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RESEARCH

Climate change-induced shifts in habitat suitability for the European roe deer (*Capreolus Capreolus* L., 1758) across Europe and Türkiye

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Abstract

European roe deer (*Capreolus capreolus* L., 1758) is a widely distributed ungulate, occurring throughout the Europe, Caucasus, and western Asia; however, populations in Türkiye are limited by habitat constraints caused by climate change. This study focuses on the habitat suitability of the species across its range and examines how future climate scenarios are expected to influence it. Using ecological niche modeling (MaxEnt), we assessed habitat suitability under present-day conditions and projected future distributions for three time periods (2041–2060, 2061–2080, and 2081–2100) across seven general circulation models (GCMs) and three Shared Socioeconomic Pathways (SSP2-4.5, SSP3-7.0, and SSP5-8.5). In addition to GBIF records for the species, occurrence data were obtained from long-term field surveys, official reports of the General Directorate of Nature Conservation and National Parks, social media records, and roadkill records. The results show that habitat suitability is largely shaped by the annual range of temperature, the seasonality of precipitation, and the mean annual temperature. Present-day projections suggest the species is predominantly associated with temperate forested regions, with high suitability in central and Eastern Europe, Scandinavia, and western Russia, and decreasing suitability in southern Europe, Türkiye, and the Mediterranean basin due to increasing climatic constraints. Future projections reveal a northward shift in suitable habitats with considerable habitat loss in southern Europe, Türkiye, and western Asia. Under SSP 5-8.5 projections, suitable habitats in Türkiye are projected to decrease by up to 66% by 2081–2100. Though habitat loss in southern part of the range is accelerating, suitable habitats are expected to appear in northern Europe, which could allow for range expansion.

Keywords Species distribution · Changing climate · European roe deer · Ecological niche modeling · Habitat loss

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Introduction

European roe deer (*Capreolus capreolus* L., 1758) is a key species belonging to the Cervidae family that plays a major role in shaping the dynamics of ecosystems in continental Europe and Anatolia through selective browsing and seed dispersal (Bobek et al. 1974; Sempéré et al. 1996). *C. capreolus*, as a medium-sized cervid, typically inhabit mosaic landscapes where forests, forest edges, and meadows intersect, and they can serve as an indicator species for habitat connectivity and forest dynamics (Evcin 2018; Lorenzini et al. 2022). Fossil records indicate that the species is among the most frequently represented mammals in the fossil record, with its presence in Europe dating back at least 600,000 years. The distribution of this species was stable during glacial and interglacial phases. Throughout the Late Quaternary, it continued to be remained one of the most frequent mammals, with almost 3,000 fossil and sub-fossil records (Sommer et al. 2009). Its historical range was extensive, encompassing temperate and boreal regions from Western Europe to the Caucasus, with its highest density in the mesic Black Sea and Marmara Regions of Türkiye, where it inhabits dense deciduous forests and temperate climates (Turan 1984; Lovari et al. 2016). In Türkiye, the species is generally distributed across the western and northern parts of the Marmara Region, the northwestern Aegean Region, the Black Sea Region, the northern slopes of Eastern Anatolia, the Southeastern Anatolia, and the central and eastern Mediterranean regions (Evcin 2018). Recent studies, however, have documented a previously unpredicted eastward expansion into Central Anatolia — a semi-arid, continental plateau that experiences extreme variation in temperature and limited cover from forest (Keten 2017; Özcan 2021) — which challenges long-standing assumptions concerning the extent of the species' range. This expansion simultaneously shows the ability of the species to expand into steppe-forest mosaics, fragmented agricultural areas, and even regions with discontinuous water availability during the dry season. It demonstrates behavioral and physiological adaptation to more arid conditions (Hewison et al. 2001; Coulon et al. 2004).

In Türkiye, the appearance of the European roe deer at Central Anatolian steppes, and most recently the Karagüney Mountains, marks a paradigm change in habitat suitability. Previously excluded (due to aridity, temperature extremes, poaching, and unregulated hunting) from the ranges of several species, these areas are now home to incipient populations, aided by reduced anthropic pressures caused by rural depopulation, habitat recovery associated with afforestation projects and climate-mediated niche opportunities (Yılmaz and Çiçek 2016; Özcan 2021). This is in contrast to global trends where cervids are restricted in their movements due to habitat fragmentation and urbanization (Tucker et al. 2018). Local data show that *C. capreolus* has used ecological corridors (i.e., linear patches, such as remnant forests, riparian buffers and shrublands) which connect fragmented habitats and allow movement between unsuitable landscapes (Zeller et al. 2012; Loro et al. 2016). Recent population estimates in Karagüney suggest 11–14 individuals, likely the descendants of migrants from the Bolu and Köroğlu mountain ranges, which highlights the importance of landscape connectivity in facilitating range shifts (Bulut et al. 2017; Evcin 2023; Özcan 2021).

Land use, animal behavior, and topography are some of the major factors that can affect the distribution of the wildlife species (Zeller et al. 2012). In contrast, *C. capreolus* use a variety of habitats at the landscape scale (Duarte et al. 2010; Loro et al. 2016). However, they favor those places where forest cover is dense, agricultural and settlement presence is low, and habitat diversity is high (Malo et al. 2004). Genetic analyses showed that European populations were established from several glacial refugia (Balkans and Carpathians), and that postglacial recolonization routes were influenced by topographic barriers and habitat connectivity (Evcin et al. 2019; Plis et al. 2022; Randi et al. 2004; Sommer et al. 2009). Ecological Niche Models (ENMs) are important tools for predicting changes in species distributions under changing habitat conditions (Benito Garzón et al. 2019; Brambilla et al. 2022; Diengdoh et al. 2022; Shan et al. 2025; Serva et al. 2025). By assessing species-environment relationships, they allow for the evaluation of habitat suitability and the description of potential geographic ranges, thus providing useful information for biodiversity conservation and ecosystem management (Brodie et al. 2022). This study explores the reasons for the European roe deer's unexpected distribution in Türkiye using a comprehensive method. We combined field observations, camera-trap data, and environmental predictors to build the ENMs. Here, the present study addresses four key questions: (1) What are the current and future habitat suitability patterns of European roe deer from Europe to Türkiye? (2) Which bioclimatic and topographic variables influence the present-day distribution of the species? (3) How does the distribution of the species in Türkiye compare to that in Europe? (4) Are the estimated shifts in habitat limits specific to Türkiye, or do they suggest wider regional adaptation patterns? Integrating ecological niche modeling with field observations refines predictions. Understanding the environmental factors that cause changes in species distributions is relevant for supporting more effective strategies. Therefore, this study provides valuable information for conservation planning and management.

Materials and methods

Target species

The European roe deer (*Capreolus capreolus* L., 1758) is the smallest deer species in its distribution range, encompassing Europe and Türkiye. Its forelegs are shorter than the hind legs, the neck is long, the ears are quite large (12–14 cm), the tail is very short (2–3 cm), and it lacks a mane. In winter, their coloration ranges from grayish-brown to dark brown, with a white rump patch, while in summer, the coloration is reddish to red-brown, and the upper part of the head is gray or brown (Danilkin 1996). The population of the species plays a significant role in both the trophic chain and nutrient cycling in nearly all European forest ecosystems. The species can utilize a wide range of habitats, including deciduous, mixed, or coniferous forests, steppes, grasslands, agricultural areas, and urban areas with extensive green spaces. Generally, it prefers landscapes with a mosaic of forests and agricultural fields, due to its biology; it can also survive in semi-arid environments and above the tree line during the summer season (Linnell and Andersen 1998; Pettorelli et al. 2003; Bobrowski et al. 2020). The species has successfully adapted to human-modified landscapes, including rural and agricultural areas. The range of European roe deer is extensive, covering almost all of Europe (outside of some of the extreme north), Türkiye, Syria, Iraq, across the Black Sea, the whole of the Caucasus region and into northwestern Iran. Its most populated coverage in Türkiye is through the Black Sea and Marmara regions. Its local distributions also extend to İzmir, Antalya and the Amanos Mountains, and Hakkari, where it has a link to the Caucasus.

