



Seasonal climate change threatens the Iberian lynx by altering predator-prey dynamics.

Photo credit: Programa de cría en cautividad del lince ibérico

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Abstract

Changes in seasonal environmental patterns under climate change are threatening biodiversity globally. The Mediterranean basin is of particular concern as it is characterized by a high seasonal variability in rainfall and temperature, which resulted in widespread adaptations to this seasonality. One important impact of climate change is to alter seasonal species interactions through differential effects across different trophic levels. In this study, I use the Iberian lynx (*Lynx pardinus*) and its main prey, the European rabbit (*Oryctolagus cuniculus*), as study species for assessing the impact of monthly changes in rainfall and maximum temperature on population dynamics of both species. I parameterized spatially explicit individual based models (IBMs) for both species using published information on demographic responses to abiotic factors and biotic interactions. The IBMs allowed me to assess joint population dynamics emerging from individual interactions, environmental variability, and demographic stochasticity. I simulated population dynamics using discrete monthly steps for 30 years under two climate scenarios using the data of various climate change models: a baseline scenario with historical (1990-2020) climatic data and a future scenario with predictions for the end of the 21st century (2070-2100). The models predict an increase of the maximum temperature and a decrease in precipitation for the study area. The simulations showed that both the rabbit and the lynx are at an increased risk of local extinction under climate change, but this risk is relatively higher for the lynx. Rabbits are compromised by a change in climate seasonality as their breeding season is likely to shorten. However, even if their densities reach low values they can recover fast if weather conditions improve. Lynxes are not directly affected by climate variables, but indirectly low rabbit densities can lead to a complete failure to reproduce. Combined with increased mortality of adults due to higher competition when rabbit densities are low, lynx number can decrease rapidly, increasing susceptibility to local extinction under stochastic mortality events. My results therefore demonstrate that, by changing species interactions, climate change can negatively

impact species seemingly buffered from direct effects of climatic variations. The high spatial variability in local extinctions further highlights the importance of improving habitat connectivity in future management strategies to allow recolonization.

Introduction

Climate-change driven increases in mean temperatures and alterations in precipitation patterns are disrupting the seasonal weather patterns worldwide. In the Northern Hemisphere, summer season has increased its length in 17 days since last century (Wang et al., 2021). Heat waves and other weather disturbances are becoming more frequent, also altering the predictability of previous seasonal patterns. Combination of long-term changes and short-term disturbances can cause very different responses in biological systems (Harris et al., 2018). For instance, in 2015 the combination of an unusually long duration of arid conditions in the Gulf of Carpentaria with local high air and water temperatures, low rainfall and low sea levels resulted in a dieback of the mangrove of unprecedented scale (Duke et al., 2017). The timing of life cycle events is usually guided by cues such as photoperiod changes that announce optimal weather conditions for these events. A shift in climate seasonality mismatches these cues with the environmental conditions that they used to indicate and impacts the life cycles of many species in ways that are now being studied (Both et al., 2009; Damien & Tougeron, 2019; Steltzer & Post, 2009; Visser & Gienapp, 2019). Thus, projections of population persistence under climate change must account for the seasonal variation in climatic patterns (Paniw et al., 2019).

Changes in seasonal weather patterns in semi-arid ecosystems, namely shorter and poorer rainy seasons and longer and more frequent droughts, are of particular concern. This is the case for the Mediterranean Basin, which is considered a climate change hotspot, with substantial increases in extreme summer temperatures and precipitation declines (Tuel & Eltahir, 2020). Droughts will also become longer and more frequent (Dai, 2011). Species in Mediterranean habitats have adapted their life cycles to match the strong seasonality of environmental factors (Maestre et al., 2012); and

alterations in seasonality can then strongly negatively affect survival, reproduction and, ultimately, population persistence and range dynamic (Paniw et al., 2019).

Climate-change driven disruptions in the life cycle of a species, their abundance or their range will impact the interspecific interactions in which the species takes part (González-Megías & Menéndez, 2012; Ovaskainen et al., 2013). In the particular case of predator-prey interactions, it is common for predators that some of their life-cycle events occur in a certain point of their prey's life cycle. For example, many predators breed after their prey, coinciding with higher prey densities (Damien & Tougeron, 2019). But predators may be slow to adapt to changes in the timing of life-cycle events in their prey (i.e., changes in phenology), leading to a phenology mismatch (Both et al., 2009; Damien & Tougeron, 2019). Such mismatches have been shown to alter the population dynamics of predators by altering demographic rates such as reproductive success (Visser & Gienapp, 2019), suggesting that higher trophic levels are at particular risk of climate-change driven alterations in species interactions (Voigt et al., 2003). Although this highlights the importance of studying interspecific dynamics under a changing environment, we still have a very limited knowledge on the direct (by changing demographic rates directly) and indirect (by changing demographic rates via species interactions) effects that climate change will have in seasonal environments.

In this study I used the Iberian lynx (*Lynx pardinus*) and its main prey, the European rabbit (*Oryctolagus cuniculus*), as study species to assess how feedbacks between demography and species interaction mediate the effects of changes in seasonal rainfall and temperatures on population persistence of both prey and predator. Specifically, I aimed to answer two questions: (i) does the risk of local extinction increase for the two species under seasonal climate change; and (ii) are lynxes relatively more threatened by the indirect effects of climate change on demographic rates of rabbits than are rabbits by direct climate-change effects on demography? To answer these questions, I parameterized individual-based models (IBMs) to jointly project spatiotemporally varying individual demographic rates of lynxes and rabbits, across 30 years and 9 sites. In the case of the rabbit, I

modelled the demographic rates explicitly as a function of climate. In the case of the lynx, I modelled the demographic rates indirectly as a function of rabbit density (and thus indirect climate effect) which determines the number of territories available for breeding and therefore reproductive success. Simulations were run in monthly time-steps under a baseline and a future climate scenario, using monthly rainfall and maximum temperature data from 10 Coupled Model Intercomparison Project 5 (CMIP5) (Taylor et al., 2012). I recorded monthly changes in stage-specific abundances of rabbits and lynxes.

Materials and methods

Study species

Rabbit

The European rabbit (*Oryctolagus cuniculus*) is a native species for the Iberian Peninsula (Callou, 1995). Human activity has led to its introduction in many countries, and now its distribution includes the majority of Europe, Australia, New Zealand, regions of South America and many islands all over the world (J.E.C. Flux & P.J. Fullagar, 1983, 1992). In many of these places it lacks predators and has been declared a pest species (Williams et al., 1995). In the southwestern Mediterranean, however it plays an important ecological role as an ecosystem engineer (Delibes-Mateos et al., 2008). It is a dominant prey species for several carnivores such as badgers, foxes, mongooses or lynxes.

Rabbits are r-strategists, short-lived mammals with population dynamics highly sensitive to reproductive output. Their breeding season depends on environmental conditions of temperature and precipitation, that determine the food availability (Gonçalves et al., 2002; Soriguer, 1981; Tablado et al., 2009). In Southern Spain, rabbits breed predominantly between the end of winter and beginning of spring (November-July). If the right conditions (warm and rainy winters and springs) last long enough, female rabbits can breed more than once a year (Soriguer, 1981). In dry years the breeding period can shorten to January-March (Gálvez Bravo, 2017). Predictions show that climate

change will likely induce a shortening of the rabbit breeding season (Tablado & Revilla, 2012), resulting in female rabbits breeding only once a year.

Rabbit mortality is very high, with a life expectancy of 1,2 years (von Holst et al., 1999), and is not likely to decrease in the future (Tablado & Revilla, 2012). A shortening of the breeding season can therefore lead to a decline in rabbit populations. This would be destabilizing for Mediterranean ecosystems, as already shown by the past declines in rabbit population after the outbreaks of myxomatosis and rabbit hemorrhagic disease (RHD) (Cabezas-Díaz, S. et al., 2009; Moreno et al., 2007). Several management measures, including rabbit introductions, were needed in order to preserve the Mediterranean scrubland ecosystem, including the Iberian lynx populations (Palomares et al., 2011; Simón et al., 2012).

Lynx

The Iberian lynx (*Lynx pardinus*) is considered to be the most endangered feline in the world (Delibes et al., 2000). Its decline began in the 20th century was mainly caused by habitat loss and decreases in food abundance, with the lynx population decline getting to critical numbers at the end of the century (Cabezas-Díaz, S. et al., 2009). In 2004, its population size was estimated to be not more than 160 individuals, divided into two isolated groups (Doñana and Sierra Morena) and occupying a total area of 500m², which implied a 99% reduction of its original distribution (Guzmán López-Ocón, 2004). Nevertheless, subsequent conservation efforts and reintroductions that began in the early 2000's have had a strongly positive effect (Simón et al., 2012) and the total number of lynxes in the Iberian Peninsula has been increasing in the past years, surpassing a thousand in 2020. Currently there are 13 populations, 12 in Spain and one in Portugal, and a total of 1365 lynxes in 2021 (*Censo del Lince Ibérico*, 2021). For this study I built IBMs for 9 nuclei of Iberian lynx populations (Table 1).

The Iberian lynx is a medium-sized carnivore. Adults weight around 12kg and measure around 45 cm in height and 80 cm in length. It is a specialist predator, up to 90% of their diet consists of rabbits, and they rarely feed on other species (Guzmán López-Ocón, 2004). Their life cycle is synchronized

with the rabbit's, with parturition occurring during periods of rabbit population increase (Palomares et al., 2005). The shortening or displacement of these periods could therefore substantially impact life-cycle dynamics of the lynx. This is because specialist predators don't usually switch their prey in case of prey shortage, but they change their behavior trying to keep feeding on their main prey species (Ferreras et al., 2011). The Iberian lynx is a long-living species, where population dynamics are governed by adult survival. This can buffer lynx population dynamics under a lower reproductive success due to low rabbit numbers, but only on the short term.

The Iberian lynx is a territorial species. When an individual becomes sexually mature (around 2 years old), they leave their mother's territory and look for their own. They can establish in new vacant territories if available, take possession of the former one of a dead lynx or take one away from another lynxes by competition. Some females also inherit their mothers' territory (Ferreras et al., 1997). Lynxes of certain ages are more likely to get a territory than others, with a ranking of 4, 5, 6, 7, 3, 8, and 9 years old for males and 4, 5, 6, 7, 3, 2, 8, and 9 for females (Ferreras et al., 1997). Those that don't establish a territory have higher mortality rates and do not reproduce. Lynxes establish territories of an average size of 10km², that can be smaller if the quality of the habitat is very good and rabbit abundance is high and bigger in cases of rabbit shortage (Ferreras et al., 1997; Palomares et al., 2001).

