Responses of an endangered brown bear population to climate change based on predictable food resource and shelter alterations

RUNNING HEAD: brown bear response to climate change

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Abstract

The survival of an increasing number of species is threatened by climate change: 20–30% of plants and animals seem to be at risk of range shift or extinction if global warming reaches levels projected to occur by the end of this century. Plant range shifts may determine whether animal species that rely on plant availability for food and shelter will be affected by new patterns of plant occupancy and availability. Brown bears in temperate forested habitats mostly forage on plants and it may be expected that climate change will affect the viability of the endangered populations of southern Europe. Here, we assessed the potential impact of climate change on seven plants that represent main food resources and shelter for the endangered population of brown bears in the Cantabrian Mountains (Spain). Our simulations suggest that the geographic range of these plants might be altered under future climate warming, with most bear resources reducing their range. As a consequence, this brown bear population is expected to decline drastically in the next fifty years. Range shifts of brown bear are also expected to displace individuals from mountainous areas towards more humanised ones, where we can expect an increase in conflicts and bear mortality rates. Additional negative effects might include: (a) a tendency to a more carnivorous diet, which would increase conflicts with cattle farmers; (b) limited fat storage before hibernation due to the reduction of oak forests; (c) increased intraspecific competition with other acorn consumers, i.e. wild ungulates and free-ranging livestock; and (d) larger displacements between seasons to find main trophic resources. The magnitude of the changes projected by our models emphasizes that conservation practices focused only on bears may not be appropriate and thus we need more dynamic conservation planning aimed at reducing the impact of climate change in forested landscapes.

1 | INTRODUCTION

The survival of an increasing number of species is threatened by climate change, yet 20–30% of plant and animal species evaluated in climate change studies seems to be at risk of range shift or extinction if global warming reaches levels projected to occur by the end of this century (Brook *et al.*, 2008; Walther, 2010; Intergovernmental Panel on Climate Change, 2014; Lenoir & Svenning, 2015). Indeed, climate change has already contributed to manifest changes in the geographic distribution and abundance of wild plants and animals over the past several decades (e.g. Root *et al.*, 2003; Parmesan, 2006; Monzón *et al.*, 2011; Bellard *et al.*, 2012; Lenoir & Svenning, 2015).

Predicting the response of plants and animals to climate change has become an extremely active field of research, as predictions (a) play a crucial role in alerting researchers and decision makers to potential future risks and (b) can support the development of proactive strategies to reduce climate change impacts on biodiversity (Bellard *et al.*, 2012). Some of the most vulnerable organisms to the alterations produced by climate change (e.g. warming temperatures and decreasing precipitation during the growing season; IPCC, 2013) are plants, given their limited ability to physically follow suitable environmental conditions (Parmesan, 2006). One of the most noticeable responses of plants to climatic changes is a shift in their geographic ranges (Malanson & Alftine, 2015). In particular, forests in temperate regions will be increasingly exposed to drought in the 21st century (Müller-Haubold *et al.*, 2013), which may accelerate rates of tree decline and mortality in Europe (Bréda *et al.*, 2006; Müller-Haubold *et al.*, 2013). Plant range shifts may determine whether those animal species that rely on plant availability for both food and shelter will be affected by new patterns of plant occupancy/abundance (Nielsen *et al.*, 2010; Shen *et al.*, 2015; Simons-Legaard *et al.*, 2016; Zang *et al.*, 2017; Cianfrani *et al.*, 2018) and/or by plant population declines or extinction cascades via bottom-up effects (Roberts *et al.*, 2014). In the case of small, isolated and/or endangered animal populations, the effects of climate change on their trophic resources may considerably override conservation and management efforts performed at other levels, e.g. reduction of human-wildlife conflicts, threat of anthropogenic footprints and activities.

Brown bears (*Ursus arctos*) dedicate considerable effort to foraging on plants, particularly in temperate forested habitats (Bojarska & Selva, 2012), with bears in south-western Europe being among the most vegetarian of the European populations (Bojarska & Selva, 2012). Accordingly, bears in the Cantabrian Mountains (NW Spain) show high proportions of plant matter in their diet (Naves *et al.*, 2006): (a) graminoids and forbs dominate their diet in spring; (b) foods such as fleshy fruits (especially blueberries *Vaccinium myrtillus*) become more important in the summer; and (3) during the early-autumn hyperphagic period (i.e. the period when bears spend most of their active time foraging to store fat, which is essential for successful hibernation and cub production; Farley and Robbins 1995, Fernández-Gil 2013) and winter, brown bears rely predominantly on hard mast, mainly acorns (Naves *et al.*, 2006). Above all, acorns and blueberry represent essential food items for Cantabrian brown bears and, thus, oak forests and formations of clumped shrubs of blueberries are critical foraging habitats for this bear population (Naves *et al.*, 2006; Rodríguez *et al.*, 2007). Few studies have focused directly on potential linkages between climate change and bear trophic plant resources (Butler, 2012; Roberts *et al.*, 2014), but some evidence exists that in the small and isolated brown bear population of Cantabrian Mountains (Rodríguez *et al.*, 2007): (a) changes in bear diet and land use in relation to changing climate conditions have already occurred in the last 30 years; and (b) a trend towards increased local temperatures over the last few decades has been observed. Moreover, climate change impacts on vegetation have recently been reported in other areas of Northern Spain, where several plant species have shown noticeable changes in the phenology of leaf unfolding, flowering, fruiting and leaf fall (Peñuelas *et al.*, 2002).

As temperature and snow conditions are among the most important factors affecting the feeding ecology of brown bears (Bojarska & Selva, 2012), it may be expected that climate change will affect brown bear food habits, for example, through changes in food availability and foraging behaviour as a result of alterations in plant distribution and phenology. Changes in the timing and intensity of fruiting and ripening of fruit and mast, as well as declines in the availability of high-quality fruits, such as *Vaccinium* sp., may have important consequences for brown bear population dynamics (Rodríguez *et al.*, 2007). Consequently, because climate change may increase the extinction risk of endangered species already threatened by their small populations or limited geographic range, a major challenge in conservation planning for small populations of endangered bears is to incorporate climate change impacts into species conservation strategies (Li *et al.*, 2015; Shen *et al.*, 2015).

The aim of this study is to conduct a comprehensive assessment of the potential impact of climate change on the future distribution of the brown bear population in the Cantabrian Mountains. Here, based on a long-term field survey on bear distribution and the latest climate projections, we applied both abiotic (i.e., climatic and geographic) and biotic (i.e., fruits and acorns distribution) variables to bioclimatic models in order to: (1) forecast the effect of potential changes in the spatial distribution of main bear food resources and shelter on the Cantabrian bear population in this century. With this aim, we evaluated two climate change scenarios (moderate and pessimistic) for 2050 and 2070 under different emissions pathways; and (2) evaluate the implication of these changes to the distribution of this small and isolated bear population.

2 | METHODS

2.1 | Study area

Our model projections took into account most of the Cantabrian range currently occupied by brown bears (Asturias, León and Palencia provinces, NW Spain), which is characterized by an Atlantic climate, at the southern distribution limit of temperate deciduous forests in Europe, with mild winters and rainy summers (Pato & Obeso, 2012; Roces-Díaz *et al.*, 2014). The Cantabrian Mountains are characterized by an oceanic and relatively warm climate, with mean precipitation exceeding 800 mm year^{-1} and reaching more than 2000 mm year^{-1} at the highest elevations. Maximum elevation is 2648 m a.s.l. and average elevation is around 1100 m (Naves *et al.*, 2003; Martínez Cano *et al.*, 2016). Woodlands mainly consist of deciduous forests of sessile oak (*Quercus petraea*), beech (*Fagus sylvatica*) and chestnut (*Castanea sativa*), with bilberry dominating the understory (Pato & Obeso, 2012). This area also represents the southern limit of the distribution of beeches, sessile oaks, pedunculate oak (*Q. robur*) and European white birch (*Betula pubescens*) (Roces-Díaz *et al.*, 2014).

The plants investigated include seven species that not only are important in the diet of Cantabrian brown bears (Naves *et al.*, 2006; Rodríguez *et al.*, 2007; Fernández-Gil, 2013b), i.e. blueberries, beeches, chestnuts, pedunculate oaks, Pyrenean oaks (*Q. pyrenaica*), sessile oaks and Scots pines (*Pinus sylvestris*), but also provide important shelter for the species (Mateo-Sánchez *et al.*, 2014, 2016; Zarzo-Arias *et al.*, 2019).

2.2 | Occurrence data collection

2.2.1 | Brown bear

The locations of brown bears were obtained from: (1) direct bear observations that were georeferenced by personnel of the Principado de Asturias and Junta de Castilla y León, primarily the Patrulla Oso, i.e. the Bear Patrol, of the Principado de Asturias and the Junta de Castilla y León, as well as all the other guards of both regional governments, by the Asturian Foundation for the Conservation of Wildlife (FAPAS, Fondo para la Protección de los Animales Salvajes), the FOA (Fundación Oso de Asturias) and the Brown Bear Foundation (FOP, Fundación Oso Pardo); and (2) personal georeferenced observations of the authors (Zarzo-Arias *et al.*, 2018). The long-term monitoring of the Cantabrian population, which started between the end of the 1980s and the beginning of the 1990s, is essentially based on yearly direct sightings and the location of indirect signs of presence, i.e. footprints, fur and scats, records of damage caused by bears to livestock, beehives, crops, human activities and infrastructures, as well as camera traps that were randomly located by the FAPAS and Bear Team during the last twenty years, mainly in forested areas where bears are less visible (FAPAS/FIEP, 2017). Viewing points used by rangers and ourselves are evenly distributed over the entire bear range in the study area. Thus, locations were both the result of yearly systematic observations and random observations, which were evenly distributed throughout the seasons. For Castilla y León (from 1985 to 2017) it was possible to collect 3,130 bear locations, whereas for Asturias (from 1995 to 2016) 5,654 bear locations were available (n = 8,784 total brown bear locations; Supplemental File 1A). Moreover, following brown bear habitat modelling by Mateo-Sánchez *et al.* (2016) 20,000 random pseudoabsence points were drawn inside the limits of the study area (Mateo-Sánchez *et al.*, 2013). Indeed, presence–absence models tend to perform better than presence-only models and, for this reason, artificial absence data (usually called pseudo-absences or background data) are usually created (Barbet-Massin *et al.*, 2012).

2.2.2 | Woody plants

We estimated foraging resources from the combination of those plant species (trees and shrubs) which sequentially provide a food supply for brown bears throughout the different seasons. Specifically, we predict habitat changes for 7 species considered to be key brown bear food resources in the Cantabrian Mountains. Information on species occurrence was drawn from the Third Spanish National Forest Inventory, SNFI3 (DGCN, 2001) (Supplemental File 1B). Few other species (e.g. Malus, Prunus and Ramnus spp.) can be important food resource seasonally (Naves *et al.*, 2006), but it was impossible to forecast their evolution under climate change scenarios because of the lack of detailed information on their spatial distribution. The plots of the SNFI3 were surveyed at two different times, i.e. once in 1998 (province of Asturias) and then in 2002-2003 (provinces of Léon and Palencia), and established at the intersections of a 1 × 1 km grid, comprising four concentric sub-plots of 5, 10, 15 and 25 m radii, with a minimum diameter at breast height threshold of 75, 125, 225 and 425 mm, respectively. We defined presence as the occurrence of one or more live beech trees in any one of the subplots. A total of 8,185 plots falling within the study area with data on the presence/absence and prevalence of analysed species were available for analysis (Table 1).

TABLE 1. Plant species considered as possible predictors for the distribution models. Prevalence = presence/total. Sites surveyed = 8185.

Species	Presences	Absences	Prevalence
Blueberry	334	7,851	0.0408
Beech	950	7,235	0.1161
Chestnut	1,426	6,759	0.1742
Pedunculate oak	1,872	6,313	0.2287
Pyrenean oak	1,680	6,505	0.2053
Sessile oak	491	7,694	0.0600
Scots pine	842	7,343	0.1029

2.3 | Spatial predictor variables

A priori, we identified 19 climate, 13 soil, 13 topography/radiative and 7 species distribution model variables for the tree species analysed (in the case of the brown bear) which we hypothesized may influence the distribution of brown bear based on our knowledge of the species and the study area (Table 2). These variables have been previously used in different studies to assess species distribution models (Roberts *et al.*, 2014; Shirk *et al.*, 2018).

TABLE 2. Environmental variables considered as possible predictors for the distribution models during the 1960-1990 reference period and in 2050 and 2070 under two future emissions scenarios (RCP 4.5 and RCP 8.5). Variables are grouped by type, including climate, hydrography, population, roads, soil, topography/radiative and species distribution models.

Variable	Class	Description	Source	Brown bear	Vegetation species
BIO_01	Climate	Annual mean temperature	WorldClim	X	X
BIO_02		Mean diurnal temperature change (Mean of monthly (max temp - min temp))	WorldClim	X	X

BIO_03		Isothermality (BIO_02/BIO_07) (*100)	WorldClim	X	X
BIO_04		Temperature seasonality (standard deviation *100)	WorldClim	X	X
BIO_05		Max temperature of warmest month (˚C)	WorldClim	X	X
BIO_06		Min temperature of coldest month (˚C)	WorldClim	X	X
BIO_07		Temperature annual range (BIO_05-BIO_06) (˚C)	WorldClim	X	X
BIO_08		Mean temperature of wettest quarter (˚C)	WorldClim	X	X
BIO_09		Mean temperature of driest quarter (˚C)	WorldClim	X	X
BIO_10		Mean temperature of warmest quarter (˚C)	WorldClim	X	X
BIO_11		Mean temperature of coldest quarter (˚C)	WorldClim	X	X
BIO_12		Annual precipitation (mm)	WorldClim	X	X
BIO_13		Precipitation of wettest month (mm)	WorldClim	X	X
BIO_14		Precipitation of driest month (mm)	WorldClim	X	X
BIO_15		Precipitation seasonality (Coefficient of variation)	WorldClim	X	X
BIO_16		Precipitation of wettest quarter (mm)	WorldClim	X	X
BIO_17		Precipitation of driest quarter (mm)	WorldClim	X	X
BIO_18		Precipitation of warmest quarter (mm)	WorldClim	X	X
BIO_19		Precipitation of coldest quarter (mm)	WorldClim	X	X
BD	Soil	Bulk density of the fine earth fraction (< 2mm) (kg m^{-3})	SoilGrids250m		X
DB		Absolute deep to bed rock (cm)	SoilGrids250m		X
DB200		Depth to bedrock (R horizon) up to 200 cm (cm)	SoilGrids250m		X
CEC		Cation exchange	SoilGrids250m		X

		capacity (cmol+/kg)			
CF		Coarse fragments (volumetric %)	SoilGrids250m		X
CLAY		Percentage of clay (weight %)	SoilGrids250m		X
Ph_H2O		Soil Ph in H2O solution	SoilGrids250m		X
Ph_KCl		Soil Ph in KCl solution	SoilGrids250m		X
SAND		Percentage of sand (weight %)	SoilGrids250m		X
SC		Soil organic carbon content (mG/ha)	SoilGrids250m		X
SC_FEF		Soil organic carbon content (fine earth fraction) (g)	SoilGrids250m		X
SILT		Percentage of silt (weight %)	SoilGrids250m		X
R		Probability occurrence of R horizon (%)	SoilGrids250m		X
ASP	Topography/Radiative	Aspect	PNOA LiDAR	X	X
CU		Curvature	PNOA LiDAR	X	X
PLC		Plan Curvature	PNOA LiDAR	X	X
PRC		Profile Curvature	PNOA LiDAR	X	X
SLP		Slope	PNOA LiDAR	X	X
TSI		Terrain Shape Index	PNOA LiDAR	X	X
WI		Wetness Index	PNOA LiDAR	X	X
EDH		Euclidean distance to nearest hydrographic network (m)	PNOA LiDAR	X	X
EDP		Euclidean distance to nearest population (m)	INE	X	
EDR		Euclidean distance to nearest roads network (m)	PNOA LiDAR	X	
SR_SS		Solar radiation in summer solstice (WH/m^2)	PNOA LiDAR		X
SR_EQ		Solar radiation in equinox (WH/m^2)	PNOA LiDAR		X
SR_WS		Solar radiation in winter solstice (WH/m^2)	PNOA LiDAR		X
SDM_BL	SDM	Species distribution model of Blueberry		X	
SDM_BE		Species distribution model of Beech		X	
SDM_CH		Species distribution model of Chestnut		X	
SDM_PO		Species distribution model of Pedunculate oak		X	
SDM_PYO		Species distribution model of Pyrenean		X	

		oak			
SDM_SO		Spatial distribution model of Sessile oak		X	
SDM_SP		Spatial distribution model of Scots pine		X	
TOTAL VARIABLES				36	43

We obtained gridded data for all climate variables with a 30-arc second resolution (approximate 800 m) from WorldClim (Hijmans *et al.*, 2005) generated for the 1960–1990 historical period. The soil variables were compiled from the SoilGrids250m (Hengl *et al.*, 2017) which provide a collection of updatable soil property and class maps of the world at a 250 m spatial resolution based on machine learning algorithms. Topography/Radiative variables were based on a 30m resolution digital elevation model (DEM) provided by the Spanish National Plan for Aerial Orthophotography (PNOA; Fomento, 2015). We used the System for Automated Geoscientific Analyses (SAGA; Conrad *et al.*, 2015) Geographical Information System (GIS) software (version 3.0.0) to calculate each of the topography/radiative variables from the DEM. We resampled all climate, soil, and topography/radiative variable raster grids at 250m resolution by using the nearest neighbour method. Finally, we extracted the values of all variables at all sampled locations.

2.4 | Species distribution modelling

We fit species distribution models using the machine learning algorithm Random Forest (RF; Breiman, 2001). Random Forest is a broadly used classification and non-parametric regression approach that consists of building an ensemble of decision trees (Gislason, P.O. Benediktsson, J.A. Sveinsson, 2006). The success of this technique is based on the use of numerous trees, developed with different independent variables that are randomly selected from the complete original set of features (e.g. Deschamps *et al.*, 2012; Wang *et al.*, 2016). Random Forest also provides a measure of the importance of input features through random permutation, which can be used for feature ranking or selection (Genuer *et al.*, 2010; Immitzer *et al.*, 2016). In machine learning, spurious data features must be removed before a model is generated (Hall, 1999). Thus, the variables that are potentially the most important are selected. For that purpose, WEKA open source software (Hall *et al.*, 2009) used for fitting the RF algorithm, uses a wrapper methodology to select the subsample of variables since it usually produces the best results (Zhiwei & Xinghua, 2010). This methodology of feature selection process selects the subsample of variables using a learning algorithm as part of the evaluation function. The RF technique was applied several times since we consider a set of a 10-fold cross-validation (i.e. models were fitting using 90% of the data for training and the remaining 10% for model evaluation).

