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Climate-Driven Habitat Shifts and Conservation Implications for the Submediterranean Oak *Quercus pyrenaica* Willd.

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Abstract

Climate change poses a major threat to forests, impacting the distribution and viability of key species. *Quercus pyrenaica* Willd., a marcescent oak endemic to the Iberian Peninsula (Portugal and Spain) and southwestern France and a structural species in submediterranean forests, is particularly susceptible to shifts in temperature and precipitation patterns. Aiming to assess its potential loss of suitable area under future climate scenarios, we developed high-resolution spatial distribution models to project the future habitat suitability of *Q. pyrenaica* under two climate change scenarios (SSP3-7.0 and SSP5-8.5) for the periods 2070 and 2100. Our model, which has an excellent predictive performance (AUC of 0.971 and a TSS of 0.834), indicates a predominantly northward shift in the potential distribution of the species, accompanied by substantial habitat loss in southern and lowland regions. Long-term potential suitable area may shrink to 42% of that currently available. This, combined with the limited natural dispersal capacity of the species, highlights the urgency of targeted management and conservation strategies. These results offer critical insights to inform conservation strategies and forest management under ongoing climate change.

Keywords: *Quercus pyrenaica*; climate change; species distribution modeling; biomod2; submediterranean forests; forest management; conservation strategies

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1. Introduction

The Pyrenean oak (*Quercus pyrenaica* Willd.) is a marcescent oak species that dominates submediterranean forests across the Iberian Peninsula (IP), occurring in ecotonal zones with sclerophyllous forests at the southern margin of its distribution range [1–3], and with deciduous forests at its northern one [4–8]. Its distribution spans southwestern France, Spain, Portugal, and northeastern Morocco, with important relict subpopulations in its southernmost range, particularly in Mediterranean mountain areas of the IP and Morocco [2,3,9]. The species thrives in areas with mean annual temperatures between 6 °C and 15 °C [2], tolerating winter cold of −5 °C and summer heat up to 22 °C [1]. However, some southern populations, particularly those in the thermo-Mediterranean fringe, occur under significantly hotter summer conditions, provided there is sufficient annual precipitation or compensatory rainfall during the warm season, a hallmark of submediterranean climate regimes [10–12]. It grows in areas with average annual precipitation ranging from 600 mm to over 3000 mm, with summer drought as a limiting factor [1,13], demanding, during the summer, 100 to 200 mm of rain [1]. It generally prefers siliceous bedrock and acidic soils [1] but can locally occur on decarbonated basic or neutral substrates due to carbonate leaching [14].

In the IP, marcescent forests dominated by *Q. pyrenaica* and *Q. faginea* define a submediterranean ecotone between the Eurosiberian and Mediterranean biogeographic regions [1,15]. This transitional zone is characterized by milder summers with increased rainfall [16,17] and represents the interface between temperate deciduous forests and Mediterranean evergreen sclerophyll woodlands [18,19]. The dynamism of submediterranean zones has been highlighted in recent studies, documenting past shifts since the late Quaternary [14], and projecting future changes [19,20]. Although the ecotone may persist or expand northward, dominant species are likely to suffer range contractions at the southern margin of their distribution range. Projected climate change, especially rising temperatures and alterations in both annual precipitation and its seasonality, is expected to reduce submediterranean areas, favoring the expansion of purely Mediterranean conditions marked by summer drought [20,21].

Predicted climate change during the 21st century will be characterized by changes in precipitation patterns, temperature rise, and extreme climatic events, particularly in the Mediterranean region [22,23]. Here, temperatures are expected to rise 20% further than what is globally expected, especially in the summer period, when they are expected to increase from 50% up to 100% further than the global average [23]. These changes will affect physical and biological systems worldwide, promoting adjustments to new realities [22], and they will be easily seen in ecotones sensitive to global changes [24–26]. Given the projected shifts in species distribution, conservation must not only focus on static preservation but also incorporate dynamic, climate-informed management frameworks.

As climate change intensifies, forest management and restoration actions must move beyond uniform solutions toward dynamic, adaptive strategies [27]. Recognizing that ecosystems vary in their sensitivity and resilience, management approaches must be tailored to specific environmental contexts [28]. In this framework, adaptive strategies can be grouped into three main categories—resistance, resilience, and response (or transition), each reflecting a different level of management intervention [27,29].

Species distribution models (SDMs), helping to map current species habitat suitability based on ecological niche [30–32], are useful for studying climate change effects on biodiversity, projecting species' suitable areas under different future scenarios, and identifying possible range shifts [33,34]. Their performance on producing accurate projections has made them increasingly valuable [35] and widely used for species conservation, management planning, and habitat restoration [34,36,37].

The Pyrenean oak plays a crucial ecological role as a key structural species in the IP submediterranean forests, providing refuge for biodiversity [38–40], contributing to ecosystem stability, and supporting a wide range of ecosystem services [11,41–43]. Although several studies have been conducted about this species [2,3,44–49], information about the current and future distribution is lacking [20]. As the submediterranean ecotone is projected to shift northwards and lose suitability in the southwestern Mediterranean [20], we hypothesize that *Q. pyrenaica* might experience a significant loss of suitable area under climate change scenarios, particularly in the southernmost parts of its current range. In this context, understanding how the species' suitable habitat may change is essential. The general goal is to predict the impact of global warming scenarios on the species under study to inform conservation and restoration efforts. The specific aims are to (1) assess the current potential distribution of *Q. pyrenaica*, (2) predict future habitat suitability under different climate change scenarios, (3) clarify priority areas for conservation and restoration, and (4) identify adaptation strategies for future conservation and restoration. To achieve these goals, we applied an ensemble modeling approach to forecast the current and future distribution of *Q. pyrenaica*, offering spatially explicit insights to support conservation planning and adaptive management under climate change.

2. Materials and Methods

2.1. Study Area and Species Occurrence Data

The study area encompasses the western Mediterranean Basin, including the IP, southwestern France, and Morocco (North Africa), where *Q. pyrenaica* populations are currently found. To mitigate spatial niche truncation and avoid clamping effects [50,51], the model was developed using a bounding box that covers the entire species distribution range, with an additional 500 km *buffer* around occurrence points (Figure 1). Species occurrence records were obtained from GBIF (https://doi.org/10.15468/dl.vggh4j (accessed on 13 March 2024)), national biodiversity databases, and expert-curated knowledge, particularly for the IP [13]. The dataset was cleaned to remove duplicates and erroneous records, ensuring high data quality for modeling. All occurrences were then standardized to a single 1 × 1 km grid, resulting in 14,554 records, with latitude and longitude coordinates in WGS 1984 (EPSG:4326) reference system grid (see Table S1).