Table 1: Nuclei of Iberian lynx distribution considered for this study, with their total area in kilometers squared and their total Lynx population size as compiled in the 2021 census.

Nucleus	Total area (km ²)	Lynx population size (2021)
Vale do Gadiana	462	209
Donana-Aljarafe	441	94
Montes de Toledo	924	221
Matachel	229	121
Ortiga	57	20
Valdeciguenas-Rio Sotillo	18	9
Setefilla-Las Minas	80	17
Valdecanas-Ibores	19	14
Sierra Morena	2222	660

IBMs

The methodology behind the two IBMs that I developed will be presented following the ODD protocol (Grimm et al., 2010).

1 Purpose

The purpose of these IBMs is to assess the predator-prey dynamic of lynx and rabbit populations under a seasonal changing environment. More precisely, these IBMs combined aim to account for the demographic development of lynx populations driven by seasonality change influence on rabbit demography.

2 State variables and scales

Rabbit

The rabbit IBM models rabbit densities per 0,1 km², which are afterwards scaled to local abundances in the total area of each site. I parameterized the rabbit model according to Tablado & Revilla (2012). In their study, the authors created a rabbit demographic model with daily time steps using equations that included the effects of climatic and biotic covariates (Tablado et al., 2009, 2012) (Table 2). Taking their model as a reference, I adapted those equations to a monthly model by raising them to ^{30.4}. For parameters like density dependence and age effect, I tested the values proposed by Tablado & Revilla (2012) and chose the set that gave the most stable and realistic populations under baseline simulations (see Table 2).

The rabbit life cycle (Figure 1) consists of three life stages: kits (less than a month old), juveniles (from 1 to 3 months) and adults (more than 3 months). Rabbits usually acquire sexual maturity at 4 months old. If the weather conditions are favorable, sexually mature female rabbits can get pregnant, which updates their pregnancy state in the IBM. After one month of gestation, pregnant females give birth the next month. After giving birth, females can get pregnant the following month. If the breeding season lasts long enough, they can breed several times a year. The average litter size is 4. The kits stay depend on their mother and stay with her for their first month. Then they become

independent juveniles. Juveniles become reproductively mature adults at 4 months old, and they stay in this stage until their death.

Table 2: Demographic rates and breeding season equations for the rabbit IBM, with their parameters as specified by Tablado & Revilla (2012) and their chosen values for my models.

Survival		$P_S = \left(\frac{e^{(\delta_A - ds \frac{n}{K})}}{1 + e^{(\delta_A - ds \frac{n}{K})}} \right) \left(1 - e^{(-\frac{v}{F_m})} \right)$
Newborns survival		$P_{SN} = 1 - M_N$
Breeding season		$P_B = \frac{1}{1 + e^{(4.542 - 0.605T^2 - 0.006D - 0.017\Delta - W)}}$
Reproductive success		$P_R = \frac{e^{(r_A - dr \frac{n}{K})}}{1 + e^{(r_A - dr \frac{n}{K})}}$
Parameter		Chosen value
Survival		
δ_A	Age effect on survival	10 for adult rabbits
		5 for juvenile rabbits
dr	Density dependence	1.5
y	Food availability effect on survival	40
Fm	Number of consecutive dry months	*
M_N	Newborns mortality	0.4
n	Population size	90 at the start ***
K	Carrying capacity	100
Breeding		
T	Maximal monthly temperature	*
D	Month average daylength	**
Δ	Photoperiod change between two consecutive months	**
W	Green pasture availability	= 0 for dry months (2T>P) = -1.592 otherwise
Fecundity		
ds	Density dependence	3
rA	Age parameter	0 for rabbits 4-6 months old
		3 for rabbits 6-9 months old
		6 for rabbits < 9 months old

* The value of these parameters depends on the climatic predictions.

**Photoperiod data obtained with the R package geosphere (Hijmans, 2021).

***Population size is updated every month as the result of the demographic processes.

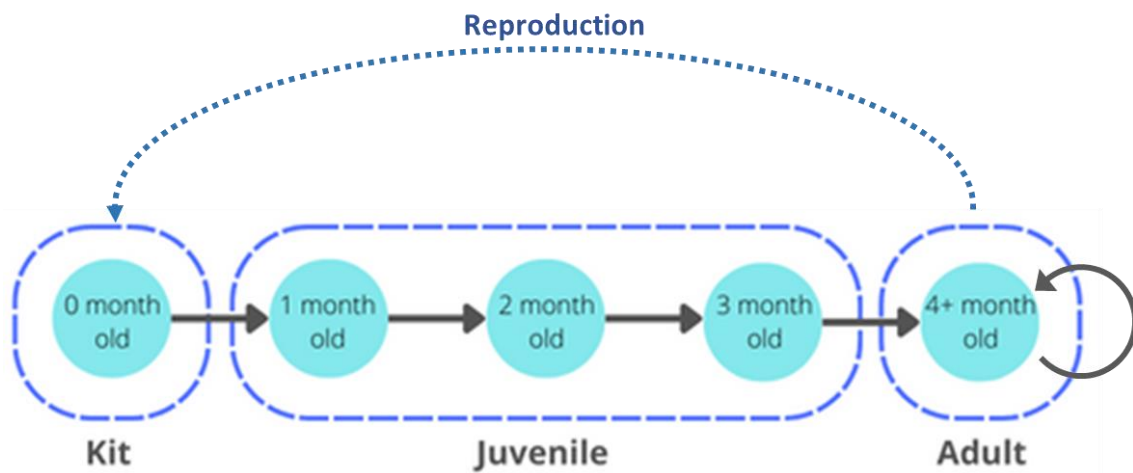


Figure 1: Life cycle of the European rabbit, used to build the IBM. Colored circles represent the ages (in months) that individuals go through, connected by solid arrows that indicate the monthly survival of an individual. The loop arrow on the 4+ circle indicates that from that age rabbits grow older-conditional on survival, but don't change their life-cycle stage. Ages that compose a life stage are grouped together by a blue dashed perimeter. The blue dashed arrow going from the adult life stage to kit represents the recruitment of new individuals via reproduction.

Lynx

The lynx IBM simulates lynx local abundances for each nucleus and was parameterized according to Fordham et al. (2013) and Gaona et al. (1998). In their study, Fordham et al. created a niche-based model for Iberian lynx and European rabbit. I adapted the demographic vital rates used by Fordham (2013) to a monthly model by setting them to $^{1/12}$ and modified them within a range of ± 0.2 deviation from their initial value to make sure they gave a realistic and stable output (Table 3).

Table 3: Lynx vital rates used to build the IBM model.

Lynx	
Monthly Survival	Cubs < 1 year $S_0 = 0.8406^{1/12}$
	Females 1-2 years $SF_1 = 0.87^{1/12}$
	Males 1-2 years $SM_1 = 0.56^{1/12}$
	Females 2 - 9 years $SF_2 = 0.99^{1/12}$
	Males 2 - 9 years $SM_2 = 0.99^{1/12}$
	Females > 9 years $SF_9 = 0.8^{1/12}$
	Males > 9 years $SM_9 = 0.8^{1/12}$
Added Mortality	$AM = 0.09$
Potential carrying capacity	$K_0 = \frac{\text{Total nucleus area (km}^2\text{)}}{10 \text{ km}^2}$

The lynx life cycle (Figure 2) consists of three stages: cubs (0 years old), pre-dispersal juveniles (1-2 years old) and dispersing adults (≥ 2 years old). Female lynxes can reproduce from 3 to 9 years of age, but only if they hold a territory. They usually give birth in March, with all the parturitions concentrated in a short interval of around 10 days. A failed breeding attempt may result in another attempt within a month (Palomares et al., 2005), but this seldomly occurs and is not considered in the IBMs. The average litter size is 3 cubs per territorial female. The cubs stay in the den and are fed by their mother up to 3 months old, afterwards they start to accompany her (up to 10 months old) and they can stay in her territory up to 2 years old (Palomares et al., 2005). For building the IBM I considered that cubs younger than 6 months will die in case of their mother's death as they highly depend on her, but older cubs can survive on their own. At 2 years old, they become sexually mature adults and begin to disperse in search of their own territory (Ferrerias et al., 1997).

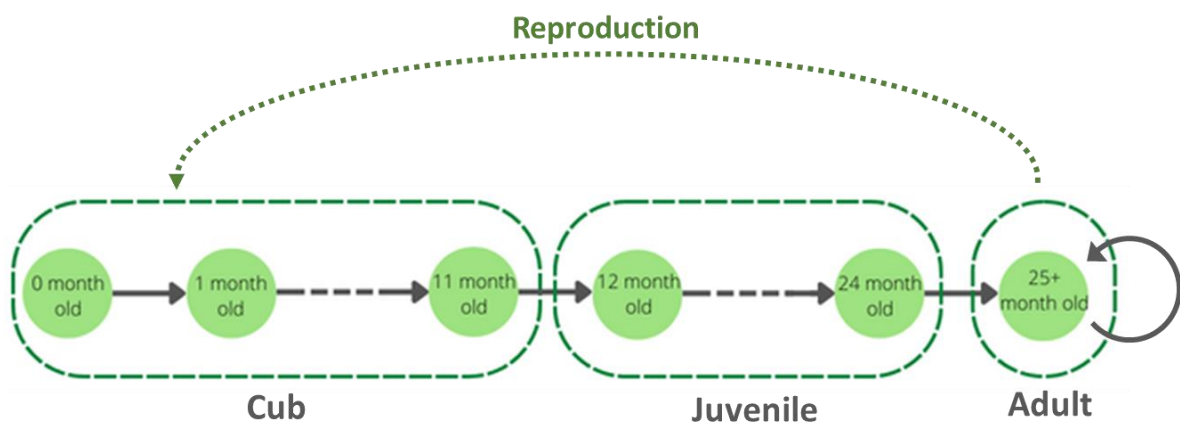


Figure 2: Life cycle of the Iberian lynx, used to build the IBM. Colored circles represent the ages (in months) that individuals go through, connected by solid arrows that indicate the monthly survival of an individual. Solid arrows with a dashed portion in the middle represent an interval of ages, belonging to the same life stage, that were omitted in order to simplify the graph. The loop arrow on the 25+ circle indicates that from that age lynxes grow older-conditional on survival, but don't change their life-cycle stage. Ages that compose a life stage are grouped together by a green dashed perimeter. The green dashed arrow going from the adult life stage to cubs represents the recruitment of new individuals via reproduction.