2.5 | Model assessment, projection and analysis for woody plants and bears

We evaluated model performance for each method and replicate in several ways, including receiver operator curve (AUC), Matthews Correlation Coefficient (MCC), True Skill Statistic (TSS; Allouche *et al.*, 2006), Cohen's Kappa (Cohen, 1968), specificity, and sensitivity. Calculating Cohen's Kappa required a binary model, which we created based on a threshold probability where sensitivity equalled specificity (i.e., we equally weighted errors of omission and commission). All modelling methods, as an output variable, report a probability of presence (PoP) for each species. To convert all other PoPs to a binary presence–absence output, a threshold PoP was selected for each species. To select a threshold for presence–absence delineation from the PoP data, the average of two methods was used: (1) the PoP that maximized the sum of sensitivity and specificity, and (2) the PoP that minimized the difference between the absolute values of sensitivity and specificity.

We projected the fitted models onto spatial projections at a 250 m resolution of the environmental variables reflecting two climate change scenarios, i.e. moderate and pessimistic (van Vuuren *et al.*, 2011; IPCC, 2013; Harris *et al.*, 2014; Dyderski *et al.*, 2017) for 2050 and 2070 under different emissions pathways. These scenarios are expressed by the representative concentration pathways (RCP), using values comparing the level of radiative forcing between the preindustrial era and 2100. The moderate scenario (RCP4.5) assumes: (a) climate policies limit greenhouse-related emissions and total radiative forcing is stabilized at 4.5Wm−2 in the year 2100 without ever exceeding that value in prior years (Thomson *et al.*, 2011); and (b) 650 ppm CO_2 and 1.0–2.6°C increase by 2100, and refers to scenario B1 of the IPCC AR4 guidelines. The pessimistic scenario (RCP8.5) assumes: (a) continued increases in greenhouse gases following recent trends, reaching a total radiative forcing of 8.5Wm−2 in the year 2100 (Riahi *et al.*, 2011); and (b) 1,350 ppm CO_2 and 2.6–4.8°C increase by 2100, and refers to scenario A1F1 of the IPCC AR4 guidelines (van Vuuren *et al.*, 2011; IPCC, 2013; Harris *et al.*, 2014; Dyderski *et al.*, 2017).

For the current and future scenarios, we used FRAGSTATS 4.2 (McGarigal *et al.*, 2016) to quantify the area of habitat and degree of habitat fragmentation based on the binary model. We quantified suitable habitat area in three ways, including total area (TA) in the study area, mean patch area (MPA), and largest patch index (LPI; the percentage of the landscape encompassed by the largest patch). Also, we quantified fragmentation using the aggregation index (AI), which equals 0 when suitable habitat is maximally disaggregated into single grid cell patches disconnected from all other patches and increases to 1 as suitable habitat is increasingly aggregated into a single, compact patch. We also quantified the degree of change for each future scenario relative to the 1960–1990 30-year normal, classifying habitat as gained, maintained or lost.

3 | RESULTS

Of the 28,874 sites surveyed, brown bears were present at 8,874 sites, resulting in a prevalence of 0.3073 (Table 1). As a result of the feature selection process, 19 of the 36 variables (Table 2) were selected as the optimal subset size by the Random Forest method (Table 3). Model performance was excellent (Table 4): AUC = 0.979, MCC = 0.828, TSS = 0.820, Kappa = 0.828. The sensitivity was 0.866 and specificity was 0.954. The functional form of the marginal response curve for brown bear with a relative importance of variables of >75%, including mean diurnal range (BIO_02), temperature seasonality (BIO_04), temperature annual range (BIO_07), mean temperature of warmest quarter (BIO_10), annual precipitation (BIO_12) and Euclidean distance to nearest hydrographic network (EDH), are shown in Figure 1.

FIGURE 1. Marginal response curves for the six variables included in the brown bear species distribution model and with a relative importance of variables >75% The normalized probability of presence (PoP) is shown as a function of each variable while holding all other variables at their median values at presence locations. The mean (black line) and standard deviation (grey area) of the probability of presence are shown.

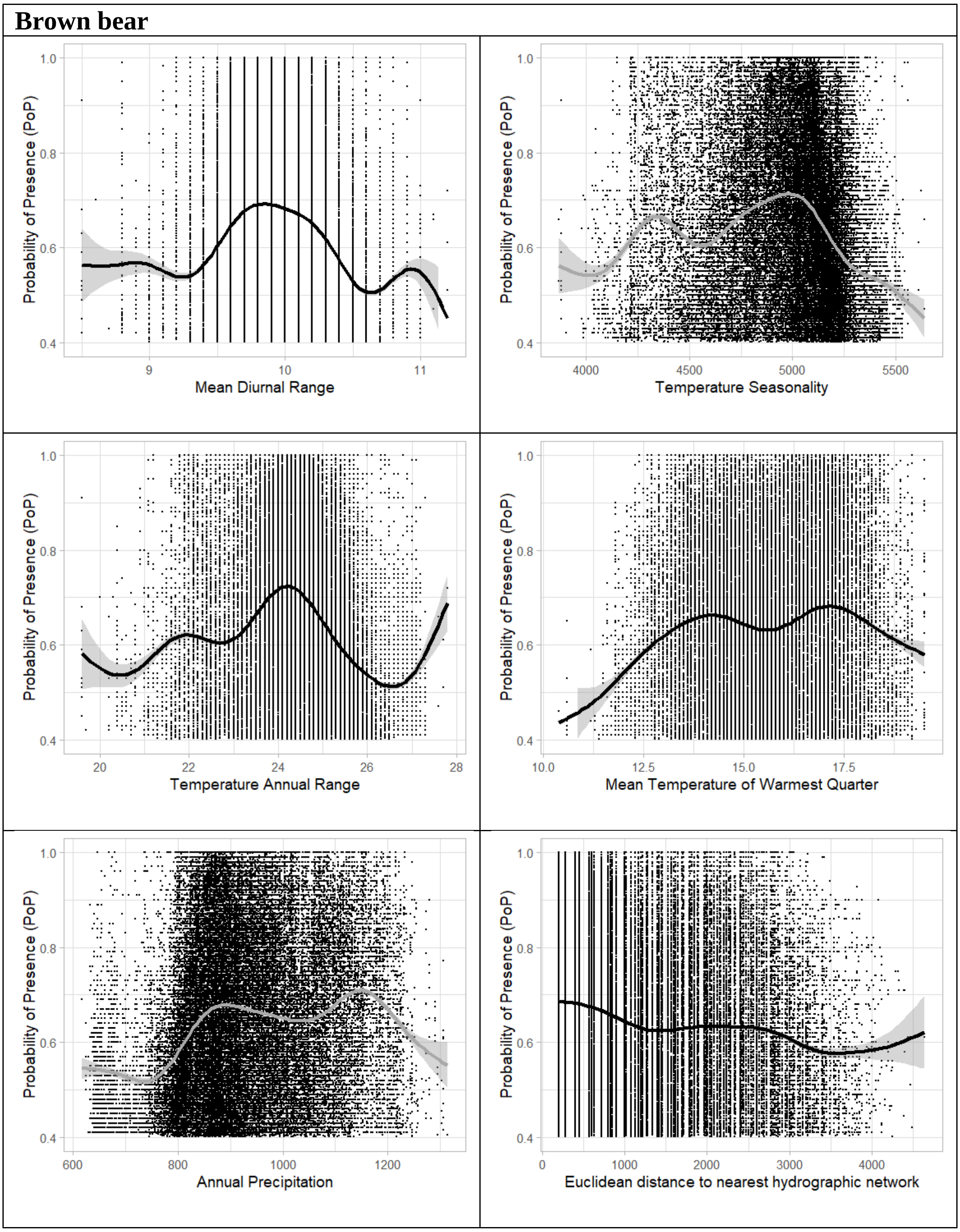

Brown bear
Probability of Presence (PoP)
Mean Diurnal Range
Temperature Seasonality
Temperature Annual Range
Mean Temperature of Warmest Quarter
Annual Precipitation
Euclidean distance to nearest hydrographic network

TABLE 3. Relative importance values calculated for environmental variables in species distribution models generated by the tested machine learning method (RF: random forest).

Variable	Class	Brown bear	Blueberry	Beech	Chestnut	Pedunculate oak	Pyrenean oak	Sessile oak	Scots pine
BIO_01	Climate				100.00	100.00		100.00	88.89
BIO_02		100.00	100.00	95.24	100.00	90.48	100.00		
BIO_03			70.59	100.00	94.74	90.48	95.45		100.00
BIO_04		92.86		76.19		71.43	81.82		83.33
BIO_05							86.36		77.78
BIO_06						71.43			
BIO_07		85.71	82.35	76.19	78.95		72.73	66.67	72.22
BIO_08						66.67			
BIO_09					73.68				
BIO_10		85.71				66.67			
BIO_11							68.18		
BIO_12		78.57		76.19	63.16	57.14			
BIO_13				66.67	57.89	47.62	54.55		
BIO_14				38.10	52.63	47.62	59.09		66.67
BIO_15		28.57	47.06	23.81	31.58	33.33	50.00	44.44	33.33
BIO_16						33.33	45.45		44.44
BIO_17		50.00	58.82			28.57			
BIO_18							36.36		
BIO_19		35.71	41.18	42.86		23.81	27.27	38.89	
BD	Soil				21.05	14.29	13.64		33.33
DB					10.53	9.52	13.64	0.00	5.56
DB200			5.88			4.76			38.89
CEC						38.10	36.36	27.78	50.00
CF				19.05	15.79	14.29	13.64		27.78
CLAY			0.00	14.29		23.81			27.78
Ph_H2O				42.86	26.32		27.27		38.89
Ph_KCl			23.53	33.33		23.81		16.67	33.33
SAND			0.00	0.00	5.26	14.29	13.64	5.56	0.00

SC			35.29		31.58		31.82		
SC_FEF						0.00	4.55		11.11
SILT				0.00	5.26	14.29			16.67
R					5.26	9.52	18.18		16.67
ASP	Terrain	57.14					13.64		
CU				19.05					
PLC		50.00		14.29					
PRC					0.00	4.76			
SLP			5.88	0.00		4.76	0.00		5.56
TSI									
WI		42.86			5.26	4.76	4.55		5.56
EDH		78.57			36.84		36.36		55.56
EDP		71.43							
EDR		71.43							
SR_SS				42.86					
SR_EQ			47.06	33.33	42.11	38.10			
SR_WS					36.84		40.91		
SDM_BL	SDM								
SDM_BE		0.00							
SDM_CH									
SDM_PO		0.00							
SDM_PYO		7.14							
SDM_SO		0.00							
SDM_SP		0.00							
TOTAL		19	13	20	22	29	26	8	23

TABLE 4. Model fit metrics for species distribution modelling (SDM) using RF applied to occurrence data within the Cantabrian Mountain range in North Spain. Model fit metrics included area under the receiver operator curve (AUC), Matthews correlation coefficient (MCC), true skill statistic (TSS), Cohen's kappa, sensitivity and specificity. Model fit was assessed on the training data used to fit the model as well as the withheld test data used for model evaluation. All the values represent the mean 10-fold cross-validation.

Model	Data set	AUC	MCC	TSS	Kappa	Sensitivity	Specificity	PoP
Brown Bear	Test	0.979	0.828	0.820	0.828	0.866	0.954	0.40
Blueberry	Test	0.935	0.281	0.524	0.230	0.559	0.965	0.20
Beech	Test	0.969	0.709	0.750	0.707	0.790	0.960	0.25
Chestnut	Test	0.885	0.441	0.541	0.423	0.658	0.883	0.35
Pedunculate oak	Test	0.884	0.482	0.537	0.475	0.673	0.864	0.40
Pyrenean oak	Test	0.877	0.491	0.601	0.470	0.732	0.869	0.35
Sessile oak	Test	0.921	0.329	0.525	0.290	0.573	0.952	0.30
Scots pine	Test	0.951	0.625	0.747	0.611	0.798	0.949	0.20

In the case of the seven plants species, prevalence at the 8,185 sites surveyed varied from 0.0408 (Blueberry) to 0.2287 (Pedunculate oak). As a result of the feature selection process, from 8 (Sessile oak) to 29 (Pedunculate oak) of the 43 variables (Table 2) were selected as the optimal subset size by the RF method (Table 3). The achieved accuracies of the classification models for the seven plants species were good (Table 4): AUC varied from 0.877 (Pedunculate oak) to 0.969 (Beech), MCC varied from 0.281 (Blueberry) to 0.709 (Beech), TSS varied from 0.524 (Blueberry) to 0.750 (Beech), sensitivity varied from 0.559 (Blueberry) to 0.790 (Beech), and specificity varied from 0.864 (Pedunculate oak) to 0.965 (Beech).

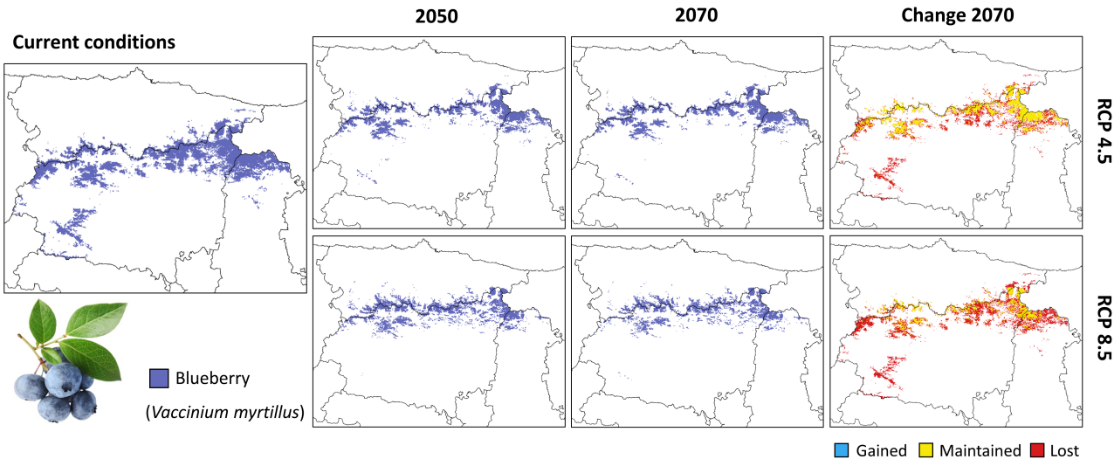
The functional form of the marginal response curves varied among the plants species analysed (Supplemental File 2); where the climate variables were the most significant ones.

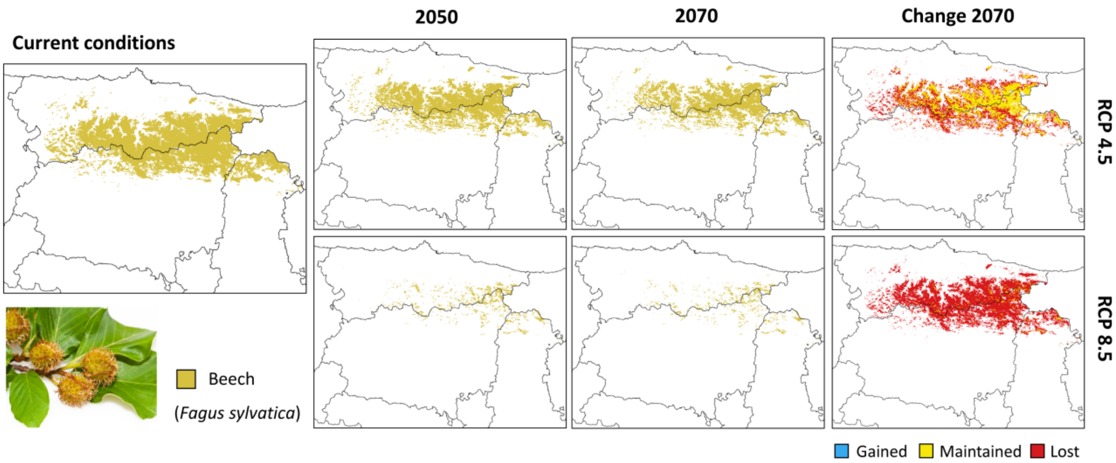
Beech forests in the Cantabrian Mountains appeared to be the most affected under the two scenarios (RPC 4.5 and 8.5, for both 2050 and 2070), as they were reduced by the half under the moderate scenario and almost disappeared under the pessimistic one (Table 5). The range of blueberries was also contracted to half its current distribution, whereas range contractions >50% were exhibited by pedunculate and sessile oaks. The latter almost disappeared under the pessimistic scenario for 2070 (Table 5). Range extensions of chestnuts and Scots pines only slightly increased/decreased (Table 5). These vegetation shifts under future climate scenarios for 2050 and 2070 are all reflected in the marked changes in distribution (mean latitude and altitude), total area and fragmentation (mean patch area, largest patch index and aggregation index) of the plant species distribution (Supplemental Files 2 and 3), such that under the most extreme future scenario (RCP 8.5) there is generally little overlap between current and future distributions (Supplemental File 3).

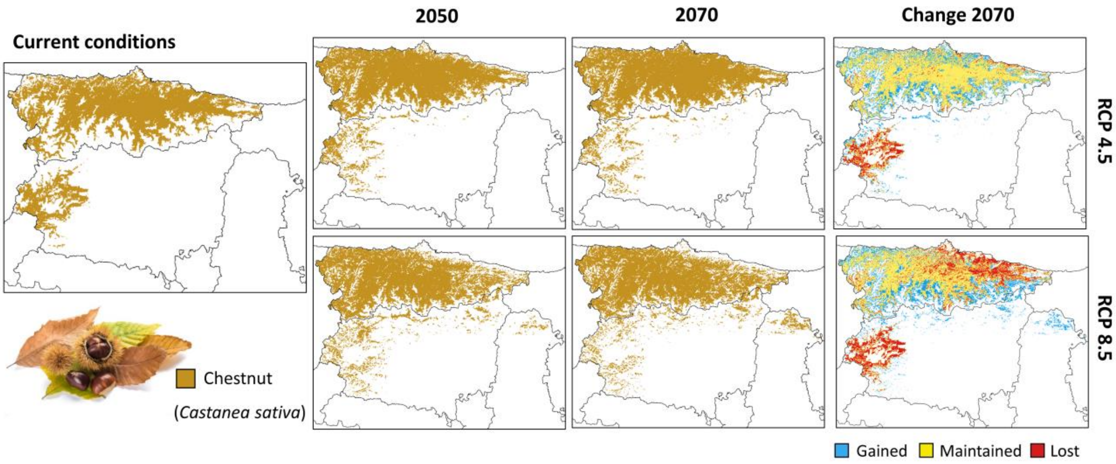
As a consequence of the extensive range contractions of most of the forest cover and blueberries in the Cantabrian Mountains, the brown bear population appeared to drastically lose its geographic range in the future (Figure 2), which: (a) is reduced by approximately half under the moderate scenario, for both 2050 and 2070; and (b) showed a dramatic contraction under the pessimistic scenario, for both 2050 (24% of the current range only) and 2070 (12%; Table 5). In addition to the range reduction, the brown bear population also showed a range shift towards the north (Figure 2), which may be mostly explained by: (a) the range shift of chestnuts towards the north; (b) the range maintenance of the Pyrenean and pedunculate oaks mainly in the north; and (c) the disappearance of blueberry, beach and sessile oak from the current brown bear distribution range (Figure 2).