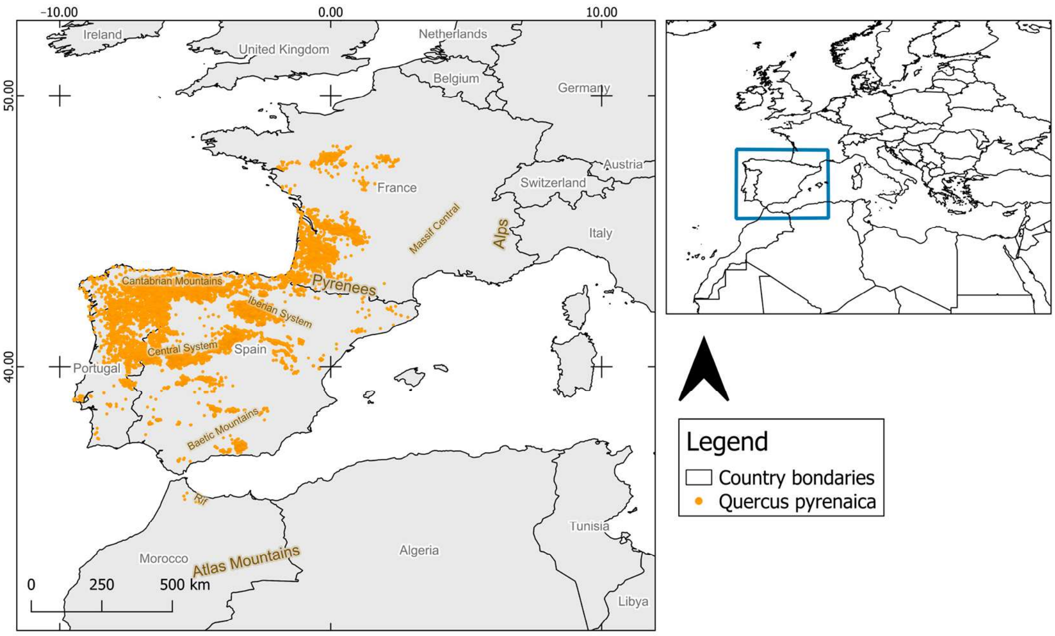

Figure 1. Study area and *Q. pyrenaica* occurrence points used in the model. Latitude/longitude coordinates in WGS 1984 (EPSG:4326) reference system grid. Maps were generated by IP in QGIS 3.34.6 (Spatial without Compromise QGIS website).

2.2. Environmental Variables

The model was calibrated using predictive environmental variables considered relevant to define the species' ecological niche (Table S2). For climatic predictors, for future and current scenarios, we selected among a set of 19 bioclimatic indices downloaded from CHELSA v.2.1 dataset [52] for the current calibration period 1981–2010. Considering the relevance of soil characteristics and terrain morphology [53] to explain *Q. pyrenaica*'s current distribution [1,8], soil pH, soil texture class at a 5 cm depth [54], Topographic Ruggedness Index [55] (TRI, as a proxy of slope and terrain complexity), and Topographic Wetness Index (TWI, as a proxy of soil moisture and flow accumulation) [56], both derived from the EarthEnv project, and elevation data at a 1 km spatial resolution were also used as predictor variables. Variable selection was employed to exclude highly collinear predictors. Using this method, we kept predictors with a pairwise correlation $|r| < 0.7$ [57] and further considered the species' ecological requirements to guide the selection process.

The climatic data used for model projections for the two-time windows (2041–2070 and 2071–2100) [52] were derived from averaged ensemble projections, which included five General Circulation Models (GCMs) (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL). These GCMs were selected since they are classified as having good performance ('Satisfactory') for Europe based on the previous CMIP5 Project [58]. We also considered two different Shared Socioeconomic Pathways (SSPs) scenarios: an intermediate scenario (SSP3-7.0) and a pessimistic scenario (SSP5-8.5) (Figure 2). Although the choice for a pessimistic scenario may not always be consensual, as some studies suggest that high-emission pathways such as SSP5-8.5 are increasingly unlikely, particularly in the latter half of this century [59,60], the use of both scenarios is intended to capture the range of potential outcomes and identify the trend between them. This approach enables us to anticipate likely tendencies, inform conservation and mitigation strategies, and further draw the attention of policymakers. All variables were re-projected and re-sampled (average) to a common reference grid at a 1 × 1 km spatial resolution (WGS 1984/EPSG:4326).

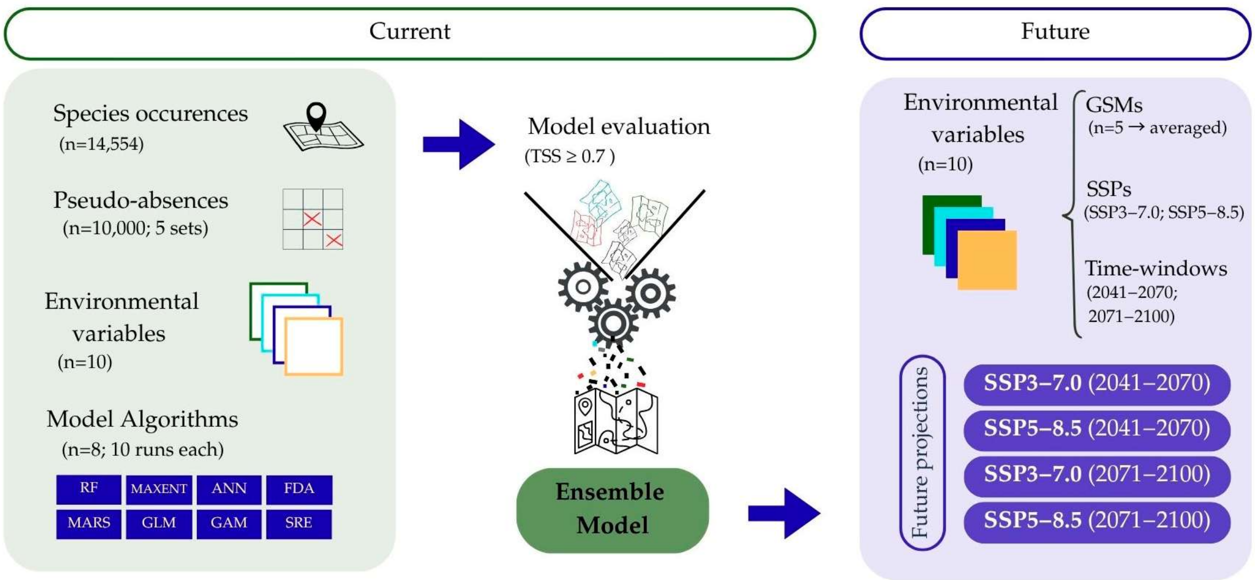

Figure 2. Modeling workflow. TSS—True Skill Statistic; GCMsGeneral Circulation Models (GCMs); SSPs—Shared Socioeconomic Pathways.

2.3. Modeling Approach: Calibration, Fitting, and Evaluation

Models were developed in the R statistical software (R 4.4.2) (R core team, 2024) using the biomod2 package [61,62]. Biomod2 package analyzes species–environment relations, applying a multi-model ensemble forecasting approach by combining several statistical and machine-learning-based algorithms [61,62]. Models were fitted using eight modeling techniques currently available in biomod2: GLM (Generalized Linear Models); GAM (Generalized Additive Models); SRE (Surface Range Envelope); ANN (Artificial Neural Networks); FDA (Flexible Discriminant Analysis); MARS (Multivariate Adaptive Regression Splines); RF (Random Forests); and MAXENT (Maximum Entropy Model). Pseudo-absence (PA) datasets were generated to calibrate the model due to the presence-only nature of the occurrence data. Five PA sets of 10,000 grid cells each were generated, with no minimum distance between PAs, to maximize the representativeness of the study area environmental space (Figure 2).

