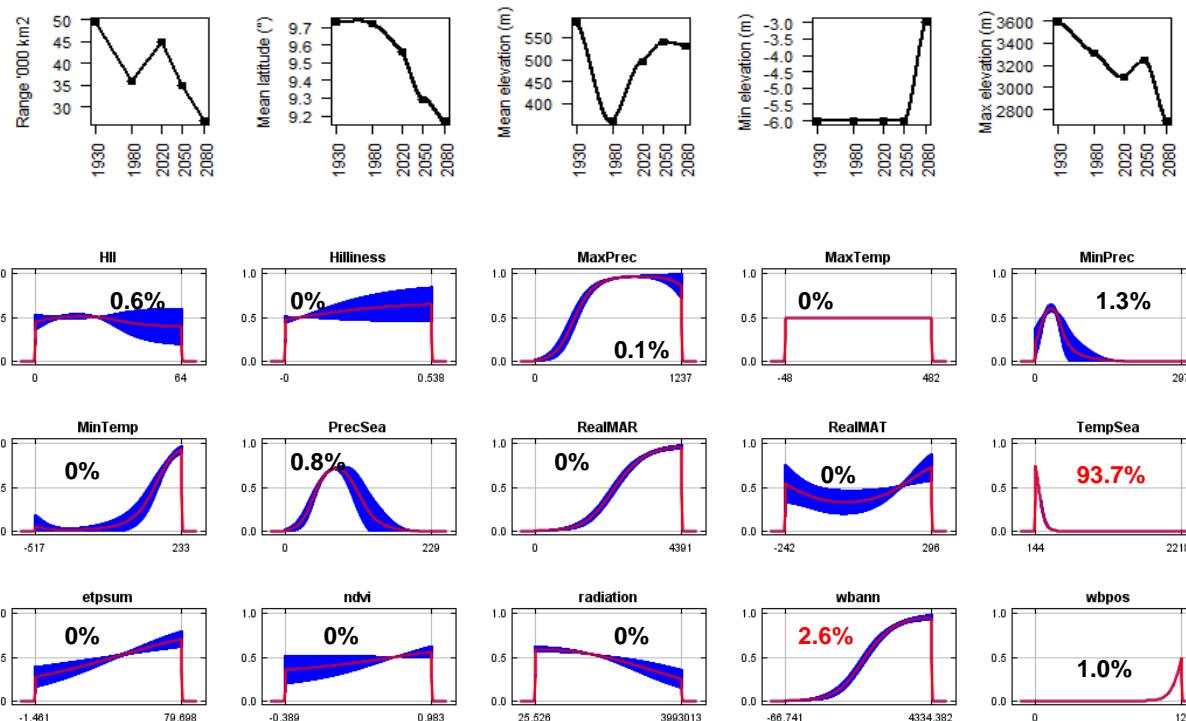
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Boyer, A.F. 2008)



#80 – Eastern cottontail (*Sylvilagus floridanus*)

n = 1104

Expert: Jorge Vazquez, Laboratorio de Ecología del Comportamiento, UAT-UNAM

Expert evaluation: Medium

Data: Modern and historic

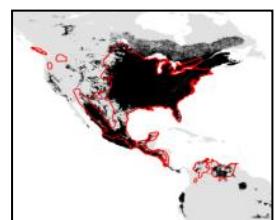
Envelope: Climatic and habitat

Dispersal distance: 7.5km/year (Similar ecology to *S.palustris*)

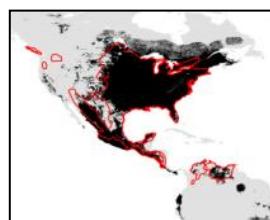
Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	0.92
Omission rate	0.09
Sensitivity	0.91
Specificity	0.93
Proportion correct	0.93
Kappa	0.69
True Skill Statistic	0.84

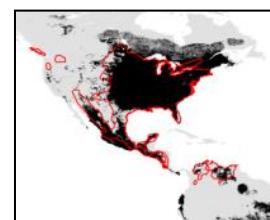
Summary: The Eastern cottontail's bioclimatic envelope is predicted to increase by 20% with a ~2° mean latitudinal polewards shift and a mean increase in elevation of ~90m driven by an increase in minimum and maximum elevation. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (29.5%), precipitation seasonality (26.2%), minimum temperature (11.5%), temperature seasonality (8.5%), minimum precipitation (8.1%), maximum temperature (3.3%), normalised difference vegetation index (2.9%), maximum precipitation (2.8%) and annual water balance (2.3%).



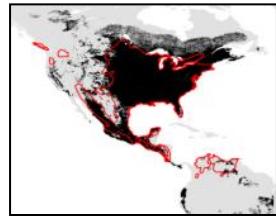
a) ~ 1930s (1900-1949)



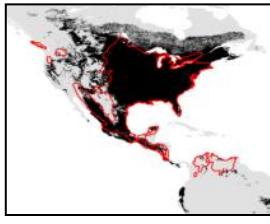
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



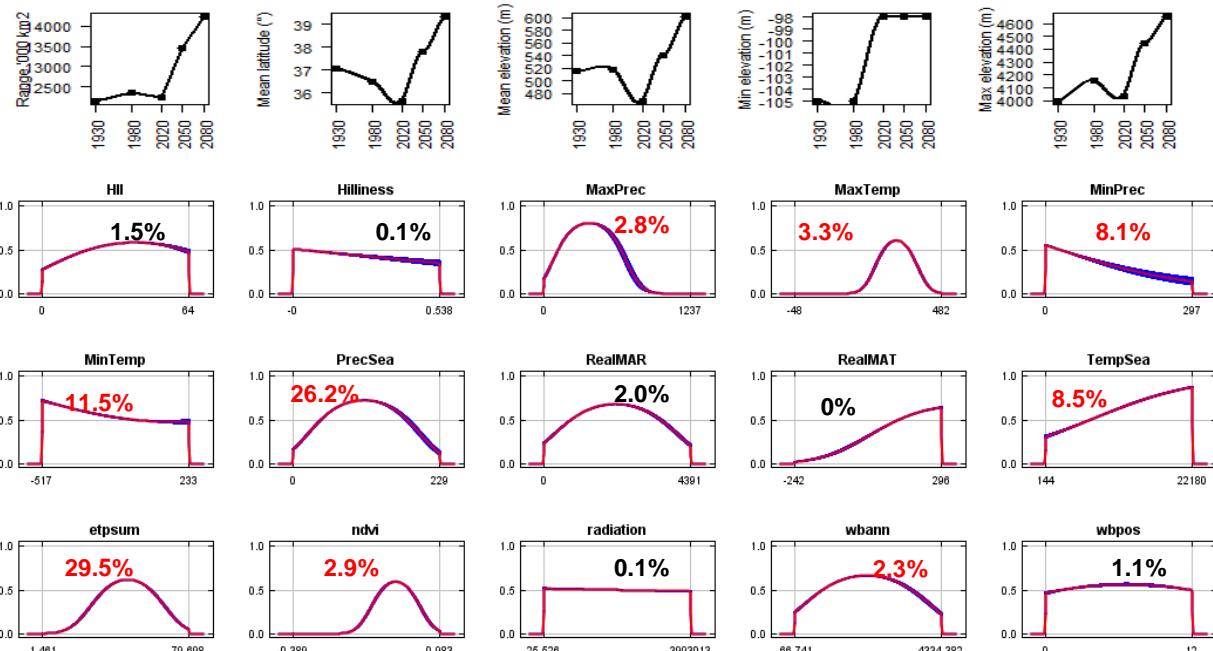
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Romero Malpica, F.J. & Rangel Cordero, H. 2008)



#81 – Tres Marias cottontail (*Sylvilagus graysoni*)