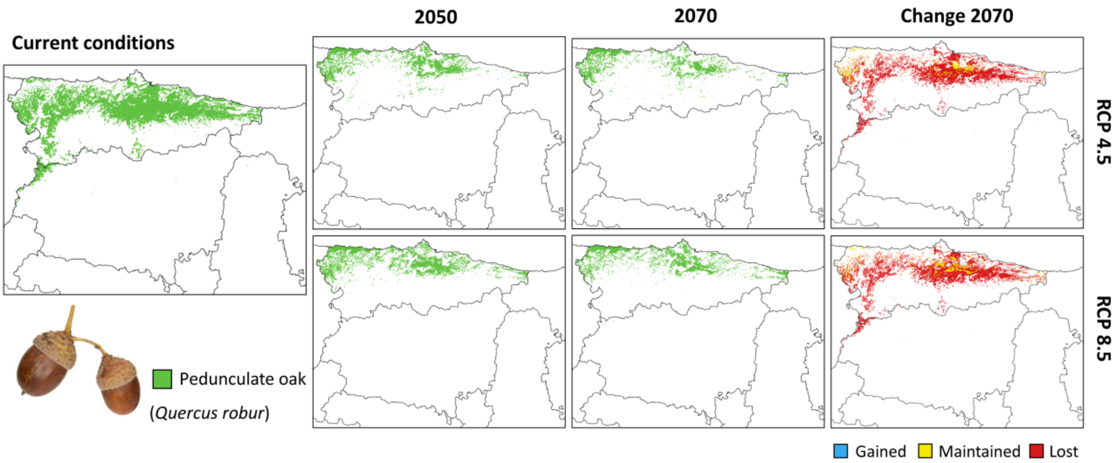
Under both RCP 4.5 and RCP 8.5, the lower and the higher emission scenarios respectively, latitudinal shifts and the aggregation index of the brown bear population only showed marginal changes (Figure 3). However, all the other parameters decreased considerably, including the total area (see also bear range contraction in Figure 2) and altitude occupied by bears, which decreased below 1000 m a.s.l. This predicted decrease in altitude supports the highlighted bear range shift towards the north (Figure 2), that is where altitudes decrease because the north of the study area is outside the bulk of the Cantabrian Mountains.

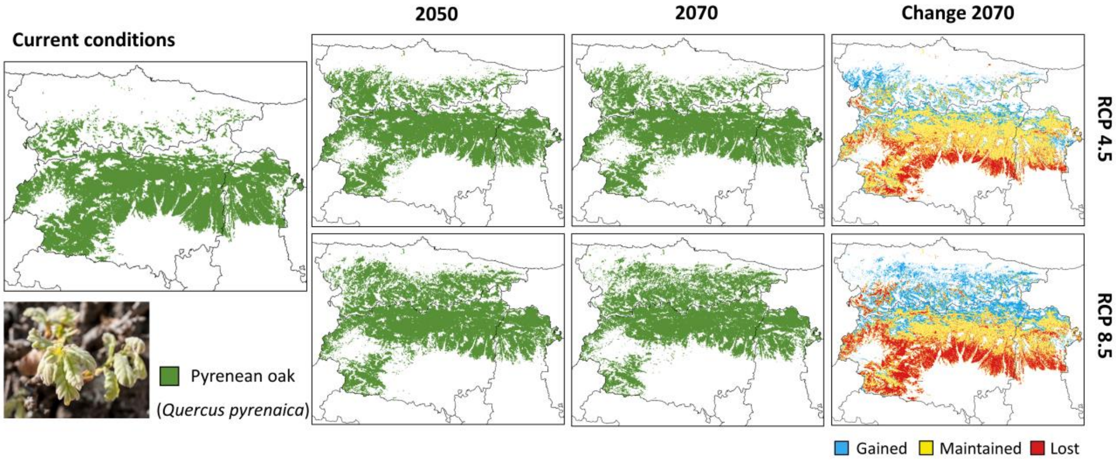
FIGURE 2. Projected changes in the future range of: (a) seven plant species (blueberry *Vaccinium myrtillus*, beech *Fagus sylvatica*, chestnut *Castanea sativa*, pedunculate oak *Quercus robur*, Pyrenean oak *Q. pyrenaica*, sessile oak *Q. petraea* and Scots pine *Pinus sylvestris*) that represent an important food resource and/or shelter for the brown bear in the Cantabrian Mountains (NW Spain); and (b) the Cantabrian brown bear population. For each species the following are shown: (a) the current distribution models; (b) the distribution models for 2050 and 2070, under both future emissions scenarios (RCP 4.5 and RCP 8.5); and (c) the range shifts in terms of gained (green), maintained (yellow) and lost (red) surface areas (grid cells) for 2070 only, under both RCP 4.5 and RCP 8.5. (The photos were downloaded from 123RF ROYALTY FREE STOCK PHOTOS, http://www.123rf.com; blueberry: ID16687172, sedneva; beech: ID9763793, Alfio Scisetti; chestnut: ID90445888, Alfio Scisetti; pedunculate oak: ID10696871, Ralf Neumann; Pyrenean oak: ID31492439, Israel Hervás; sessile oak: ID12474697, Israel Hervás; Scots pine: ID63105314, Juha Remes; brown bear: ID7250879, Eric Isselee).

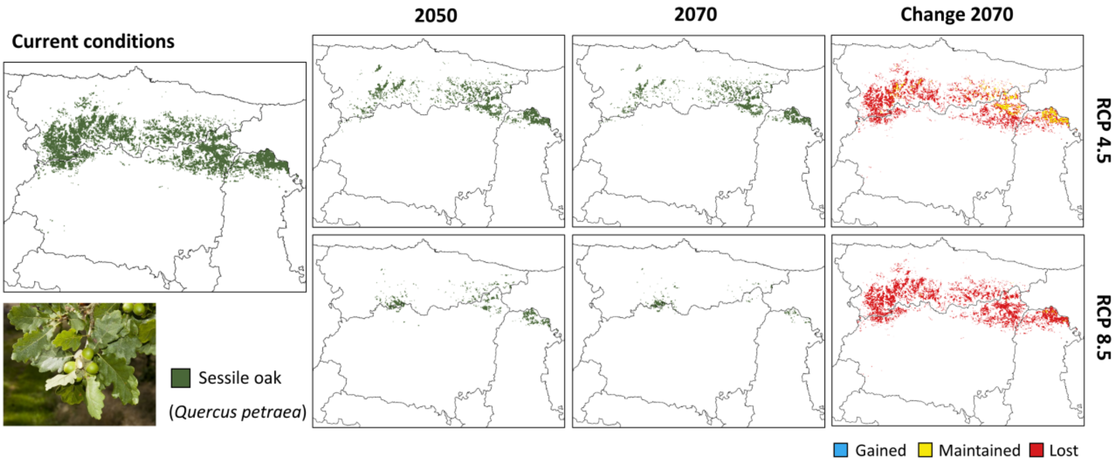

Current conditions
2050
2070
Change 2070
RCP 4.5
RCP 8.5
Blueberry
(Vaccinium myrtillus)
Gained
Maintained
Lost

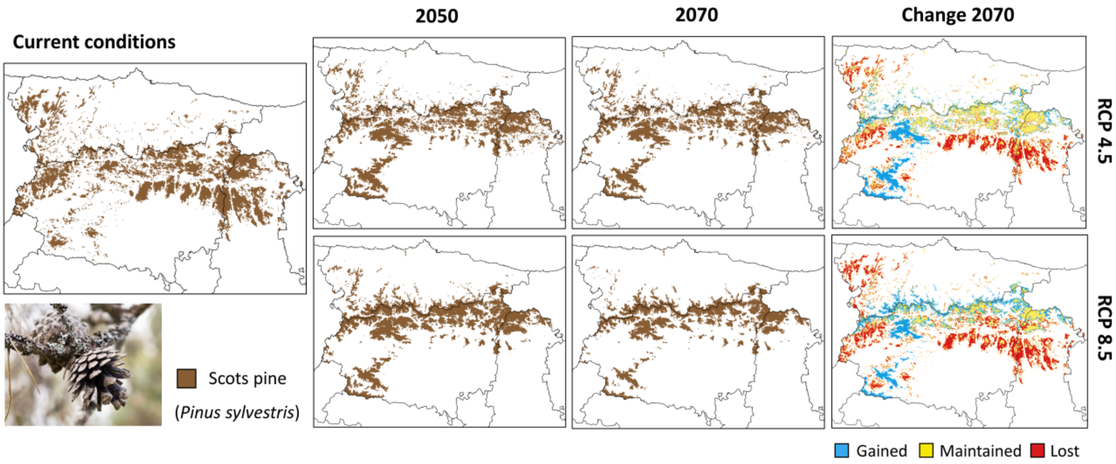

Current conditions
2050
2070
Change 2070
RCP 4.5
RCP 8.5
Beech
(Fagus sylvatica)
Gained
Maintained
Lost

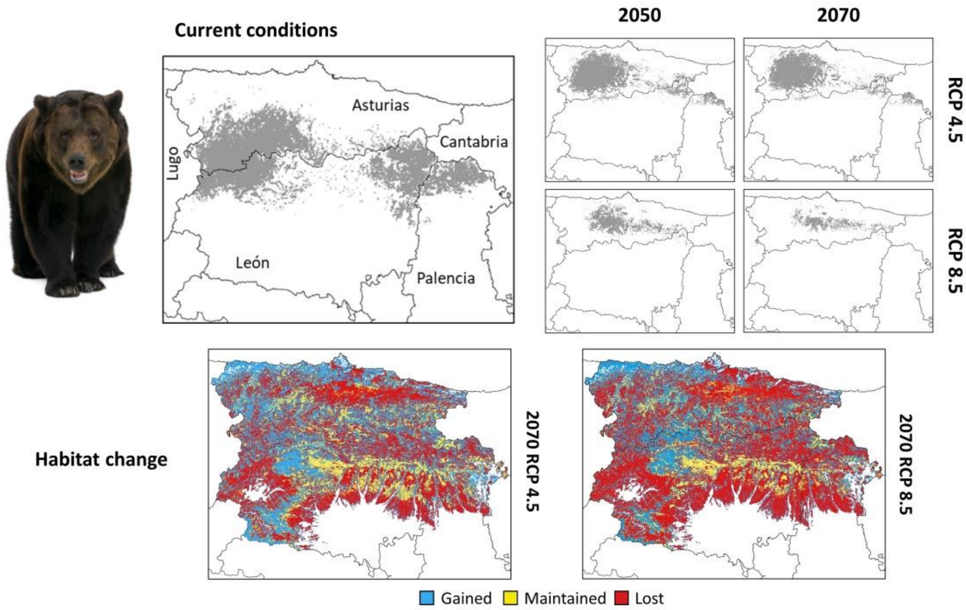

Current conditions
2050
2070
Change 2070
RCP 4.5
RCP 8.5
Chestnut
(Castanea sativa)
Gained
Maintained
Lost


Current conditions
2050
2070
Change 2070
RCP 4.5
RCP 8.5
Pedunculate oak
(Quercus robur)
Gained
Maintained
Lost


Current conditions
2050
2070
Change 2070
RCP 4.5
RCP 8.5
Pyrenean oak
(Quercus pyrenaica)
Gained
Maintained
Lost


Current conditions
2050
2070
Change 2070
RCP 4.5
RCP 8.5
Sessile oak
(Quercus petraea)
Gained
Maintained
Lost





At sites where brown bear were present, the distribution of the four climate variables shifts under the two future climate scenarios (RCP 4.5 and 8.5) for 2050 and 2070 (Figure 4). The future projections reveal a large shift towards warmer summer temperatures (BIO_10). The future projections also reveal a shift towards less annual precipitation (BIO_12), although the magnitude is small compared to that of the temperature-related variables (Supplemental File 4).

FIGURE 3. Changes in the distribution (mean latitude and altitude), area (total area), fragmentation (mean patch area), largest patch index (i.e. the percent of the bear population encompassed by the single largest patch) and aggregation index (a measure of fragmentation that varies from 0 to 100, with zero reflecting conditions where all occupied grid cells are maximally dispersed from each other across the landscape) of the brown bear population in the Cantabrian Mountains, under five scenarios: (1) the current reference period; (2) 2050 under the RCP 4.5 emissions scenario; (3) 2050 under the RCP 8.5 emissions scenario; (4) 2070 under the RCP 4.5 emissions scenario; and (5) 2070 under the RCP 8.5 emissions scenario.

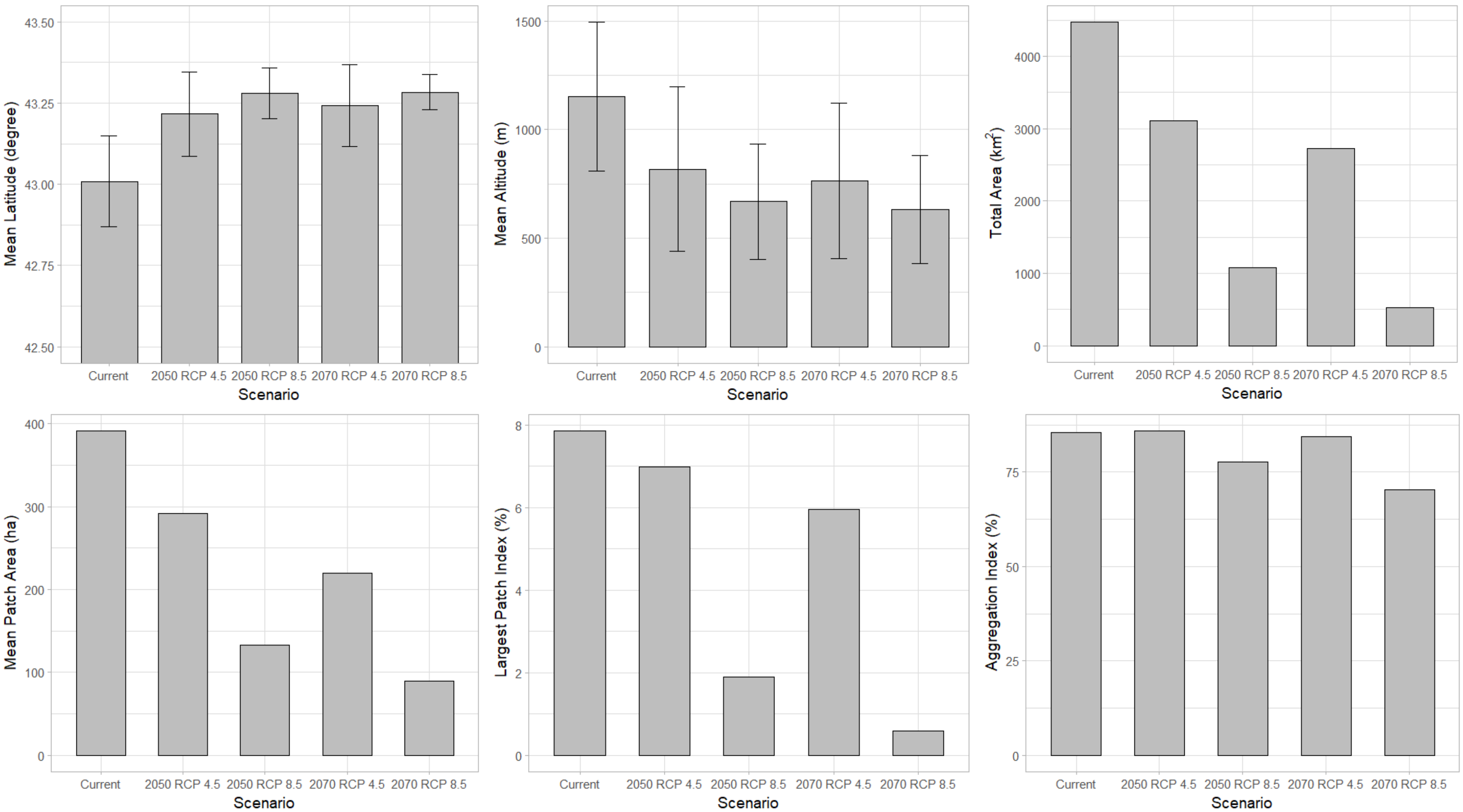
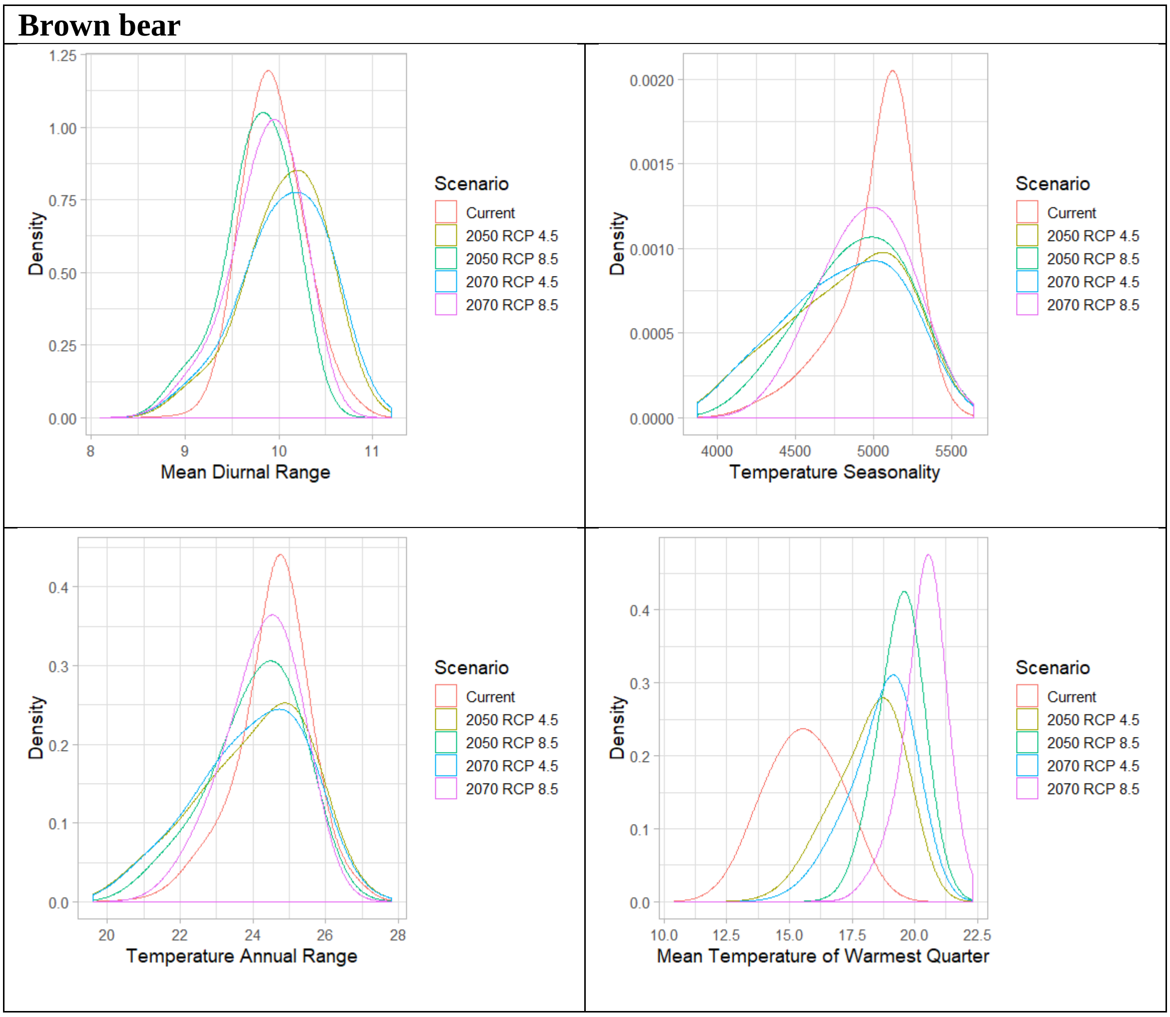
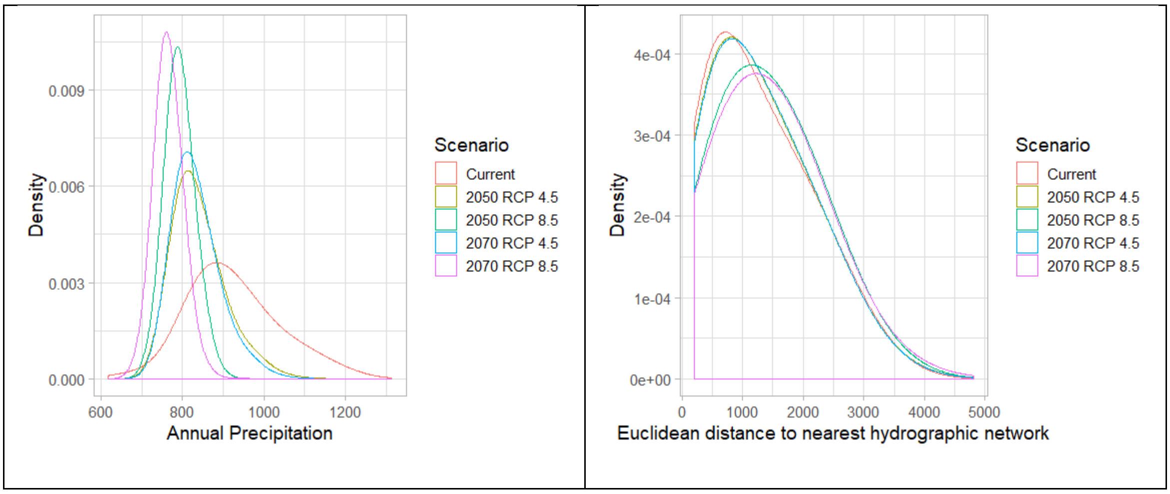