Model evaluation was performed in 10 rounds using holdout cross-validation, with 80% of the input records used for model fitting and 20% for model evaluation at each round. To assess model performance, different accuracy measures were calculated: Area Under the Receiver Operating Curve (AUC), True Skill Statistic (TSS), and sensitivity and specificity [61]. The AUC can assume values between 0 and 1 and can be classified as excellent (0.9–1.0), very good (0.8–0.9), good (0.7–0.8), fair (0.6–0.7), and poor (0.5–0.6) [63]. The TSS values vary between -1 and 1 and can be classified as excellent (TSS > 0.8), good (0.6–0.8), fair (0.4–0.6), poor (0.4–0.2), and very poor (TSS $\leq$ 0.2) [64]. The threshold value maximizing the TSS was used to 'binarize' model results into suitable/unsuitable habitats [65]. The best-performing models were selected before model ensembling using a threshold of TSS $\geq$ 0.7 [66]. These models were used to calculate an ensemble model based on their average, reducing inter-model uncertainty [35,67].

Variable importance was assessed using a permutation method, an internal biomod2 procedure. A score of zero indicates no influence of a given variable, while higher values reflect a greater impact on model predictions.

2.4. Present-to-Future Range Shifts

The model representing current suitable areas was used as a baseline to assess range shifts between present and future scenarios. The current model was overlapped with the different future projections to evaluate changes in habitat suitability, allowing for the identification of areas with suitability gains, losses, and areas that remain consistently suitable or unsuitable (Figure 3). These operations were performed in ArcGIS Pro® 3.2.2. using the Raster Calculator tool. To visualize future variation spatially, a many-to-many matrix was constructed by combining all possible present-to-future comparisons, enabling comprehensive mapping of projected range shifts.

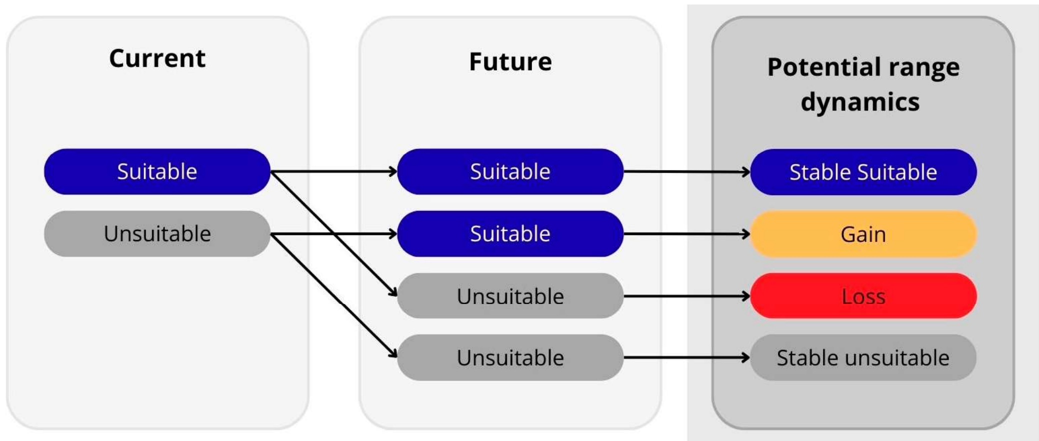

Figure 3. *Quercus pyrenaica* potential range/distribution dynamics by combining current and future projected distributions.

To identify areas with a higher likelihood of future suitability for *Q. pyrenaica*, projected range shifts under various scenarios were overlaid. Areas classified as either stable or showing suitability gains across all future projections were defined as long-rm suitable areas, as they consistently remain favorable for the species (Figure 4). In contrast, areas identified as unsuitable or experiencing a loss of suitability in at least one scenario were designated as transitional zones, indicating that suitability is shifting, either increasing or decreasing, but not necessarily temporary (Figure 4).

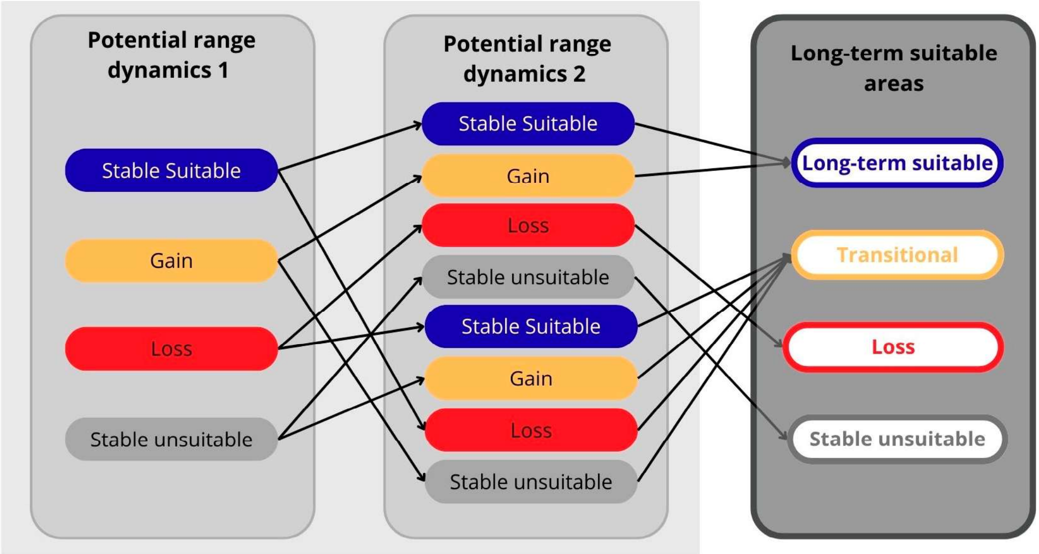

Figure 4. Long-term-suitable areas, obtained by the overlap of possible future range shifts of projections of *Q. pyrenaica*.

3. Results

3.1. Model Evaluation and Environmental Variable Contribution

With an AUC of 0.971 and a TSS of 0.834, the model demonstrates excellent predictive performance, indicating a high level of accuracy in estimating *Q. pyrenaica*'s potential distribution (Table S3). Sensitivity and specificity scores were above 88, highlighting that the model can accurately predict presences and absences (Table S3).

The most important variables defining the distribution of *Q. pyrenaica* were annual precipitation (Bio12), precipitation during the warmest quarter (Bio18), and soil pH. Other variables, including mean temperature of warmest quarter (Bio10), precipitation seasonality (Bio15), isothermality (Bio03), and the minimum temperature of the coldest month (Bio06), had smaller contributions to the model (Table S4). The contributions of soil texture (TEX), TRI (Topographic Ruggedness Index), and TWI (Topographic Wetness Index) were negligible (Figure 5 and Table S4).

Variables related to annual or seasonal precipitation (Bio12, Bio18, and Bio15) were those that most contributed ~64% (Figure 5 and Table S4). Regarding annual precipitation (Bio12), a variable that contributes ~30% to the model, the species acknowledge values over 500 mm (Figure 6), with a peak around 700 to 1000 mm (Figure 6). Summer rainfall is also important (~26%), while some values of precipitation during the warmest quarter exist (Bio18) (Figure 6). Precipitation seasonality (Bio15) seems to have the lowest importance among precipitation variables but with higher than ~8% contribution to the model. Temperature-related variables (Bio10, Bio03, and Bio06) contributed ~19% to the model. The temperature of the warmest quarter (Bio10) peaks within 17 to 22 °C, contributing ~11% to the model. The isothermality (Bio03) values are lower than 0.45, suggesting large differences between seasons compared to daily temperature ranges. The minimum temperature of the coldest month (Bio06) is the lowest contributor of temperature variables to the model (~1%). Density values show more points in positive temperatures, around 2 to 3 °C (Figure 6). Soil pH contributed ~16% to the model, mostly ranging between 5 to 7 values, revealing the species' predominance in acidic soils (Figure 6).