n = 6

Expert: Consuelo Lorenzo, Departamento Conservación de la Biodiversidad, Chiapas

Expert evaluation: Good

Data: Modern and historic

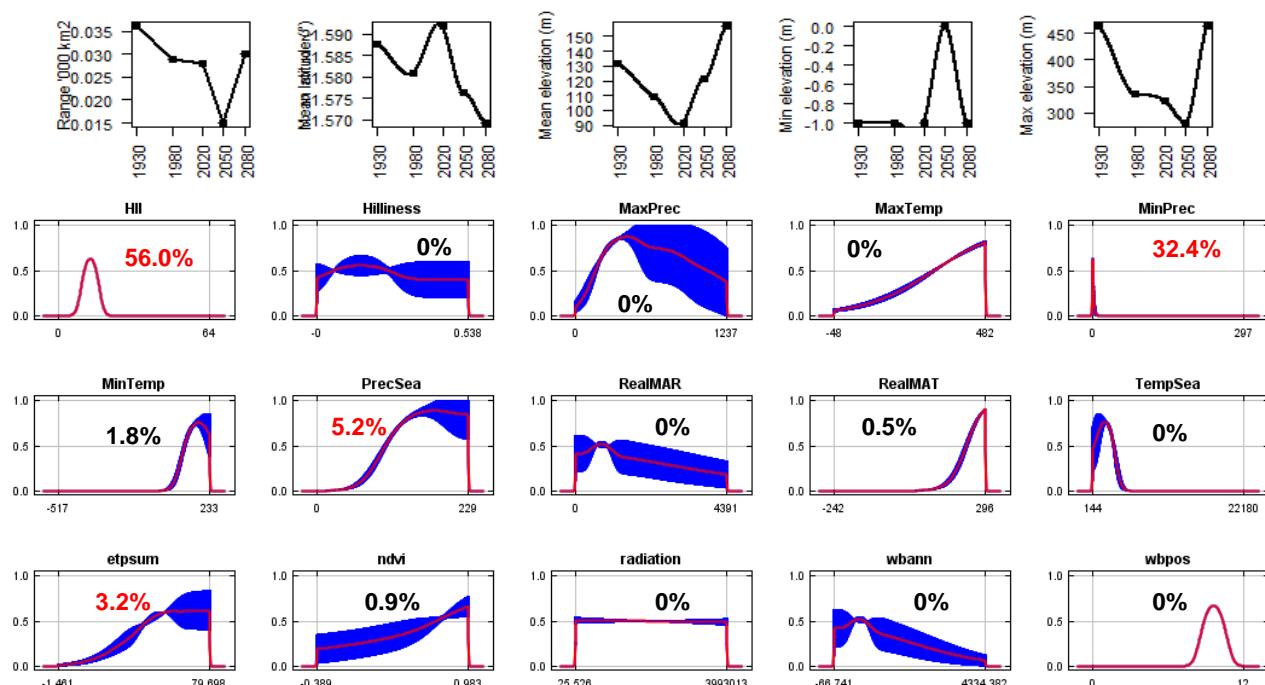
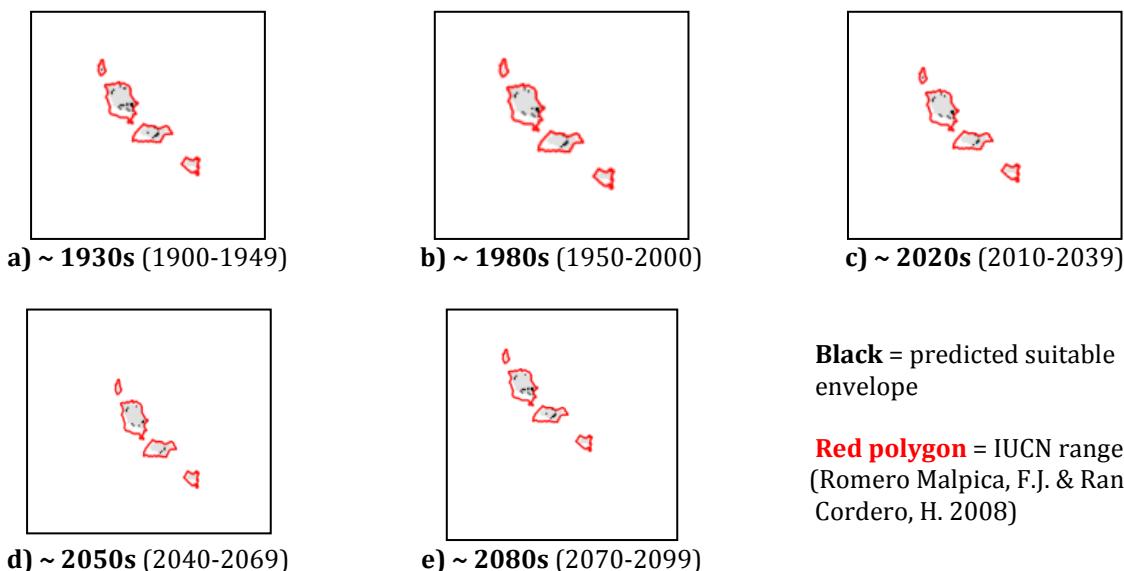
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Island species, range 0.01-0.01)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	1.00
Omission rate	0.00
Sensitivity	1.00
Specificity	1.00
Proportion correct	1.00
Kappa	1.00
True Skill Statistic	1.00

Summary: The Tres Marias cottontail's bioclimatic envelope is predicted to decrease by 20% with a no latitudinal polewards shift and a mean increase in elevation of ~25m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by human influence index (56.0%), minimum precipitation (32.4%), precipitation seasonality (5.2%) and annual evapotranspiration (3.2%).



#82 – Omilteme cottontail (*Sylvilagus insonus*)

n = 3

Expert: Alejandro Velazquez, UNAM-Canada

Expert evaluation: Good

Data: Only modern

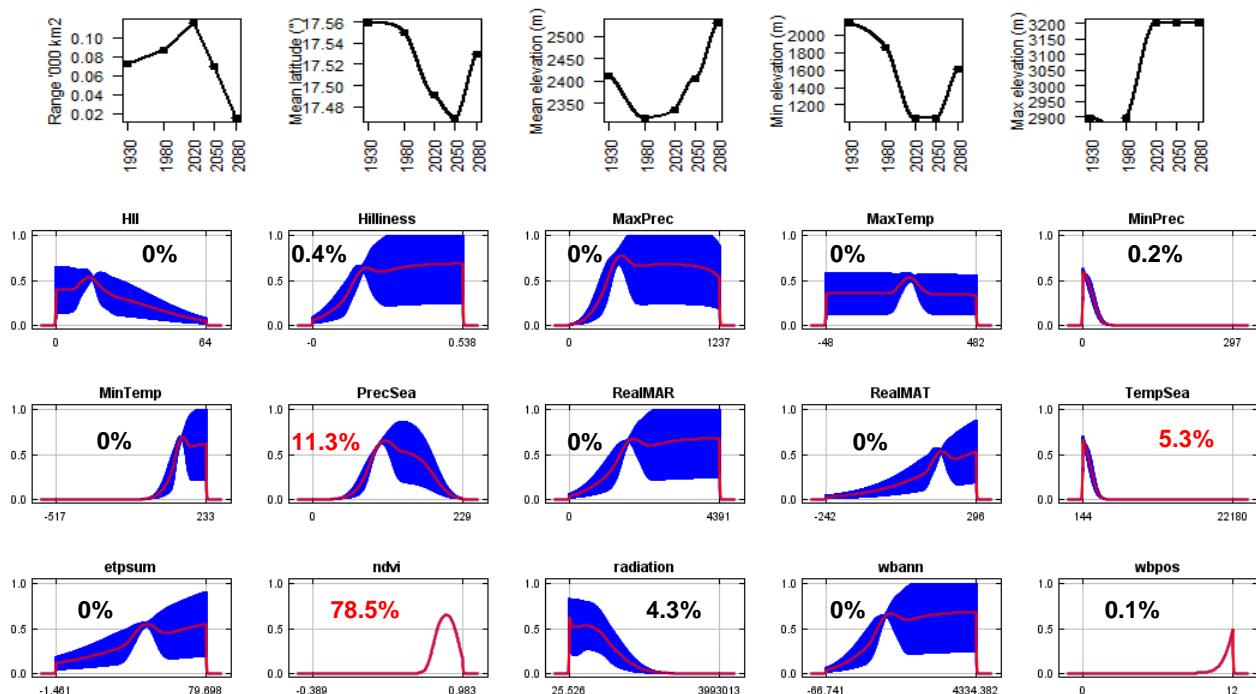
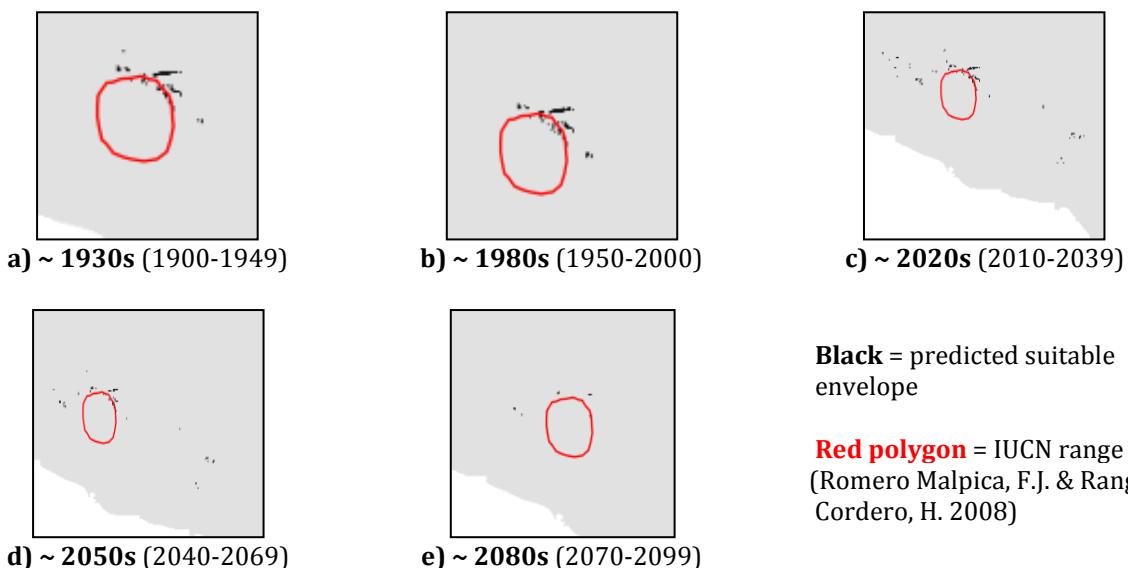
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Similar ecology to *S.dicei*)

Status: MODELLABLE; Included in final analysis: ✓

Model evaluation metric	
AUC	1.00
Omission rate	0.00
Sensitivity	1.00
Specificity	1.00
Proportion correct	1.00
Kappa	1.00
True Skill Statistic	1.00

Summary: The Omilteme cottontail's bioclimatic envelope is predicted to decrease by 80% with a no latitudinal polewards shift and a mean increase in elevation of ~120m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by normalised difference vegetation index (78.5%), precipitation seasonality (11.3%) and temperature seasonality (5.3%).