Occurrence data

Species occurrence data on a global scale was acquired from the Global Biodiversity Information Facility (GBIF 2025) whereas Türkiye's data were obtained through field studies conducted over the last 20 years, reports from the General Directorate of Nature Conservation and National Parks (DKMPGM) representatives, events shared on social networks, and reports including road-kill data. The General Directorate of Nature Conservation and National Parks (DKMPGM) maintains a central database of wildlife records in Türkiye (Fig. 1).

This database includes data such as species presence records, inventory records containing population data, and causes of mortality for various species. These data are collected and reported by the general directorate

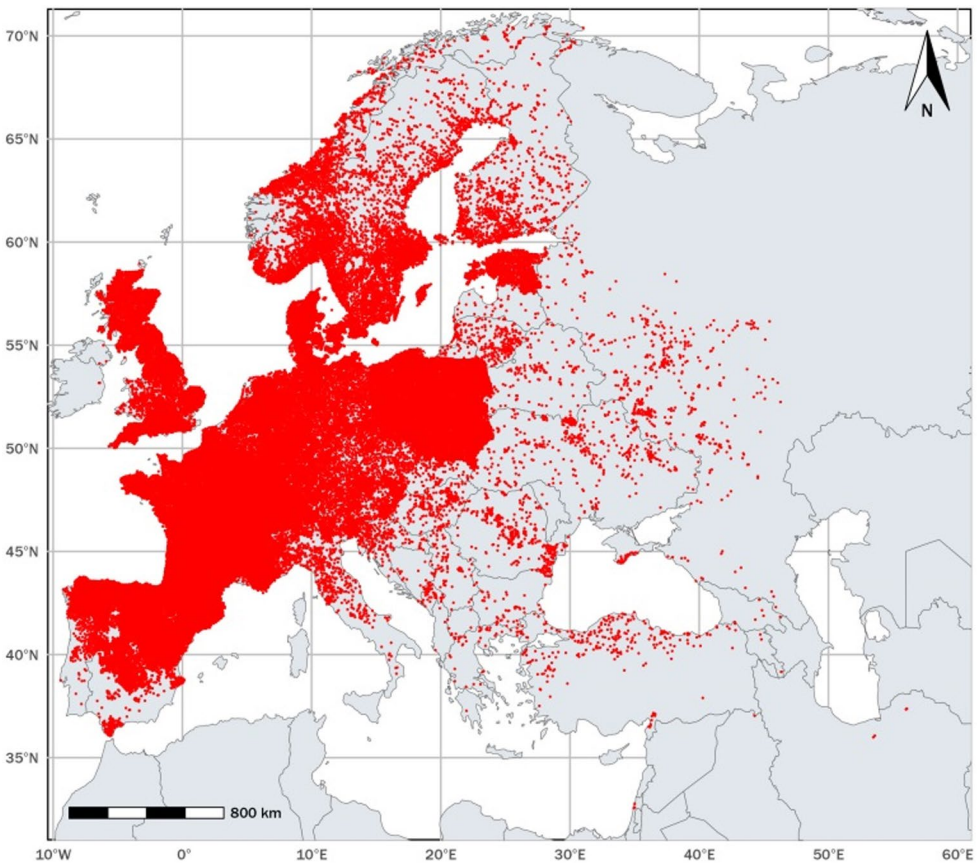

Fig. 1 The geographical location of the occurrence data (red points indicate occurrence records)

staff, park rangers, and affiliated field personnel using standard forms and protocols. For this study, species records covering the period [2005–2025] were obtained from the provincial directorates of DKMPGM. We also searched publicly available posts on Facebook, Instagram, Twitter (X), and YouTube between January 2020 and December 2024 using combinations of Turkish and English keywords (e.g., "karaca" and "Capreolus capreolus" combined with provincial names or "wildlife" terms) and related hashtags (e.g., #karaca, #roedeer). Search results were manually screened, and posts without clear date or location information were excluded. Each candidate record was reviewed for species identification by at least two independent authors who evaluated the accompanying photos or videos based on diagnostic morphological characteristics (e.g., body size, coat color, antler structure). The post's metadata (geographic tags, textual description) were checked for internal consistency and compared to known distribution boundaries. Posts with ambiguous identification, implausible locations, or missing verifiable dates were excluded. Where possible, we verified locations by consulting the original posting author or local authorities. The records that passed all criteria were retained. A total of 2,235,880 occurrence records were obtained for the species, of which 2,235,620 were retrieved from the GBIF database, and 260 records were acquired from field studies. The data-editing process produced 2,216,533 occurrence records, after the removal of duplicates, potential errors, and redundancies.

All records were georeferenced to the WGS84 coordinate system and validated for accuracy using ArcMap (v10.7, ESRI, California, USA). Combining occurrence data obtained from different fieldwork procedures in multiple studies can result in an increased prediction of distribution and a rise in spatial autocorrelation (Fick and Hijmans 2017). In order to reduce sampling bias and have an even sampling effort (Merow et al. 2013; Boria et al. 2014; Fourcade et al. 2014; Sillero et al. 2021), we applied a random sub-selection process, keeping only one occurrence point per 5-km radius grid cell. Occurrence records were processed using the spThin R package (Aiello-Lammens et al. 2015), reducing the initial 2,216,533 records to 45,506 thinned records. The study area was considered to be the region from which European roe deer have access, at present and in the future. A five-degree buffer was applied around occurrence data. The records are distributed across Western, Central, Northern, and parts of Eastern Europe. This resulted in a study area (M) sensu (Soberón and Peterson 2005) delimited by 30.98°N to 71.33°N latitude and −11.07°E to 61.08°E longitude, which encompasses the accessible regions for the species. The study area (G) used for projections corresponds to Europe.

Environmental data

Climate data were obtained from WorldClim v2.1 a global dataset (Fick and Hijmans, 2017; www.worldclim. org) at 2.5' (~4.7 km) spatial resolution and topographic data from the EarthEnv database (Amatulli et al. 2018, https://www.earthenv.org/topography). The 19 WorldClim variables were formulated as averages of monthly temperature and rainfall data from 1970 until 2000. We used 15 recent bioclimatic variables, which were produced without four variables that revealed some spatial artifacts in previous studies (bio8, bio9, bio18, bio19; e.g. Campbell et al. 2015; Escobar et al. 2014). Five of the topographic variables [mean slope, roughness, topographic position index, and terrain ruggedness index] were extracted from the 250 m GMTED2010 global digital elevation model products (Amatulli et al. 2018). All topographic variables were resampled to the spatial resolution and extent of the bioclimatic variables using the nearest-neighbour method to ensure spatial consistency among predictors prior to modeling.

To reduce multicollinearity and improve model stability and performance among environmental variables (Heikkinen et al. 2006; Dormann et al. 2013), we firstly removed variables with a variance inflation factors (VIF) > 5 and applied a correlation threshold of 0.70 (Zuur et al. 2010). This was done using the usdm package (Naimi 2015). Eight bioclimatic variables were chosen as predictors based on the species' ecological preferences (Mysterud and Sæther 2010; Gaillard et al. 2013): bio1 (Annual Mean Temperature), bio2 (Mean Diurnal Range [Mean of monthly (max temp - min temp)]); bio7 (Temperature Annual Range [bio5-bio6]); bio13 (Precipitation of Wettest Month); bio14 (Precipitation of Driest Month), and bio15 (Precipitation Seasonality [Coefficient of Variation]), topographic position index (tpi), terrain ruggedness index (tri).