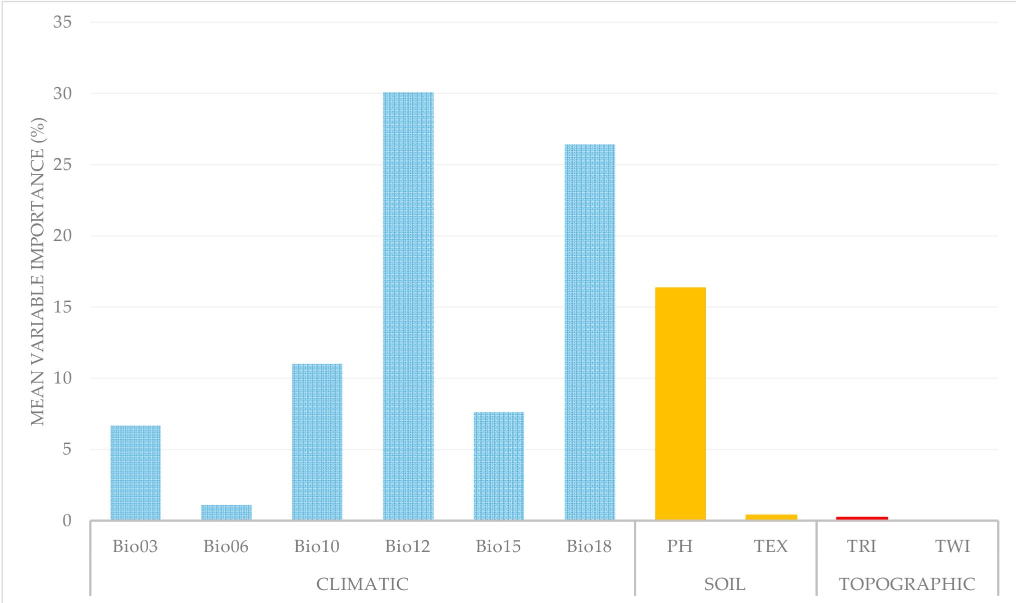

Figure 5. Variable importance for *Q. pyrenaica* considering the three groups of predictors, climatic (precipitation and temperature), soil, and topographic: Bio03—isothermality (Bio02/Bio07) (×100); Bio06—minimum temperature of the coldest month; Bio10—mean temperature of warmest quarter; Bio12—annual precipitation; Bio15—precipitation seasonality (coefficient of variation); Bio18—precipitation of warmest quarter; pH (soil pH at 5 cm); TEX (soil texture class at 5 cm); TRI (Topographic Ruggedness Index), and TWI (Topographic Wetness Index).

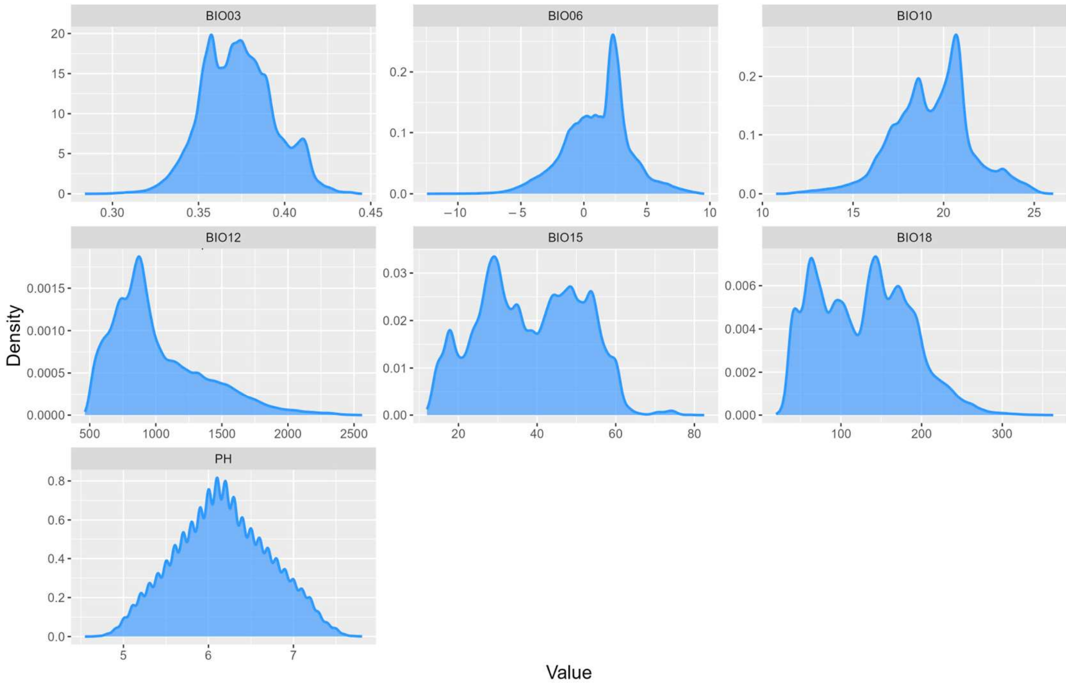

Figure 6. Density estimation for each selected environmental variable: Bio03—isothermality (Bio02/Bio07) (×100); Bio06—minimum temperature of the coldest month; Bio10—mean temperature of warmest quarter; Bio12—annual precipitation; Bio15—precipitation seasonality (Coefficient of Variation); Bio18—precipitation of warmest quarter; pH (soil pH at 5 cm).

3.2. Potential Current Distribution and Future Range Shifts

According to the final ensemble model, the current potential distribution of *Q. pyrenaica* extends from North Africa (specifically the Rif and Middle Atlas regions of Morocco) across the north/northwest of the IP, and it extends further to the west coast of France until Brittany, with isolated areas in the southeast of France, covering an estimated area of 485,887 km^2. The distribution is largely continuous from central–western Iberia to northwestern France, primarily along coastal zones. Additionally, more fragmented presences are projected in North Africa, southern and southeastern France, as well as scattered locations across the IP, Sardinia, and Corsica.

The model also identified climatically suitable areas in the Algerian Atlas, Corsica, and Sardinia, despite the absence of known occurrences in these regions for *Q. pyrenaica*.