Process overview and scheduling

In both models, the fate of every individual is simulated from their birth or the beginning of the simulation, up until their death or the end of the simulation. Both IBMs were built and run using RStudio (RStudio Team, 2020).

Rabbit

In the rabbit IBM, the first step each month is to calculate the survival rate as a function of the climate and density covariates (Table 2). The survival of each individual (1 or 0) is sampled from a Binomial distribution with the mean given by the survival rate.

Surviving reproductive individuals then recruit offspring. If a female pregnant in a month t survives to $t+1$, she gives birth at the beginning of $t+1$. Her offspring number is sampled from a Poisson distribution of mean 4 (average litter size) weighted by S_0 (Table 2), which represent very early mortality right after birth. The kits are added to the population as new individuals of age 0 and stage “kits”. Their sex is randomly assigned, with a 1:1 ratio.

After determining last month’s offspring and setting the reproductive success of every female back to 0, the IBM calculates the breeding season probability for that month (P_B , Table 2). If it is > 0.5 (Tablado & Revilla, 2012), that month is considered to be inside the breeding season.

Subsequently, the next step is reproductive success. Inside the breeding season, every adult female that survived the month is considered likely to get pregnant and has her reproductive success (1 or 0) sampled from a binomial distribution with the mean given by the probability corresponding to their age (P_R , Table 2). Breeding outside the breeding period is not considered.

Finally, dead individuals are removed from the data frame and the surviving ones are aged one month, updating their stage to their new age.

Lynx

In the lynx IBM, the first step in each monthly simulation was to determine the carrying capacity for a given population. Carrying capacity is calculated as a function of the total area of the population and the rabbit density at the beginning of that month. The average size of an adult lynx territorial area, 10km^2 , is considered a potential territory, so the potential carrying capacity is calculated (K_0 , Table 3). The actual number of available territories depends on how many territories can have ≥ 1 rabbit per ha (less is considered non-viable for lynxes). In case of rabbit shortage, the number of available territories gets reduced until the remaining number has at least a 1 rabbit per ha density. The IBM follows the age ranking of likelihood of getting a territory (Ferrerias et al., 1997) to assign territories. From October to January, the months when younger lynxes are more likely to disperse in search of a territory, lynxes of ages low in the ranking (less competitive) that hold a territory lose it to lynxes of ages higher in the ranking (more competitive). If a resident and disperser lynx are of the same age, the resident lynx keeps the territory. For the rest of the months, non-resident lynxes don't compete for territories, but residents do if there is a reduction in the number of territories.

Once the territories are assigned, the next step of the IBM is to determine survival (0 or 1). The monthly survival probability depends on age, sex, and, for adults, on whether or not they hold a territory. Adult lynxes without territory face a higher mortality rate (AM , Table 3). The survival is sampled for every individual from a binomial distribution with the mean corresponding to the monthly survival probability (Monthly survival, Table 3). Additionally, if a female mother of cubs < 6 months doesn't survive, her cubs are also assigned survival = 0.

The last step is the recruitment of offspring. Only the female lynxes that hold a territory reproduce. Territorial females are considered able to breed from 2 to 9 years old (Palomares et al., 2005). Recruitment occurs in March, and the litter size for every territorial female is sampled from a Poisson distribution with mean 3.5 and weighted by S_0 . The newborn cubs are added to the population with

a new ID (specifying the year where they were born), age 0, sex randomly assigned (ratio 1:1) and with their mother's ID.

4 Design concepts

Basic principles

For both IBMs, the key idea is the link between an environmental factor (climatic changes for the rabbit and rabbit density for the lynx) affecting individual processes such as survival or reproduction and scaling up to population dynamic.

Emergence

In both IBMs emerging population dynamics are derived from the individual outcome of the members in a population. This outcome is stochastically imposed from the relationship (known from previous empirical studies) between demographic process that depend on individual traits, such as age or sex, and on environmental factors. These demographic processes introduce new trait values and population characteristics every month, which are then become the background of the following month. Group dynamics are the final emergence of this relationship net.

Interaction

In the rabbit model, individuals indirectly interact via the density, affecting their survival rates as many of them are a function of the carrying capacity (See Table 2). Lynxes interact in a spatially implicit manner, via the probability of obtaining a territory, which in turn affects their survival and reproduction probabilities. In addition, juveniles < 6 months of age depend on their mother for survival.

Stochasticity

Demographic stochasticity is introduced in both models by sampling survival and reproduction success from a binomial distribution. Uncertainty in the climatic projections is also accounted for by running simulations for different Global Change Models (GCMs, see *Climate data*).

Observation

For both models, the ID, sex, age, stage, and reproductive and survival success is saved for every individual. The general and stage-specific densities are also stored. In the lynxes IBM, the possession or not of a territory is also recorded, as well as the mother's ID for newborns. This allows to oversee the development of the simulated populations and each of their individuals.

5 Initialization

Rabbit

The initial populations are composed of 90 individuals. Their sex is assigned randomly, assuming a 1:1 sex ratio and their age is sampled from a distribution of mean 17 months and deviation 5 months (Tablado & Revilla, 2012). The carrying capacity is set to 100 individuals.

Lynx

The initial lynx populations have for each nucleus the same size as the real ones from the 2021 census (*Censo del Lince Ibérico, 2021*), each individual characterized with an ID specifying that they were part of the initial population. Their sex is assigned randomly, assuming a 1:1 sex ratio. The age structure was sampled once for each nucleus from a distribution with mean 65 months, maximum 9 years (180 months) and a deviation of 65 months (Fordham et al., 2013; Gaona et al., 1998); the same age distribution was used for every simulation on the same nuclei.

6 Input data

In the rabbit IBM, the input data are the climatic variables calculated from the CMIP5 climatic models' data (see the *Climate data* section). In the lynx IBM, the input data is the initial rabbit density of a certain month obtained in the rabbit IBM.

Final output

I calculated the extinction probability (k) for every nucleus. I ran 100 simulations (10 runs of each of the 10 climatic scenarios) in each nucleus and calculated the percentage of simulations when population abundance decreased to < 1 . In populations that persisted for 30 years I also recorded

monthly abundances of different life-cycle stages. Extinction rates and abundances were compared between baseline and future climate scenarios.

Climate data

In order to project my IBMs, I required past and future climatic projections. I chose to use the models from the CIMP5, an internationally coordinated effort aimed to comprehend current, past and future climate changes as a result of both natural variability and anthropogenic radiative forcing (Taylor et al., 2012). The institutes participating in this project generated several GCMs that modelled many climatic variables across a set of experiments. The outputs of these models for the different experiments are accessible at <https://esgf-node.llnl.gov/search/cmip5/>. I chose to use two of these experiments: the “historical” run, forced by observed atmospheric characteristics over the late 19th and the 20th century; and the RCP 8.5, the most dramatic future scenario of atmospheric greenhouse gas Representative Concentration Pathways (RCP) that portrays a level of radiative forcing of 8.5 Watts per square meter by the year 2100. I chose 10 GCMs (Table 4) that have been used in other recent ecological studies (Paniw et al., 2022). For every model and experiment, several runs are produced differing in their initialization conditions (e.g., the starting date for historical runs). Each of these runs has an identification ensemble code. I chose the ensemble r1i1p1 for all the models. I downloaded the maximal temperature and precipitation data, both the historical (1850-2006) and the RCP 8.5 predictions (2006-2101). These models are global datasets, so for each Iberian lynx nucleus, I sampled a random point and extracted the climate data for those coordinates. To do this, I georeferenced the last map of the lynx distribution by the Life Lynx Connect project website (<https://lifelynxconnect.eu/censos/>) (Life Lynx Connect, 2020) in QGIS 3.10.5 and sampled one random point for each nucleus.

The annual means of the temperature data and the summatory of the precipitation data are displayed in Figure 3. The 10 models have different underlying assumptions and therefore provide different climatic scenarios despite all of them having similar tendencies. This differences between

them allow the IBMs simulations to account for uncertainty in the predictions. In all models, maximum temperature shows a clear tendency to increase. Rainfall does not have such clear pattern: although there is a decreasing tendency in all models, there is a lot of variability between years.

Table 4: CMIP5 GCMs from which climate data was obtained for this study. Table available at: <https://pcmdi.llnl.gov/mips/cmip5/availability.html> .

Modeling Center	Model	Institution	Terms of use
BCC	bcc-csm1.1-m	Beijing Climate Center, China Meteorological Administration	unrestricted
CNRM-CERFACS	CNRM-CM5	Centre National de Recherches Meteorologiques / Centre Europeen de Recherche et Formation Avancees en Calcul Scientifique	unrestricted
CSIRO-BOM	ACCESS1.0	CSIRO (Commonwealth Scientific and Industrial Research Organisation, Australia), and BOM (Bureau of Meteorology, Australia)	unrestricted
EC-EARTH	EC-EARTH	EC-EARTH consortium	unrestricted
IPSL	IPSL-CM5A-LR	Institut Pierre-Simon Laplace	unrestricted
MIROC	MIROC-ESM-CHEM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies	unrestricted
MPI-M	MPI-ESM-MR	Max Planck Institute for Meteorology (MPI-M)	unrestricted
MRI	MRI-CGCM3	Meteorological Research Institute	unrestricted
NASA GISS	GISS-E2-R	NASA Goddard Institute for Space Studies	unrestricted

With the maximum temperature and precipitation data, I calculated the variables needed for the rabbit's vital rates equations (Table 2). These variables, taken from Tablado & Revilla (2012), account for different aspects of climate conditions that affect the rabbit's life cycle.

- F_m , the number of consecutive dry months, is calculated for each month as the sum of all the previous consecutive months where precipitation < 2 * temperature.
- W is an estimate of the green pasture availability. Its value was assigned as a function of the month's dryness: 0 if precipitation < 2 * temperature and -1.592 otherwise.