Future habitat suitability of European roe deer was predicted by projecting the fitted models onto eight different global circulation models – (GCM): ACCESS-CM2 (Dix et al. 2019), BCC-CSM2-MR (Wu et al. 2019), CMCC-ESM2 (Cherchi et al. 2019), IPSL-CM6A-LR (Boucher et al. 2020), MIROC6 (Tatebe et al. 2019), MPI-ESM1-2-HR (Müller et al. 2018), MRI-ESM2-0 (Yukimoto et al. 2019), and UKESM1-0-LL (Sellar et al. 2020). This was done to have a reasonable level of uncertainty in climate model projections (Sanderson et al. 2015). Future datasets for the periods 2041–2060, 2061–2080, and 2081–2100 were acquired from the 6th Climate Model Inter-comparison Project (CMIP6, www.wcrp-climate.org/wgcm-cmip/wgcm-cmip6) and three socioeconomic pathways (for a relatively optimistic scenario - SSP2-4.5, a mid-range scenario – SSP3-7.0 and a high-emission, worst-case scenario — SSP5-8.5).

Ecological niche modeling

We used maximum entropy modeling (Maxent v3.4.1, Phillips et al. 2006, 2017) to predict the current and future habitat suitability of the species under the existing climatic conditions, as well as under three future climate projections. Cross-validation was implemented using a random 10-fold approach, in which occurrence points were randomly assigned to 10 subsets. To implement the cross-validation method (Phillips and Dudik, 2008), we set the number of bins (k) equal to the number of occurrences in the species dataset. To optimize model complexity, balance goodness of fit and predictive ability, and calculate maximum entropy models, we utilized the R package ENMeval v2.0.5 (Muscarella et al. 2014; Kass et al. 2021). Background points were randomly sampled from the defined accessible area, corresponding to the continental extent of Europe buffered by five degrees around occurrence records. A total of 10,000 background points were used, following common practice in MaxEnt-based ecological niche modeling (Soberón and Peterson 2005). Our modeling process involved constructing models with regularization multiplier values varying from 0.5 to 10 (in 0.5 increments) and incorporating six distinct feature class combinations (l, lq, h, lqh, lqhp, and lqhpt). Therefore, we ran 120 individual models for the species.

We assessed the accuracy of our models using (1) the area under the curve (AUC) of the receiver operating characteristic (ROC) plot for test localities (AUC_{TEST}; Hanley and McNeil 1982; Peterson et al. 2011), (2) the difference between training and test AUC (AUC_{DIFF}; Warren and Seifert 2011), (3) OR_{10} (10% training omission rate) for test localities (Fielding and Bell 1997; Peterson et al. 2011) and (4) the Akaike information criterion corrected for small sample size (AICc; Burnham and Anderson 2004; Warren and Seifert 2011) evaluation metrics in ENMeval (Muscarella et al. 2014; Kass et al. 2021). Although the Boyce Index is commonly applied to presence-only models, we adopted a multi-criteria evaluation framework including AUCTEST, AUCDIFF, OR10, AICc, and null model comparisons. This approach was used to balance model discrimination, overfitting, and transferability across broad and environmentally heterogeneous regions, and to reduce reliance on any single evaluation metric when generating large-scale current and future projections (Liu et al. 2025).

To further calculate the performance of our models, we operated the null model approach (Raes and ter Steege 2007). Null ENMs were generated with 100 iterations using the method of Bohl et al. (2019) and expanded by Kass et al. (2021). The performance of the empirical model was compared against the mean of the null model.

The selected model was then extrapolated over the present-time and future scenarios. Thus, we performed 72 projections (8 GCMs × 3 SSPs × 3 time-periods) and generated the mean rasters for the GCMs scenarios and time periods. Predictions were presented in the 'cloglog' output format in the range of 0 (unsuitable) and 1 (suitable) (Phillips et al. 2017).

The model's cloglog probability outputs were binarized using multiple threshold methods, as suggested in the literature (Hellegers et al. 2025). Four threshold methods were employed to mitigate the risk of bias (over- or under-prediction) associated with a single threshold approach: Maximum test sensitivity plus specificity, Equal training sensitivity and specificity, 10 percentile training presence and Balance training omission, predicted area and threshold value. A consensus (0–4) layer was produced by combining the 0–1 rasters for each method; each pixel took a value between 0 (none) and 4 (all) based on the number of methods that predicted 'present'. In the main analyses, species presence was defined using a ≥ 2 consensus threshold (to balance sensitivity and specificity), and an additional ≥ 3 consensus threshold was tested for sensitivity analysis.

Future projections (SSP 2–4.5.5/370/585; 2041–2060, 2061–2080 and 2081–2100) were resampled using the nearest neighbour method (CRS, extent and resolution) to align with the current raster. Area values were calculated using the 'cellSize' function in the 'terra' package with the unit set to 'km'; calculations performed in the geographic coordinate system were repeated in the equal-area Mollweide projection for verification purposes. The results were visualized using the terra (Hijmans et al. 2025) and rasterVis (Lamigueiro and Hijmans 2021) packages.

Results

The VIF results demonstrated severe multicollinearity among several bioclimatic variables, with values exceeding 1000 for bio10, bio5, and bio7. In contrast, topographic variables showed low collinearity, as presented in Table 1. We chose the best model for European roe deer based on its statistical performance and low complexity, reduced to four evaluation metrics and null models. The best model was based on statistical significance (AUC_{DIFF} = 0.008, SD = 0.004), good performance (%10 OR = 0.102 SD = 0.015) and low complexity (AICc = 113618). It included linear, quadratic, hinge, and product features with a regularization parameter 0.5 and a good average area under the curve for test data (AUC_{TEST} = 0.797). We calculated performance metrics for our model with null models and found that our empirical model significantly

Table 1 Variance inflation factors (VIF) for environmental predictors. Bioclimatic variables (bio1–bio17) were derived from worldclim data (Fick and Hijmans 2017). Topographic predictors include topographic position index (tpi), terrain ruggedness index (tri), and roughness

Variables	VIF
bio6	6.45
bio15	11.83
bio11	15.77
bio3	38.65
bio 2	112.16
bio14	139.79
bio1	188.54
bio17	228.46
bio13	256.04
bio12	317.69
bio16	528.82
bio4	827.50
bio7	1327.43
bio10	1620.34
bio5	2216.45
tpi	1.58
slope	174.70
tri	189.75
roughness	278.01

differed from those computed for a series of null models ($AUC_{TRAIN-NULL}$ = 0.606, SD = 0.004, Z-value = 46.303; p = < 0.01).

Bioclimatic variables related to temperature and precipitation and topographic factors have played a major role in shaping the distribution of the species. Our results show that the habitat suitability of the species is explained by temperature annual range (bio7, 77.9%), mean diurnal range (bio2, 7.7%), precipitation seasonality (bio15, 4.2%), precipitation of the wettest month (bio13, 4%), precipitation of the driest month (bio14, 2.7%), and annual mean temperature (bio1, 2.3%). In addition, the terrain ruggedness index (tri, 1.2%) and the topographic position index (tpi, <1%) also influenced its distribution.

Under current climatic conditions, the model projections show that European roe deer is broadly distributed throughout Europe, parts of the Caucasus, and western Asia (Figs. 2 and 3).

In general, the distribution of the species is in accordance with temperate deciduous and mixed forests, where temperature and precipitation gradients are significant in determining habitat suitability. While this species remains largely confined to regions with intermediate climate variability and stable precipitation regimes, it occurs in both core and marginal habitats.