#83 – San Jose brush rabbit (*Sylvilagus mansuetus*)

n = 9

Expert: Tamara Rioja Pardela, Universidad de Ciencias y Artes de Chiapas, Mexico

Expert evaluation: Good

Data: Only modern

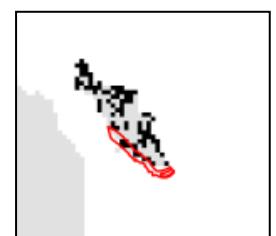
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Island species, range 0.01-0.01)

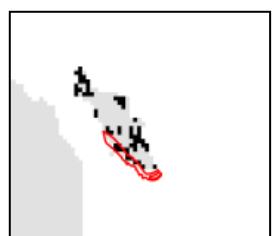
Status: MODELLABLE; Included in final analysis: ✓

AUC	1.00
Omission rate	0.00
Sensitivity	1.00
Specificity	1.00
Proportion correct	1.00
Kappa	1.00
True Skill Statistic	1.00

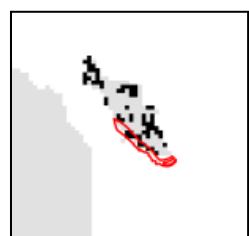
Summary: The San Jose brush rabbit's bioclimatic envelope is predicted to decrease by 25% with a no latitudinal polewards shift and a mean increase in elevation of ~30m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (36.7%), human influence index (34.0%), minimum precipitation (21.8%) and precipitation seasonality (3.2%).



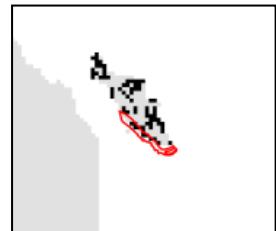
a) ~ 1930s (1900-1949)



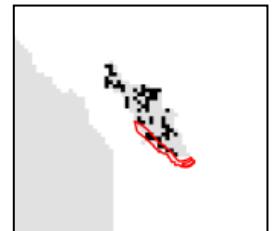
b) ~ 1980s (1950-2000)



c) ~ 2020s (2010-2039)



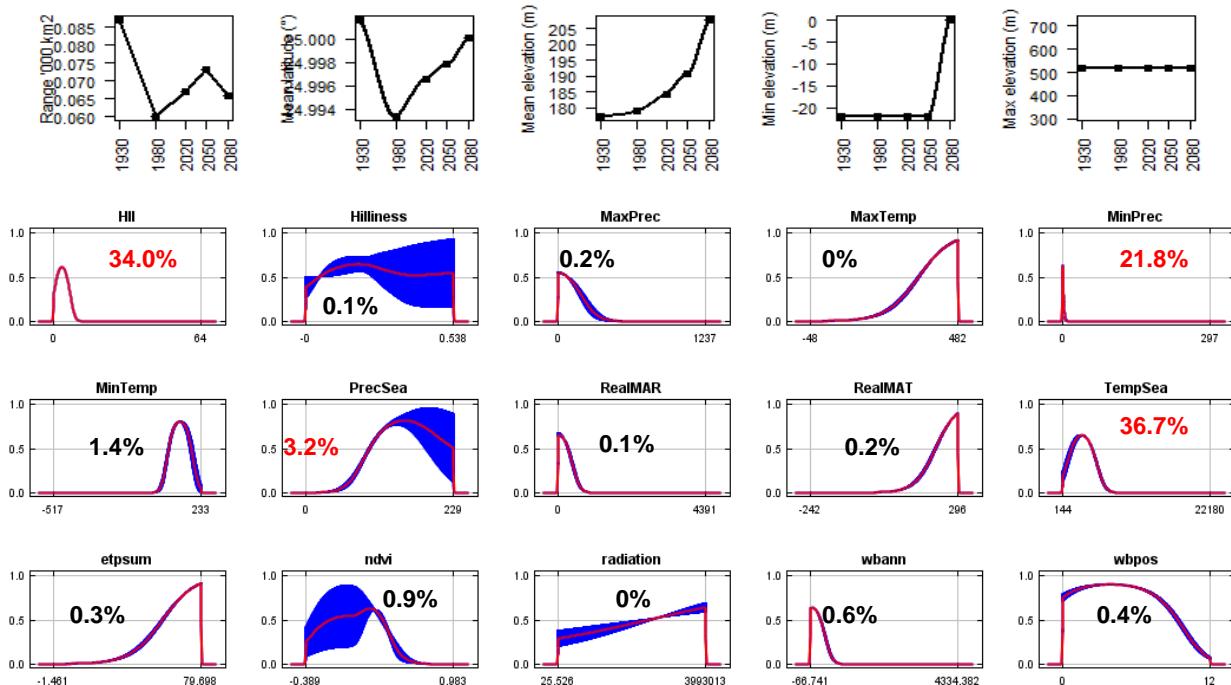
d) ~ 2050s (2040-2069)



e) ~ 2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Lorenzo, C. & Álvarez-Castañeda, S. 2011)



#84 – Mountain cottontail (*Sylvilagus nuttallii*)

n = 290

Expert: Jennifer Frey, New Mexico State University

Expert evaluation: Medium

Data: Modern and historic

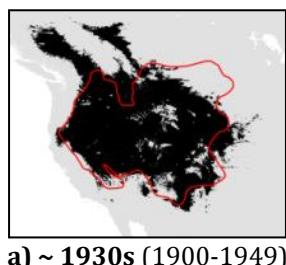
Envelope: Climatic and habitat

Dispersal distance: 7.5km/year (Similar ecology to *S.palustris*)

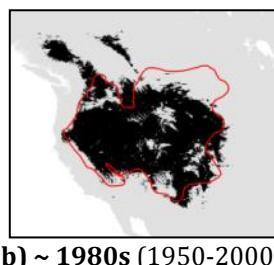
Status: MODELLABLE; Included in final analysis: ✓

AUC	0.95
Omission rate	0.09
Sensitivity	0.91
Specificity	0.99
Proportion correct	0.99
Kappa	0.78
True Skill Statistic	0.90

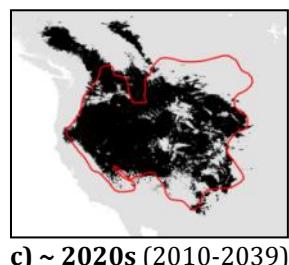
Summary: The Mountain cottontail's bioclimatic envelope is predicted to decrease by 20% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~40m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by mean annual temperature (64.0%), maximum temperature (26.9%), temperature seasonality (2.8%) and minimum precipitation (1.4%).



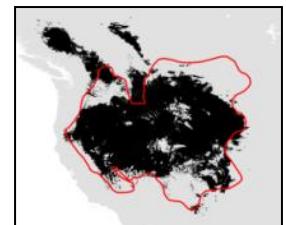
a) ~1930s (1900-1949)



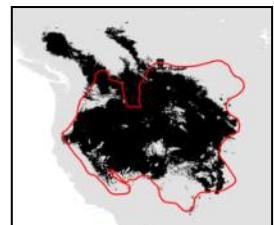
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



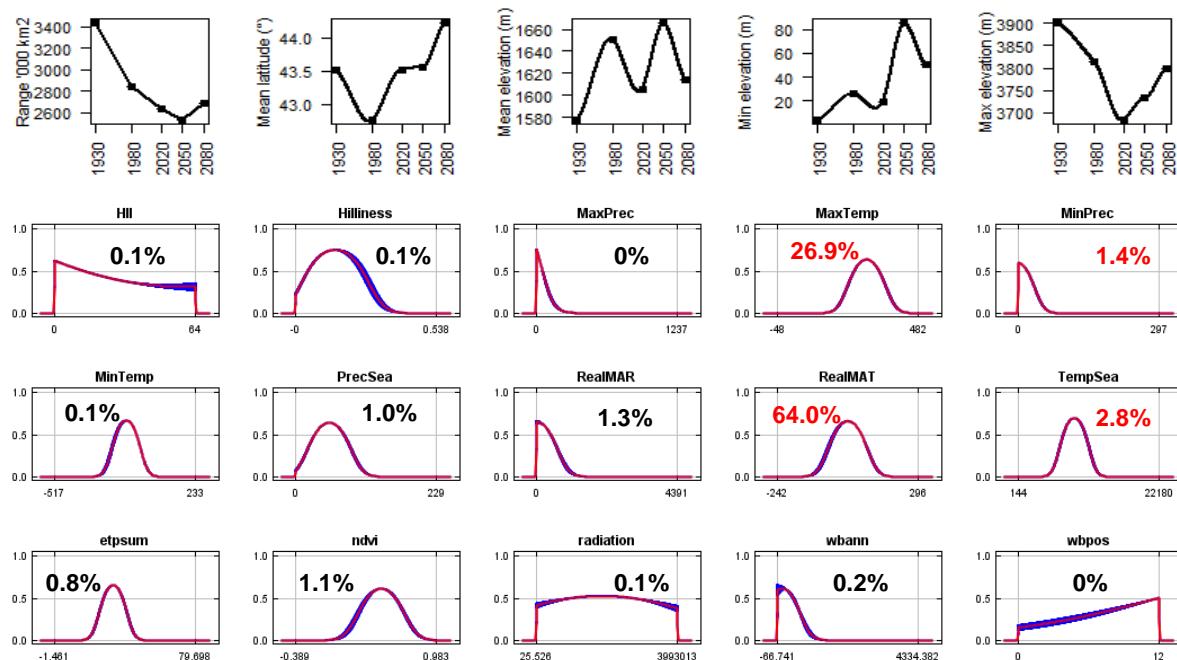
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Smith, A.T. & Boyer, A.F. 2008)