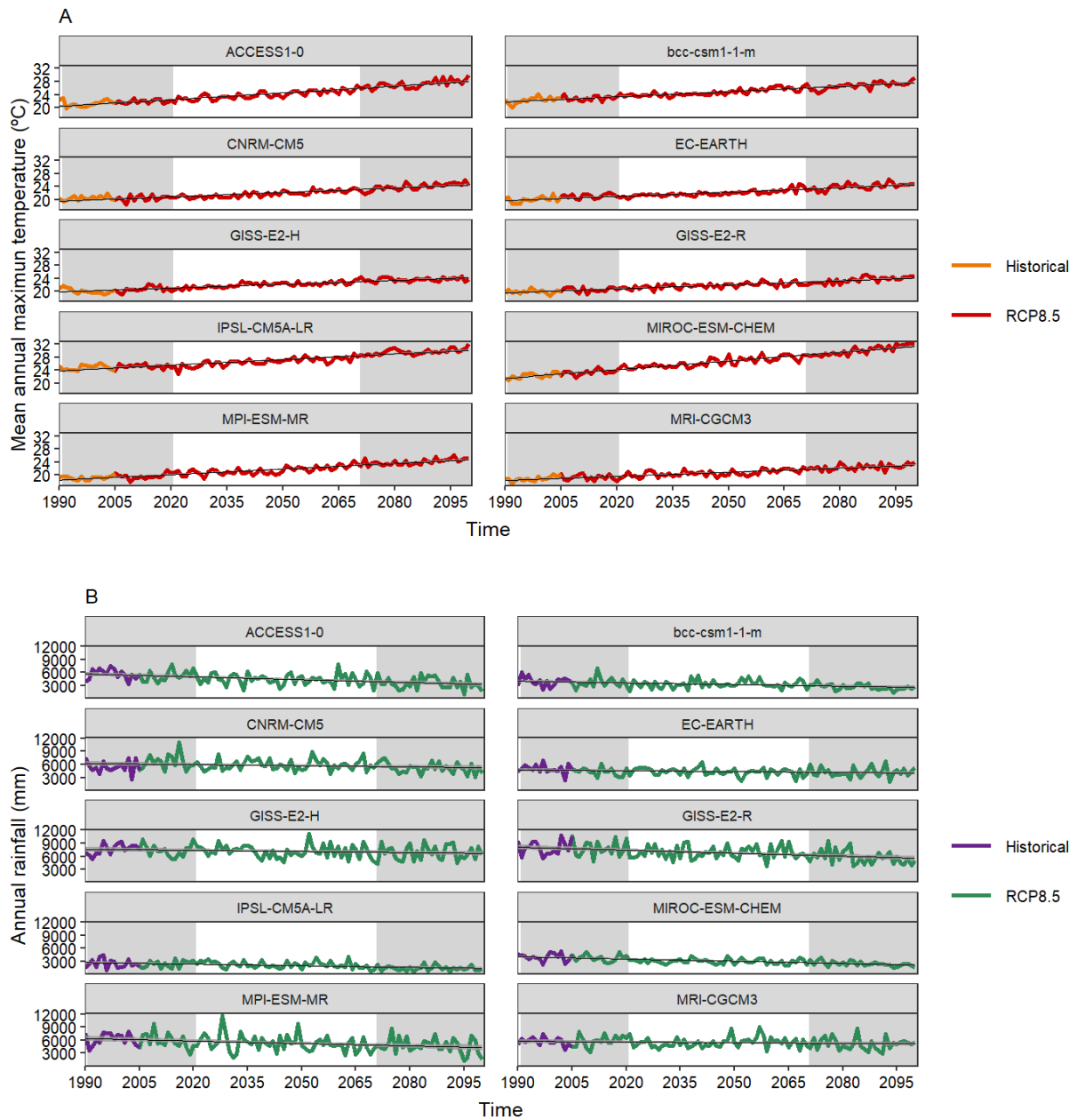


Figure 3: Mean annual maximum temperature in °C (A) and summed annual rainfall in mm (B) projected by the 10 models selected for this study. The different colors indicate the periods of historical and RCP8.5 climate simulations. The general tendency of each model is represented with a thin black line. Shaded areas indicate the time periods for which the IBMs were run.

Results

The probability of extinction is, on average, 32 percentage points higher for the rabbit and 25 percentage points higher for the lynx under future climate simulations, i.e., simulating projected rainfall and maximum temperatures for 2070-2100, compared to the baseline, i.e., simulating historical and projected rainfall and maximum temperatures for 1980-2020 (Figure 4). For the lynx, smaller nuclei (<100 km²; corresponding to smaller initial lynx abundance and number of territories), consistently show a higher extinction probability.

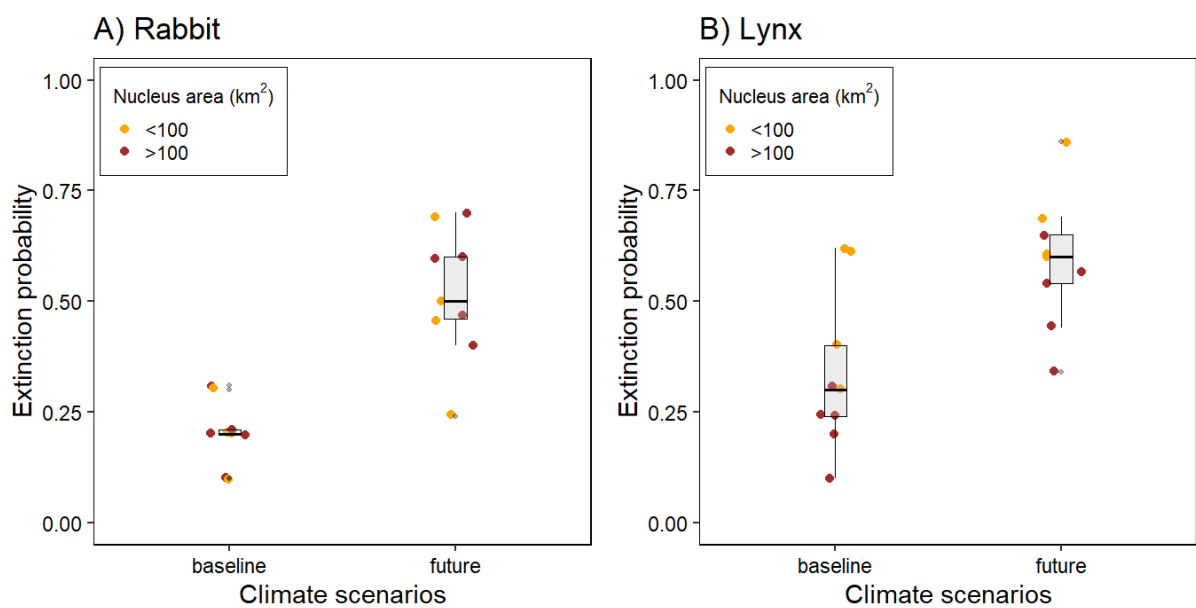


Figure 4: Extinction probabilities for the rabbit (A) and the lynx (B) under baseline and future climate scenarios, calculated as the proportion of simulations for each nucleus where a population went extinct (< 1 individual left in the population). Probabilities corresponding to large nuclei (>100 km²) are colored in dark red, and the ones corresponding to small nuclei (<100 km²) are colored in gold. The boxplots show the distribution of the frequency of extinction probabilities. The grey box marks the interquartile ranges, from quantile Q1 (25% of the data, lower limit) to Q3 (75% of the data, upper limit), indicating the median (50% of the data) with a black line). The whiskers go from the box until the last data point that it's not an outlier, i.e., inside the limits defined by 1.5*Q1.

The IBMs projections show that even in those populations that do not go extinct, abundances are significantly lower under future scenarios than baseline scenarios (Table 5; Figure 5). For both species the decrease between baseline and future simulations is significant in every nucleus, i.e., the upper limit of the 95% confidence interval (CI) of the future simulation does not cross the mean of the baseline simulation.

A stage-specific comparison of abundances for both species can be found in the Supporting materials S1 (Figures S1.2 and S1.3). For the lynx, the biggest differences from baseline to future simulations are found in the cub stage, followed by pre-dispersal juveniles, and finally dispersing adults, who show the smallest variations. The impact of rabbit decreases seems therefore stronger in recruitment than in survival, as expected because low rabbit densities affect mainly reproductive success of lynxes.

Table 5: Confidence interval of 95% for the mean abundances of each IBM's successful populations in both scenarios for each nucleus.

Nucleus	Mean densities through the years [CI 95%]			
	Rabbit baseline	Rabbit future	Lynx baseline	Lynx future
Doñana - Aljarafe	3876 [3737 , 4014]	2742 [2635 , 2850]	285 [279 , 290]	225 [221 , 229]
Matachel	2163 [2083 , 2242]	1832 [1764 , 1899]	150 [147 , 152]	124 [123 , 126]
Montes de Toledo	9266 [8946 , 9586]	8068 [7769 , 8366]	574 [563 , 586]	476 [468 , 485]
Ortiga	538 [519 , 558]	450 [433 , 467]	37 [37 , 38]	32 [32 , 33]
Setefilla - Las Minas	716 [690 , 742]	542 [521 , 562]	50 [49 , 51]	41 [40 , 42]
Sierra Morena	20995 [20232 , 21757]	17940 [17218 , 18662]	1421 [1394 , 1448]	1215 [1188 , 1242]
Valdecañas - Ibores	188 [182 , 195]	161 [155 , 166]	14 [13 , 14]	12 [12 , 12]
Valdecigüeñas - Rio Sotillo	166 [160 , 172]	139 [133 , 144]	14 [14 , 14]	12 [12 , 13]
Vale do Guadiana	3883 [3743 , 4022]	2945 [2823 , 3068]	293 [288 , 298]	238 [234 , 241]