These results indicate that climate will greatly govern future habitat suitability, causing substantial regional contractions or expansions as shown in Fig. 4. Future ENM projections suggest significant changes in the potential distribution of European roe deer under different climate change scenarios for three future periods: 2041–2060, 2061–2080, and 2081–2100. The extent of these changes varied across Shared Socioeconomic Pathways (SSP 2–4.5.5, SSP 3–7.0, SSP 5–8.5.5) due to the future climatic fluctuations. As climate change intensity increases, habitat suitability is

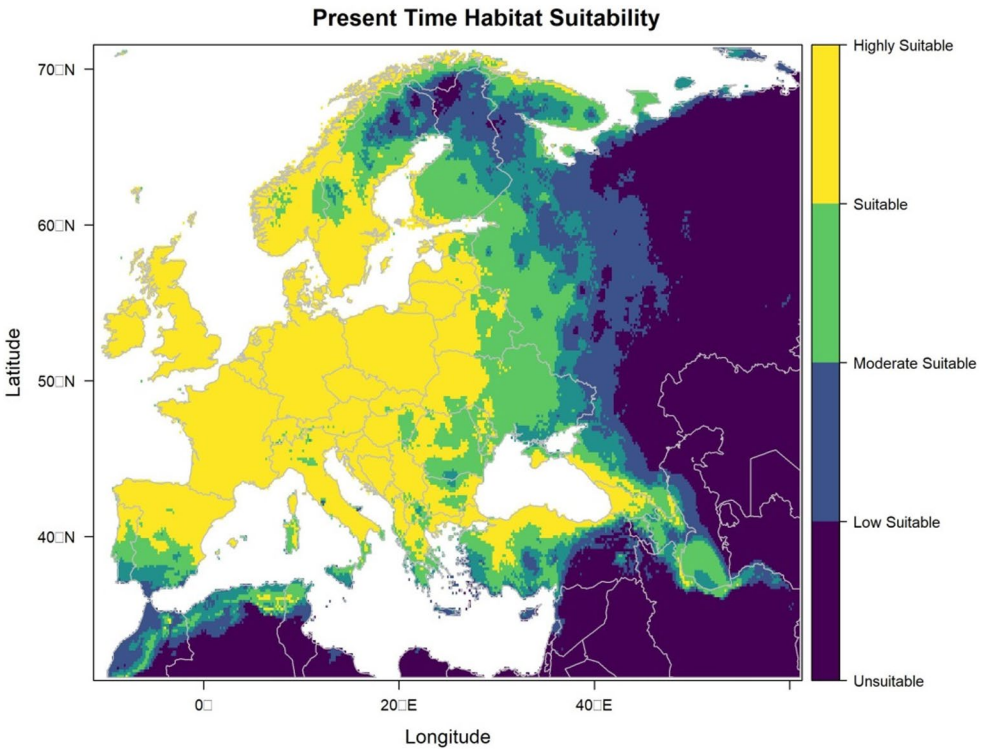

Fig. 2 Study area extent projected current potential distribution, and recorded occurrences of the European roe deer across its overall distribution range. Red dots represent occurrence records. The probability of occurrence ranges from 0 (dark blue, lowest probability) to 1 (yellow, highest probability)

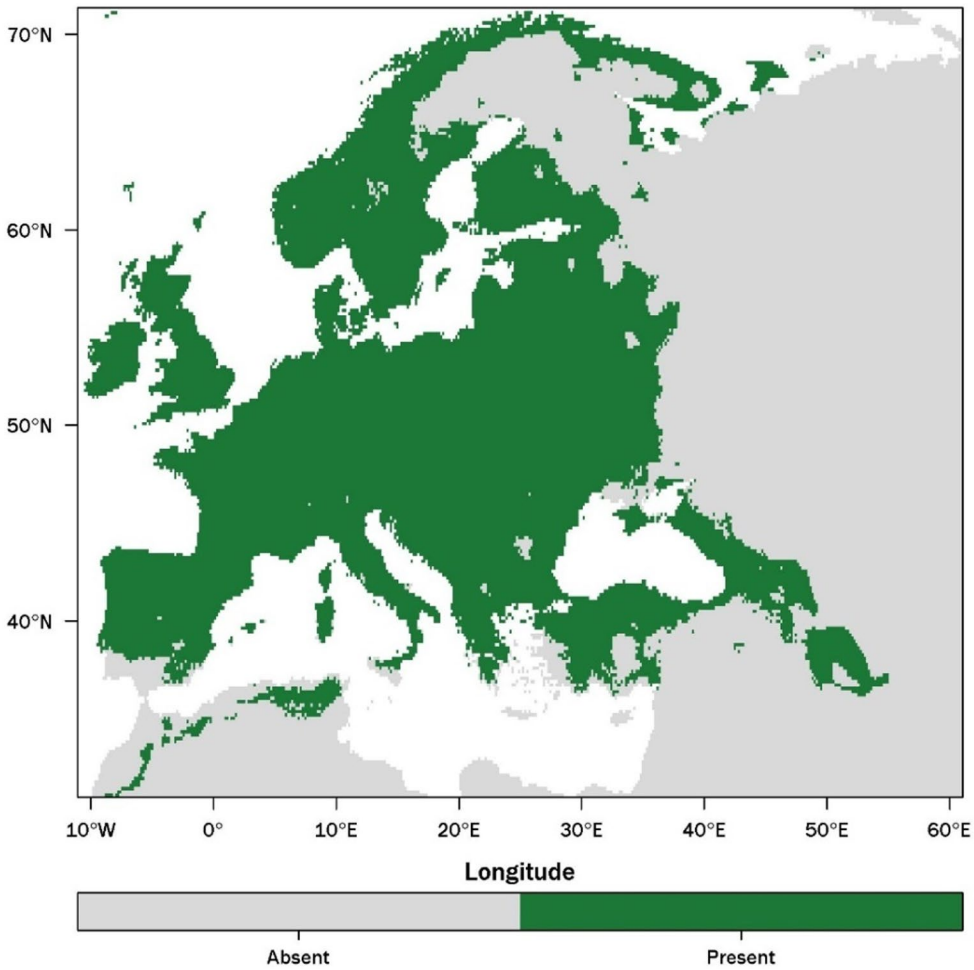

Fig. 3 Average binary prediction for European roe deer under present-day climate conditions. Gray represents unsuitable habitats, while green indicates suitable habitats

expected to shift northward, accompanied by considerable losses in southern and lower elevation regions. This trend is more apparent in the worst-case scenario (SSP 5–8.5.5). A significant reduction in habitat suitability is observed in southern Europe, the Balkans, Türkiye, western Asia, and the Caucasus (Fig. 5).

Moderate habitat loss is projected for southern regions in 2041–2060, especially in the Mediterranean basin. However, core habitats in central and Eastern Europe and western Russia remain highly suitable. Predictions for 2061–2080 show continued habitat loss in southern and southeastern Europe and an increase in habitat suitability in northern latitudes, including Scandinavia, and higher altitudes in the Urals. Predictions for the period 2081–2100 point to the most extreme habitat reductions occurring in the southern limits of the species' distribution, especially under SSP 5–8.5.5. These changes imply a major climate-induced poleward and elevational shift in the species' range.

By 2100, models predict an overall decrease in habitat suitability under all climate scenarios. Compared with the present-day estimate (676.02 million ha), suitable area declines by 6.2% (SSP 2–4.5.5), 5.3% (SSP 3–7.0), and 8.4% (SSP 5–8.5.5) by 2041–2060; by 2061–2080 the losses deepen to 7.4% (SSP 2–4.5.5), 8.2% (SSP 3–7.0), and 11.5% (SSP 5–8.5.5). By 2081–2100, suitable area is reduced by 10.1% under both SSP 2–4.5.5 and SSP 3–7.0 and by 16.3% under SSP 5–8.5.5, indicating persistent contraction rather than expansion (Table 2).