#85 – Appalachian cottontail (*Sylvilagus obscurus*)

n = 39

Expert: Michael Barbour, Alabama Natural Heritage Program

Expert evaluation: Medium

Data: Modern and historic

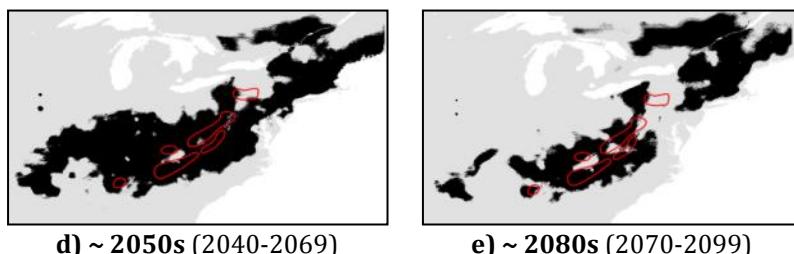
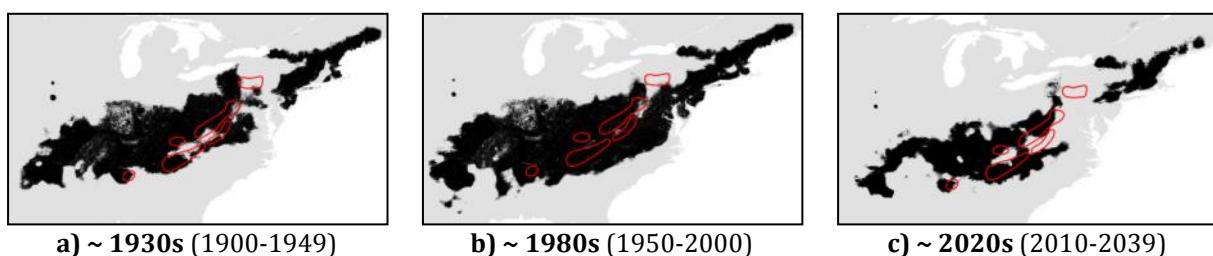
Envelope: Climatic only

Dispersal distance: 0.01km/year (Similar ecology to *S.dicei*)

Status: MODELLABLE; Included in final analysis: ✓

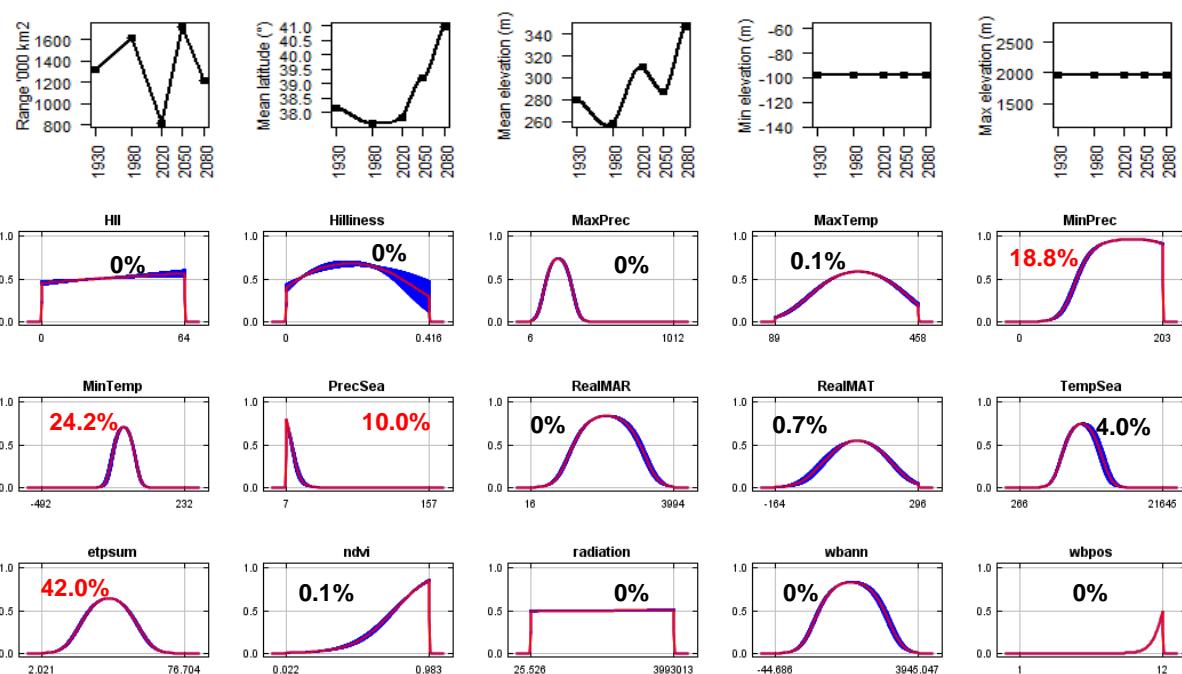
AUC	0.97
Omission rate	0.05
Sensitivity	0.95
Specificity	0.99
Proportion correct	0.99
Kappa	0.73
True Skill Statistic	0.95

Summary: The Appalachian cottontail's bioclimatic envelope is predicted to decrease by 10% with a ~3° mean latitudinal polewards shift and a mean increase in elevation of ~70m. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (42.0%), minimum temperature (24.2%), minimum precipitation (18.8%) and precipitation seasonality (10.0%).



Black = predicted suitable envelope

Red polygon = IUCN range
(Barry, R. & Lazell, J. 2008)



#86 – Marsh rabbit (*Sylvilagus palustris*)

n = 25

Expert: Bob McCleery, University of Florida

Expert evaluation: Good

Data: Only modern

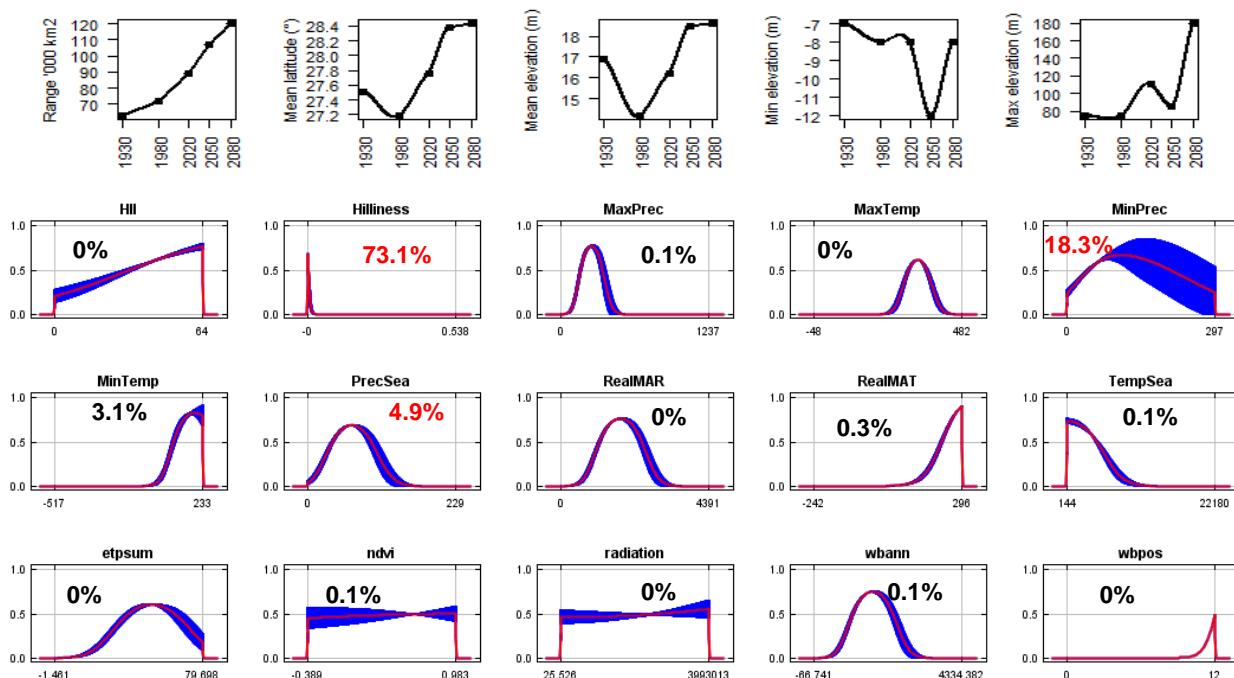
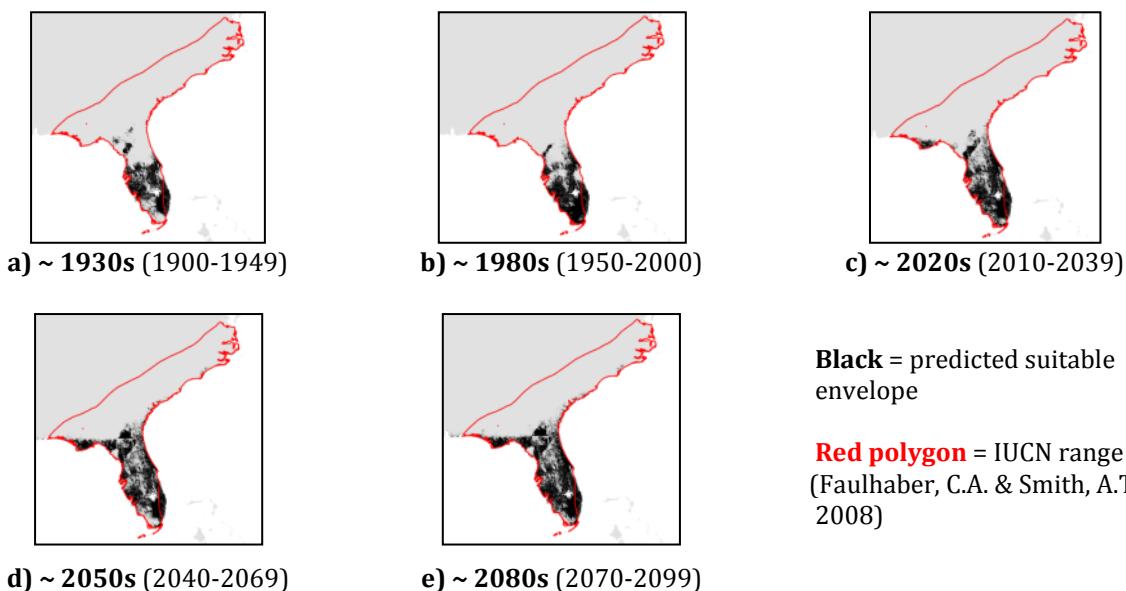
Envelope: Climatic and habitat