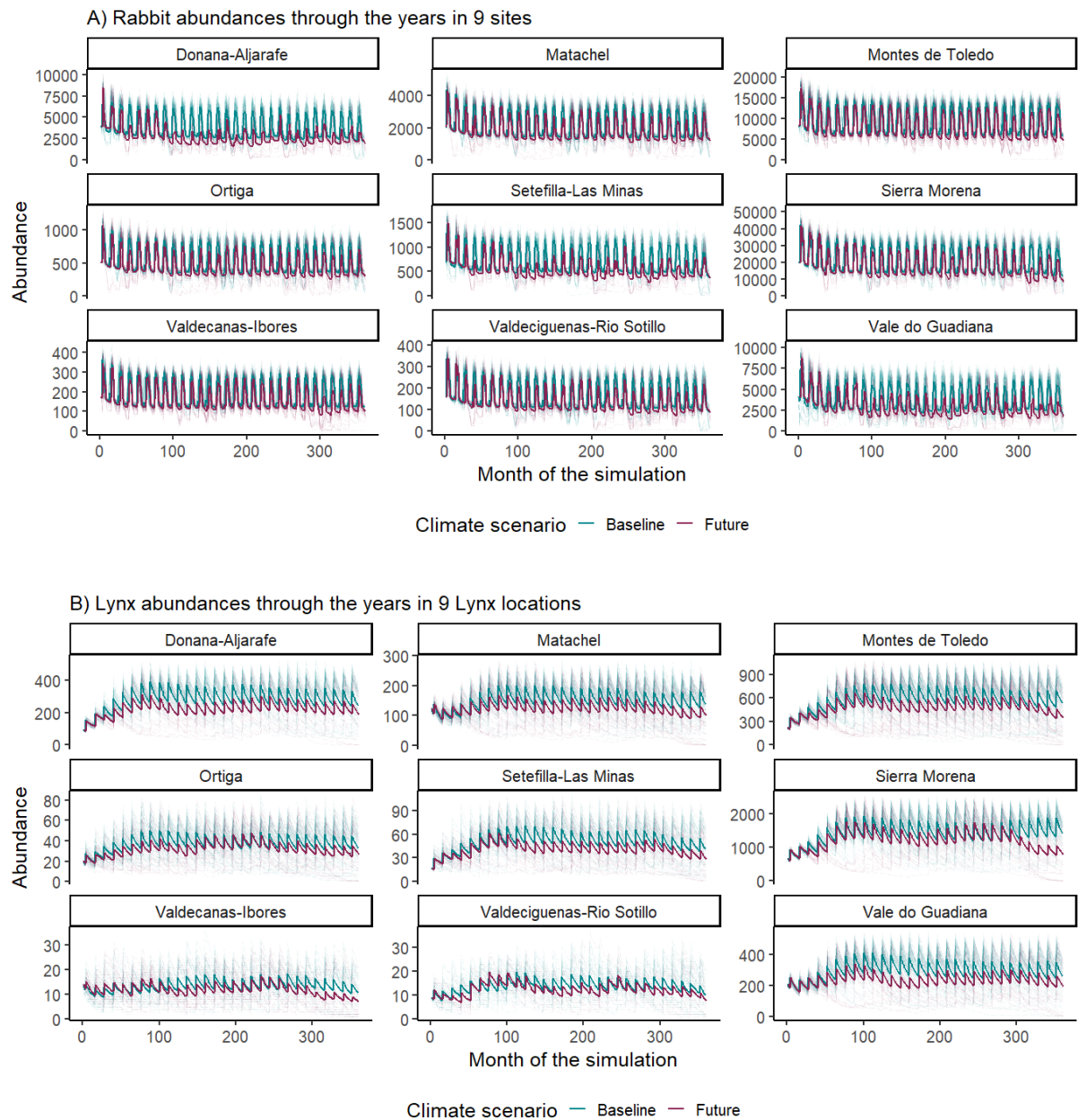


Figure 5: Rabbit (A) and lynx (B) persisting populations abundances for each nucleus under baseline and future climatic scenarios. The mean abundances over the years are represented by robust lines, and each singular successful simulation is portrayed by a shaded line.

Discussion

The IBMs that I parameterized in this study simulated populations of the Iberian lynx and the European rabbit and the dynamic among them through the different climatic seasonality of a baseline and a future scenario. The results show higher extinction rates under future climatic scenarios than in the baseline simulations, thus exposing that the risk of local extinction is higher for both species under seasonal climate change. Comparisons between both species show that the extinction risk of the lynx is higher in the future climatic scenario. This implies that the indirect effects of climate change on the lynx via the alteration of rabbit's demography pose a bigger threat for the lynx than the direct climate-change effects on rabbits themselves do for the rabbit. Is important to note that the rabbit IBM is conservative while addressing mortality, as it doesn't consider the probability of epidemics and new diseases growing as an effect of climate change, something that is likely to happen. Lynx lower densities could also negatively impact rabbit populations, as they have shown to control mesopredators and have an overall positive effect on maintaining rabbit populations stable (Jiménez et al., 2019).

Overall, extinction probabilities of lynxes are higher in the IBM simulations than those of the rabbits. The Iberian lynx is a specialist predator, and even if they are not known to die from starvation there are existing records of behavioral changes caused by rabbit insufficiency, primarily affecting breeding and dispersal. The annual breeding period for the lynx is short and restricted to a month. Low rabbit densities during that short period imply little or zero reproduction for the lynx, and while rabbits may recover on a later favorable weather the lynx population won't have more offspring that year. This was the case in previous cases of observed rabbit population decreases. In the rabbit shortage following the RHD outbreak in 1980, female lynxes amplified their territories, and for a year, no younger lynxes dispersed (they stayed in their mother's territory), and no reproduction was observed (Ferreras et al., 2011). In the RHDV2 outbreak in 2011 the number of territorial females got drastically reduced, negatively impacting breeding (Monterroso et al., 2016). Several years without or with very little reproduction, combined with higher mortality due to the lack of available

territories lead to population collapses, as shown in the IBMs. An occasional adaptation to this seasonally changing climate is more likely to occur for the rabbit, as fast-paced mammals are more likely to adapt their phenology to new climatic conditions (Bronson, 2009). Longer lived species as the lynx may not do so well, and while generalist predators can switch to more favorable preys, specialist like the Iberian lynx will have to deal with a mismatch between their life cycle and their prey's (Damien & Tougeron, 2019).

The results show a clear effect of nucleus size in the lynx's probability of extinction. Smaller nuclei show higher probabilities as an effect of demographic stochasticity. Demographic stochasticity can be defined as the randomness in population demographic rates derived from the probabilistic nature of biological processes themselves (Melbourne, 2012). This implies that smaller populations will face higher extinction risks simply for having less individuals, as it is more likely for all individuals to die out of pure hazard than in larger populations. That explains the two highest values of extinction probability for the baseline scenarios, both belonging to smaller populations. This is not the case for the rabbit as the nucleus size is not considered in the IBM, all initial populations have the same size. Both in populations and communities demographic stochasticity can drive outcomes far from determinist models predictions (Legault et al., 2019), thus the importance of accounting for it when modeling future populations and dynamics of endangered species.

It is important to note that the IBMs I built are spatially implicit. In reality, lynxes from larger nuclei could colonize smaller nuclei where extinction is higher. When rabbit abundance is low and there are less territories available, adult lynxes can travel longer distances in search of a territory, sometimes leaving their nucleus and ending in another one (Ferrerias et al., 1997). Old lynxes (around 9 years old) that are displaced by younger individuals can also disperse long distances (Ferrerias et al., 1997). However, even if movement is not directly addressed, this study shows that the spatiotemporal variation of lynx population dynamics is high. This means that lynxes will need to remain mobile in

the future in order to preserve their populations viability. Management must become more adaptive therefore, focusing on connectivity and habitat protection (Olds et al., 2012; Pitman et al., 2017).

My work supports previous studies analyzing future changes in lynx ranges. In particular, Fordham et al. (2013) accounted for the difference between managed and unmanaged areas in the lynx's vital rates and obtained evidence to enforce adapting conservation measures to preserve the lynx's habitat more efficiently. However, their approach uses population models and not IBMs and therefore does not account for demographic stochasticity. In addition, my work is the first explicitly modelling feedbacks between rabbit and lynx demography under seasonal changes in climatic conditions, thus gaining a mechanistic understanding of the seasonal biotic processes that mediate changes in lynx abundances under climate change. IBMs have become frequent in population ecology as they provide strong and more realistic predictions (Bauduin et al., 2020; Paniw et al., 2022) in changing environments than population models (Stillman et al., 2015).

This study illustrates the importance of accounting for seasonal biotic interactions under global change while also considering demographic stochasticity. The effect of seasonal climate change on future lynx populations was only addressed as an indirect effect altering the rabbit's demographic rates, and yet it caused a 25% increase of the lynx's extinction probability. This shows how in a seasonally changing climate altered interspecific interactions can be an important driver of species extinction, especially in higher trophic levels. In order to understand how seasonality change will affect complex communities, we need to understand how it will impact the underlying interactions that sustain these communities (Maestre et al., 2012; Tylianakis et al., 2008). This requires a strong analytical framework, that studies these interactions as a result of demography changes driven by individual fates under a changing environment (Foden et al., 2019; Grimm et al., 2017). Approaches like this study allow to better understand the mechanisms through which seasonal climatic change can threaten biological systems. Moreover, by accounting for demographic stochasticity it provides a more realistic insight on how these mechanisms act on populations of different characteristics. This

grants a better idea on how real-life populations will behave on future seasonal changing climate conditions, but also furnishes support to enhance better management practices that prevent smaller populations to go extinct. Future predictions on species response to climate change should dig deeply into the complex effects that a changing seasonal environment can have on interspecific interactions, aiming to achieve a more broadly understanding of the mechanisms involved and to guide future conservation practices through the best path.

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References

- Bauduin, S., Grente, O., Santostasi, N. L., Ciucci, P., Duchamp, C., & Gimenez, O. (2020). An individual-based model to explore the impacts of lesser-known social dynamics on wolf populations. *Ecological Modelling*, 433, 109209. <https://doi.org/10.1016/j.ecolmodel.2020.109209>
- Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B., & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *Journal of Animal Ecology*, 78(1), 73-83. <https://doi.org/10.1111/j.1365-2656.2008.01458.x>
- Bronson, F. H. (2009). Climate change and seasonal reproduction in mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1534), 3331-3340. <https://doi.org/10.1098/rstb.2009.0140>

- Cabezas-Díaz, S., Lozano, J., & Virgós, E. (2009). The declines of the wild rabbit (*Oryctolagus cuniculus*) and the Iberian lynx (*Lynx pardinus*) in Spain: Redirecting conservation efforts. Handbook of nature conservation: Global, environmental and economic issues. En *Handbook of nature conservation: Global, environmental and economic issues* (pp. 238-231). Nova Science Publishers.
- Callou, C. (1995). Modifications de l'aire de répartition du lapin (*Oryctolagus cuniculus*) en France et en Espagne, du pléistocène à l'époque actuelle. État de la question. *Antropozoologica*, 21, 95-114.
- Censo del Lince Ibérico*. (2021). Ministerio para la Transición Ecológica y el Reto Demográfico (MITECO).
- Dai, A. (2011). Drought under global warming: A review. *WIREs Climate Change*, 2(1), 45-65.
<https://doi.org/10.1002/wcc.81>
- Damien, M., & Tougeron, K. (2019). Prey–predator phenological mismatch under climate change. *Current Opinion in Insect Science*, 35, 60-68. <https://doi.org/10.1016/j.cois.2019.07.002>
- Delibes, M., Rodríguez, A., & Ferreras, P. (2000). *Action plan for the conservation of the Iberian lynx (Lynx pardinus) in Europe*. Council of Europe Publishing.
- Delibes-Mateos, M., Delibes, M., Ferreras, P., & Villafuerte, R. (2008). Key Role of European Rabbits in the Conservation of the Western Mediterranean Basin Hotspot. *Conservation Biology*, 22(5), 1106-1117. <https://doi.org/10.1111/j.1523-1739.2008.00993.x>
- Duke, N. C., Kovacs, J. M., Griffiths, A. D., Preece, L., Hill, D. J. E., van Oosterzee, P., Mackenzie, J., Morning, H. S., & Burrows, D. (2017). Large-scale dieback of mangroves in Australia. *Marine and Freshwater Research*, 68(10), 1816. <https://doi.org/10.1071/MF16322>
- Ferreras, P., Beltrán, J. F., Aldama, J. J., & Delibes, M. (1997). Spatial organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*). *Journal of Zoology*, 243(1), 163-189.
<https://doi.org/10.1111/j.1469-7998.1997.tb05762.x>