Habitat suitability in Türkiye is expected to decrease dramatically in all scenarios, which is in contrast to its wider distribution pattern. Current potential habitat is estimated at 43.79 million ha, but this area shrinks significantly, particularly in the later periods. According to the SSP 2–4.5.5 climate scenario, suitable habitats in the country decrease by 31.1% for 2041–2060, while they drop by 35.5% and 39.0% under SSP 3–7.0 and SSP 5–8.5.5, respectively. The contraction of suitable habitat continues to amplify by 2061–2080 to 48.8% under SSP 3–7.0 and 55.6% under SSP 5–8.5.5, showing severe limitations for populations of the species. By 2081–2100, Türkiye is predicted to experience drastic habitat loss, exceeding 45.3% (SSP 3–7.0) and 66.2% (SSP 5–8.5.5), indicating that a considerable part of the suitable habitats of the country will become unsuitable due to climate change.

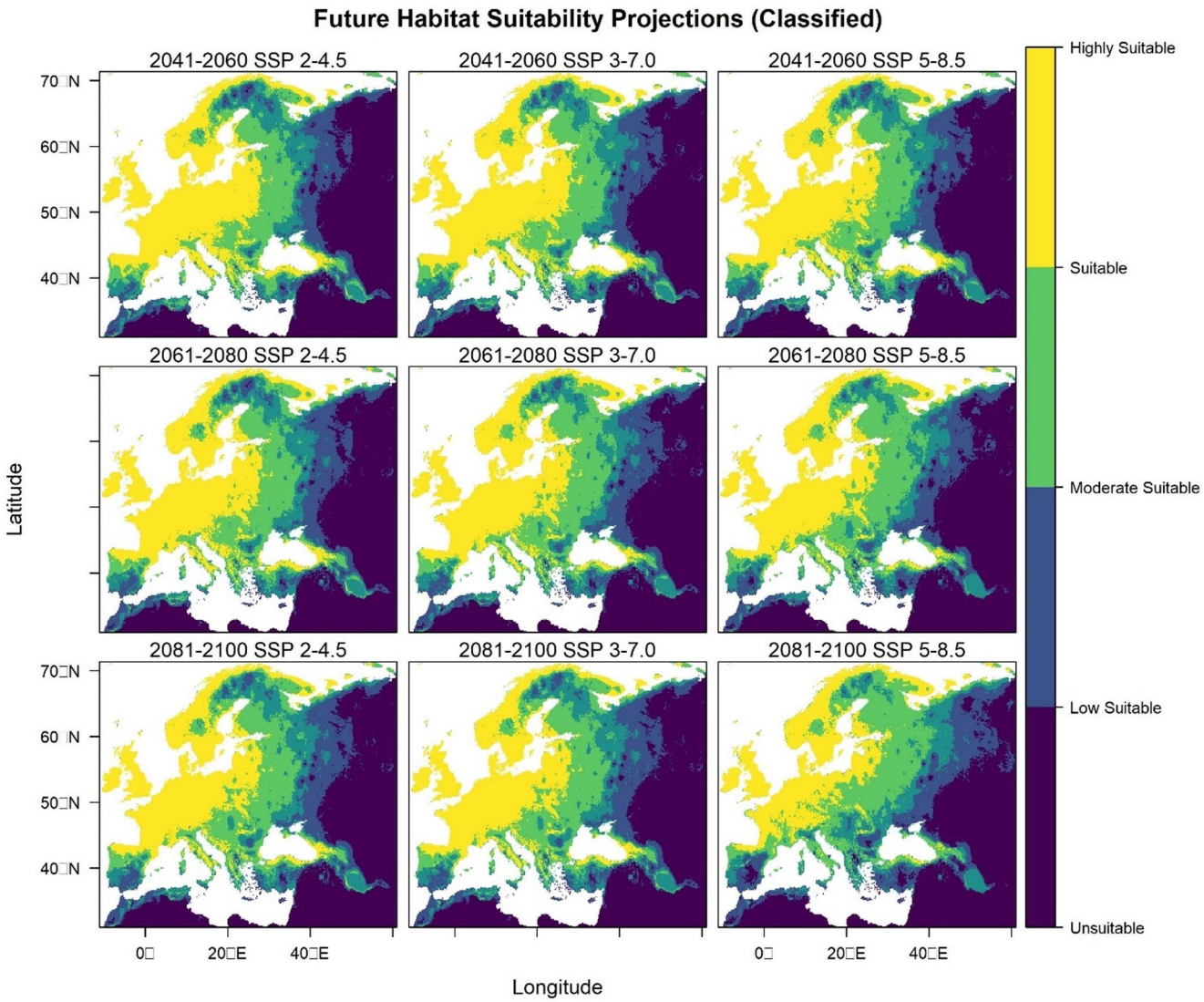

Fig. 4 Average binary prediction for European roe deer under future climate scenarios. Gray color represents unsuitable habitats, while green color indicates suitable habitats

The maps showing average binary prediction for the species under future climate scenarios indicate three key patterns of habitat change: contraction (red), expansion (green), and stable areas (gray). In the 2041–2060 period, contraction is already evident under all three scenarios, with the most notable habitat loss occurring in the western and central regions of Türkiye (Fig. 6).

Expansion areas, in green, are limited to the far northeast of the country, along the Black Sea coast. Contraction is more regionally concentrated under SSP 2–4.5.5 compared to SSP 3–7.0 and SSP 5–8.5.5, which are associated with more widespread habitat loss (i.e., mostly distributed in central Anatolia). In the 2061–2080 period, the contraction areas continue to expand under all scenarios (Fig. 7). This is particularly obvious in the SSP 3–7.0 and SSP 5–8.5.5 scenarios, where large portions of previously stable habitats in the western and central regions become unsuitable for European roe deer. Some small areas of expansion can be seen in the northeast, but they do not seem to make up for the loss of habitat. The contraction areas were thus even more pronounced under all scenarios by 2081–2100, with the most severe habitat loss across most of the country under SSP 585. The central and western regions show widespread contraction, while the northeast, particularly along the Black Sea region, retains a few small patches of stable habitat. In SSP 2–4.5.5, habitat loss is equally extensive although some northern areas are relatively stable. The SSP 3–7.0 scenario presents an intermediate level of contraction, with the general trend showing