Dispersal distance: 7.5km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.75
True Skill Statistic	0.99

Summary: The Marsh rabbit's bioclimatic envelope is predicted to increase by 90% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~2m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by surface roughness index (73.1%), minimum precipitation (18.3%) and precipitation seasonality (4.9%).



#87 – Robust cottontail (*Sylvilagus robustus*)

n = 9

Expert: Dana Lee, Oklahoma State University

Expert evaluation: Poor

Data: Modern and historic

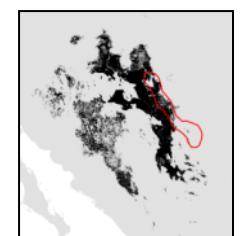
Envelope: Climatic and habitat

Dispersal distance: 0.01km/year (Similar ecology to *S.dicei*)

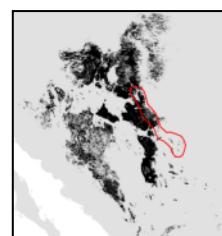
Status: UNMODELLABLE; Included in final analysis: X

AUC	0.94
Omission rate	0.11
Sensitivity	0.89
Specificity	0.99
Proportion correct	0.99
Kappa	0.27
True Skill Statistic	0.88

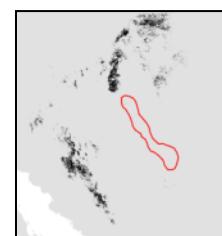
Summary: The Robust cottontail's bioclimatic envelope is predicted to decrease by 90% with a ~4° mean latitudinal polewards shift and a mean increase in elevation of ~480m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by precipitation seasonality (68.5%), minimum precipitation (8.2%), temperature seasonality (7.1%), minimum temperature (4.5%), mean annual precipitation (3.6%), annual water balance (2.6%) and number of months with a positive water balance (1.6%).



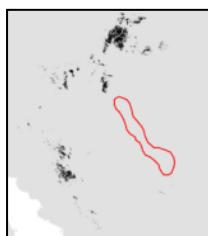
a) ~1930s (1900-1949)



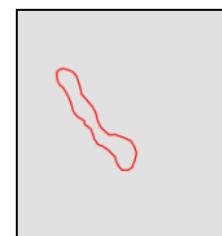
b) ~1980s (1950-2000)



c) ~2020s (2010-2039)



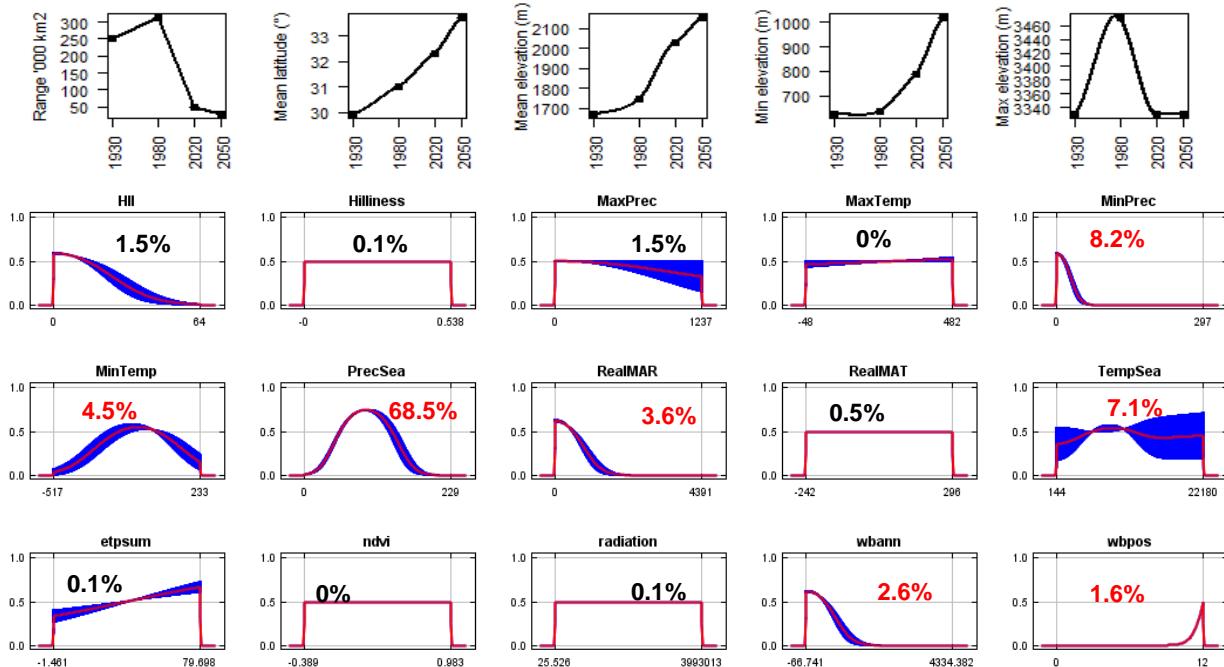
d) ~2050s (2040-2069)



e) ~2080s (2070-2099)

Black = predicted suitable envelope

Red polygon = IUCN range
(Ruedas, L. & Smith, A.T. 2008)



#88 – New England cottontail (*Sylvilagus transitionalis*)