- Ferreras, P., Travaini, A., Cristina Zapata, S., & Delibes, M. (2011). Short-term responses of mammalian carnivores to a sudden collapse of rabbits in Mediterranean Spain. *Basic and Applied Ecology*, 12(2), 116-124. <https://doi.org/10.1016/j.baae.2011.01.005>
- Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G., Martin, T. G., Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M., & Huntley, B. (2019). Climate change vulnerability assessment of species. *WIREs Climate Change*, 10(1). <https://doi.org/10.1002/wcc.551>
- Fordham, D. A., Akçakaya, H. R., Brook, B. W., Rodríguez, A., Alves, P. C., Civantos, E., Triviño, M., Watts, M. J., & Araújo, M. B. (2013). Adapted conservation measures are required to save the Iberian lynx in a changing climate. *Nature Climate Change*, 3(10), 899-903. <https://doi.org/10.1038/nclimate1954>
- Gálvez Bravo, L. (2017). Conejo – *Oryctolagus cuniculus* (Linnaeus, 1758). En A. Salvador Milla, J. Cassinello, & I. Barja (Eds.), *Enciclopedia Virtual de los Vertebrados Españoles*. CSIC - Museo Nacional de Ciencias Naturales (MNCN). <https://digital.csic.es/handle/10261/112112>
- Gaona, P., Ferreras, P., & Delibes, M. (1998). Dynamics and Viability of a Metapopulation of the Endangered Iberian Lynx (*Lynx pardinus*). *Ecological Monographs*, 68(3), 349-370.
- Gonçalves, H., Alves, P. C., & Rocha, A. (2002). Seasonal variation in the reproductive activity of the wild rabbit (*Oryctolagus cuniculus algirus*) in a Mediterranean ecosystem. *Wildlife Research*, 29(2), 165-173. <https://doi.org/10.1071/wr00048>
- González-Megías, A., & Menéndez, R. (2012). Climate change effects on above- and below-ground interactions in a dryland ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1606), 3115-3124. <https://doi.org/10.1098/rstb.2011.0346>
- Grimm, V., Ayllón, D., & Railsback, S. F. (2017). Next-Generation Individual-Based Models Integrate Biodiversity and Ecosystems: Yes We Can, and Yes We Must. *Ecosystems*, 20(2), 229-236. <https://doi.org/10.1007/s10021-016-0071-2>

- Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., & Railsback, S. F. (2010). The ODD protocol: A review and first update. *Ecological Modelling*, 221(23), 2760-2768.
<https://doi.org/10.1016/j.ecolmodel.2010.08.019>
- Guzmán López-Ocón, J. N. (Ed.). (2004). *El lince ibérico (Lynx pardinus) en España y Portugal: Censo-diagnóstico de sus poblaciones*. Ministerio de Medio Ambiente, Direccion General para la Biodiversidad.
- Harris, R. M. B., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M.-S., Keatley, M. R., Woodward, C. A., Williamson, G., ... Bowman, D. M. J. S. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change*, 8(7), 579-587.
<https://doi.org/10.1038/s41558-018-0187-9>
- J.E.C. Flux, & P.J. Fullagar. (1983). World distribution of the rabbit (*Oryctolagus cuniculus*). *Acta Zool. Fennica*, 174, 75-77.
- J.E.C. Flux, & P.J. Fullagar. (1992). World distribution of the Rabbit *Oryctolagus funiculus* on islands. *Mammal Review*, 22(3/4), 151-205.
- Jiménez, J., Nuñez-Arjona, J. C., Mougeot, F., Ferreras, P., González, L. M., García-Domínguez, F., Muñoz-Igualada, J., Palacios, M. J., Pla, S., Rueda, C., Villaespesa, F., Nájera, F., Palomares, F., & López-Bao, J. V. (2019). Restoring apex predators can reduce mesopredator abundances. *Biological Conservation*, 238, 108234. <https://doi.org/10.1016/j.biocon.2019.108234>
- Legault, G., Fox, J. W., & Melbourne, B. A. (2019). Demographic stochasticity alters expected outcomes in experimental and simulated non-neutral communities. *Oikos*, 128(12), 1704-1715. <https://doi.org/10.1111/oik.06028>
- Life Lynx Connect. (2020). *Censos – Life Lynxconnect*. <https://lifelynxconnect.eu/censos/>
- Maestre, F. T., Salguero-Gómez, R., & Quero, J. L. (2012). It is getting hotter in here: Determining and projecting the impacts of global environmental change on drylands. *Philosophical*

Transactions of the Royal Society B: Biological Sciences, 367(1606), 3062-3075.

<https://doi.org/10.1098/rstb.2011.0323>

Melbourne, B. A. (2012). Demographic stochasticity. *Encyclopedia of theoretical ecology*. Univ. of California Press, p 848.

Monterroso, P., Garrote, G., Serronha, A., Santos, E., Delibes-Mateos, M., Abrantes, J., Perez de Ayala, R., Silvestre, F., Carvalho, J., Vasco, I., Lopes, A. M., Maio, E., Magalhães, M. J., Mills, L. S., Esteves, P. J., Simón, M. Á., & Alves, P. C. (2016). Disease-mediated bottom-up regulation: An emergent virus affects a keystone prey, and alters the dynamics of trophic webs. *Scientific Reports*, 6(1), 36072. <https://doi.org/10.1038/srep36072>

Moreno, S., Beltrán, J. F., Cotilla, I., Kuffner, B., Laffite, R., Jordán, G., Ayala, J., Quintero, C., Jiménez, A., Castro, F., Cabezas, S., & Villafuerte, R. (2007). Long-term decline of the European wild rabbit (*Oryctolagus cuniculus*) in south-western Spain. *Wildlife Research*, 34(8), 652. <https://doi.org/10.1071/WR06142>

Olds, A. D., Connolly, R. M., Pitt, K. A., & Maxwell, P. S. (2012). Habitat connectivity improves reserve performance: Connectivity improves reserve performance. *Conservation Letters*, 5(1), 56-63. <https://doi.org/10.1111/j.1755-263X.2011.00204.x>

Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E., & Delgado, M. del M. (2013). Community-level phenological response to climate change. *Proceedings of the National Academy of Sciences*, 110(33), 13434-13439. <https://doi.org/10.1073/pnas.1305533110>

Palomares, F., Delibes, M., Revilla, E., Calzada, J., & Fedriani, J. M. (2001). Spatial Ecology of Iberian Lynx and Abundance of European Rabbits in Southwestern Spain. *Wildlife Monographs*, 148, 1-36.

Palomares, F., Revilla, E., Calzada, J., Fernández, N., & Delibes, M. (2005). Reproduction and pre-dispersal survival of Iberian lynx in a subpopulation of the Doñana National Park. *Biological Conservation*, 122(1), 53-59. <https://doi.org/10.1016/j.biocon.2004.06.020>

- Palomares, F., Rodriguez, A., Revilla, E., López-Bao, J. V., & Calzada, J. (2011). Assessment of the Conservation Efforts to Prevent Extinction of the Iberian Lynx. *Conservation biology : the journal of the Society for Conservation Biology*, 25, 4-8. <https://doi.org/10.1111/j.1523-1739.2010.01607.x>
- Paniw, M., Duncan, C., Groenewoud, F., Drewe, J. A., Manser, M., Ozgul, A., & Clutton-Brock, T. (2022). Higher temperature extremes exacerbate negative disease effects in a social mammal. *Nature Climate Change*, 12(3), 284-290. <https://doi.org/10.1038/s41558-022-01284-x>
- Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T., & Ozgul, A. (2019). Life history responses of meerkats to seasonal changes in extreme environments. *Science*, 363(6427), 631-635. <https://doi.org/10.1126/science.aau5905>
- Pitman, R. T., Fattebert, J., Williams, S. T., Williams, K. S., Hill, R. A., Hunter, L. T. B., Robinson, H., Power, J., Swanepoel, L., Slotow, R., & Balme, G. A. (2017). Cats, connectivity and conservation: Incorporating data sets and integrating scales for wildlife management. *Journal of Applied Ecology*, 54(6), 1687-1698. <https://doi.org/10.1111/1365-2664.12851>
- RStudio Team. (2020). *RStudio: Integrated Development for R*. RStudio, PBC, Boston, MA URL. <http://www.rstudio.com/>
- Simón, M. A., Gil-Sánchez, J. M., Ruiz, G., Garrote, G., McCain, E. B., Fernández, L., López-Parra, M., Rojas, E., Arenas-Rojas, R., Rey, T. D., García-Tardío, M., & López, G. (2012). Reverse of the Decline of the Endangered Iberian Lynx: Saving the Iberian Lynx. *Conservation Biology*, 26(4), 731-736. <https://doi.org/10.1111/j.1523-1739.2012.01871.x>
- Soriguer, R. C. (1981). Biología y dinámica de una población de conejos (*Oryctolagus cuniculus*, L.) en Andalucía occidental. *Doñana Acta Vertebrata*, 8 (Volumen especial 3). <https://digital.csic.es/handle/10261/44353>
- Steltzer, H., & Post, E. (2009). Seasons and Life Cycles. *Science*, 324(5929), 886-887. <https://doi.org/10.1126/science.1171542>