Future climate scenarios project a predominantly northward (latitudinal) and altitudinal shift in the geographic range of *Q. pyrenaica*, with a general decrease in the area suitable for the species (Table 1). Habitat gains are anticipated in northern France, England, and Wales, potentially expanding into Ireland under the most extreme scenario (SSP5-8.5; Figure 7d). Smaller suitable areas may also persist or emerge in northern Iberia and Morocco and southeastern Spain mountainous regions under less severe climatic scenarios for the short time period (2041–2070) (Figure 7a). However, these southern and upslope refugia progressively shrink under more severe climate scenarios and in later periods (2070–2100), reflecting increasing habitat contraction and even extirpation (Figure 7b,d). Conversely, along the Pyrenees and in southern France, habitat suitability increases under more severe climate scenarios and in later time frames, suggesting that these regions may become increasingly favorable for *Q. pyrenaica*. (Figure 7d). In the IP, the entire Mediterranean fringe loses suitability for *Q. pyrenaica*, with suitable areas remaining mainly on the siliceous slopes of the Baetic system. In the pessimistic scenario, losses in central–western France could lead to the isolation of northern populations from those in the south (Figure 7d). Across all analyzed scenarios, the gains in new suitable areas are consistently smaller than the losses in unsuitable areas (Table 1). Stable suitable areas exceed 50% in only one scenario (SSP3-7.0, 2041–2070). Furthermore, in the 2071–2100 time frame, losses account for approximately 50% of the current suitable area in both SSP scenarios, representing larger areas than those that remain suitable. The results for both scenarios (SSP3-7.0 and SSP5-8.5) present a higher loss and lower suitable area (gain + stable) for the long term (2071–2100) (Table 1).

Table 1. Percentage of change (%) in the predicted distributions (gained, stable, or loss) of *Q. pyrenaica* under different scenarios and time frames. Total suitable area: gain and stable area.

SSP Scenarios	Time Frames	Gain		Stable		Loss		Total Suitable Area
		Km^2	%	Km^2	%	Km^2	%	Km^2
SSP3-7.0	2041–2070	56,540	10.42	303,008	55.86	182,879	33.71	359,548
	2071–2100	77,272	13.72	209,214	37.15	276,673	49.13	286,486
SSP5-8.5	2041–2070	89,047	15.49	282,048	49.06	203,839	35.45	371,095
	2071–2100	150,728	23.68	161,301	25.34	324,586	50.99	312,029

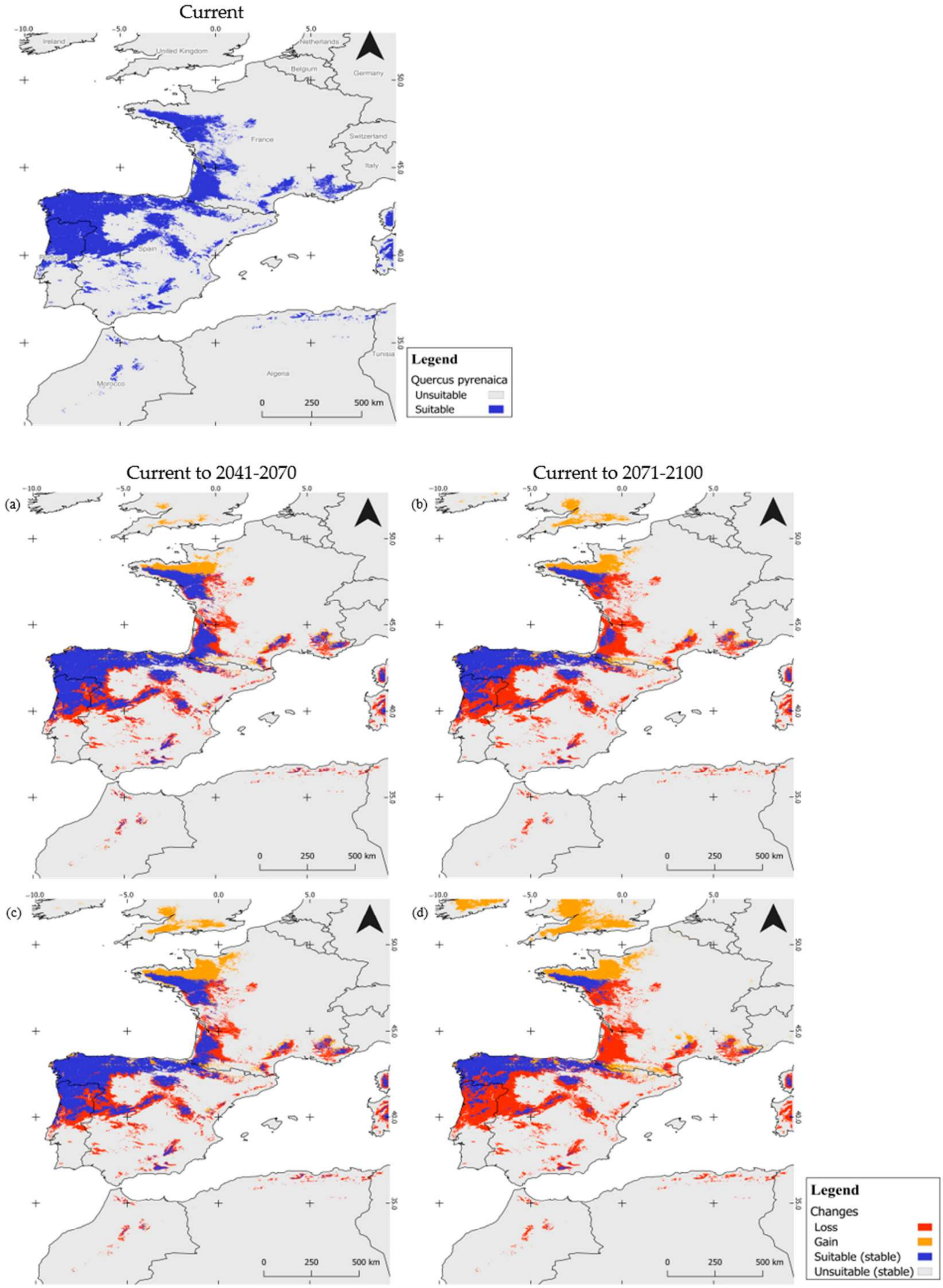

Figure 7. Suitable climatic distribution of *Q. pyrenaica* under current conditions and changes in predicted distributions (gain, loss, or stable) under different scenarios: (**a**) 2041–2070 SSP3-7.0; (**b**) 2071–2100 SSP3-7.0; (**c**) 2041–2070 SSP5-8.5; (**d**) 2071–2100 SSP5-8.5.

3.3. Long-Term-Suitable Areas and Implications for Species Conservation

The gain and stable suitable areas were analyzed across different scenarios to identify locations with a higher long-term probability for *Q. pyrenaica*, since these may be potential key conservation zones for the species. This analysis, as shown in Figure 5, was conducted for two-time frames (2041–2070 and 2071–2100), considering the overlap between the two SSP scenarios. In the 2041–2070 period, the total area of long-term-suitable zones represents 69% of the total suitable areas under current conditions. In contrast, the 2071–2100 time frame shows a reduction in the potential conservation area to 48% of the suitable area under current conditions. Conversely, transitional zones expand over 100%, from 2041–2070 to 2071–2100 (Figure 8a,b).