n = 18

Expert: John Litvaitis, University of New Hampshire

Expert evaluation: Medium

Data: Modern and historic

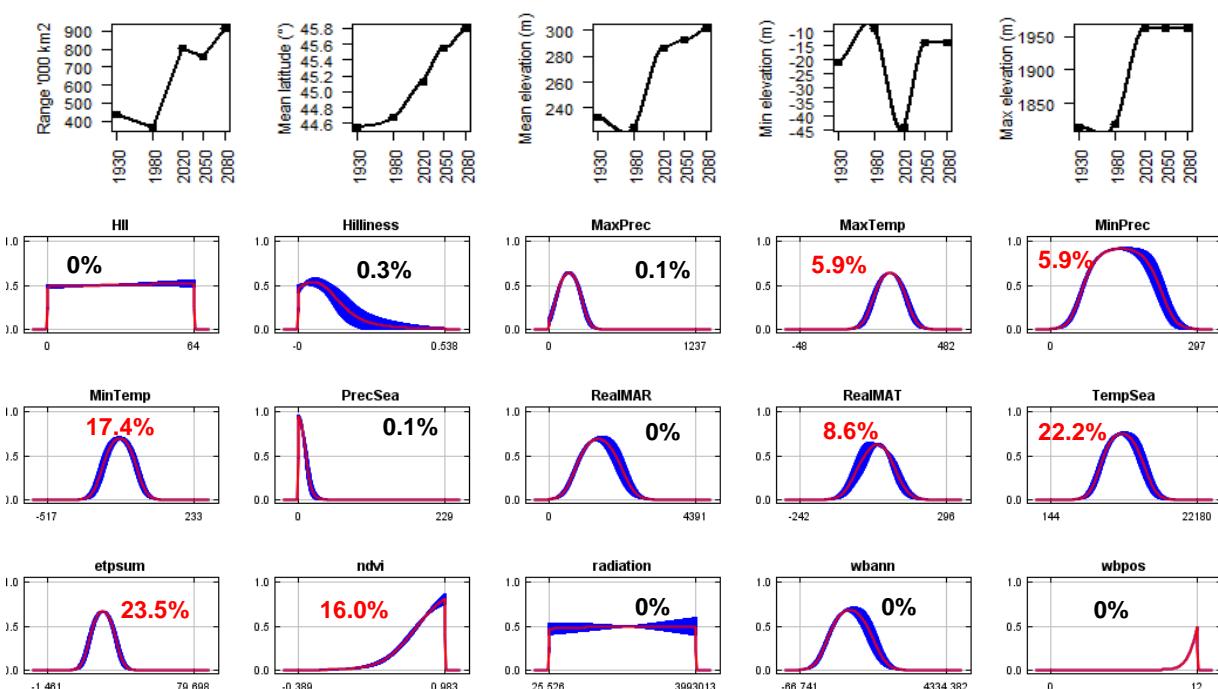
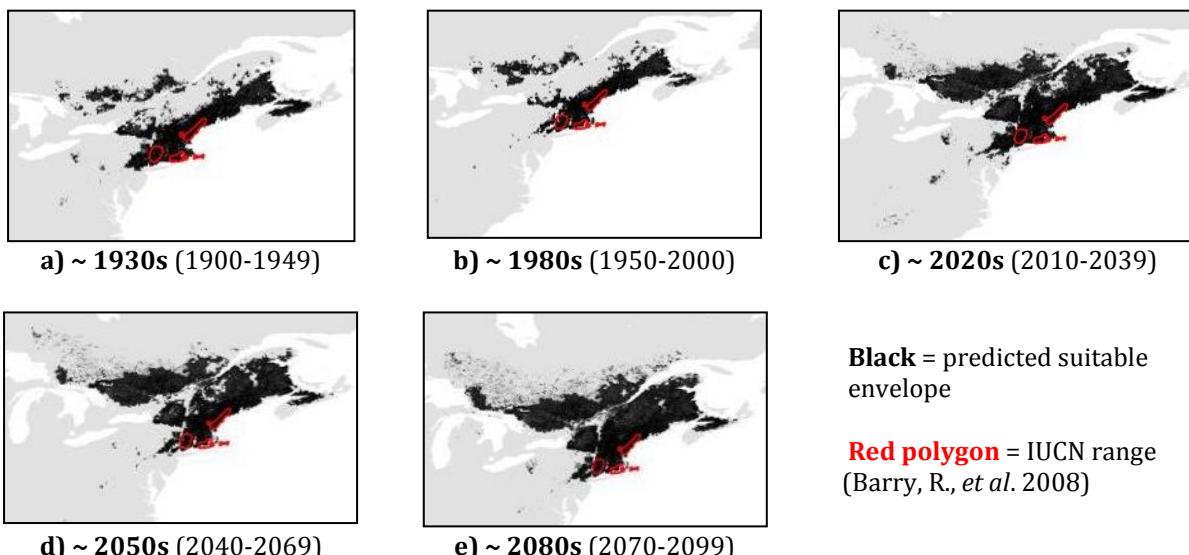
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Expert)

Status: MODELLABLE; Included in final analysis: ✓

AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.68
True Skill Statistic	0.99

Summary: The New England cottontail's bioclimatic envelope is predicted to increase by 110% with a ~1° mean latitudinal polewards shift and a mean increase in elevation of ~70m driven by an increase in maximum elevation. 95% of the permutation importance of the model was contributed to by annual evapotranspiration (23.5%), temperature seasonality (22.2%), minimum temperature (17.4%), normalised difference vegetation index (16.0%), mean annual temperature (8.6%), maximum temperature (5.9%) and minimum precipitation (5.9%).



#89 – Venezuelan lowland rabbit (*Sylvilagus varynaensis*)

n = 6

Expert: Daniel Lew, Venezuelan Institute of Scientific Research, Ecology Centre, Biodiversity Unit

Expert evaluation: Poor

Data: Only modern

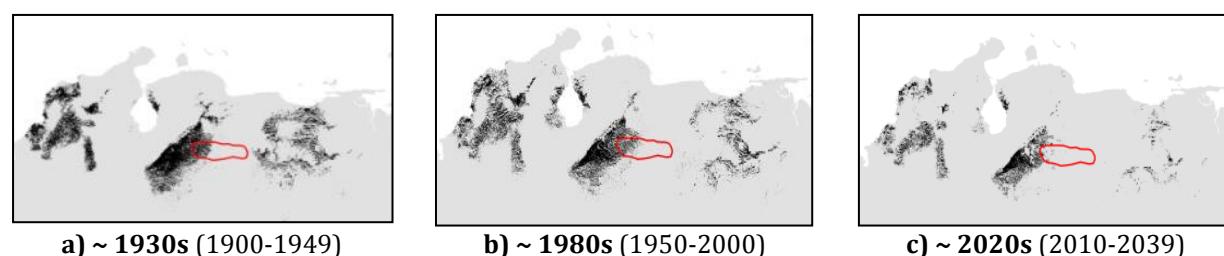
Envelope: Climatic and habitat

Dispersal distance: 3km/year (Similar ecology to *S.transitionalis*)

Status: UNMODELLABLE; Included in final analysis: X

AUC	0.99
Omission rate	0.00
Sensitivity	1.00
Specificity	0.99
Proportion correct	0.99
Kappa	0.92
True Skill Statistic	0.99

Summary: The Venezuelan lowland rabbit's bioclimatic envelope is predicted to decrease by 100% with a ~1.5° mean latitudinal polewards shift and a mean increase in elevation of ~275m driven by an increase in minimum elevation. 95% of the permutation importance of the model was contributed to by temperature seasonality (97.7%).

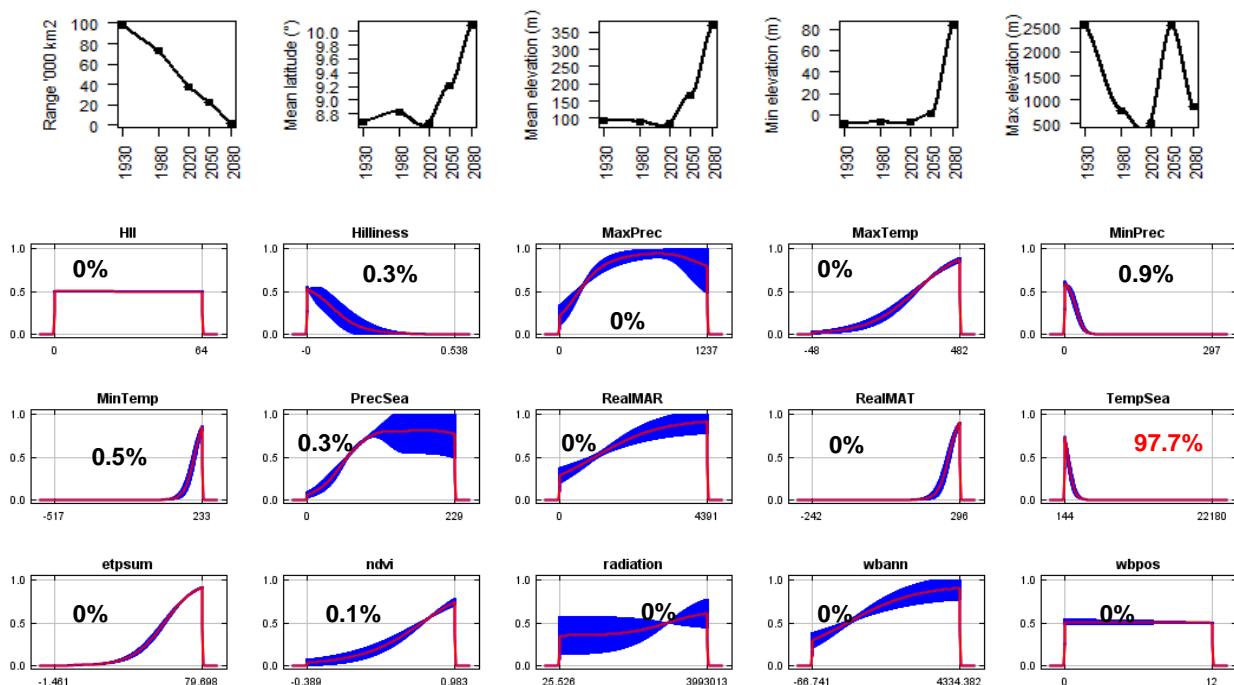


Black = predicted suitable envelope

Red polygon = IUCN range
(Durant, P. & Guevara, M.A. 2008)

d) ~2050s (2040-2069)

e) ~2080s (2070-2099)



Appendix 2. Additional tables and figures - Chapter 3

Table 2.1. Lagomorph experts, institutions and species evaluated.