Mean Latitude (degree)
Mean Altitude (m)
Total Area (km2)
Mean Patch Area (ha)
Largest Patch Index (%)
Aggregation Index (%)
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5

TABLE 5. Extension (km^2 and %) of range contractions and expansions (+%) of the brown bear and the seven plant species used by bears as food and shelter in the Cantabrian Mountains under five scenarios: (1) the current reference period; (2) 2050 under the RCP 4.5 emissions scenario; (3) 2050 under the RCP 8.5 emissions scenario; (4) 2070 under the RCP 4.5 emissions scenario; and (5) 2070 under the RCP 8.5 emissions scenario.

	Brown bear		**Blueberry**		**Beech**		**Chestnut**		**Pedunculate oak**		**Pyrenean oak**		**Sessile oak**		**Scots pine**	
	Km^2	%	Km^2	%	Km^2	%	Km^2	%	Km^2	%	Km^2	%	Km^2	%	Km^2	%
Scenario																
Current	4476		2621		4861		5676		2754		9231		2177		3662	
2050 RCP 4.5	3105	69	1557	59	3202	66	6577	+16	788	29	9338	+1	641	29	3714	+1
2050 RCP 8.5	1079	24	1325	51	302	6	5797	+2	908	33	9385	+2	218	10	4066	+11
2070 RCP 4.5	2729	61	1580	60	2472	51	6855	+21	611	22	8963	97	481	22	3391	93
2070 RCP 8.5	527	12	1090	42	225	5	5812	+2	708	26	8460	92	80	4	3013	82

FIGURE 4. Distribution of climate variables at sites where brown bears are present in the Cantabrian Mountains, under five scenarios: (1) the current reference period; (2) 2050 under the RCP 4.5 emissions scenario; (3) 2050 under the RCP 8.5 emissions scenario; (4) 2070 under the RCP 4.5 emissions scenario; and (5) 2070 under the RCP 8.5 emissions scenario.





4 | DISCUSSION

Our simulations suggest that the geographic range of the seven plant species used by brown bears as food and shelter in the Cantabrian Mountains might respond in different ways under future climate warming, with most bear resources reducing their range. As a consequence, the available brown bear range in the Cantabrian Mountains is expected to reduce (Figure 2) in the next fifty years, mostly due to the effect of climate change on vegetation range shifts.

Current wilderness areas of the Cantabrian Mountains are largely located in mountainous regions, which are expected to experience some of the largest climatic changes (Root *et al.*, 2003), with montane species being subject to increasing temperatures and changing precipitation regimes (Monzón *et al.*, 2011). For example, among the recognised effects of global warming, we know that: (a) drought reduces blueberry growth, as well as fruit size and maturation (Bădescu *et al.*, 2017), an effect that is expected to be stronger at the southern limit of its European geographic range, such as in northern Spain (Pato & Obeso, 2012); (b) beech forests are particularly affected by an increase in periods of drought in summer and heavy rains in autumn and spring, which cause oxygen depletion in the soil, as well as by their limited capability to take advantage of the increasing atmospheric CO_2 content (Rennenberg *et al.*, 2004; Müller-Haubold *et al.*, 2013; Latte *et al.*, 2016). Indeed, the beech is more drought sensitive than other European broadleaved tree species, such as oaks (e.g. *Quercus petraea* and *Q. robur*) (Dulamsuren *et al.*, 2017), which supports the extreme beech range contraction predicted by our model. Recent observations of long-term growth decline in beech forests at the southern edge of their distribution (Italy and northern Spain) have already been linked to drought effects associated with climate change (Müller-Haubold *et al.*, 2013; Dulamsuren *et al.*, 2017); and, as is widely recognized, (c) more severe climate change scenarios may also affect tree species otherwise relatively resistant, like pedunculate and sessile oaks (Doležal *et al.*, 2010; Dyderski *et al.*, 2017). In particular, sessile oak growth reduction is connected with water deficit, i.e. little growth in hot, dry conditions, especially for trees growing in an oceanic climate (Doležal *et al.*, 2010; Mérian *et al.*, 2014).

Range shifts of brown bear are expected to displace individuals from wilder mountainous areas towards more humanised ones, where we can expect an increase in conflicts and bear mortality rates. Indeed, the distribution range of Pyrenean and pedunculate oaks is expected to shift largely towards the north of Asturias (Figure 2), closer to lowlands, where the density of people and human infrastructures is highest. Here, the high density of crops, livestock, human settlements and roads may increase rates of human-bear conflict and mortality. A similar increase in bear-human conflict has been suggested for grizzlies in North America due to the reduction of whitebark pine *Pinus albicaulis* forests as a result of climate change (Mattson *et al.*, 2001; Schrag *et al.*, 2008). Without these forests, whitebark pine seeds become unavailable as a food source which induces grizzly to move to lower elevations to find alternative food sources, where they are more likely to experience conflicts with humans. Such anthropogenic causes of mortality, which have not been taken into account in our models, can be additive to bear range contraction and produce an even greater decline of the species during the 21st century. Additionally, the projected reduction of Cantabrian plant species might also: (a) modify the currently mostly vegetarian diet of bears (Naves *et al.*, 2006; Rodríguez *et al.*, 2007; Fernández-Gil, 2013b), which may replace less available fruits and acorns with more meat (Bastille-Rousseau *et al.*, 2017); and/or (b) increase the interest of bears in apiaries and crops. Both possibilities can increase the probability of local conflicts with humans and change the generally positive attitude that people currently have towards brown bears in the Cantabrian Mountains.

Three additional negative effects on bears may be expected as a consequence of the vegetation changes in the Cantabrian Mountains. First, because acorns constitute the bulk of the autumn and winter diet for this population (Naves *et al.*, 2006), a drastic reduction in oak forests may affect fat storage before den entry, which is essential for successful hibernation and cub production (Farley & Robbins, 1995b; Robbins *et al.*, 2012). Indeed, a decrease in acorn consumption may reduce protein intake from plant material, which might affect Cantabrian brown bears during hyperphagia (Rodríguez *et al.*, 2007). Bear reproduction might be even more affected by this low protein intake under the predicted warming climate. Yet, under future climate change scenarios, winter temperature is expected to increase and, consequently, energy demands of hibernating mammals will increase because the energetic costs of torpor increase, i.e. less energy can be allocated to reproduction during warm winters (Humphries *et al.*, 2002; Albrecht *et al.*, 2017). Secondly, under such a scenario of low acorn availability, current rates of intraspecific competition with other acorn consumers, i.e. wild ungulates such as the wild boar *Sus scrofa* and free-ranging livestock, may increase (Naves *et al.*, 2006; Rodríguez *et al.*, 2007). Thirdly, because the distances between oaks and blueberry bushes seem to be destined to increase due to both their range shift and contraction (Figure 2), bears might need to make larger displacements between seasons to find main trophic resources. For example, increased distances between the area inhabited by a typical summer food like blueberries and oak forests, where bears get most of their autumn food, may expose bears to greater risks than before (e.g. car collisions and increased energy consumption) because of the longer distances they need to cover during the hyperphagia period. Indeed, the distribution and availability of limited resources may be more spatially dispersed and, thus, may influence bear space use. When resources are not concentrated in space or time, individuals may require greater areas to gain the resources necessary to sustain their body size and successfully reproduce (Mangipane *et al.*, 2018).

Because human pressure (e.g. land use, fire) in human-modified landscapes is already stressing several mammal species, it may possibly enhance the negative influence that climate change will have (Maiorano *et al.*, 2011). For example, livestock grazing pressure has already been observed to impact bear consumption of *Vaccinium* shrubs in the Cantabrian Mountains because of their reduced availability (Rodríguez *et al.*, 2007; Fernández-Gil, 2013b). As a consequence, cattle numbers and/or periods of grazing should be reduced within the brown bear range in the Cantabrian Mountains, as already suggested by Naves *et al.* (2006), Rodríguez *et al.* (2007) and Fernández-Gil (2013).

We consider it important to highlight here one limitation of our study. In our projections species distributions are only determined by environmental factors controlling their niche (e.g. climate, soil and topography/radiative), whereas tree plant distributions may also be influenced by biotic interactions among species such as competition, predation, amensalism and mutualism, further modulated by abiotic disturbances like fires and forest management practices (Shirk *et al.*, 2018). Phenotypic plasticity and local adaptation may also modify rates of tree species contraction and expansion (Valladares *et al.*, 2014), but the magnitude of the projected range shift for some species might make relying on these natural mechanisms of resiliency alone insufficient. Evidently, our projections on the impact of climate change on the distribution and availability of bear food plant species cannot take into account potentially complex adaptive behavioural responses of bears, which are well-known habitat generalists (Roberts *et al.*, 2014). The wide nutritional niche of brown bears might allow them to cope with the nutritional challenges associated with changes in available food resources due to climate change (Roberts *et al.*, 2014; Coogan *et al.*, 2018). In spite of these caveats, our model predictions allow us to make inferences on possible general patterns of future plant range shifts and bear population dynamics under different climate scenarios. Yet, there is a strong need to develop forecasts of what could happen under different climate change scenarios given certain assumptions (e.g. Bond *et al.*, 2014; Li *et al.*, 2015) and, accepting the basic assumptions and limitations of predictive models, we regard our projections as a useful first step and plausible null model to rely on for future bear conservation, rather than assuming that the present distributions of brown bears and their resources will remain unchanged.

The expected reduction and shift of brown bears and their feeding resources/habitats in the Cantabrian Mountains will profoundly impact the conservation effectiveness of the current protected areas. Nevertheless, climate change will likely reduce the distributions of bears in these reserves. It is thus necessary to upgrade the spatial distribution of protected areas to improve species protection under the processes engendered by climate change (Hannah *et al.*, 2007). The integration of potential range shifts into conservation planning is a proactive way to confront the effect of climate change on vegetation and, consequently, on the animal species linked to the affected plant species. Conservation plans that overlook potential range shifts have poor expected outcomes for most species (Bond *et al.*, 2014; Li *et al.*, 2015). Indeed, projecting future scenarios of forest shifts given climate change predictions for the region can help inform conservation planning to mitigate bear food and shelter range contractions. For example, plant assisted colonization, i.e. intentionally moving species to climatically suitable locations outside their current ranges (Iverson & McKenzie, 2013), as well as assisted gene flow, are strategies being explored to maximize tree plant resistance and adaptation to a changing regional climate (Aitken *et al.*, 2008; Iverson & McKenzie, 2013; Travis *et al.*, 2013). For example, assisted gene flow might be used to introduce individuals with adaptive genotypes into populations that lack those traits (Aitken & Bemmels, 2016). Given that natural colonization is unlikely to occur within the projected range shift, assisted colonization into areas our study identified as suitable in the future may also be warranted (Vitt *et al.*, 2010). Thus, our results provide a preview of the potential future distribution of shrubs and tree species suitable for brown bear food and shelter, providing lead-time to enact forward-looking strategies designed to conserve forest ecosystems within the study area. The magnitude of the forest changes projected by our models emphasizes that, to conserve the Cantabrian brown bear population, conservation practices only focused on bears may not be appropriate; rather, we also need more dynamic conservation planning aimed to reduce the impact of climate change in the forested landscapes of the Cantabrian Mountains. One strategy is to accept the future changes in species ranges and to focus on those areas into which these species will move (Monzón *et al.*, 2011). Thus, together with conservation actions aimed at maintaining bears in their historical and current ranges, we encourage practices targeted at managing species range shifts and which start to conserve and manage those areas potentially favourable to be inhabited by bears as a consequence of the modifications due to climate change. As we cannot force plant species to remain in a geographical space that no longer represents their evolved climate envelope, or animal species to persist where their main resources have disappeared, a pre-emptive strategy based on climate change shifts may be better aligned with reality.

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AUTHOR CONTRIBUTION

VP & CAL-S conceived the study and gathered all the data; CAL-S conducted the data analyses; CAL-S and AN-F prepared the geodatabases; CAL-S and AZ-A prepared most of the figures; VP & CAL-S led the writing of the manuscript with suggestions and idea developments from all authors.

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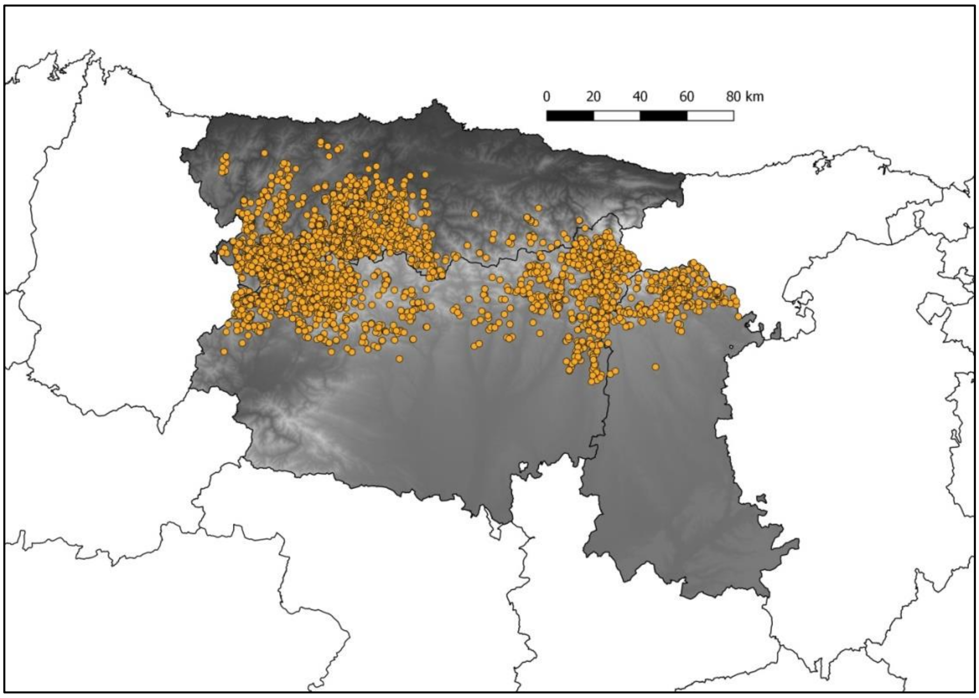
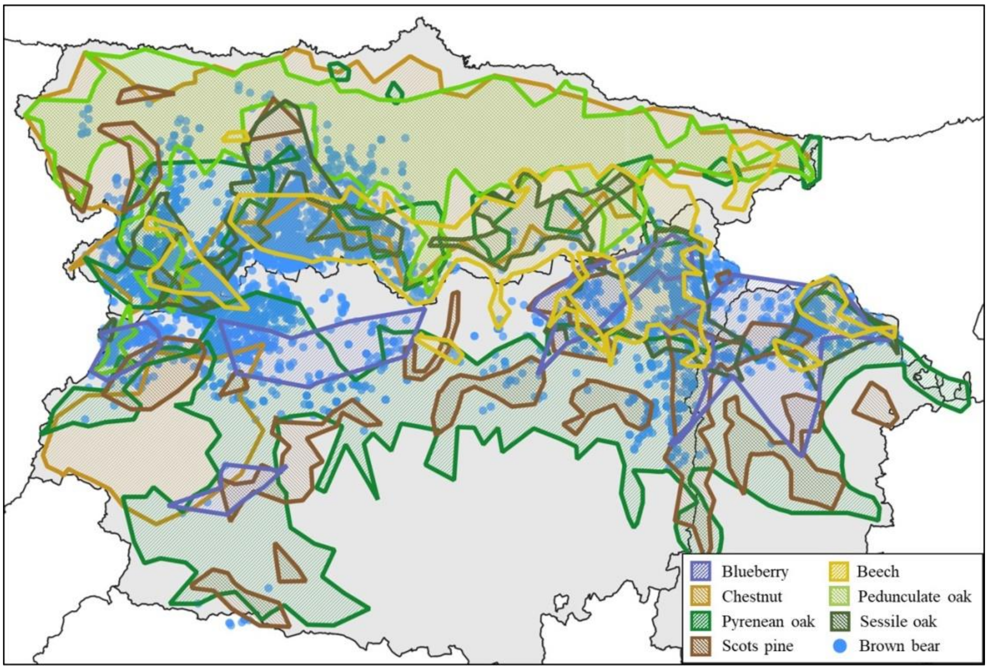
SUPPLEMENTAL FILES

SUPPLEMENTAL FILE 1. (A) The spatial distribution of the sampling effort for brown bear occurrence data (n = 8,784 locations), which covered the whole range of bear distribution in the Cantabrian Mountains.