- Stillman, R. A., Railsback, S. F., Giske, J., Berger, U., & Grimm, V. (2015). Making Predictions in a Changing World: The Benefits of Individual-Based Ecology. *BioScience*, 65(2), 140-150.
<https://doi.org/10.1093/biosci/biu192>
- Tablado, Z., & Revilla, E. (2012). Contrasting Effects of Climate Change on Rabbit Populations through Reproduction. *PLoS ONE*, 7(11), e48988. <https://doi.org/10.1371/journal.pone.0048988>
- Tablado, Z., Revilla, E., & Palomares, F. (2009). Breeding like rabbits: Global patterns of variability and determinants of European wild rabbit reproduction. *Ecography*, 32(2), 310-320.
<https://doi.org/10.1111/j.1600-0587.2008.05532.x>
- Tablado, Z., Revilla, E., & Palomares, F. (2012). Dying like rabbits: General determinants of spatio-temporal variability in survival: Determinants of global survival patterns in rabbits. *Journal of Animal Ecology*, 81(1), 150-161. <https://doi.org/10.1111/j.1365-2656.2011.01884.x>
- Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An Overview of CMIP5 and the Experiment Design. *Bulletin of the American Meteorological Society*, 93(4), 485-498.
<https://doi.org/10.1175/BAMS-D-11-00094.1>
- Tuel, A., & Eltahir, E. A. B. (2020). Why Is the Mediterranean a Climate Change Hot Spot? *JOURNAL OF CLIMATE*, 33, 15.
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12), 1351-1363.
<https://doi.org/10.1111/j.1461-0248.2008.01250.x>
- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, 3(6), 879-885. <https://doi.org/10.1038/s41559-019-0880-8>
- Voigt, W., Perner, J., Davis, A. J., Eggers, T., Schumacher, J., Bährmann, R., Fabian, B., Heinrich, W., Köhler, G., Lichter, D., Marsteller, R., & Sander, F. W. (2003). Trophic levels are differentially sensitive to climate. *Ecology*, 84(9), 2444-2453. <https://doi.org/10.1890/02-0266>

von Holst, D., Hutzelmeyer, H., Kaetzke, P., Khaschei, M., & Schönheiter, R. (1999). Social Rank, Stress, Fitness, and Life Expectancy in Wild Rabbits. *Naturwissenschaften*, 86(8), 388-393.
<https://doi.org/10.1007/s001140050638>

Wang, J., Guan, Y., Wu, L., Guan, X., Cai, W., Huang, J., Dong, W., & Zhang, B. (2021). Changing Lengths of the Four Seasons by Global Warming. *Geophysical Research Letters*, 48(6).
<https://doi.org/10.1029/2020GL091753>

Williams, C. K., Parer, I., Coman, B. J., Burley, J., & Braysher, M. L. (1995). *Managing vertebrate pests: Rabbits*. Australian Government Publishing Services.

Supporting material S1

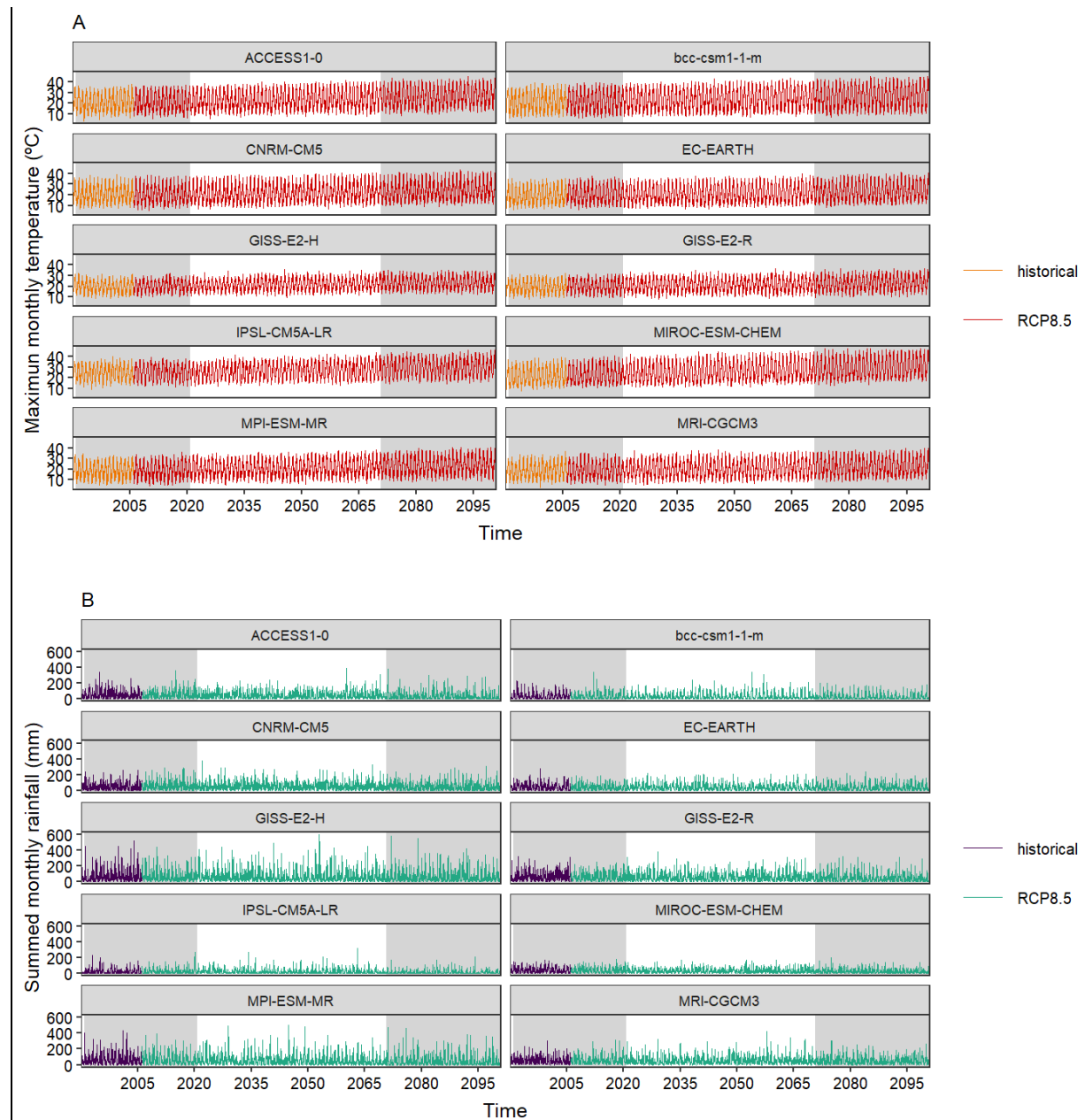
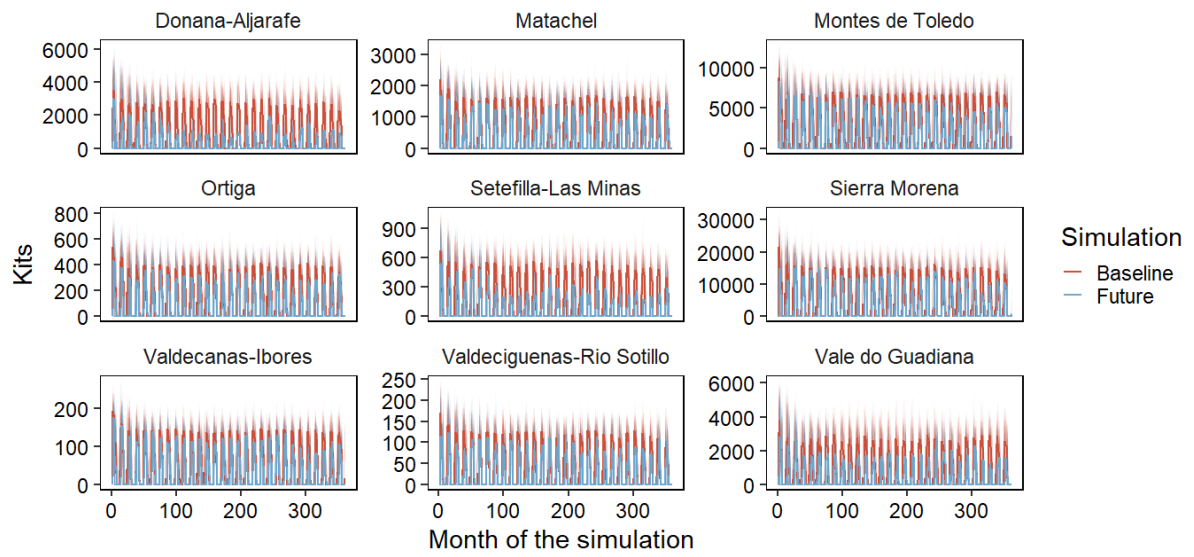
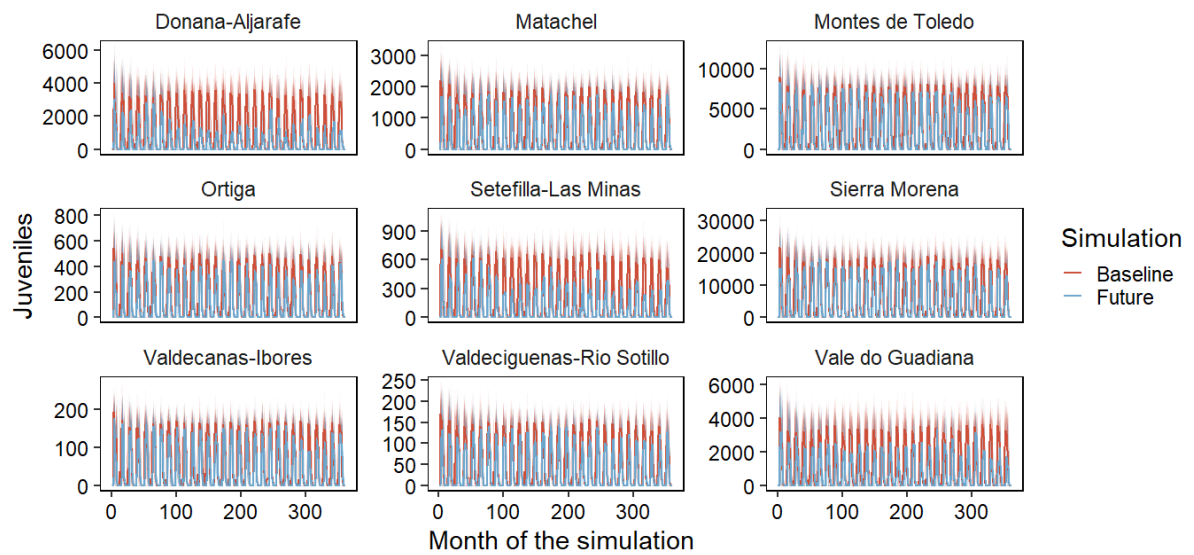


Figure S1.1: Monthly maximum temperature in °C (A) and summed monthly rainfall in mm (B) projected by the 10 models selected for this study. The different colors indicate the periods of historical and RCP8.5 climate simulations. Shaded areas indicate the time periods for which the IBMs were run.