Expert	Institution	Species evaluated
Alejandro Velazquez	UNAM-Canada	<i>Lepus californicus</i> <i>Sylvilagus insonus</i>
Andrew Smith	Arizona State University	<i>Ochotona argentata</i> <i>Ochotona curzoniae</i> <i>Ochotona dauurica</i> <i>Ochotona erythrotis</i> <i>Ochotona forresti</i> <i>Ochotona gloveri</i> <i>Ochotona iliensis</i> <i>Ochotona koslowi</i> <i>Ochotona ladacensis</i> <i>Ochotona princeps</i> <i>Ochotona pusilla</i> <i>Ochotona thomasi</i>
Andrew Tilker	University of Texas Austin	<i>Nesolagus timminsi</i>
Andrey Lissovsky	Zoological Museum of Moscow State University	<i>Ochotona hoffmanni</i> <i>Ochotona pallasi</i> <i>Ochotona rufile</i> <i>Ochotona turuchanensis</i>
Arturo Carillo-Reyes	Universidad de Ciencias y Artes de Chiapas	<i>Lepus flavigularis</i>
Bob McCleery	University of Florida	<i>Sylvilagus palustris</i>
Charles Krebs	University of British Columbia	<i>Lepus americanus</i>
Chelmala Srinivasulu	Osmania University, India	<i>Lepus tibetanus</i> <i>Lepus tolai</i> <i>Ochotona rufescens</i>
Consuelo Lorenzo	Departamento Conservación de la Biodiversidad, Chiapas	<i>Sylvilagus audubonii</i> <i>Sylvilagus bachmani</i> <i>Sylvilagus graysoni</i>
Dana Lee	Oklahoma State University	<i>Sylvilagus robustus</i>
Daniel Lew	Venezuelan Institute of Scientific Research, Ecology Centre, Biodiversity Unit	<i>Sylvilagus varynaensis</i>
David Gray	Grayhound Information Services	<i>Lepus arcticus</i>
David Happold	Australian National University	<i>Poelagus marjorita</i> <i>Pronolagus saundersiae</i>
Deyan Ge	Institute of Zoology, Chinese Academy of Sciences	<i>Lepus mandschuricus</i> <i>Ochotona thibetana</i>
Eric Waltari	City University of New York	<i>Lepus othus</i> <i>Lepus townsendii</i>
Francesco Angelici	Italian Foundation of Vertebrate Zoology	<i>Lepus corsicanus</i>
Fumio Yamada	Forestry and Forest Products Research Institute, Japan	<i>Pentalagus furnessi</i>
Gopinathan Maheswaran	Zoological Survey of India	<i>Caprolagus hispidus</i> <i>Lepus nigricollis</i>

Hariyo Wibisono	Wildlife Conservation Society, Indonesia	<i>Nesolagus netscheri</i>
Hayley Lanier	University of Michigan	<i>Ochotona collaris</i>
Jan Schipper	Arizona State University	<i>Sylvilagus dicei</i>
Jennifer Frey	New Mexico State University	<i>Lepus callotis</i> <i>Sylvilagus cognatus</i> <i>Sylvilagus nuttallii</i>
John Flux	IUCN Lagomorph Specialist Group	<i>Lepus capensis</i> <i>Lepus microtis</i>
John Litvaitis	University of New Hampshire	<i>Sylvilagus transitionalis</i>
Jorge Salazar-Bravo	Texas Tech University	<i>Sylvilagus brasiliensis</i>
Jorge Vazquez	Laboratorio de Ecología del Comportamiento, UAT-UNAM	<i>Sylvilagus cunicularius</i> <i>Sylvilagus floridanus</i>
Jose Antonio Martinez-Garcia	Universidad Autónoma Metropolitana, Mexico	<i>Romerolagus diazi</i>
Julia Witczuk	Warsaw Agricultural University, Poland	<i>Ochotona hyperborea</i>
Kai Collins	University of Pretoria	<i>Bunolagus monticularis</i> <i>Lepus saxatilis</i> <i>Pronolagus crassicaudatus</i> <i>Pronolagus randensis</i> <i>Pronolagus rupestris</i>
Koji Shimano	Shinshu University, Japan	<i>Lepus brachyurus</i>
Michael Barbour	Alabama Natural Heritage Program	<i>Sylvilagus obscurus</i>
Neil Reid	Queen's University Belfast	<i>Lepus europaeus</i> <i>Lepus timidus</i> <i>Oryctolagus cuniculus</i>
Nishma Dahal	National Centre for Biological Sciences, India	<i>Ochotona macrotis</i> <i>Ochotona nubrica</i>
Paul Krausman	University of Montana	<i>Lepus alleni</i>
Pelayo Acevedo	University of Porto	<i>Lepus castroviejoi</i> <i>Lepus granatensis</i>
Penny Becker	Washington Dept. of Fish & Wildlife, USA	<i>Brachylagus idahoensis</i>
Robert Kissell	Memphis State University	<i>Sylvilagus aquaticus</i>
Rudy Boonstra	University of Toronto Scarborough	<i>Lepus americanus</i>
Sabuj Bhattacharya	Wildlife Institute of India	<i>Ochotona roylei</i>
Sumiya Ganzorig	Hokkaido University	<i>Ochotona alpina</i>
Tamara Rioja Pardela	Universidad de Ciencias y Artes de Chiapas, Mexico	<i>Lepus insularis</i> <i>Sylvilagus mansuetus</i>
Thomas Gray	WWF Greater Mekong	<i>Lepus peguensis</i>
Weihe Yang	Institute of Zoology, Chinese Academy of Sciences	<i>Lepus comus</i> <i>Lepus coreanus</i> <i>Lepus oiostolus</i> <i>Lepus sinensis</i> <i>Lepus yarkandensis</i>
Youhua Chen	Wuhan University, China	<i>Lepus hainanus</i>
Zelalem Tolesa	Addis Ababa University	<i>Lepus fagani</i> <i>Lepus habessinicus</i> <i>Lepus starcki</i>

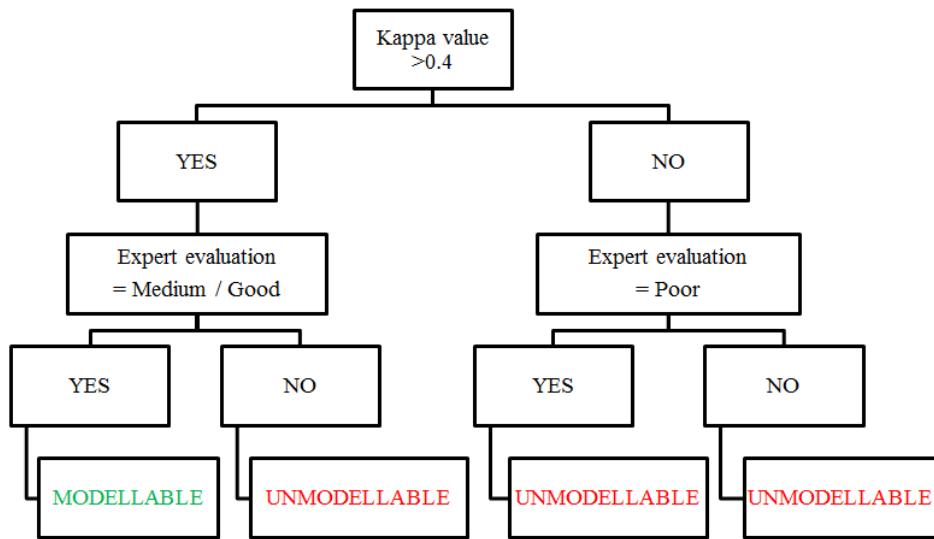


Fig. 2.1. Framework for assessing whether species were “modellable” or “unmodellable” based on Kappa values and expert evaluation classification.

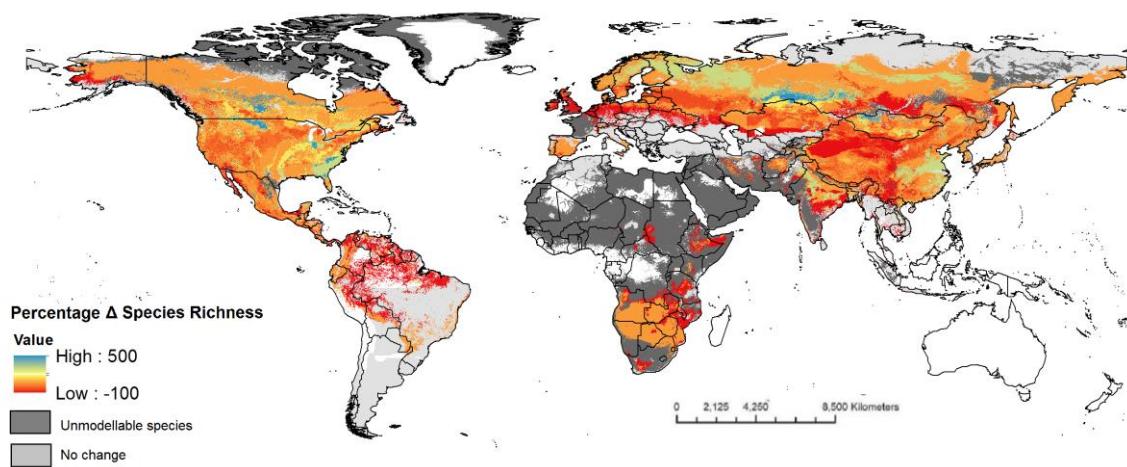


Fig. 2.2. Percentage change in predicted lagomorph species richness from the 1930s to 2080s. Light grey areas indicate no change in species richness and dark grey indicates areas occupied by “unmodellable” species with uncertain outcomes.

Table 2.2. Results of generalised least square models characterising predicted lagomorph bioclimatic envelope changes. Significant p values are in bold. Group refers to lagomorph taxonomy, i.e. pikas, rabbits and hares & jackrabbits.