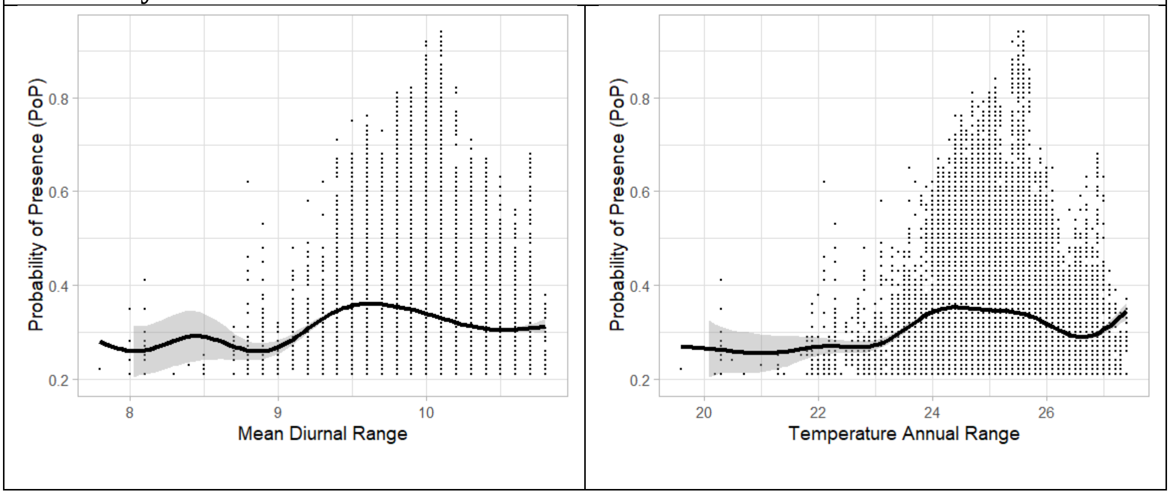


(B) The spatial distribution of plant species and brown bear locations.

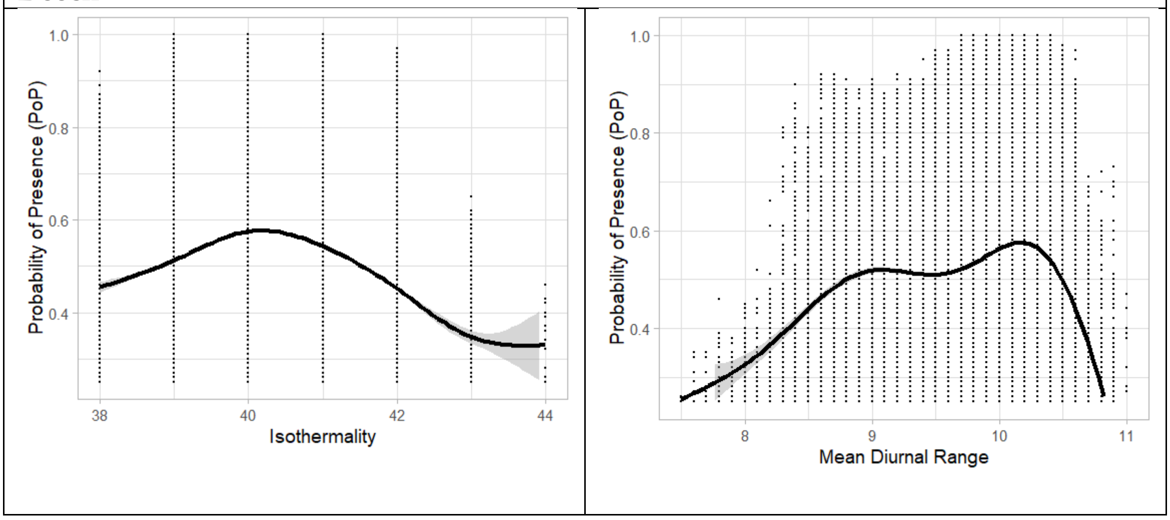


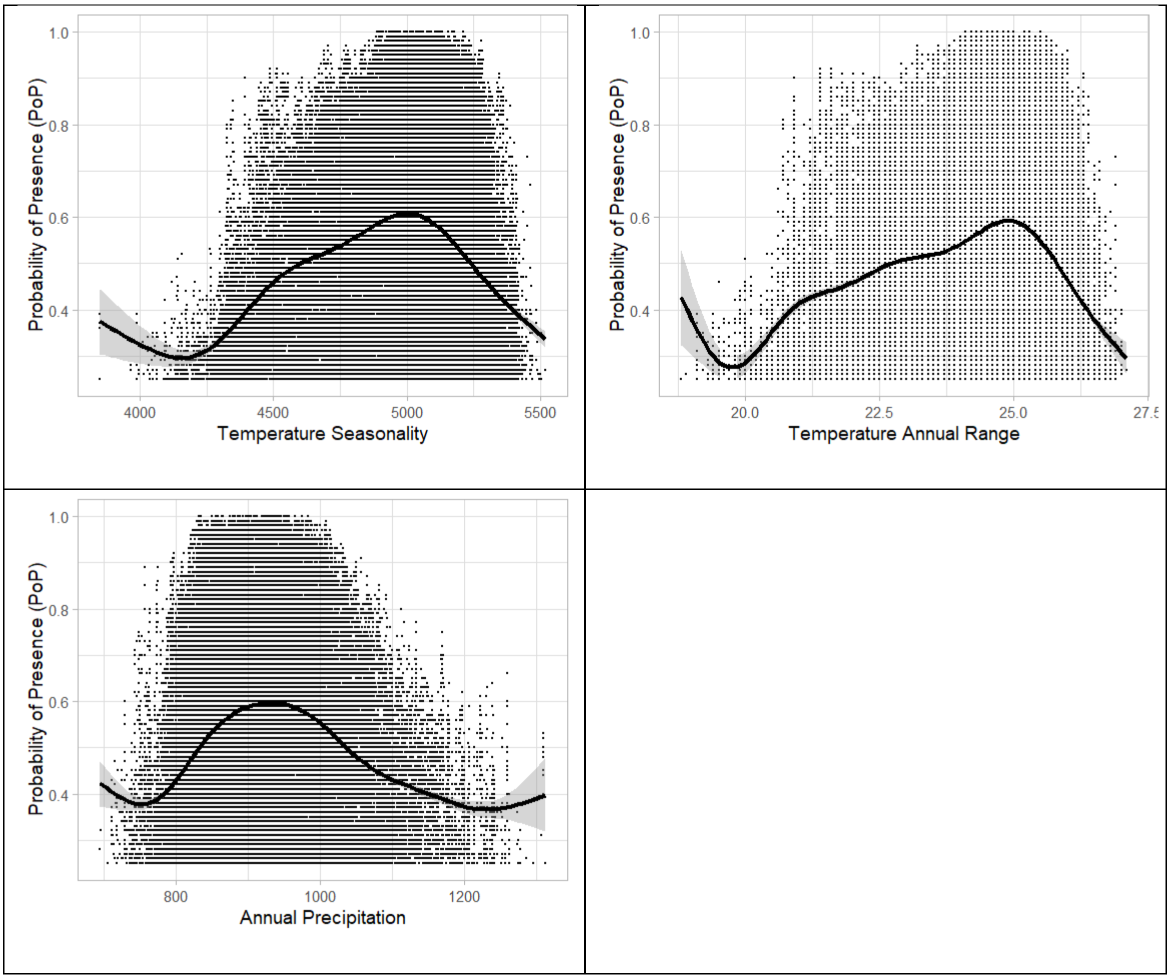
SUPPLEMENTAL FILE 2. Marginal response curves for the variables included in the seven plant species distribution models and with a relative importance of variables >75%. The normalized probability of presence (PoP) is shown as a function of each variable while holding all other variables at their median values at presence locations. The mean (black line) and standard deviation (grey area) of the probability of presence are shown.

Blueberry

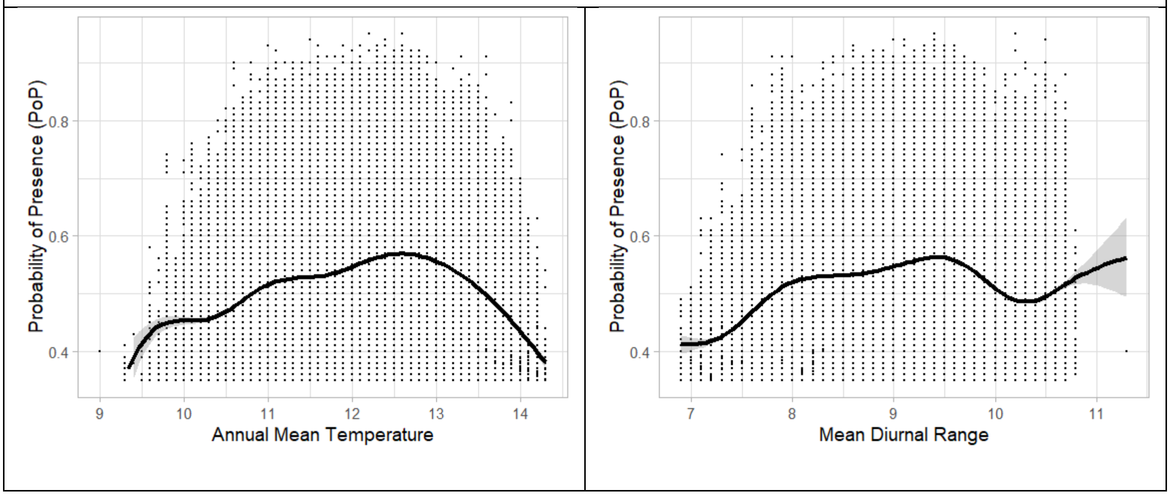


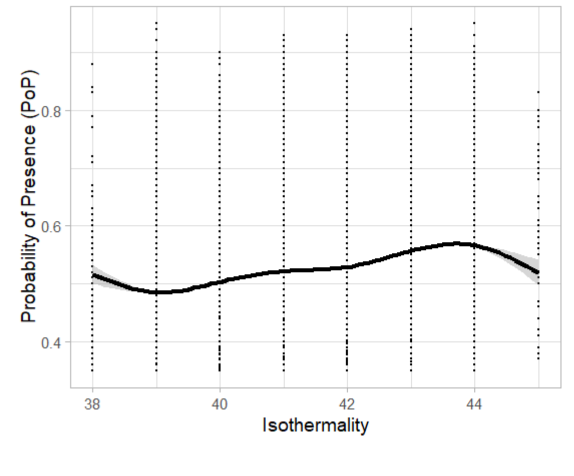
Beech

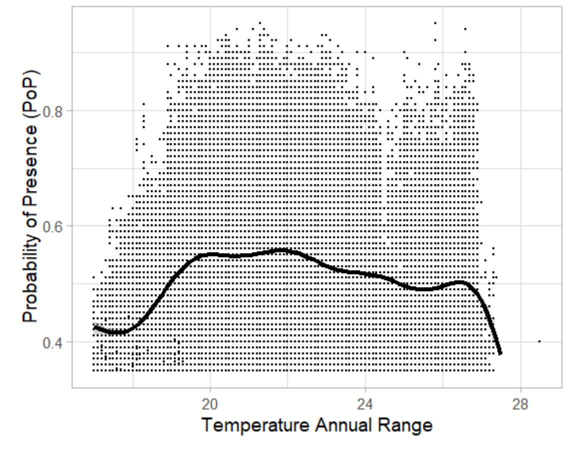



Probability of Presence (PoP)
1.0
0.8
0.6
0.4
4000
4500
5000
5500
Temperature Seasonality
22.5
20.0
25.0
27.5
Temperature Annual Range
800
1000
1200
Annual Precipitation

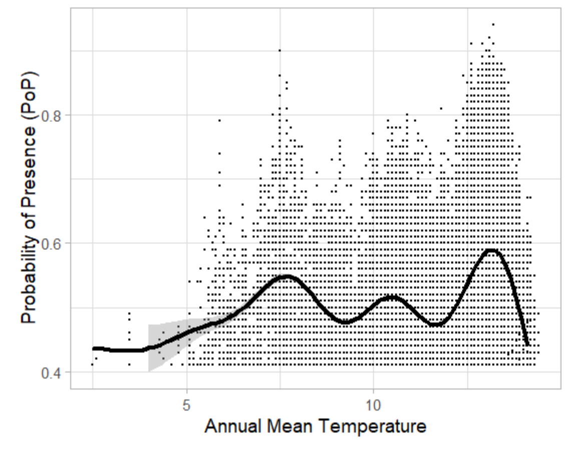
Chestnut

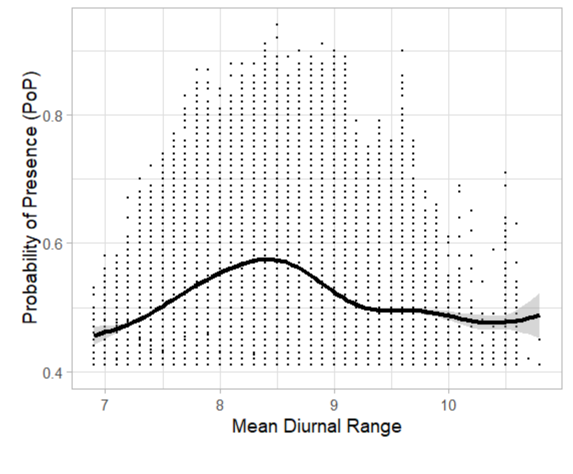

Probability of Presence (PoP)
0.8
0.6
0.4
9
10
11
12
13
14
Annual Mean Temperature
7
8
9
10
11
Mean Diurnal Range