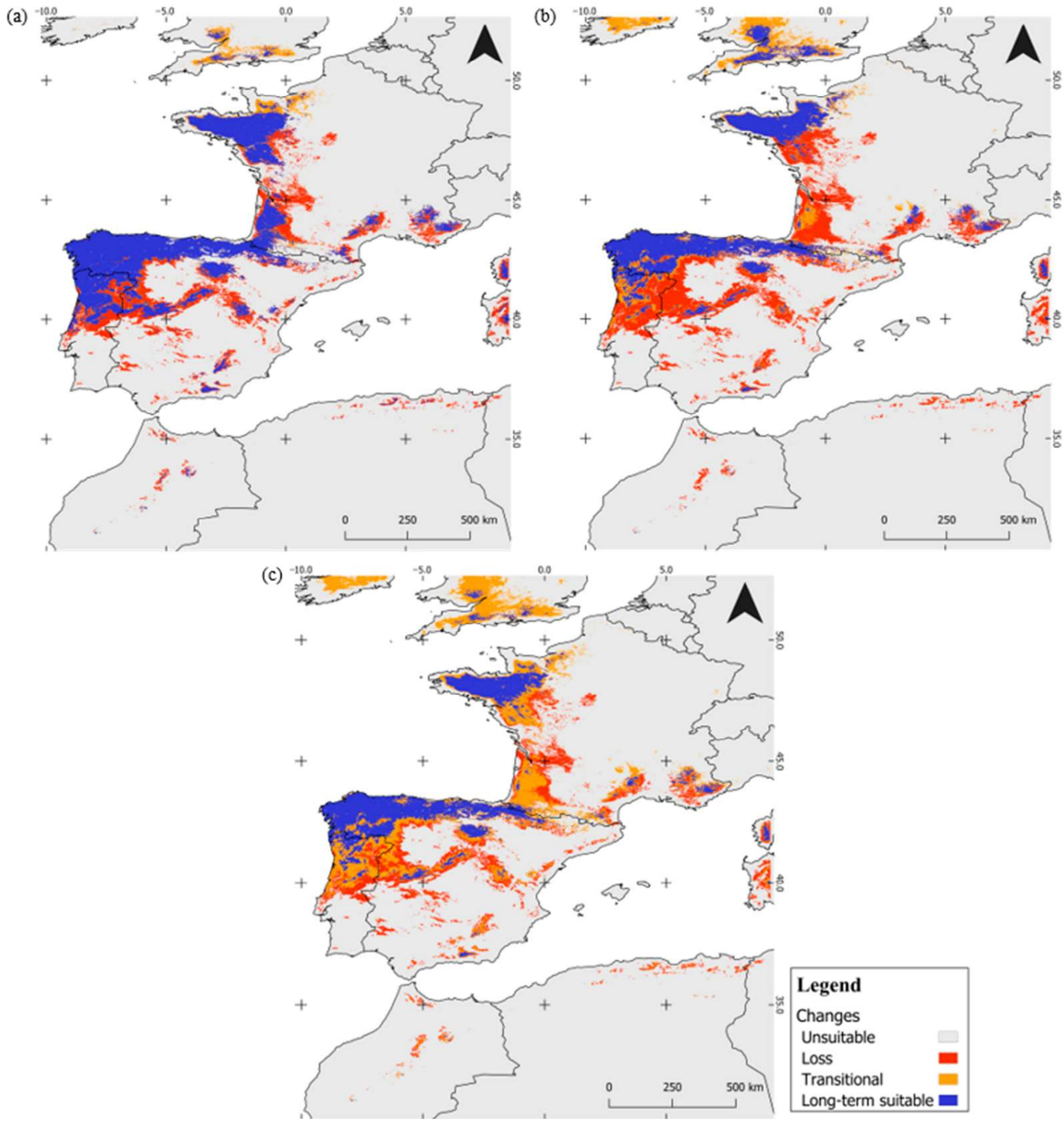

Figure 8. Overlap of changes in predicted distributions (gain, loss, or stable) of *Q. pyrenaica* between the two SSPs for two different time frames: (**a**) 2041–2070 and (**b**) 2071–2100; (**c**) between all the considered scenarios and time frames.

When all scenarios are overlapped, the potential area that remains suitable across all scenarios is about 42% of the currently suitable areas, a lower value than when the two-time frames are considered separately, meaning that 58% of the current suitable areas are lost (Figure 8c). Transitional zones increase over 100% when all scenarios are overlapped, compared to the 2071–2100 period (Figure 8c). In North Africa, stable and newly suitable areas for *Q. pyrenaica* are limited, primarily restricted to high elevations in the Atlas Mountains (above 3000 m in Morocco and 1500 m in Algeria), although the species is currently absent from the latter. In the IP, mountain ranges in the southern and central regions continue to provide suitable habitats. However, gains in these areas are minimal and confined to small high-altitude zones such as the Baetic and Iberian system and the peaks of Moncayo (Figure 8c). The northern and northwestern parts of the IP retain suitability for the species across all scenarios, forming a continuous corridor. Gains in these regions are also limited and mostly occur in small coastal areas or along the slopes of the Pyrenees. In southern France, small patches of suitable habitat are projected to persist or emerge on the southern and eastern slopes of the Alps. The most substantial area of newly suitable habitat is found in northern France, which, when combined with the existing stable range, could form a significant continuous distribution for the species (Figure 8c).

4. Discussion

4.1. Current and Future Scenarios

The ensemble model yielded high predictive performance and identified extensive areas currently suitable for *Q. pyrenaica*. Suitable habitats for this species occur across broad areas of the western IP and western France, although they become increasingly fragmented in the southern and southeastern portions of the range (North Africa, southern IP, and southeastern France). The spatial distribution of *Q. pyrenaica* is primarily governed by climatic variables, especially temperature and precipitation, as well as edaphic factors, such as the soil pH. Among precipitation-related parameters, total annual precipitation and rainfall during the warmest quarter emerged as the most influential predictors. A minimum annual precipitation threshold of approximately 500 mm appears critical for the species' persistence, although it tolerates pronounced seasonal variation in both temperature and precipitation. Despite its climatic tolerance to lower values of annual precipitation, *Q. pyrenaica* remains dependent on adequate water availability during the hot and dry season—a typical trait of submediterranean oaks [13,17,20]. Temperature-related variables, such as minimum winter temperatures and temperature seasonality, exert comparatively less influence. Nonetheless, these factors underscore the species' presence in continental regions, where it endures marked thermal seasonality and demonstrates substantial winter cold tolerance and, to a lesser extent, tolerance to dry summer conditions. Future projections consistently indicate a significant range contraction in the southern distribution, combined with a northward and upslope expansion, regardless of scenario. The model shows that suitable areas are consistently smaller than unsuitable ones, leading to overall habitat loss. Furthermore, stable suitable areas are usually under 50%, showing highly dynamic range shifts. Indeed, future climate projections indicate significant changes in precipitation spatiotemporal patterns, with decreased rainfall and frequent and severe summer droughts, especially during the warm season [68]. Temperatures are also expected to rise, with longer and more frequent heatwaves [69], potentially rendering many areas unsuitable for the species. This aligns with broader trends projected for the submediterranean ecotone [20] and for Mediterranean tree species, where climate change is anticipated to drive both latitudinal (poleward) and altitudinal (upslope) shifts in species distributions [70–72]. In this study, the total putative area gained by *Q. pyrenaica* is higher under more severe climate scenarios than for moderate ones, which is counterintuitive. This may be linked to a more pronounced altitudinal shift in these harsher scenarios, as habitat suitability increases along the Pyrenees and southern France under more severe climate projections and in later time frames. Additionally, the latitudinal response is also projected to be stronger, with new projected suitable areas appearing in northern France, England, Wales, and Ireland, particularly in the most severe scenario [73–78]. According to these projections, *Q. pyrenaica* may expand into areas currently dominated by temperate deciduous species [79] currently occupying the Eurosiberian region and leading to a potential shift from deciduous temperate forests to submediterranean marcescent forests [20]. Temperate species, such as the Iberian and European pedunculate and sessile oaks (*Q. robur* L., *Q. orocantabrica* Rivas Mart., Penas, T.E.Díaz & Llamas (=*Q. robur subsp. broteroana*), and *Q. petraea* (Matt.) Liebl.) or beech (*Fagus sylvatica* L.), which are particularly vulnerable to drought-induced stress, are likely to suffer significantly from future heatwaves and reduced precipitation. This could result in increased mortality and diminished recruitment for these species [7,80], resulting in a species turnover, compounded by ongoing habitat fragmentation and land use changes [81].