A



B



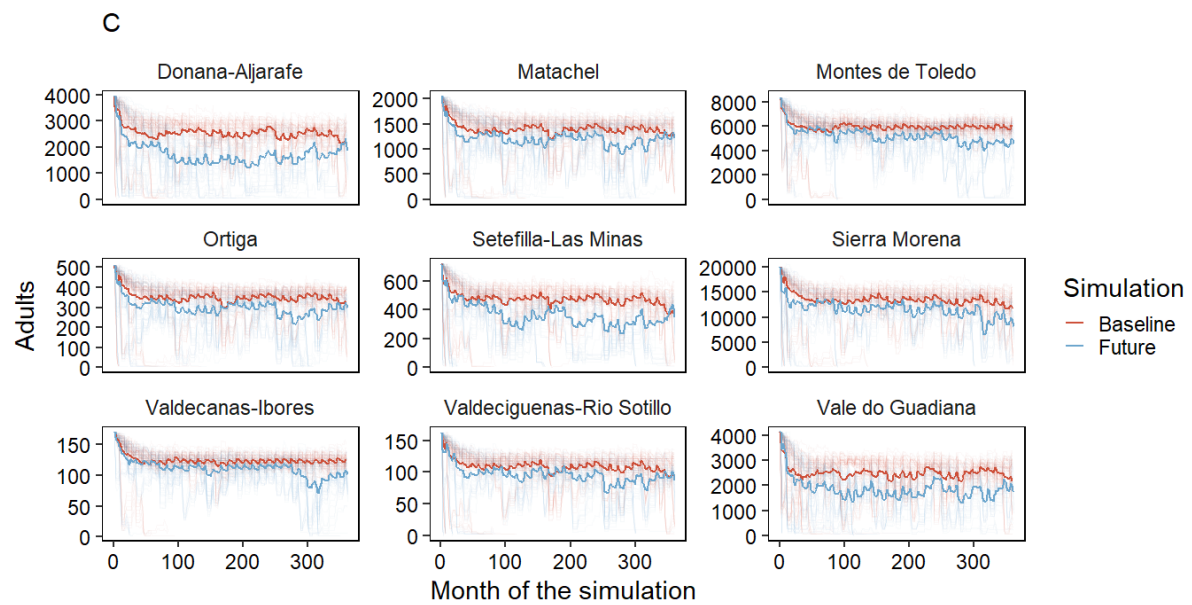
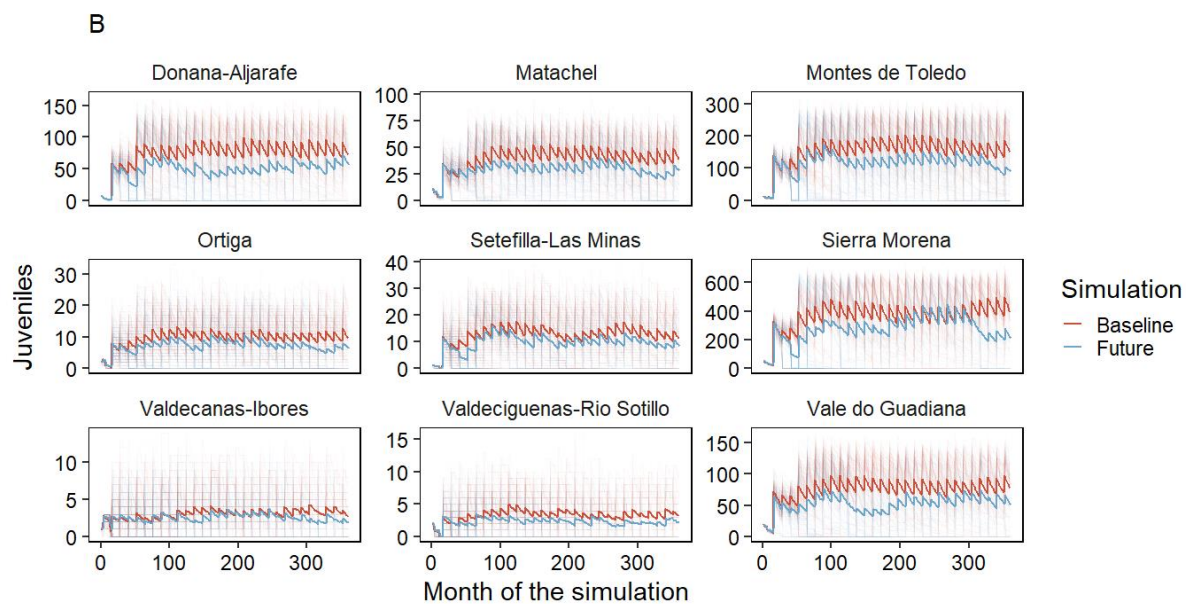
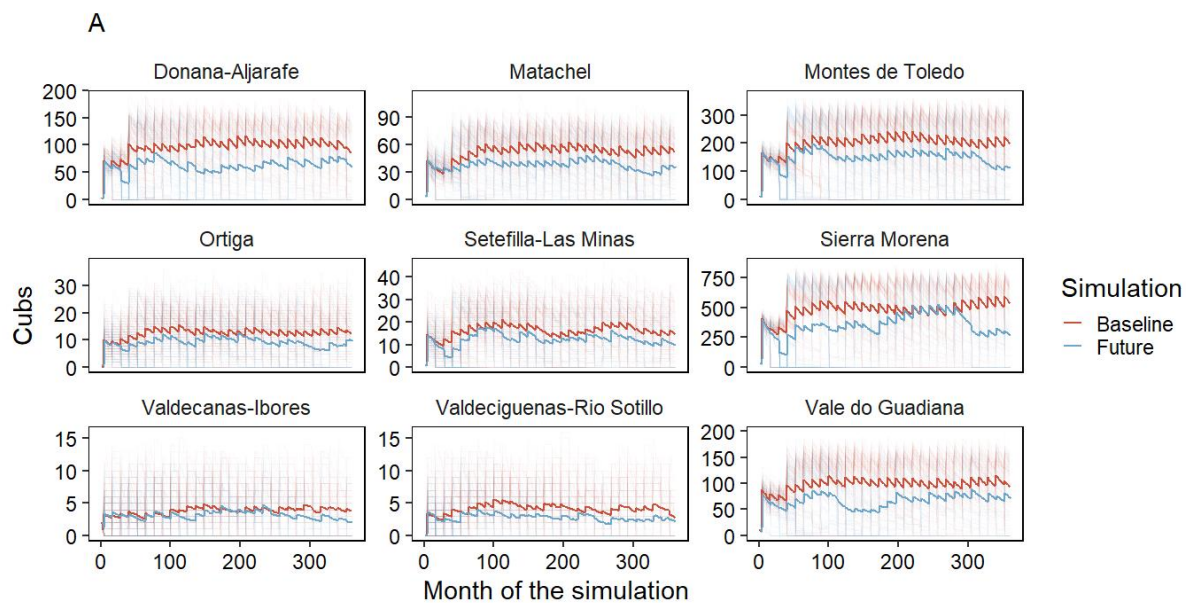


Figure S1.2: Abundances and mean abundances of each rabbit stage in the simulated populations over the 360 months of simulation. A) Kits abundances, B) Juveniles abundances, and C) Adults abundances. Thick lines represent mean abundances and shaded lines represent every single simulated population. The different colors differentiate populations simulated under baseline or future climate conditions.



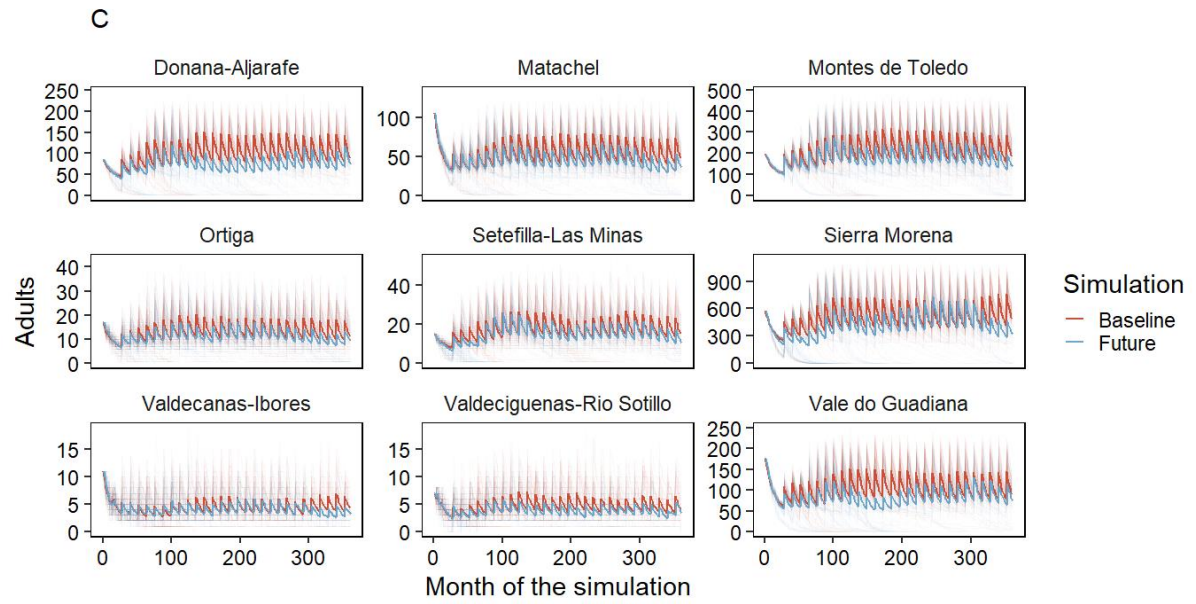


Figure S1.2: Abundances and mean abundances of each lynx stage in the simulated populations over the 360 months of simulation. A) Cubs abundances, B) Juvenile abundances, C) Adults abundances. Thick lines represent mean abundances and shaded lines represent every single simulated population. The different colors differentiate populations simulated under baseline or future climate conditions.