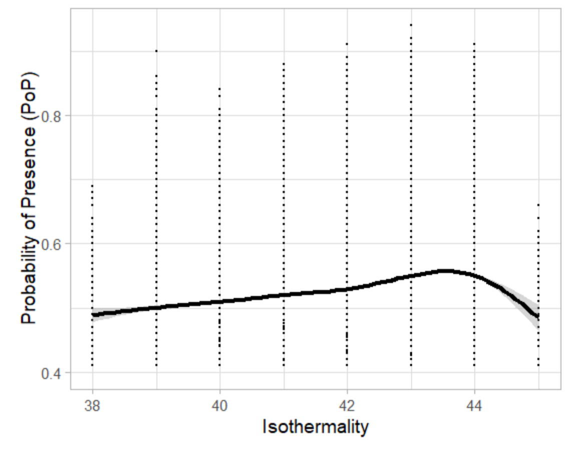




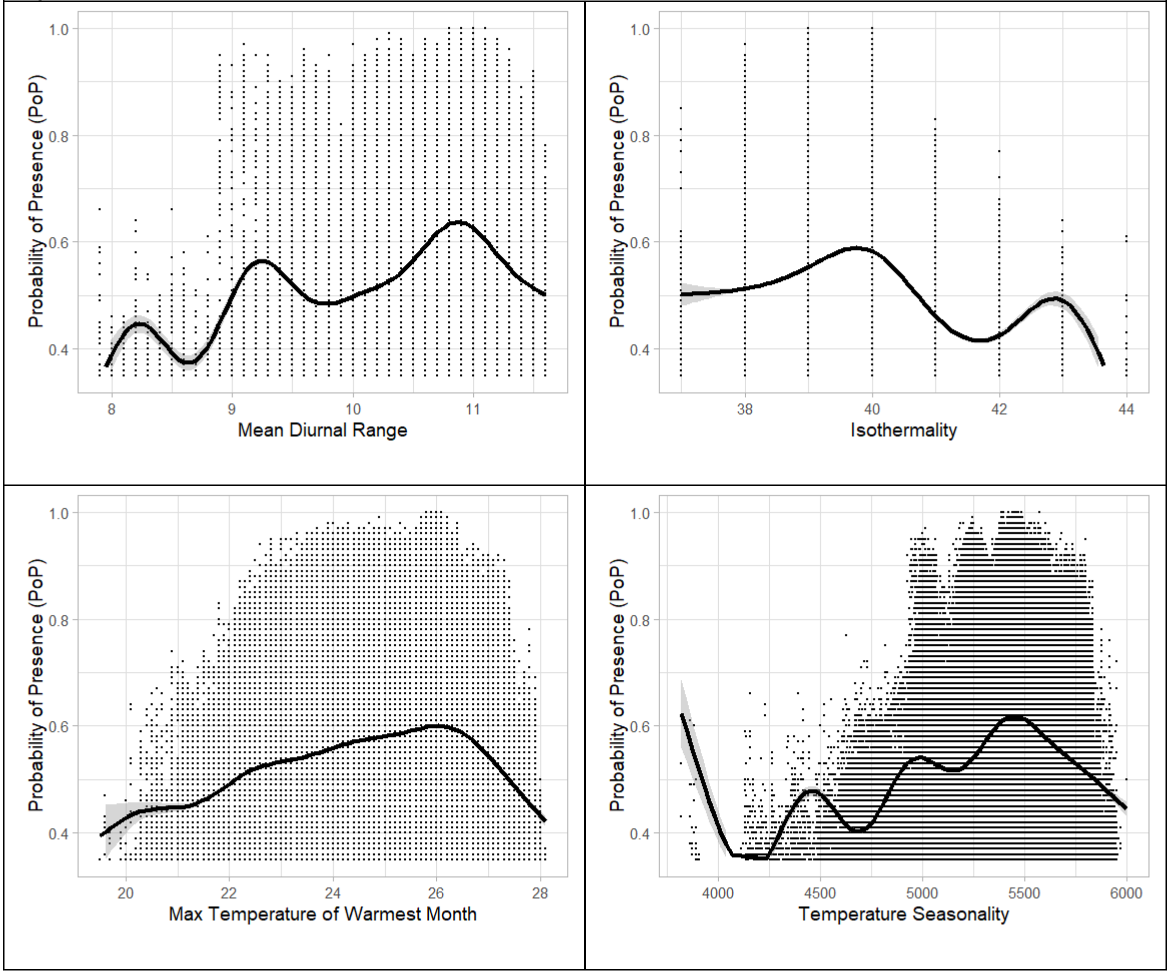
Pedunculate oak



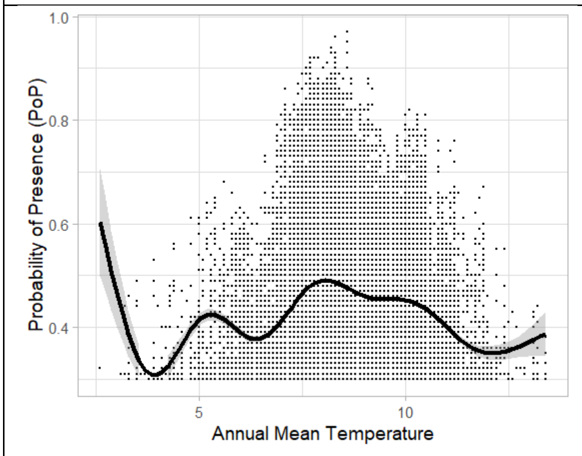




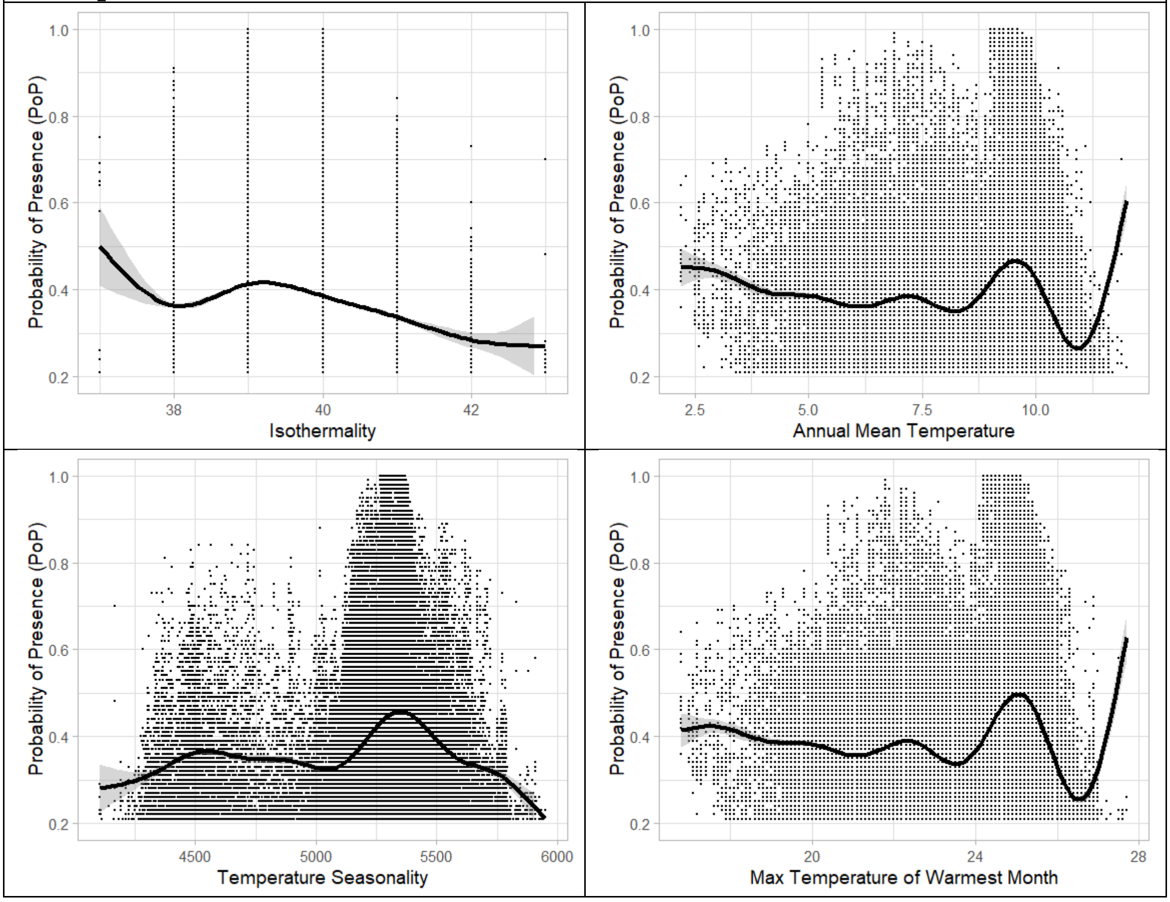
Pyrenean oak



Sessile oak

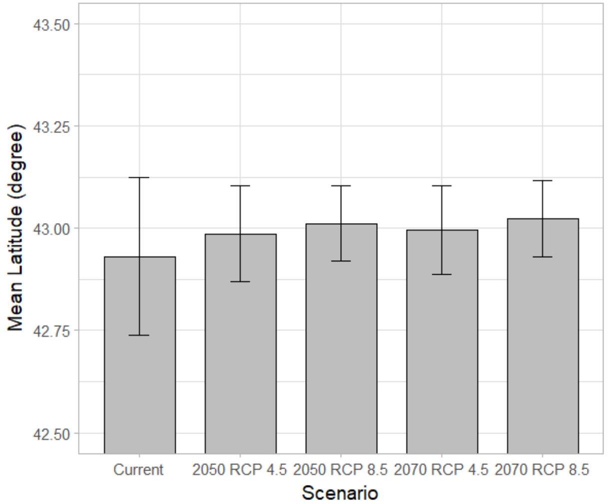


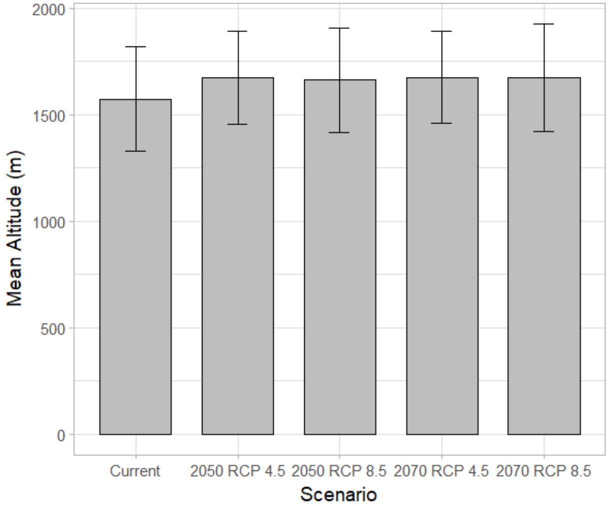
Scots pine

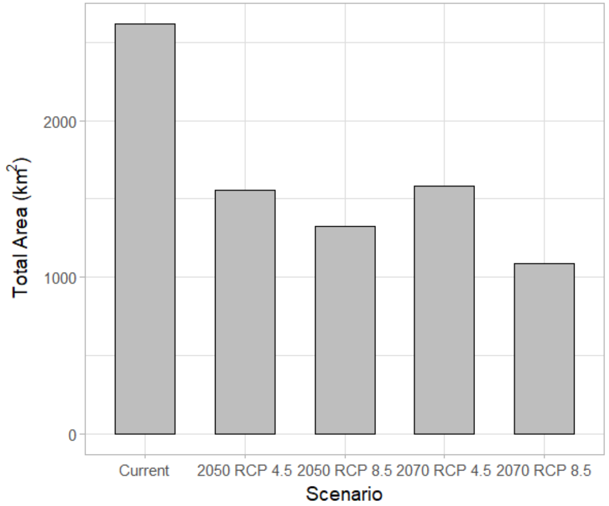

Probability of Presence (PoP)
1.0
0.8
0.6
0.4
0.2
38
40
42
Isothermality
2.5
5.0
7.5
10.0
Annual Mean Temperature
4500
5000
5500
6000
Temperature Seasonality
20
24
28
Max Temperature of Warmest Month

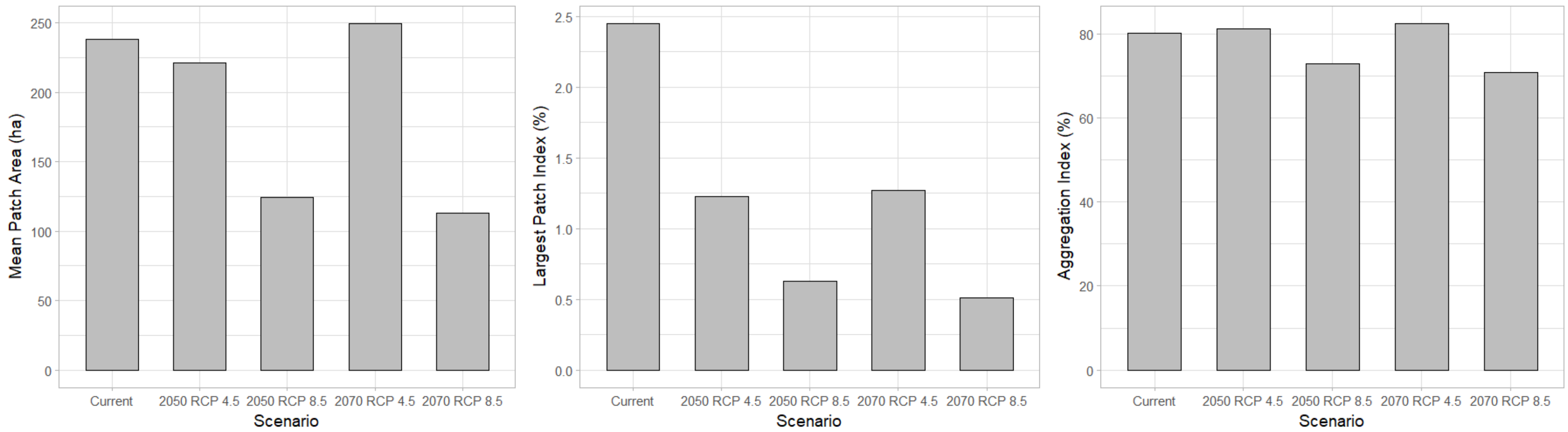
SUPPLEMENTAL FILE 3. Changes in the distribution (mean latitude and altitude), area (total area) and fragmentation (mean patch area; largest patch index, i.e. the percent of the study area occupied by the single largest patch; and aggregation index, a measure of fragmentation that varies from 0 to 100, with zero reflecting conditions where all suitable grid cells are maximally dispersed from each other across the landscape) of the habitat for the seven plant species used by brown bears as food and shelter in the Cantabrian Mountains, under five scenarios: (1) the current reference period; (2) 2050 under the RCP 4.5 emissions scenario; (3) 2050 under the RCP 8.5 emissions scenario; (4) 2070 under the RCP 4.5 emissions scenario; and (5) 2070 under the RCP 8.5 emissions scenario.

Blueberry

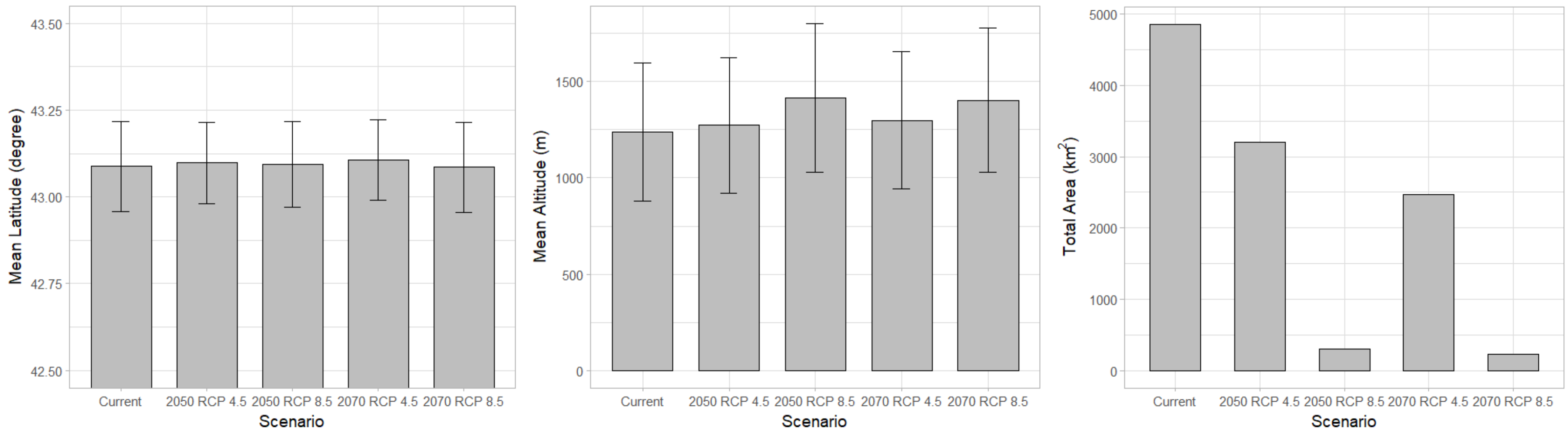


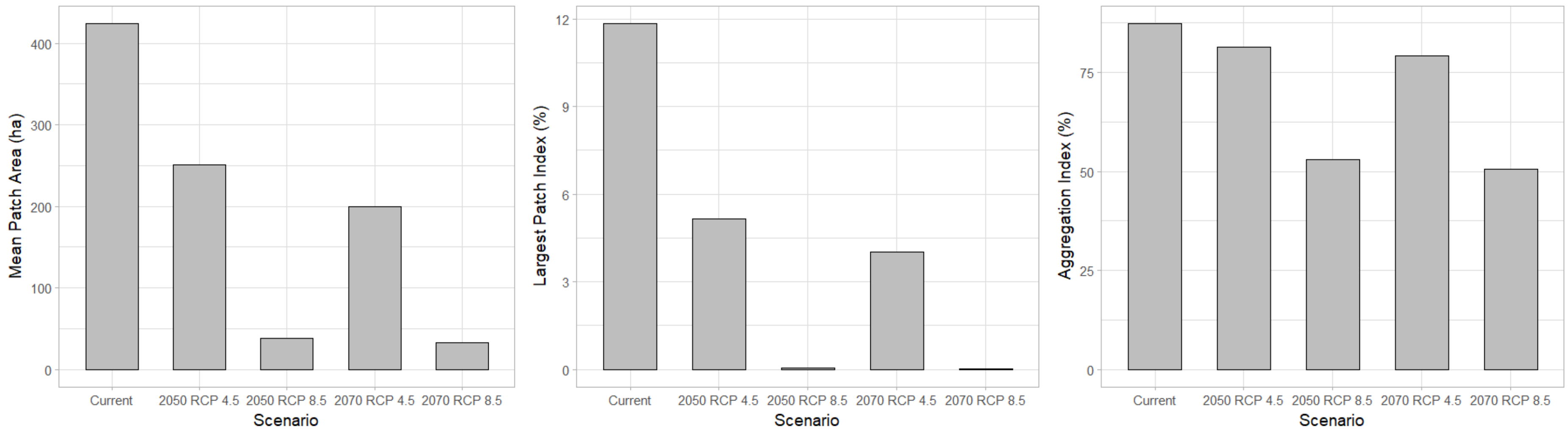




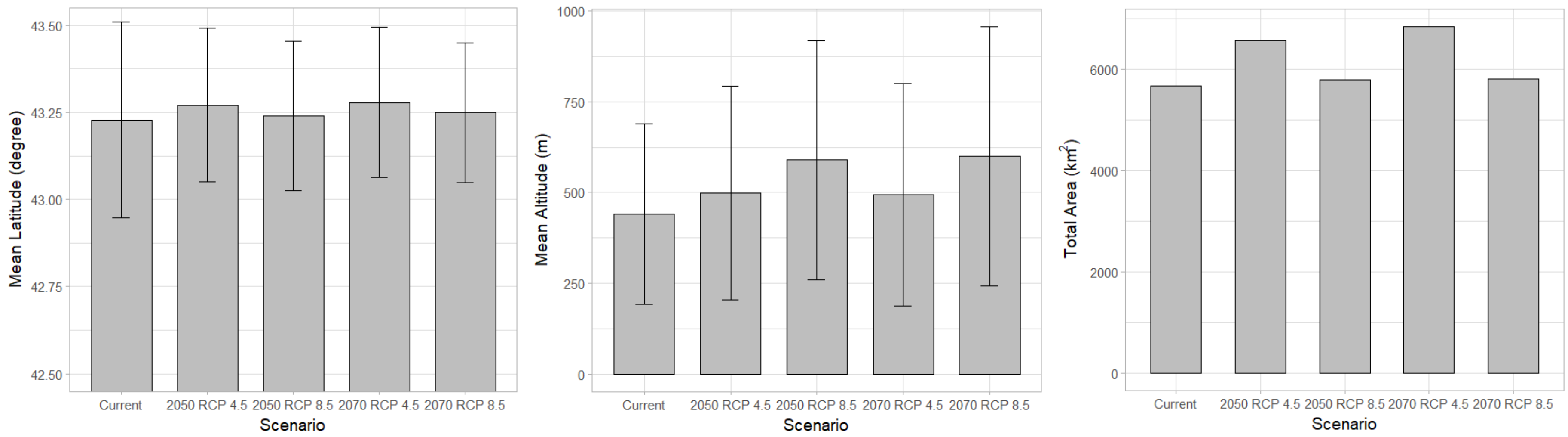

Mean Patch Area (ha)
250
200
150
100
50
0
Largest Patch Index (%)
2.5
2.0
1.5
1.0
0.5
0.0
Aggregation Index (%)
80
60
40
20
0
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Scenario

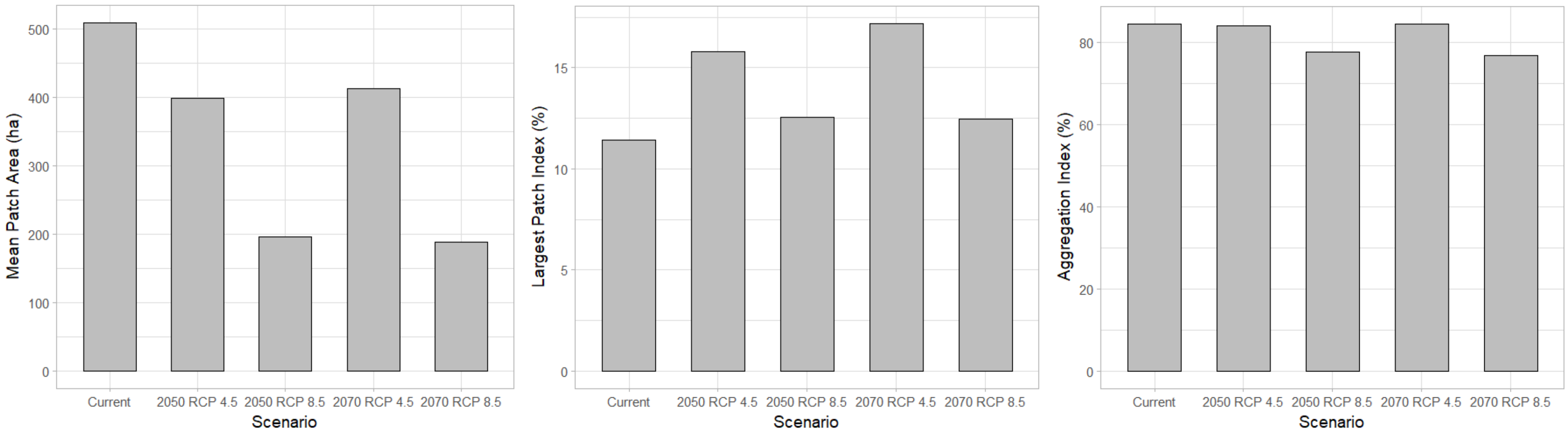
Beech


Mean Latitude (degree)
43.50
43.25
43.00
42.75
42.50
Mean Altitude (m)
1500
1000
500
0
Total Area (km^2)
5000
4000
3000
2000
1000
0
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Scenario