Severe habitat loss is expected in the southern IP, North Africa, and southern and eastern France, especially in the Mediterranean fringe and at lower altitudes. Habitat loss is projected to be ca. 34%–51%, depending on the scenario. In pessimistic scenarios, the northern European populations may be isolated from the IP ones, and several smaller suitable areas may persist or arise in northern Iberia and in Morocco and southeastern Spain mountainous regions, as well as the southern and eastern slopes of the Alps in southern France. However, these southern and high-altitude putative refugia will progressively shrink under more severe climate scenarios and in later time periods (2070–2100), reflecting habitat contraction and displacement. In lower latitudes, especially in North Africa, the species may be confined to extremely small and diffuse areas, trapped in a few high-altitude mountains, which may function as important refuges for the species, as happened in the past during the last glaciations with, e.g., *Cupressus dupreziana* A. Camus in Algeria and *Abies pinsapo* Boiss. in southern Spain [82–85]. Indeed, Mediterranean species may have genetic and ecological resilience to changing conditions, allowing them to adapt to new climates over time. However, the speed of climate change may outpace the species' ability to adapt, especially if migration is hindered by fragmented landscapes [86]. The increase in the species' habitat fragmentation may accelerate genetic drift, with a potential decrease in genetic variability and, therefore, the species' adaptability to future harsh climatic conditions. Nevertheless, refuge areas from the last glaciation contain reservoirs of genetic diversity, but the pace of current changes is dramatically higher and the potential for genetic loss is huge, despite other helpful mechanisms, plasticity vs. evolution, and maintenance of population size over time [86] (and references therein). Habitat loss in low-altitude regions suggests that *Q. pyrenaica* may experience local extinctions in areas with increased aridity. In these locations, this species may progressively lose suitable areas for species adapted to drier, hotter climates, with a shift toward evergreen species such as cork oak (*Q. suber* L.) and holm oak (*Q. rotundifolia* Lam.) [87] and strawberry tree (*Arbutus unedo* L.) [71], in a process antagonistic to what will happen in the northern rear edge [82–85].

Restoration and management measures are important to improve the resilience to climate change and guarantee the conservation of *Q. pyrenaica* forests, including small marginal areas. These actions for managing and adapting forests require a longer-term perspective, since forests have to cope with the rapid pace of changes in climate conditions over at least several decades [28,73], emphasizing the need for adaptive management strategies [28,88].

The results highlighted in the current study suggest that many currently suitable locations may not remain viable for long-term conservation efforts, as the total suitable area in each projection is smaller than the predicted area for current conditions. The projections indicate an overall decline in suitable habitat, representing 69% of the total suitable area under current conditions for the period 2041–2070 and 48% for 2071–2100. Two large areas emerge as key areas for *Q. pyrenaica* conservation: northern Iberia and northern France, which may be geographically disconnected under future climatic scenarios. In northern Iberia, habitat suitability remains largely stable across all scenarios. The species is already present in most of these locations as a dominant species and in mixed stands dominated by deciduous temperate species [87,89]. Across this region, the species has the conditions to expand to new areas by gaining a competitive advantage over others as the climate changes [7]. In the north of France, a large part of the long-term-suitable area corresponds to new colonization areas, in locations where the presence of the species is scarce or absent. In this case, the species' capacity for colonizing new suitable areas might be a limiting factor [73], especially if we consider the existence of large areas with unfavorable land use (e.g., agriculture). Acorns, *Quercus* spp. fruits, have high predation rates, including post-dispersal seed predation by insects, rodents, birds, and wild boars [74–77] and a dispersal distance smaller than a 100 m radius from the origin [76–78]. Even so, the species' expansion to higher elevations and northern latitudes, like northern France, might be a conservation opportunity for *Q. pyrenaica* and other submediterranean species. Also, using *Q. pyrenaica* in temperate forest conservation actions may delay climate change effects in these locations, promoting their resistance and resilience to extreme climate events and maintaining their capacity to provide important ecosystem services (ES) [90,91].

4.2. What Can We Do in the Future to Conserve and Restore?

Quercus pyrenaica forests have long been shaped by human activity [1,92]. This long-term anthropogenic shaping makes it essential to spatially tailor conservation strategies based on future habitat dynamics identified in our models. Its stands have traditionally been managed through pruning and felling to supply firewood, charcoal, cattle forage, and other products, such as tannins. Coppice management and the use of prescribed fire to promote herbaceous growth and stimulate sprouting, resources highly valued by livestock, have been common practices in *Q. pyrenaica* woodlands since Antiquity [45,93,94]. These traditional uses, along with more recent silvicultural interventions, may have significantly altered the natural gene pools of these forest trees, potentially impacting the genetic structure of their populations [95] (and references therein).

A full spectrum of adaptation strategies might be used in adaptive forest management and restoration [27], but it is important to consider that specific measures can vary significantly across regions, according to local conditions [28]. The strategies to adopt can be categorized into several levels: resistance, resilience, and response (now often referred to as transition) [96]. Resistance strategies aim to maintain core forest composition in a stable state by enhancing their defenses against anticipated climate change impacts. These approaches are most suitable for low-sensitivity ecosystems or areas buffered from severe climate effects, such as refugia [27,29,96]. Resilience strategies want to enhance an ecosystem's capacity to absorb disturbances and adapt to new conditions by promoting species genetic diversity within its natural range. These actions may include assisted population expansion, a form of assisted migration involving short-distance movement of genotypes or populations within their current range or in limited range expansion [27,29,96]. Transition strategies anticipate and facilitate ecosystem change by shifting forest composition toward species better adapted to future climates, especially in areas where native species are becoming unsuitable. These actions may involve assisted population expansion or, where appropriate, the introduction of better-adapted species through assisted range expansion [27,29,96].