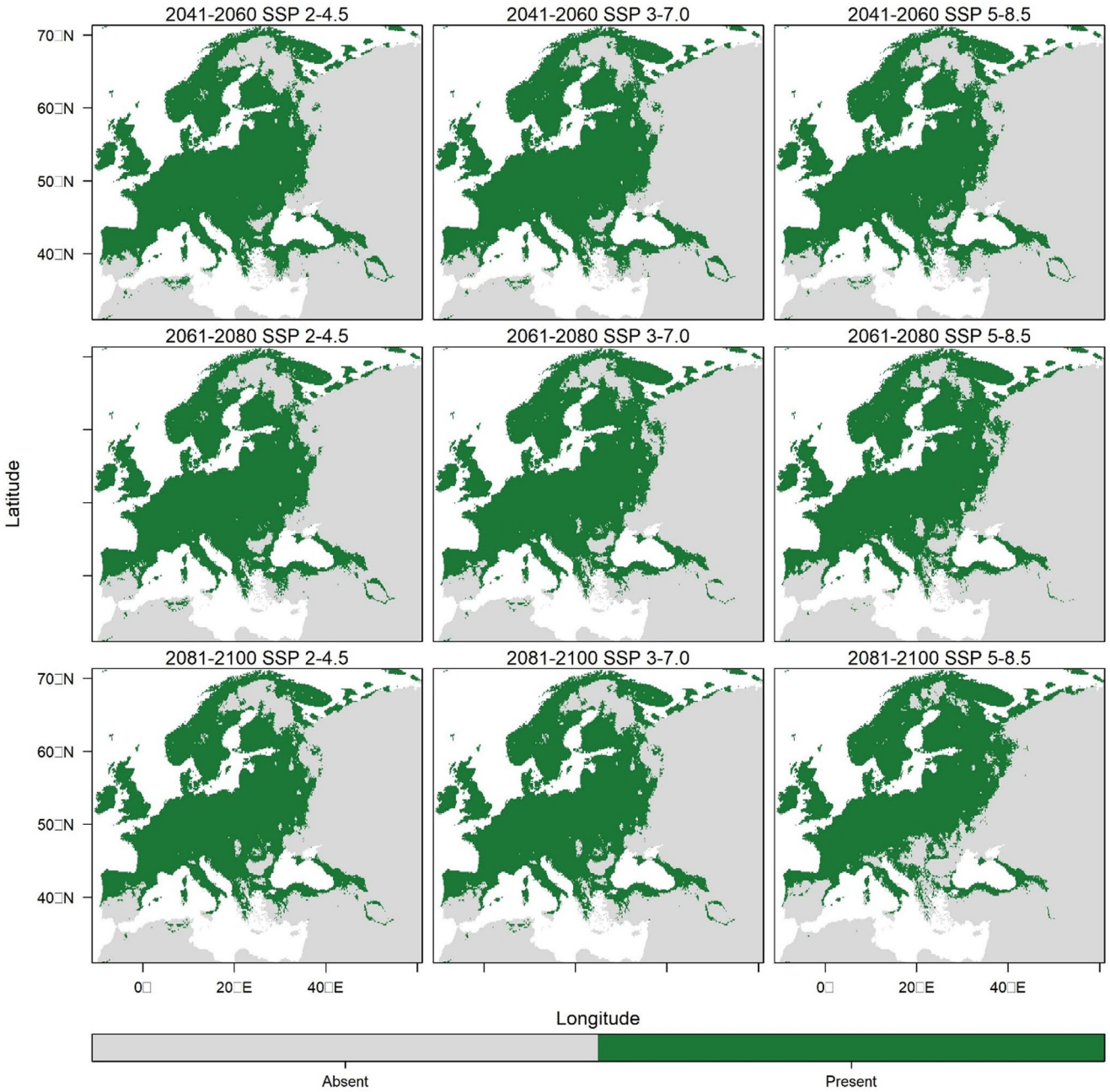

Fig. 5 Average projected climate habitat suitability maps for European roe deer across its overall distribution range under future climate scenarios. Projections are shown for three time periods (2041–2060, 2061–2080, and 2081–2100) and three Shared Socioeconomic Pathways (SSPs): optimistic (SSP 2–4.5.5), middle-of-the-road (SSP 3–7.0), and worst-case (SSP 5–8.5.5). The probability of occurrence ranges from 0 (dark blue, lowest probability) to 1 (yellow, highest probability)

a progressive loss of its habitat from west to east. The reduction in stable habitat across all time frames suggests a consistent trend of habitat shrinkage over time, with some areas retaining stability only in the most favorable climatic regions. The northeastern Black Sea region continues to be the primary location for habitat expansion, albeit on a small scale.

Discussion

The European roe deer (*Capreolus capreolus*) is a species that shows high ecological flexibility and is widespread in Europe. Although the species generally prefers forested areas, it has also begun to be seen frequently in human-influenced habitats such as agricultural lands and, in recent

Table 2 Spatiotemporal changes in the potential distribution of European roe deer under climate change (three shared socioeconomic pathways [SSPs]: optimistic [SSP 2–4.5.5], middle-of-the-road [SSP 3–7.0], and worst-case [SSP 5–8.5.5])

Projection	Overall Potential Area (ha)	Change Rate (%)	Türkiye Potential Area (ha)	Change Rate (%)
Present Day	676,015,200	–	43,790,700	–
2041–2060 SSP2-4.5	633,802,900	−6.2	30,164,700	−31.1
2041–2060 SSP3-7.0	639,939,800	−5.3	28,254,500	−35.5
2041–2060 SSP5-8.5	619,075,500	−8.4	26,700,100	−39.0
2061–2080 SSP2-4.5	626,057,200	−7.4	26,801,900	−38.8
2061–2080 SSP3-7.0	620,510,300	−8.2	22,432,500	−48.8
2061–2080 SSP5-8.5	598,270,100	−11.5	19,421,400	−55.6
2081–2100 SSP2-4.5	607,673,500	−10.1	23,959,300	−45.3
2081–2100 SSP3-7.0	607,673,500	−10.1	23,959,300	−45.3
2081–2100 SSP5-8.5	565,667,600	−16.3	14,798,600	−66.2

years, city parks (Lorenzini et al. 2022). Although urbanization and land-use changes are important drivers that can influence the habitat preferences of the species, our models focused on climatic and topographic predictors. Furthermore, temperature fluctuations have the potential to modify European roe deer habitats and, although the species shows ecological adaptability, these changes may still influence its feeding behavior and survival.

C. capreolus is very sensitive to extreme temperature changes. As a result of our study, the most important variables, bio7 (annual temperature variability) and bio2 (mean diurnal range) emphasize the potential of roe deer to change their habitat preferences and to affect their biological cycles, such as breeding cycles. High temperatures and low precipitation lead to extreme drought, reducing the vital resources of roe deer, especially food and water availability (Kamieniarz et al. 2024). Such temperature fluctuations have the potential to affect the habitats of this species, despite its broad ecological adaptability, and thus its feeding behavior and survival abilities.

Roe deer mate in the summer months and can adjust their reproductive cycle to the most appropriate time by slowing down embryonic development thanks to embryonic diapause (Danilkin 1996). Roe deer can skip ovulation during extremely hot and dry summer months and have an alternative mating period in autumn. Kamieniarz et al. (2024), in their study of the Puszcza Zielonka Experimental Forest, observed that females that ovulated in autumn were more likely to give birth to twins and stated that individuals participating in hot summer mating usually gave birth to a single offspring. Similarly, Gaillard et al. (2013) noted that severe summer droughts may increase female mortality rates in roe deer.

Changing weather conditions can affect the availability of resources essential for roe deer in different ways. In Scandinavia and Central Europe, roe deer's access to food is restricted by prolonged snow cover in the winter months (Mysterud et al. 1997). In contrast, our revised models indicate that the most severe contractions will occur in the Mediterranean regions, where hot and dry summers and declining rainfall are projected to further reduce food quantity and quality. Although minor new habitats are projected in northern Europe, these gains are negligible compared to the extensive losses in the south. It is also known that heavy rain at unexpected times also damages the vegetation on which the roe deer feed and take shelter (Lombardini et al. 2017). Decreases in snow cover and depth due to climate change suggest that there will be a shift in the winter distribution of roe deer towards higher altitudes and northern latitudes (Mysterud and Sæther 2010; Hagen et al. 2021).

The difference between daily maximum and minimum temperatures can affect the movement of roe deer and their preferences for shelter and browsing areas. Extreme temperature changes during the day may cause them to spend time in different regions. Mancinelli et al. (2015) stated that roe deer prefer dense canopy cover to avoid heat stress on hot summer days. In addition to climatic variables, topographic features also play a determining role in the distribution of roe deer (Evcin et al. 2019; Franchini et al. 2023). In our model, terrain roughness explained only a small proportion of habitat suitability (1.2%). This suggests that while roe deer may benefit from landscapes with some structural heterogeneity, terrain roughness is not a strong determinant of their distribution in Türkiye. The low contribution of topographic variables in our model suggests that climatic drivers are more influential for future distribution patterns. This also indicates that roe deer, while broadly adaptable to different landscapes, face limits under the projected climatic constraints (Milošević-Zlatanović et al. 2018).