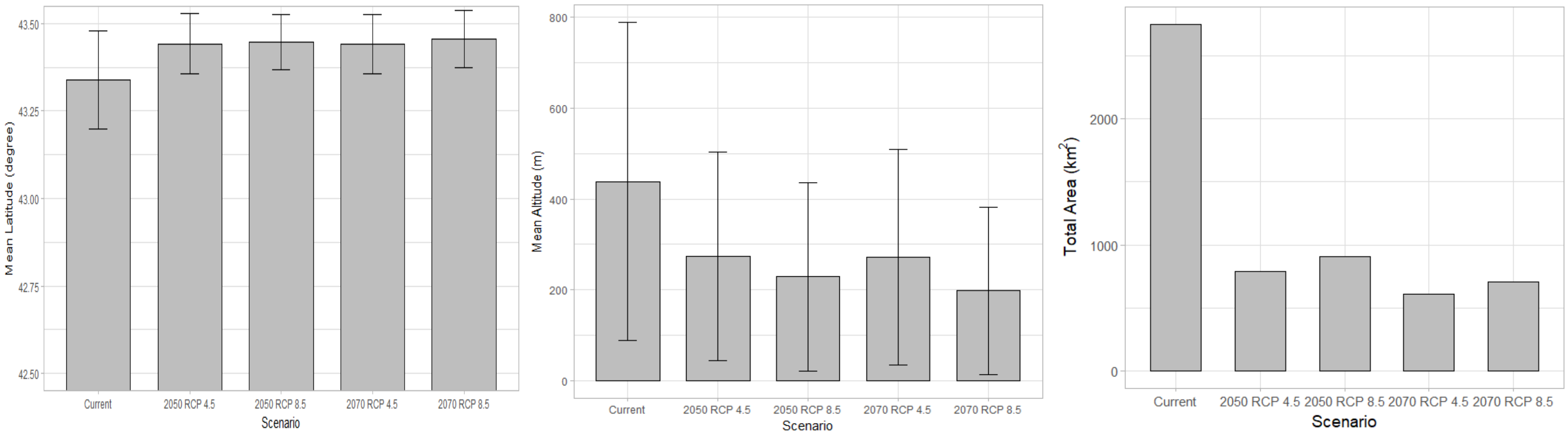

Mean Patch Area (ha)
0
100
200
300
400
Largest Patch Index (%)
0
3
6
9
12
Aggregation Index (%)
0
25
50
75
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Scenario

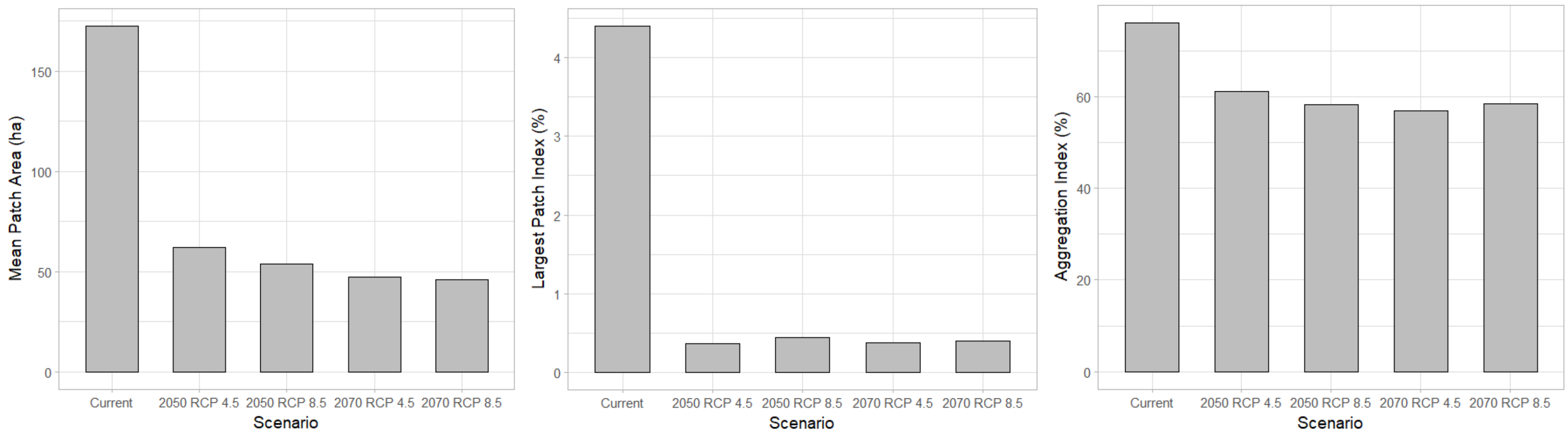
Chestnut


Mean Latitude (degree)
42.50
42.75
43.00
43.25
43.50
Mean Altitude (m)
0
250
500
750
1000
Total Area (km²)
0
2000
4000
6000
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Scenario

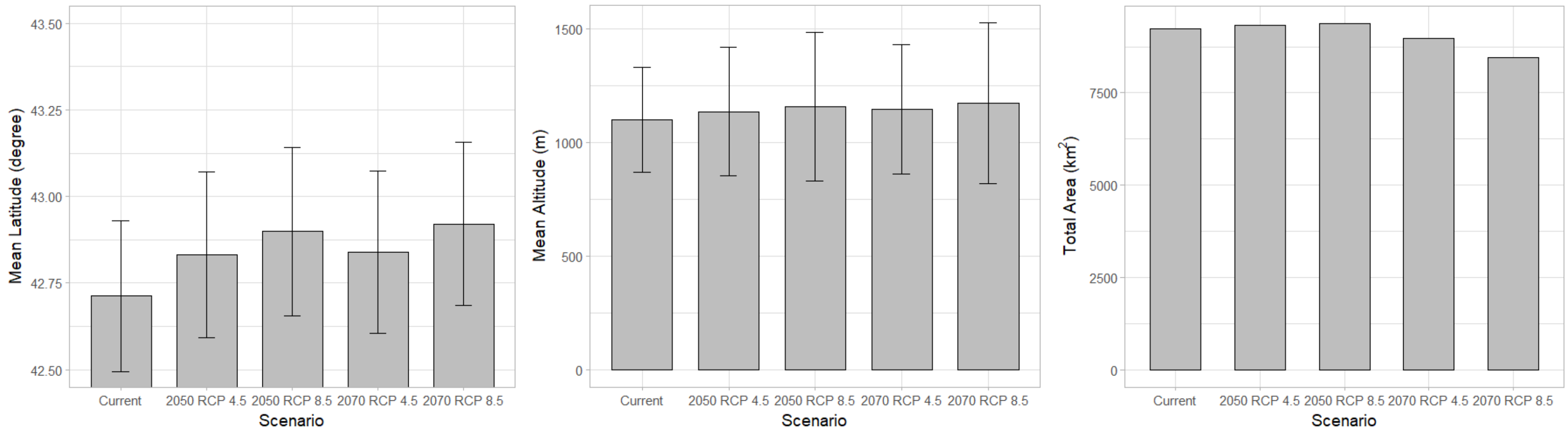


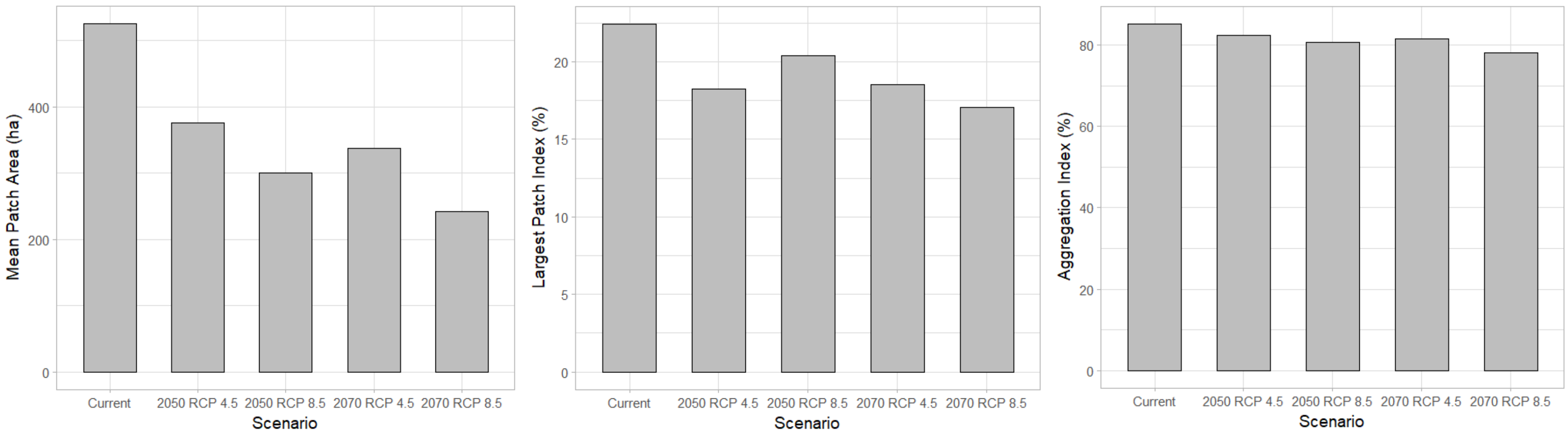
Pedunculate oak



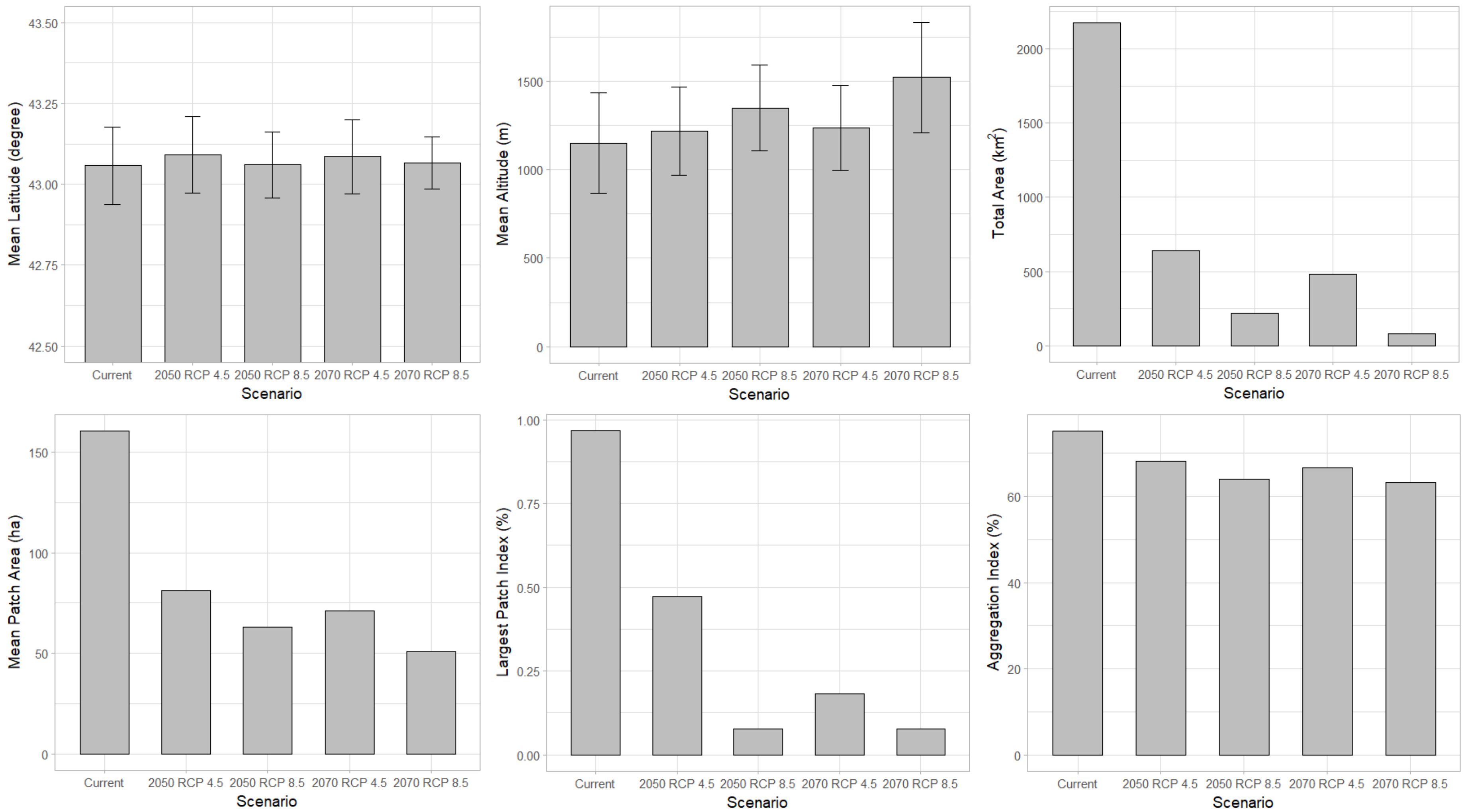


Pyrenean oak



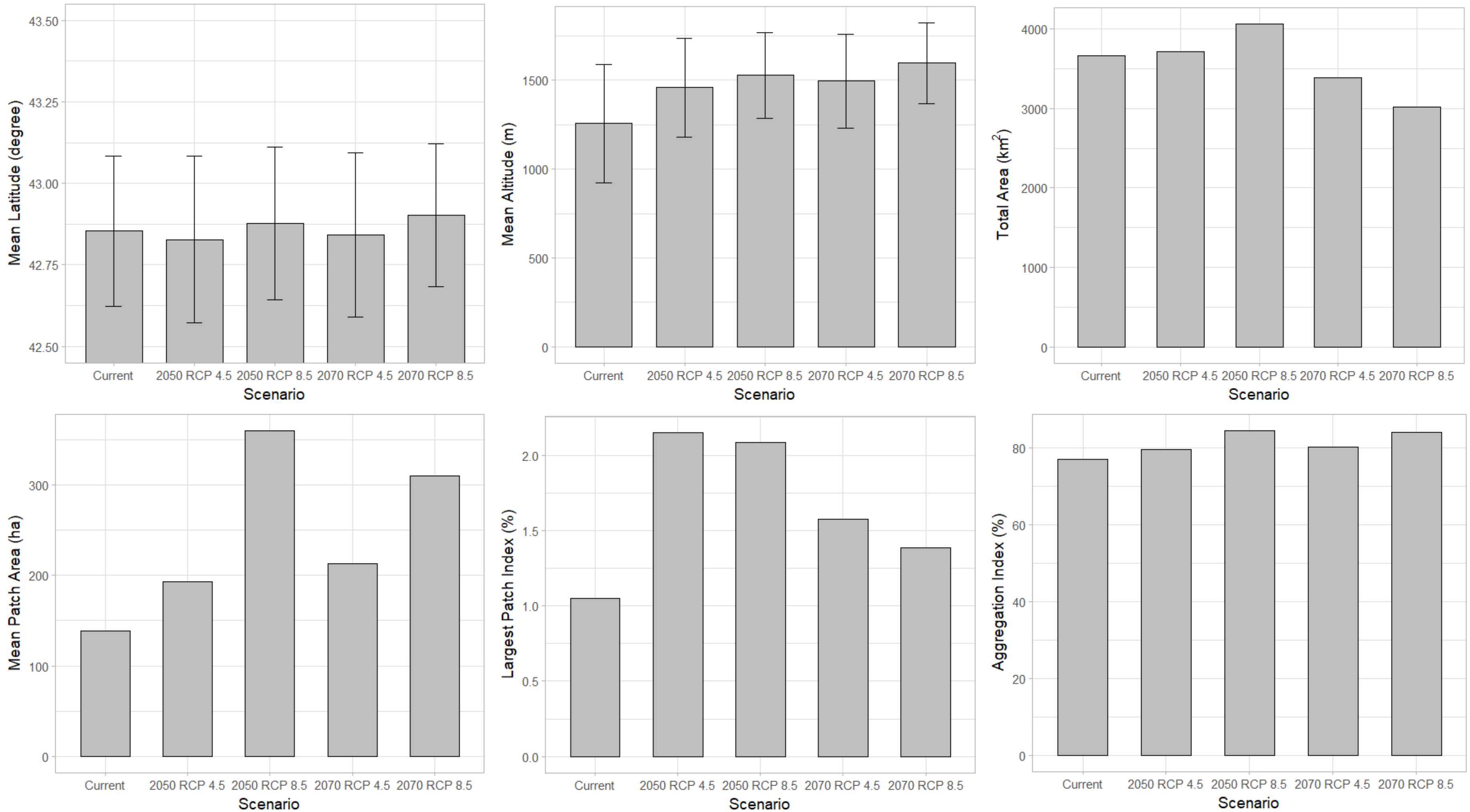

Mean Patch Area (ha)
0
200
400
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Scenario
Largest Patch Index (%)
0
5
10
15
20
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Scenario
Aggregation Index (%)
0
20
40
60
80
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Scenario

Sessile oak



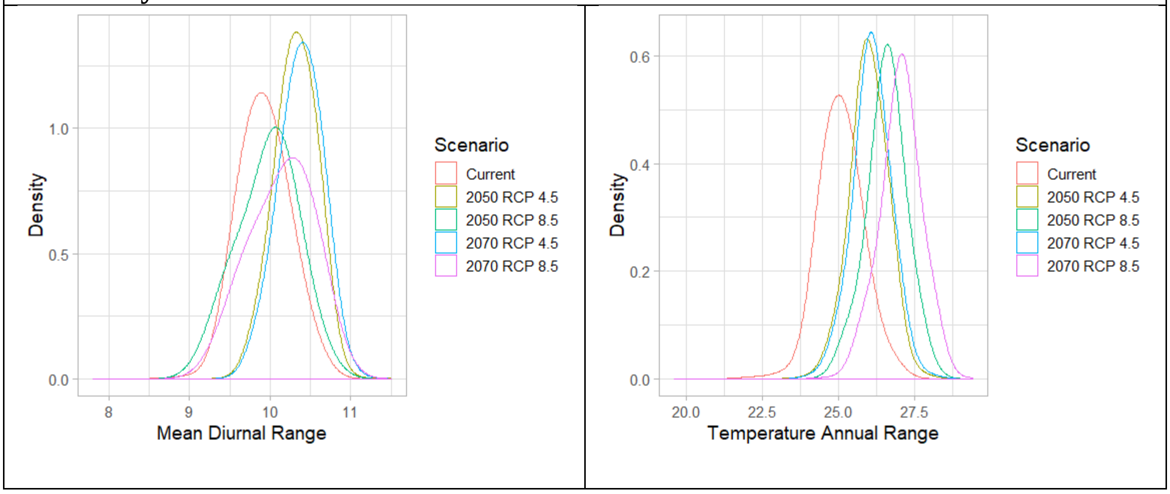
Mean Latitude (degree)
Mean Altitude (m)
Total Area (km^2)
Mean Patch Area (ha)
Largest Patch Index (%)
Aggregation Index (%)
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Scenario