Response variable	Term	F	df	p
Range change (km) $F_{df=1,234}=0.586, p=0.445$	Group	0.004	2, 229	0.950
	Year	3.710	1, 228	0.026
	Group: Year	0.537	2, 226	0.585
Mean latitudinal change (°) $F_{df=1,234}=13.460, p<0.001$	Group	12.798	2, 229	<0.001
	Year	1.603	1, 228	0.204
	Group: Year	0.448	2, 226	0.640
Mean elevation change (m) $F_{df=1,234}=44.184, p<0.001$	Group	19.458	2, 229	<0.001
	Year	21.140	1, 228	<0.001
	Group: Year	3.541	2, 226	0.031

Table 2.3. Results of phylogenetically-controlled generalised least square regressions. Significant p values for model-averaged coefficients are in bold. F and p values for the top model are listed under each response variables; asterisks (*) indicate traits in the top model. Lambda (λ) confidence intervals and significance from 0 and 1 are also shown.

Response variable	Trait	$\beta \pm \text{s.e.}$	F	p
Range change (km) $F_{df=4, 52}=4.28, p=0.005$ Lambda 95%CI=0, 0.147 N.S. from 0, $p<0.01$ from 1	Adult body mass (g)*	0.258 ± 0.112	2.308	0.021
	Diet breadth	0.137 ± 0.088	1.552	0.121
	Gestation length (days)	-0.154 ± 0.121	1.269	0.204
	Litters per year	0.090 ± 0.084	1.073	0.283
	Litter size	-0.062 ± 0.098	0.634	0.526
	Home range size (km ²)	-0.069 ± 0.099	0.698	0.485
	Population density (n/km ²)	-0.079 ± 0.090	0.878	0.380
	Age at sexual maturity	-0.062 ± 0.089	0.694	0.488
	Activity cycle	0.020 ± 0.134	0.151	0.880
	Habitat breadth	0.050 ± 0.101	0.493	0.622
Mean latitudinal change (°) $F_{df=5, 49}=6.10, p<0.001$ Lambda 95%CI=0, 0.209 N.S. from 0, $p<0.01$ from 1	Adult body mass (g)*	0.196 ± 0.099	1.989	0.047
	Diet breadth*	0.181 ± 0.082	2.190	0.029
	Litter size*	0.128 ± 0.097	1.320	0.187
	Litters per year*	0.215 ± 0.079	2.731	0.006
	Activity cycle	0.097 ± 0.124	0.787	0.431
	Age at sexual maturity	-0.106 ± 0.084	1.254	0.210
	Home range size (km ²)	-0.088 ± 0.113	0.787	0.438
	Gestation length (days)	0.147 ± 0.132	1.112	0.266
	Habitat breadth	0.028 ± 0.093	0.304	0.761
	Population density (n/km ²)	0.027 ± 0.084	0.318	0.750
Mean elevation change (m) $F_{df=2, 50}=5.92, p=0.005$ Lambda 95%CI=0, 0.205 N.S. from 0, $p<0.01$ from 1	Adult body mass (g)*	-0.183 ± 0.091	2.019	0.043
	Gestation length (days)	0.099 ± 0.106	0.932	0.351
	Diet breadth	-0.110 ± 0.079	1.386	0.166
	Home range size (km ²)	0.074 ± 0.075	0.986	0.324
	Litters per year	-0.057 ± 0.070	0.813	0.416
	Age at sexual maturity	0.055 ± 0.075	0.731	0.324
	Activity cycle	0.075 ± 0.105	0.708	0.479
	Population density (n/km ²)	0.064 ± 0.071	0.902	0.367
	Litter size	0.019 ± 0.079	0.235	0.814
	Habitat breadth	-0.005 ± 0.085	0.058	0.953
Max. elevation change (m) $F_{df=2, 53}=3.54, p=0.036$ Lambda 95%CI=0, 0.384 N.S. from 0, $p<0.01$ from 1	Litters per year *	0.160 ± 0.092	1.746	0.081
	Gestation length (days)	-0.136 ± 0.116	1.169	0.242
	Habitat breadth	0.095 ± 0.102	0.934	0.351
	Age at sexual maturity	-0.098 ± 0.096	1.020	0.308
	Activity cycle	0.041 ± 0.118	0.348	0.728
	Litter size	0.014 ± 0.104	0.137	0.891
	Population density (n/km ²)	0.054 ± 0.091	0.596	0.551
	Adult body mass (g)	0.034 ± 0.121	0.280	0.780
	Home range size (km ²)	-0.003 ± 0.107	0.029	0.977
	Diet breadth	0.004 ± 0.093	0.047	0.962

Appendix 3. Additional table - Chapter 4

Table. 3.1. Results of Generalized Linear Models. Significant *p* values are in bold.

Response variable	Term	$\beta \pm \text{s.e.}$	<i>t</i>	<i>p</i>
Mean phylogenetic distance <i>F</i> _{2,3738} =19.80 (<i>p</i> <0.001)	Sympatry-Interaction & Sympatry- No Interaction	39.971 ± 7.791	5.130	<0.001
	Sympatry-Interaction & Allopatry	-46.311 ± 7.729	-5.992	<0.001
	Sympatry-No Interaction & Allopatry	-6.340 ± 3.078	-2.060	0.040
Mean adult body mass (g) <i>F</i> _{2,3738} =22.26 (<i>p</i> <0.001)	Sympatry-Interaction & Sympatry- No Interaction	-838.100 ± 162.500	-5.159	<0.001
	Sympatry-Interaction & Allopatry	419.790 ± 170.930	2.456	0.014
	Sympatry-No Interaction & Allopatry	-418.300 ± 68.080	-6.144	<0.001
Difference in adult body mass (g) <i>F</i> _{2,3738} =26.81 (<i>p</i> <0.001)	Sympatry-Interaction & Sympatry- No Interaction	176.100 ± 152.000	1.159	0.248
	Sympatry-Interaction & Allopatry	-616.590 ± 171.230	-3.601	<0.001
	Sympatry-No Interaction & Allopatry	-440.470 ± 68.200	-6.458	<0.001
Mean ecoregional climate stability <i>F</i> _{2,3738} =0.03 (<i>p</i> =0.969)	Sympatry-Interaction & Sympatry- No Interaction	0.004 ± 0.020	0.188	0.851
	Sympatry-Interaction & Allopatry	-0.001 ± 0.025	-0.053	0.958
	Sympatry-No Interaction & Allopatry	0.002 ± 0.010	0.243	0.808
Mean human population density <i>F</i> _{2,3738} =5.02 (<i>p</i> <0.001)	Sympatry-Interaction & Sympatry- No Interaction	-81.760 ± 49.480	-1.653	0.099
	Sympatry-Interaction & Allopatry	-29.580 ± 88.508	-0.334	0.738
	Sympatry-No Interaction & Allopatry	-111.342 ± 35.253	-3.158	0.002
Mean % of occurrence records in human-converted habitats <i>F</i> _{2,3738} =6.30 (<i>p</i> =0.002)	Sympatry-Interaction & Sympatry- No Interaction	-8.538 ± 3.269	-2.612	0.010
	Sympatry-Interaction & Allopatry	2.600 ± 4.283	0.607	0.544
	Sympatry-No Interaction & Allopatry	-5.940 ± 1.706	-3.482	<0.001

Appendix 4. Additional figures - Chapter 7



Fig. 4.1. Changes in betweenness centrality for each North and South American lagomorph species from the present day to the 2050s and 2070s.

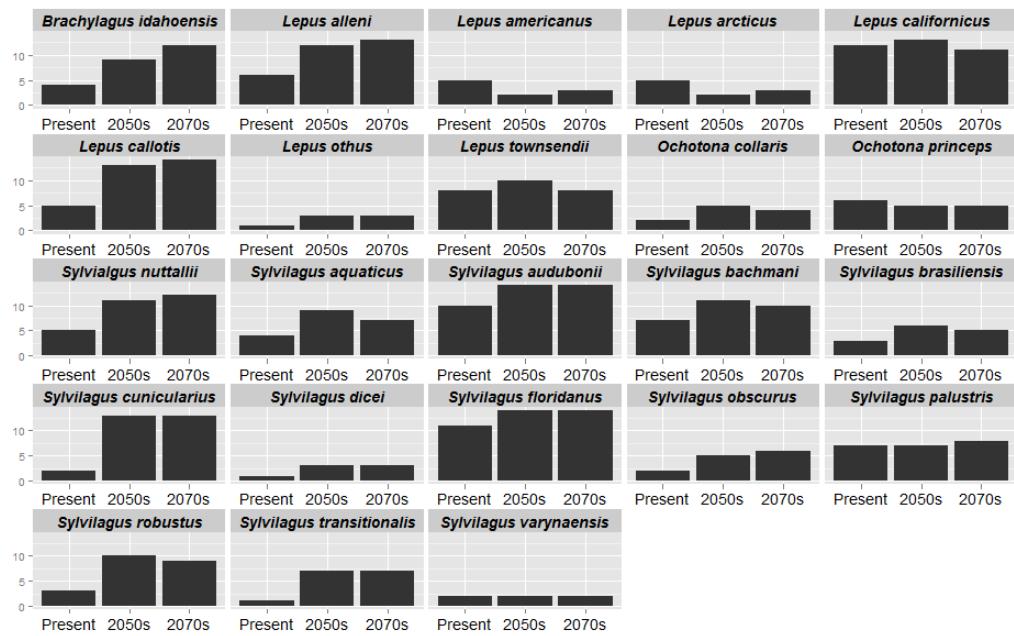


Fig. 4.2. Changes in degree distribution for each North and South American lagomorph species from the present day to the 2050s and 2070s.