The present-day distribution pattern of roe deer in Türkiye is mainly concentrated in the Black Sea and Marmara Regions. In addition, the species has a fragmented distribution extending from Central Anatolia to İzmir, Antalya, the Amanos Mountains, and even Hakkari (Evcin 2018). Since the early 2000 s, local reports and field studies have indicated localized increases in observations and reported abundances within fragmented ranges, along with increased human-deer conflict incidents, vehicle collisions, and observation frequency. Possible reasons for these local patterns include the species' popularity with local communities, the

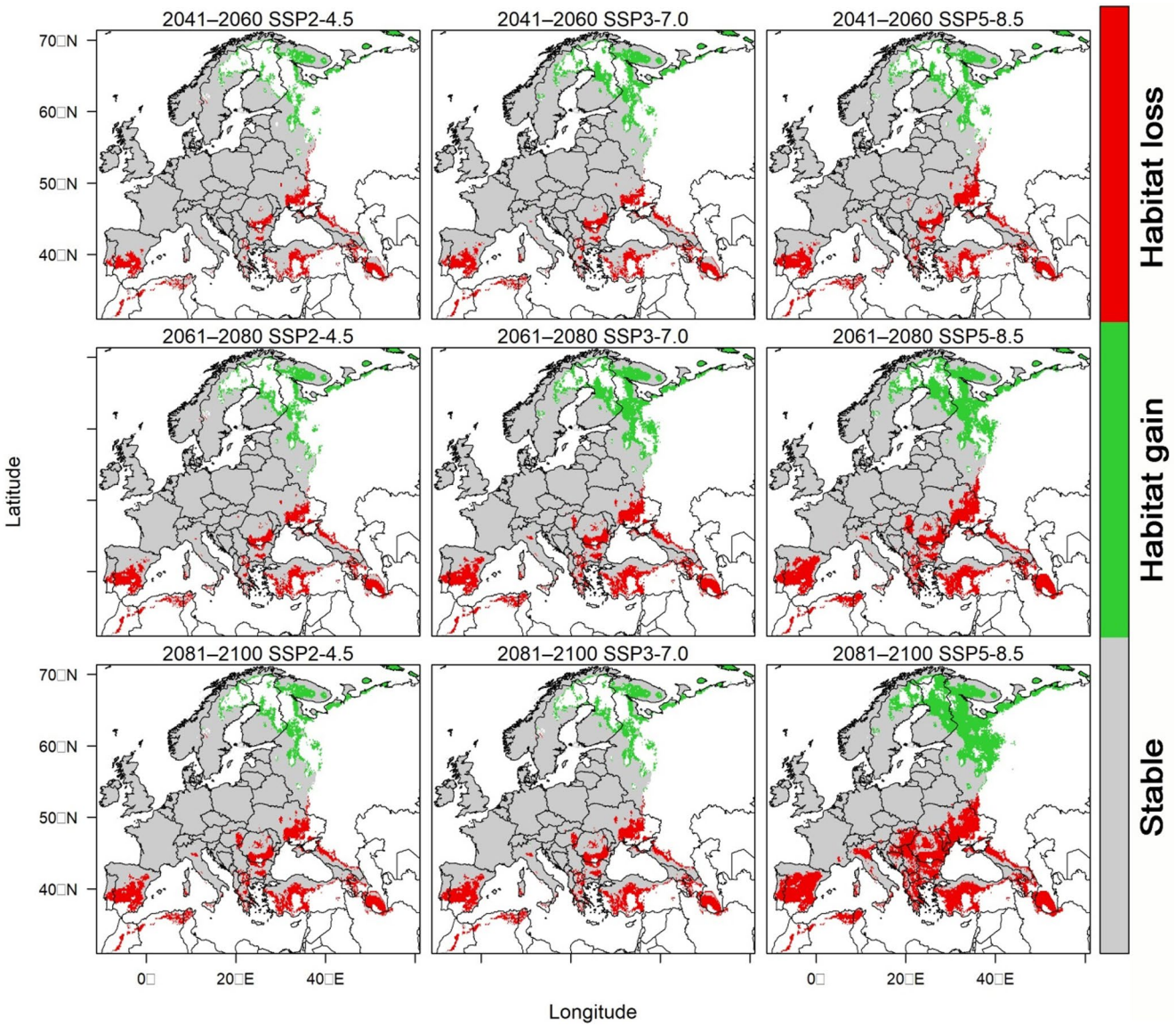

Fig. 6 The habitat change map for European roe deer overall distribution under future climate scenarios (Gray = Stable, Green = Gains, Red = Losses)

relatively low density of predators, and its broad ecological tolerance. However, our models suggest that such local patterns may not persist under future climate conditions, as severe contractions are projected across much of Türkiye.

Dispersal ability is an important determinant of the potential range shifts projected by our ENM. Although only limited refugia are projected in northern and high-altitude regions, colonization of these areas will depend on the capacity of populations to move across the surrounding matrix habitats, which often consist of agricultural land, settlements, or fragmented woodlands. Although dispersal was not explicitly modeled, literature suggests limited dispersal ability may impede northward shifts (Kerr 2020). The occurrence dataset also included roadkill records, which may introduce spatial bias by overrepresenting accessible areas. As human-related predictors were not explicitly incorporated into the models, this bias represents an additional limitation that should be considered when interpreting suitability patterns, particularly at local scales. The species is known to use heterogeneous landscapes, including farmland and mosaic habitats, to establish new ranges (Coulon et al. 2004; Hewison et al. 2009; Ducros et al. 2020; Evcin 2023). However, dispersal distances are limited to a few kilometers in general, with most juveniles settling within 5–20 km of their natal ranges (Strandgaard 1972; Wahlström and Liberg 1995). Some colonization of adjacent areas can occur through matrix habitats that allow movement, but major barriers such as highways, dense urban zones, or deep valleys can strongly restrict their movements (Passoni et al. 2021). The recent colonization of the Karagüney

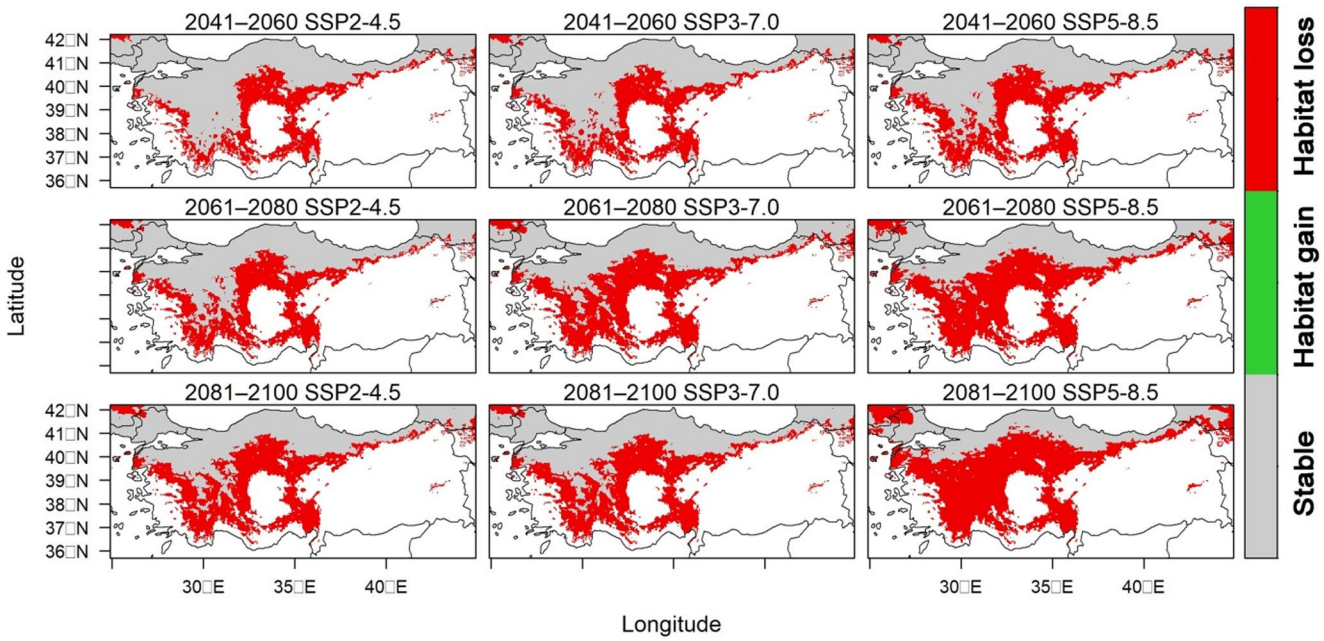

Fig. 7 The habitat change map for European roe deer focusing on Türkiye under future climate scenarios

Mountains in Türkiye demonstrates that roe deer are able to occupy contiguous suitable areas (Özcan 2021). Nevertheless, ecological and anthropogenic constraints indicate that its dispersal is unlikely to keep pace with the distributional changes projected under future climate scenarios.