Scots pine

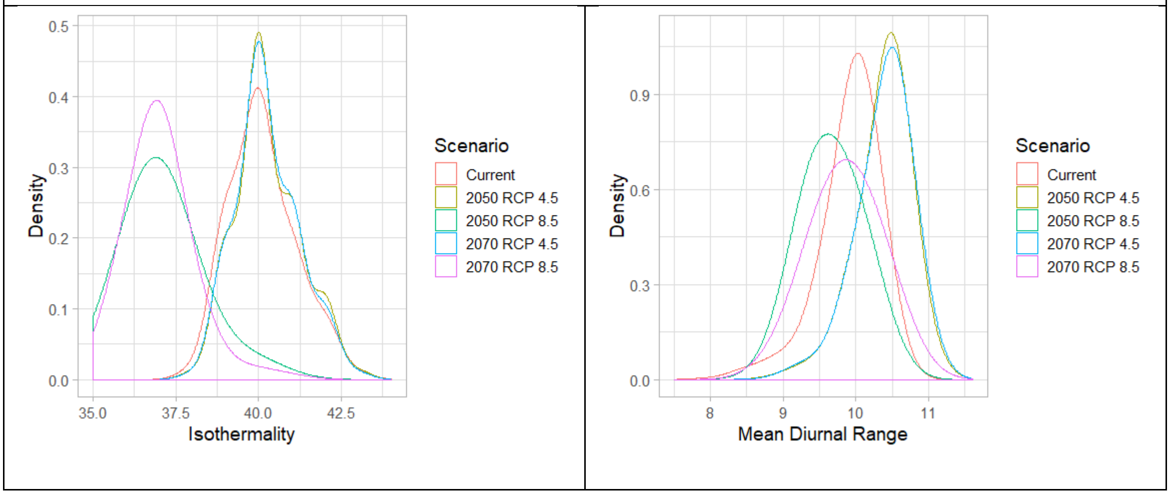

Mean Latitude (degree)
43.50
43.25
43.00
42.75
42.50
Mean Altitude (m)
1500
1000
500
0
Total Area (km2)
4000
3000
2000
1000
0
Mean Patch Area (ha)
300
200
100
0
Largest Patch Index (%)
2.0
1.5
1.0
0.5
0.0
Aggregation Index (%)
80
60
40
20
0
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Scenario

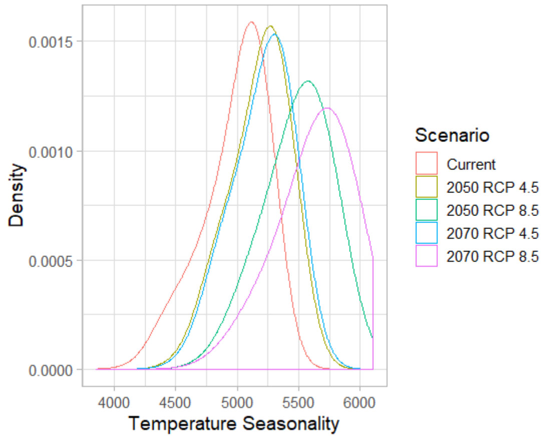
SUPPLEMENTAL FILE 4. Distribution of those variables that contributed more than 75% to the model algorithm for the seven plant species in the Cantabrian Mountains, under five scenarios: (1) the current reference period; (2) 2050 under the RCP 4.5 emissions scenario; (3) 2050 under the RCP 8.5 emissions scenario; (4) 2070 under the RCP 4.5 emissions scenario; and (5) 2070 under the RCP 8.5 emissions scenario.

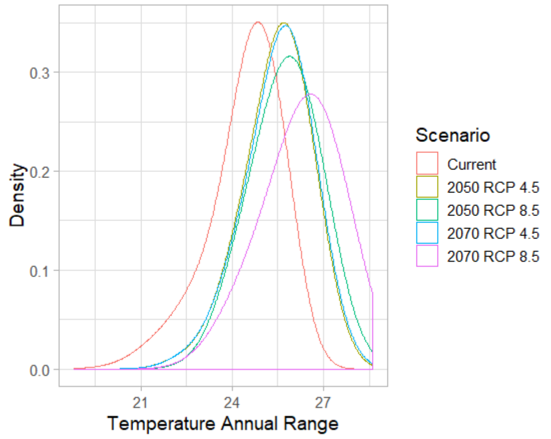
Blueberry

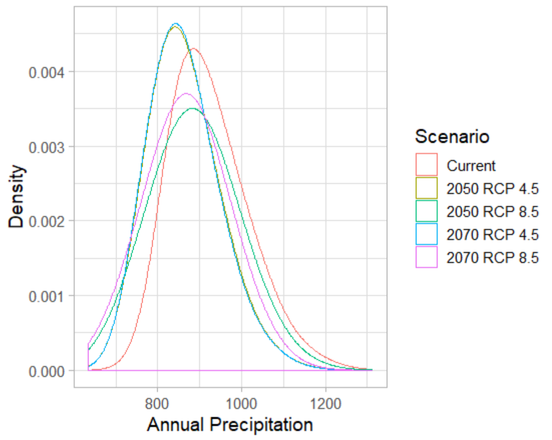


Beech

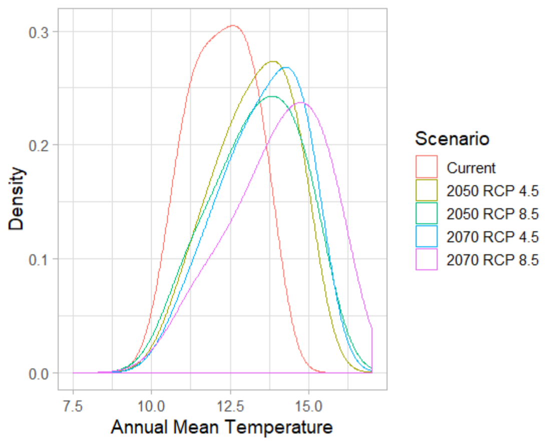


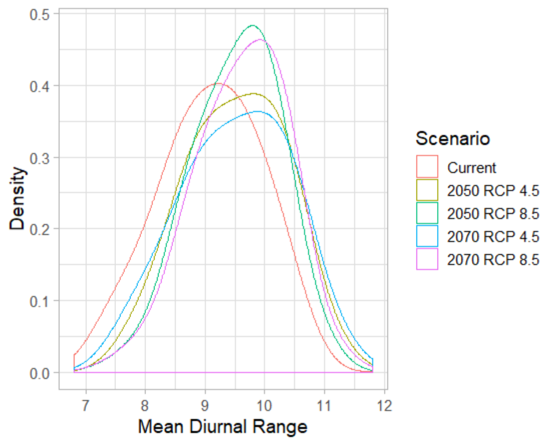

Density
0.0015
0.0010
0.0005
0.0000
4000
4500
5000
5500
6000
Temperature Seasonality
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5

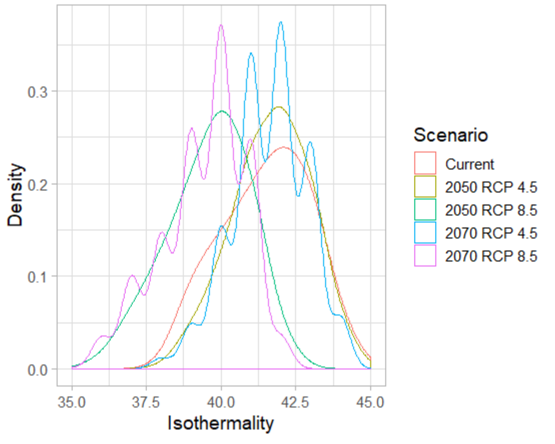

Density
0.3
0.2
0.1
0.0
21
24
27
Temperature Annual Range
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5

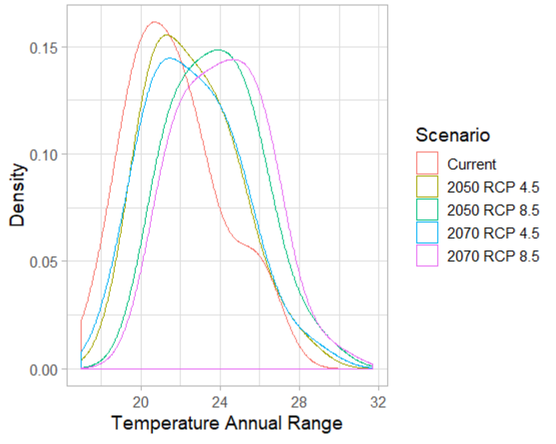

Density
0.004
0.003
0.002
0.001
0.000
800
1000
1200
Annual Precipitation
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5

Chestnut

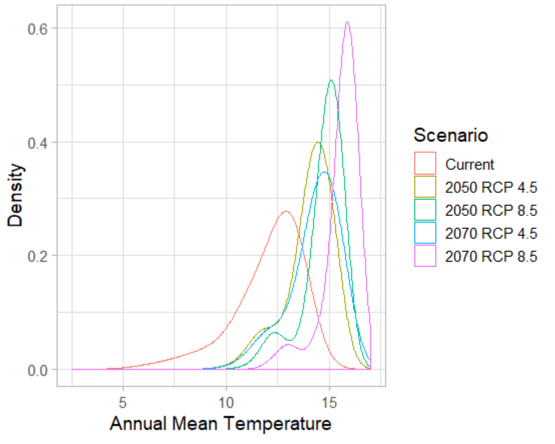

Density
0.3
0.2
0.1
0.0
7.5
10.0
12.5
15.0
Annual Mean Temperature
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5

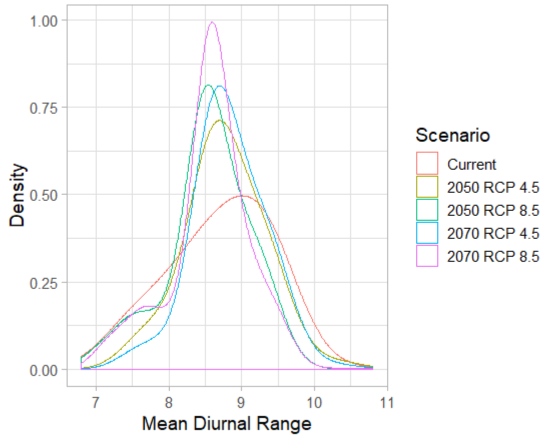

Density
0.5
0.4
0.3
0.2
0.1
0.0
7
8
9
10
11
12
Mean Diurnal Range
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5

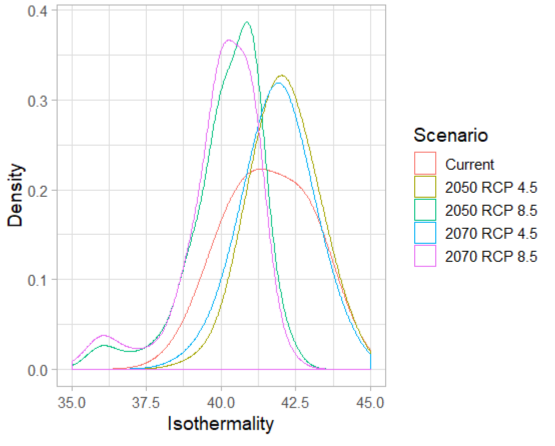




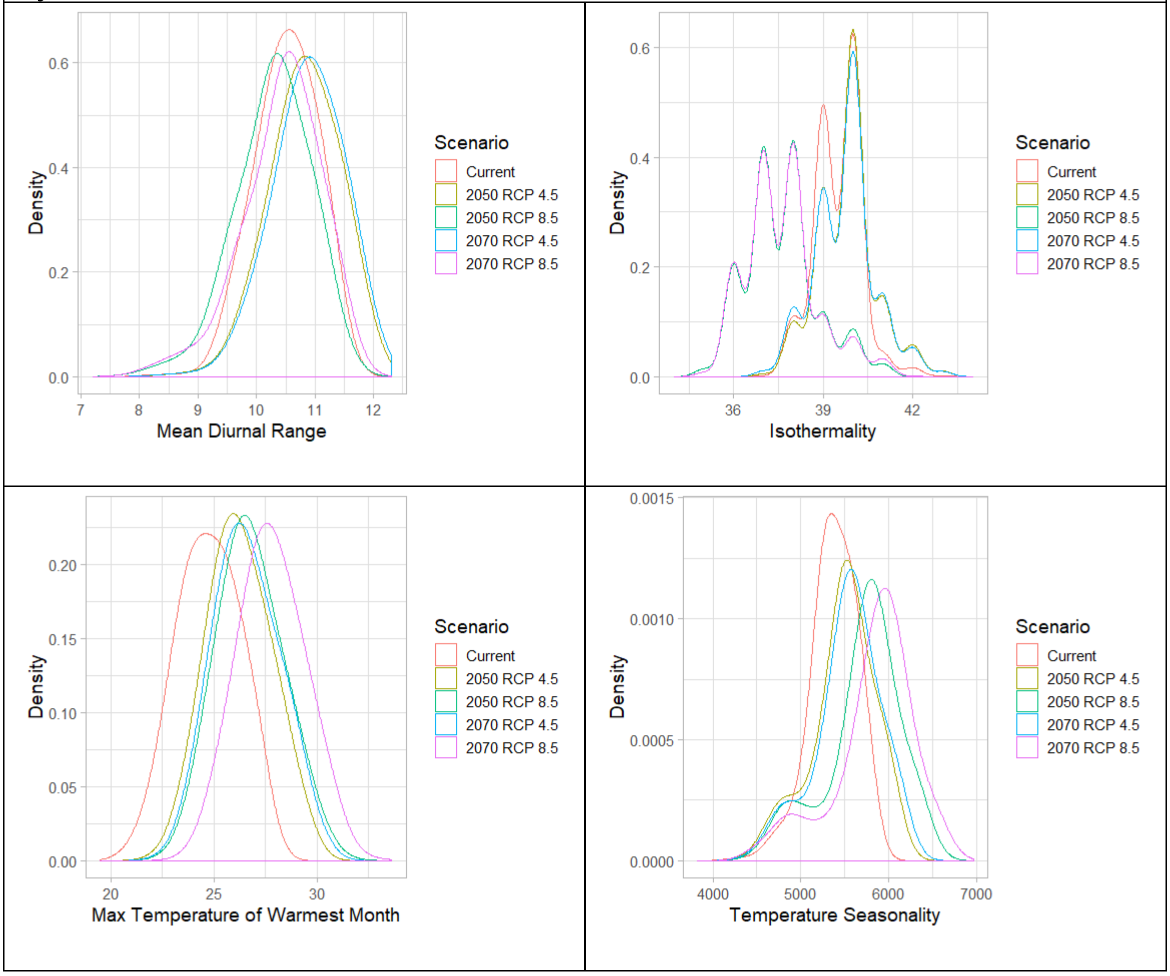
Pedunculate oak



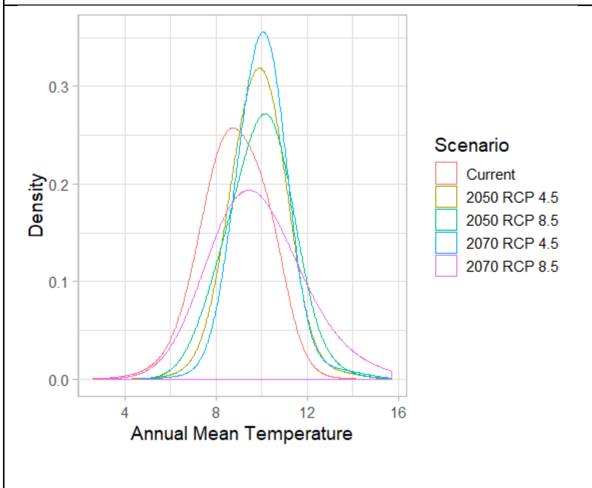




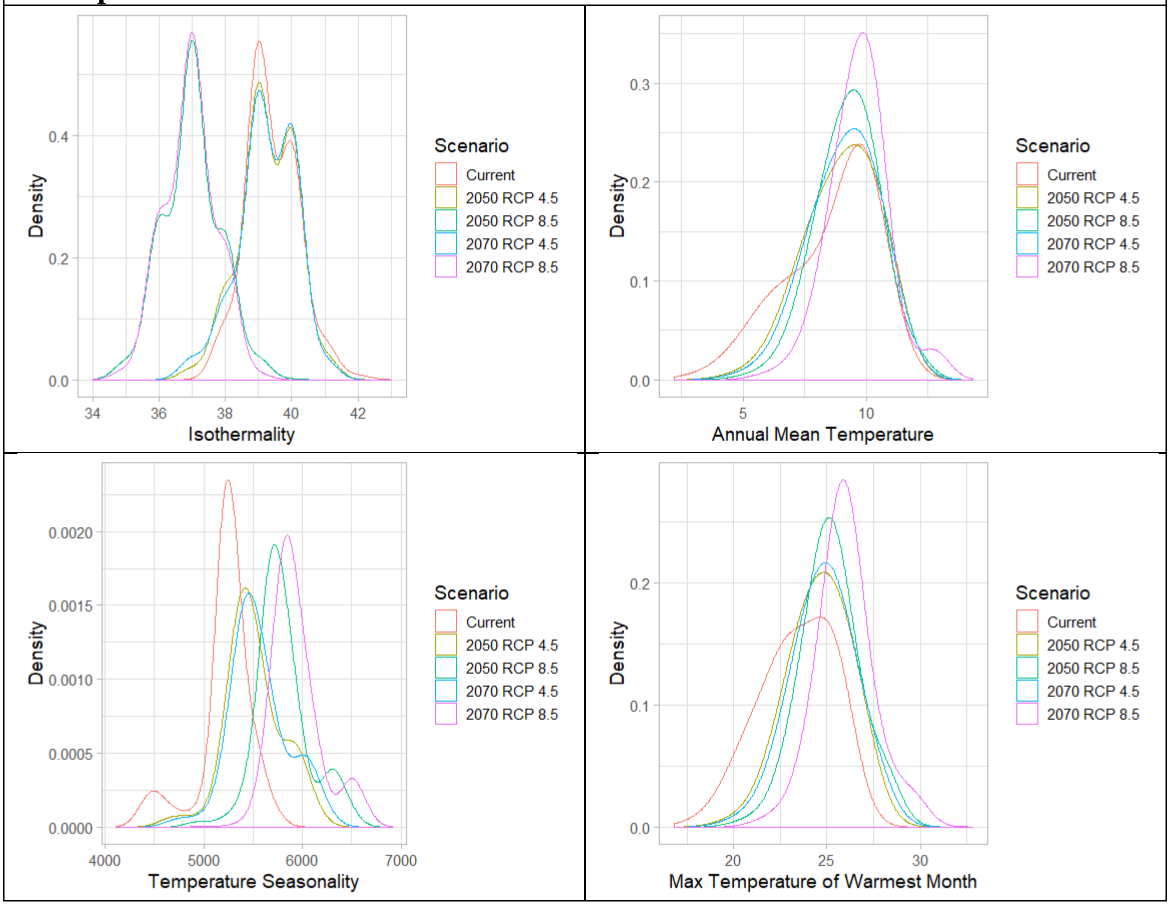
Pyrenean oak



Sessile oak



Scots pine


Density
Isothermality
Scenario
Current
2050 RCP 4.5
2050 RCP 8.5
2070 RCP 4.5
2070 RCP 8.5
Annual Mean Temperature
Temperature Seasonality
Max Temperature of Warmest Month