Protecting key suitable areas and small southern refugia may be crucial [97,98]. This protection can be achieved by conferring a protected status to these locations or even taking appropriate management measures now to maintain or create areas that may guarantee the species' persistence or a place to migrate to in the future [99], for instance, by preserving soil conditions and seedling protection. *Quercus pyrenaica* ecosystem restoration through forest management could be part of a resistance or resilience strategy, depending on the target areas. Currently, due to land abandonment, this species is recovering in abandoned rural areas [100]. This movement should be embraced by decision makers and included in restoration programs, intending to increase resilience and decrease fragmentation and promote biodiversity conservation, soil stability, and other ES. A less fragmented forest will be more resilient, enhancing the species' capacity to cope with future changes [101]. Measures for restoration should include the following: (i) habitat identification, meaning that restoration should focus on areas where this species was historically present, but was lost due to land use change, deforestation, wildfires, or climate impacts; (ii) identifying suitable sites, involving assessing soil types, moisture availability, altitude, and temperature conditions, including the results from the study herein; and foreseeing regions where the species is currently taking over due to land abandonment and to species turnover molded by climate change [101] (and references therein). *Quercus pyrenaica*'s ongoing natural regeneration from existing seed banks or nearby mature trees, along with seedlings or seeds collected in situ and genetically adapted to local conditions, provides a strong foundation for restoration. This can be complemented by assisted population expansion of *Q. pyrenaica* from southern or low-altitude locations to selected northern and upward sites [29,102], as studies show that provenances from warm climates can survive in experimental sites where the climate is anticipated to be warm in the future [29,102,103]. The idea is to enhance the stress tolerance of populations in currently highly suitable areas by introducing individuals from populations already adapted to some environmental stresses [104,105] to promote both resilience and resistance [90]. This approach may be applied in areas currently suitable and projected to remain so in the long term, as well as in transitional zones currently occupied by *Q. pyrenaica* forests. The goal of this is to enhance habitat suitability and resilience while promoting population connectivity [27].

The use of tree shelters or protection from herbivory may be undertaken to ensure regeneration success. Introducing other native species alongside *Q. pyrenaica* (e.g., *A. unedo*, *Laurus*, *Phyllirea*, *Crataegus*, *Sorbus aucuparia* L., *Pyrus cordata* Desv., *Cistus*, *Lavandula*, or other native nurse shrubs) can enhance a rapid take-over of the biodiversity and resilience by mimicking the natural composition of the ecosystems and providing safe sites for protection against acorn and/or seedling consumers and enhancing the possibility of dispersal [74,75].

Assisted migration could, theoretically, be used as a proactive transition strategy aimed at facilitating the shift from current to future forest conditions [73]. This strategy may promote the introduction of *Q. pyrenaica* in particular areas where it is not present [90] by transporting it into areas that are predicted to be suitable under future climatic conditions and where the species would have difficulties dispersing on their own (assisted range expansion) [29,102,106]. This strategy can help increase forest species diversity, strengthen ecosystem resilience to natural hazards [105,107], and ensure the presence of species capable of withstanding prolonged periods of harsher climatic conditions. Despite its potential benefits, this technique has faced criticism for introducing individuals, assumed to be fit, that may be outnumbered by the local population [29]. As a result, their alleles may not effectively spread within the recipient population, particularly since population size is a factor [108]. Additionally, relocating species carries the risk of losing locally adapted traits that are essential for survival. For instance, species may be specifically adapted to local soil conditions, climate patterns, or ecological interactions. If these species are moved to an environment that does not align well with their adaptive traits, such as bud phenology or resistance to extreme climatic events, they may struggle to survive or fail to thrive. An example of this was the introduction of *Pinus pinaster* seeds from Portugal and Galicia to Aquitaine, France, after World War II, which caused huge devastation to this forest. The outcome was disastrous, with high stand mortality following the exceptionally cold winter of 1985 [109]. This incident underscores the need for targeted studies to identify areas likely to offer suitable conditions for the species under future climate scenarios. For many species, it is still unclear whether such relocations will result in long-term survival or if the species will struggle to establish stable populations in new environments. Therefore, caution is necessary in planning assisted migration. Future research should prioritize transitional zones, focusing on locations where species turnover is likely to occur soon. These studies will help managers select species for assisted range expansion or migration efforts.

Ex situ conservation may also be an option [110], particularly by preserving the genetic diversity of populations in areas that are at risk of becoming extinct, such as prioritizing marginal populations in the Baetic and Rif ranges, where rapid loss of climatic suitability is projected.

Additionally, studying the species' genetic structure across its entire range would be a valuable tool in selecting genetically diverse and divergent stands for preservation and in forecasting the species' genetic variability, since only a few studies were carried out at the local scale [95]. Anthropic and natural disturbances, such as ground fires, are frequent in the submediterranean region, conferring a selective advantage to *Q. pyrenaica* in comparison to other hardwood species with lower sprout capability. This species has a high sprouting capability, mainly due to root-sucker sprouts [111], a characteristic that provides an ecological advantage under frequent disturbance regimes. Yet, it may also promote clonality, and the consequences to the genetic diversity from this type of behavior were examined in an open woodland and a coppice forest [95]. The genetic diversity and allelic richness were high in both cases; nevertheless, clonal assemblies were found. Caution should be taken when selecting material for ex situ conservation, and acorns should be collected from trees far apart to avoid clonality and inbreeding, particularly biparental inbreeding. Thus, conservation and management strategies should balance ecosystem-level resilience and the conservation of genetic diversity.

5. Conclusions

This study provides a comprehensive assessment of the potential impacts of climate change on *Q. pyrenaica* distribution, a key submediterranean forest species in the western Mediterranean Basin. Using an ensemble modeling approach, we found strong evidence of significant range shifts, with a clear trend toward habitat loss in southern and low-altitude areas and a potential expansion into northern and higher-altitude regions under future climate scenarios. Notably, long-term-suitable zones shrink by up to 58% when all scenarios are overlapped, while transitional areas expand markedly, calling for spatially explicit conservation prioritization.

Precipitation-related variables, especially annual and summer rainfall, emerged as the main drivers of habitat suitability, highlighting the species' dependence on sufficient water availability during the dry season. While *Q. pyrenaica* displays some tolerance to temperature seasonality and continental conditions, its long-term persistence will be challenged by increasing drought severity and more frequent heatwaves, especially in its southern range.

The projected contraction of suitable habitat, combined with the limited natural dispersal capacity of the species within a highly fragmented habitat, and potential clonality raise concerns for its future distribution. Although putative new suitable areas emerge in northern France, the British Isles, and high-altitude refugia, active conservation strategies such as ecosystem restoration, habitat protection, and ex situ conservation will be essential to support species survival. Our findings underscore the urgency of integrating predictive models into conservation planning, focusing on long-term resilience and adaptability. Future research should incorporate genetic, ecological, and demographic data to refine projections and guide management actions. Beyond its vulnerability, *Q. pyrenaica* represents a key biogeographical sentinel and an indicator species for the stability of submediterranean forest mosaics under climatic pressure.

Restoring *Q. pyrenaica* ecosystems requires a comprehensive approach that combines ecological, social, and economic factors. By improving habitat quality, enhancing species resilience, and promoting sustainable land management practices, we can ensure the long-term conservation of this valuable tree species and its role in Mediterranean ecosystems. Given the increasing pressure from climate change, active restoration is a crucial step toward safeguarding *Q. pyrenaica* forests for future generations.

To wrap up, based on the species knowledge from the results of the current study, the following management guidelines are proposed for habitat maintenance and species conservation: (1) raise awareness among the general public and policy makers, and provide training and incentives for landowners to adopt conservation-friendly forestry practices; (2) protect and restore suitable habitats to prevent fragmentation and support healthy plant communities; (3) study and conserve the species' genetic diversity through in situ and ex situ methods, including germplasm preservation; (4) apply adaptive conservation strategies focused on resistance, resilience, and transition.

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Abbreviations

The following abbreviations are used in this manuscript:

SDM	Species Distribution Models
IP	Iberian Peninsula
ES	Ecosystem Services

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