The current network of protected areas in Türkiye is often insufficient to protect its diverse ecosystems. The existing protected areas have been increasingly threatened by non-conservation uses such as mining, energy projects, and intensive forest management for timber production. The lack of comprehensive management plans and the resulting habitat fragmentation increases the threats to wildlife and emphasize the need for stronger conservation strategies that prioritize biodiversity and ecosystem integrity (Şekercioğlu et al. 2011). Understanding the environmental factors that affect species distributions is crucial for supporting their adaptation to climate change. In particular, integrating ecological niche modeling with field observations can improve predictions and allow for more accurate assessments of habitat suitability and future range shifts. This study, which projects severe future contractions in roe deer habitat under multiple climate scenarios, provides information for conservation planning and species management.

At the European scale, model performance assessments have indicated that predictions of roe deer absences tend to be less reliable than those for other ungulates (ENETWILD-consortium 2022). This limitation increases the risk of false positives when projecting suitable habitats. To address this, we defined the binary threshold by balancing sensitivity and specificity, thereby reducing the bias toward overprediction. In addition, we reported alternative thresholds through a sensitivity analysis to demonstrate the robustness of our results under different binarization criteria. By incorporating the findings in conservation frameworks, local and regional authorities can develop more effective, data-driven strategies to protect wildlife and enhance biodiversity conservation.

Bioclimatic and topographic variables suggest a future loss of suitable habitat in southern Türkiye, according to model projections. While the species shows ecological adaptability, the consistent and severe contractions projected across all scenarios indicate that its persistence remains highly uncertain. Hence, national conservation plans for the species are vital to continue its existence in the face of environmental change.

The consistent declines observed in Table 1 highlight the profound impact of climate change on species distributions. While limited gains are projected in northern and high-altitude regions, the species faces extreme challenges in Türkiye, where suitable habitat is projected to decline drastically. These findings suggest that climate change will not have uniform effects across all regions but will instead create largely adverse and spatially heterogeneous impacts, with contractions dominating southern and central areas, and only restricted refugia remaining suitable in the north.

Rising temperatures are likely behind the habitat losses in Türkiye, the decreased water availability, and the changing patterns of vegetation that may no longer meet the species' ecological needs. The heightened aridity and extreme climatic events projected under higher-emission scenarios

will worsen these challenges, resulting in a high risk of population decline and possible local extinction. With these projections in mind, the need for urgent conservation efforts to combat the challenges of climate change is necessary. Strategies such as habitat restoration, protected area expansion, and climate adaptation planning could help mitigate some of the negative impacts and support the long-term viability of roe deer populations in the country.

Modeling habitat suitability is particularly essential for European roe deer since the species is significant for both ecology and culture. Predicting future contractions or shifts in range can aid in pinpointing possible refugia, enhancing habitat connectivity, and informing initiatives to mitigate biodiversity loss. Our results align with previous SDM studies on roe deer that documented latitudinal and altitudinal responses to warming, including northward movements in Central and Northern Europe (Mysterud and Saether 2010; Lorenzini et al. 2022). Comparable trends have been seen in other temperate ungulates, including red deer and wild boar, which have expanded their distributions to higher latitudes and altitudes in response to warmer winters (Veličković et al. 2016; Büntgen et al. 2017). In contrast to the severe contractions expected for southern Europe and Türkiye, this study emphasizes the need to consider both range expansion and contraction when establishing adaptive conservation measures under climate change.

Finally, it is important to acknowledge a few limitations of this study. First, the choice of emission scenarios and general circulation models (GCMs) affects the projections of habitat suitability. Second, because different regions have varying levels of monitoring intensity, occurrence records—some of which are based on opportunistic observations—may show geographic biases. Third, the coarse spatial resolution of the climatic and topographic data limits how much these projections can inform site-level conservation planning, because many small-scale habitat features important for roe deer do not appear at this resolution. Fourth, our models mainly focus on abiotic factors and neglect possible biotic interactions that could also affect roe deer distribution in the context of climate change, such as competition, predation, genetic diversity or disease dynamics.

Recent research has shown that European roe deer do not form a genetically homogeneous population across their range (Niedziałkowska et al. 2024). Instead, several genetically differentiated groups exist, shaped by post-glacial range expansions and long-term geographical separation, and such genetic differences may influence population responses to environmental change. Although these findings provide important insights into population-level processes, our modeling framework intentionally focused on the species-level climatic niche at the continental scale. Integrating genetic structure into ecological niche models represents a valuable direction for future research, particularly for assessing local adaptation, but was beyond the scope of the present large-scale climate-driven analysis. Since our assessment does not include this variation, it cannot fully represent differences in adaptive potential across regions. Future study that combines climate-based estimates with land use information and genetic data would provide a clearer understanding of present habitat conditions and potential range changes. While these limitations are common in SDM applications, we used sensitivity analysis, model calibration, and variable selection to increase robustness of the applied methodology. We also recommend that mapping the main movement routes of roe deer across Europe, as identifying important corridors would help assess whether the species can follow the projected range shifts. As highlighted by Serva et al. (2025), including connectivity modeling in landscape planning would also help improve the design of long-term conservation measures.

Conclusions

This study shows how climate change has substantial effects on roe deer distribution across Europe and Türkiye. ENMs suggest that the most important climatic factors determining habitat suitability are the annual temperature range, precipitation seasonality, and mean annual temperature. Under the present-day conditions, the majority of suitable habitat can be found in the temperate forest areas of central and Eastern Europe, Scandinavia, and western Russia. Future climate projections under SSP 2–4.5.5, SSP 3–7.0, and SSP 5–8.5.5 indicated a northward shift of suitable habitats, with considerable losses in southern Europe, Türkiye, and western Asia, particularly under the worst-case scenario (SSP 5–8.5.5). The large-scale northward shift in habitat suitability indicates that some populations are likely to find climate refuge at higher latitudes, whereas many southern populations appear to be at high risk of decline and local extinction.

It is important to note that habitat suitability maps represent climate-induced potential habitat suitability, not actual habitat occupancy. Therefore, areas predicted to be highly suitable may also include areas that are locally unsuitable due to anthropogenic factors such as urbanization, transportation infrastructure, and land use. While these factors strongly influence local habitat availability, they have not been included in the modeling framework to avoid scale mismatch and limited transferability under future climate scenarios. Integrating human-induced constraints at regional and local scales into the models is considered even more beneficial for climate-focused conservation planning.

Adaptation and management measures to support roe deer populations can be achieved through the establishment and designation of protected areas, particularly where

populations are disturbed or facing threats. A key priority is to expand and connect protected areas in regions where roe deer populations are most vulnerable. This emphasizes the need to identify possible refugia and to develop management plans that prioritize biodiversity and ecosystem integrity. In this context, adaptation measures can be applied to mitigate the adverse effects of climate change, such as habitat restoration, assisted migration, and other measures to enhance the adaptability of roe deer populations. Encouraging further research and monitoring is also important for understanding the interactions and future impacts of climate change on both roe deer and other wildlife species through the assessment of the capacity of species to adapt, delineation of potential refugia, and refinement of predictions of future habitat suitability.

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Data availability The data supporting this study's findings are not openly available due to privacy and data protection policies; however, they can be obtained from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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